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MUSCLE SYNERGIES DURING STANDING

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by

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ABSTRACT

The main aim of this dissertation is to define the notion of a postural muscle synergy and to develop a method of identifying and analyzing muscle synergies during different tasks in standing persons. The term muscle synergy has been widely used in the motor control literature without a clear operational definition. With the introduction of the uncontrolled manifold (UCM) hypothesis, it has become possible to offer an operational definition: synergies are task-specific groups of control variables, which stabilize particular performance variables.

This approach provides a framework for the identification and analysis of synergies. The hypothesis assumes that the controller (the central nervous system, CNS) acts in the state space of control variables (CVs) and selects in this space a manifold (UCM) corresponding to a value of a performance variable, which needs to be stabilized. The CNS selectively restricts variability of CVs in directions that do not span the UCM as compared to those within the UCM. If several attempts at a task are analyzed, variance per degree of freedom within the manifold is expected to be higher than orthogonal to such a manifold.

The UCM approach has been applied to kinematic and kinetic variables and has been successful in identifying important performance variables that are selectively stabilized in several tasks. This dissertation is the first attempt to extend the use of this approach to a more physiological variable, muscle activation recorded by electromyography (EMG).

This dissertation has two main parts. In the first part, we develop a method of using the UCM approach to identify muscle synergies during different postural tasks in stable standing. Our next goal has been to investigate the effects of standing on a surface with decreased area of support (unstable conditions) and of additional finger touch or hand grasp on the organization of muscle synergies.

In order to use the UCM approach to identify muscle synergies, the first step is to identify CVs manipulated by the controller. We have assumed that the CNS does not manipulate levels of activation of individual muscles, but unites muscles into groups within which the activity of the muscles is scaled in parallel with the help of CVs. In the first study, we identified three such CVs, which we called muscle modes or M-modes and have shown that these M-modes are very similar across subjects and several postural tasks performed on a stable support surface.

In the next study, we related changes in these three M-modes to shifts of an important performance variable in postural control, the center of pressure (COP). UCM analysis revealed that the three M-modes co-varied to stabilize a particular magnitude of the COP shift. An additional finding has been that there are separate synergies for COP shifts to the front and back.

In the second part of this dissertation, we focus on the effects of changes in the support surface stability and availability of additional touch or grasp on the formation of and interaction among M-modes. We first performed an experiment to investigate the effects of different types of touch on postural sway. It is known that even a mechanically inefficient finger touch is enough to stabilize posture. Results of our study show that both the availability of a stable reference point as well as modulation of contact forces play important roles in reducing postural sway. Further, it is not finger touch alone that has a stabilizing effect. Even touch to the side of the head or neck can reduce sway, possibly because of the high sensitivity of the receptors of the head and neck to shear forces. These results demonstrate the amazing versatility of the system for postural stabilization, which can use information from different sensory sources related to different mechanical interactions with external objects.

Support surface instability and availability of a finger touch or grasp have an effect on anticipatory changes in the activity of postural muscles prior to self-induced perturbations. We conducted an experiment to reveal the effects of these factors on the formation and co-variation of M-modes. We first compared M-modes during a postural task under four stability conditions: stable support surface with no touch, unstable support surface with no touch, unstable support surface with light touch, and unstable support surface with grasp to an external stable object.

Across all these conditions, there was a “menu” of five modes from which three were chosen in any given condition in a subject specific way. Among the five modes, two modes showed reciprocal patterns of muscle activity that spanned all three major leg/trunk joints and resulted in displacement of the center of mass either forward or backwards (“push-forward” and “push-back” modes). The remaining three modes corresponded to joint-specific co-contraction patterns. Of the four conditions studied, the co-contraction patterns predominated over the reciprocal patterns during standing in unstable conditions with a hand grasp as compared to the other three conditions. UCM analysis failed to identify M-mode synergies in the three conditions studied: stable, unstable, and unstable with touch. This was possibly because there are no pre-existing synergies for the unstable conditions as these are not tasks that are commonly performed in everyday life.

In this dissertation we have shown that the UCM method can be used to identify muscle synergies using a physiological variable, that is, muscle activity measured by EMG. When subjects performed various postural tasks under stable standing conditions, we found that M-modes were robust across tasks and subjects. Further analysis, under different stability conditions revealed that the organization of M-modes and their co-variation to preserve a particular magnitude of COP shift is task and subject specific.

The UCM method can be applied in the future to study abnormal synergies in postural disorders. The method can also be used to study the evolution of synergies across the lifespan as well as during the learning of novel tasks.

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Chapter 1

INTRODUCTION

Coordination between posture and movement

The central theme of this dissertation is the study of control of upright human posture. A standing person is required to stabilize and support the trunk, upper limbs and the head over the two lower limbs against internal and external forces. Thus, the postural control system serves several purposes. First, it needs to ensure that appropriate muscles are contracted to support the body against the force of gravity. Second, it is required to stabilize the supporting segments of the body when other segments are moving. Finally, it must ensure that the body is balanced on its base of support, that is, its center of gravity projects on to the base of support (in quiet standing; Rothwell 1994).

Upright human posture is inherently unstable because of its narrow base of support (of the order of one square foot) and relatively high center of gravity (in the pelvic region). The human body has often been modeled as an inverted pendulum (Fitzpatrick et al. 1992a; Day et al. 1993; MacKinnon and Winter 1993; Winter et al. 1993; Fitzpatrick and McCloskey 1994; Winter et al. 1998; Morasso and Schieppati 1999). Such a system with only a single joint is difficult to equilibrate even when there are no forces acting on it. In reality however, there are not only several joints to be controlled along the long axis of the body and a number of muscles crossing each of these joints but also numerous forces act on the body at all times. In order to support, stabilize and balance the body, postural muscles need to be finely controlled and coordinated so that the center of mass (COM) projects within the small base of support.

Posture is affected by mechanical perturbations and/or available sensory information. Examples of mechanical perturbations are: being pushed while standing or

performing a voluntary movement. Perturbations may also arise from reduced or conflicting sensory information, such as muscle vibration or lack of vision (Lackner and Levine 1979; Allum and Pfaltz 1985; Fitzpatrick et al. 1992a; Schumann et al. 1995). On the other hand, additional sensory information, such as a touch to a stable surface can reduce postural sway and have a stabilizing effect (Jeka 1997).

Any movement performed by a standing person requires simultaneous control of posture. For example, quick motion of the arms results in forces and moments at the shoulder joint of such magnitude that they could disturb postural equilibrium (Bouisset and Zattara 1983; Bouisset and Zattara 1987; Ramos and Stark 1990). Then again, there can be situations where the postural requirements themselves may limit voluntary movements. For example, if one were to attempt the same arm movement while standing on a narrow beam, the postural task of staying upright itself may interfere with the person's ability to perform the movement in the same way as in the first example.

Thus, control of posture and movements are very closely linked and fine coordination between the two is required to effectively perform most daily tasks. This dissertation is aimed at understanding the control of postural muscles during different types of voluntary movements and under different types of stability conditions.

Postural synergies

Since execution of voluntary movements is so closely linked with the control of posture, it has been suggested that every movement comprises of two distinct components, one of which is related to the desired movement (the focal component) and the other one which is related to maintenance of posture (postural component) (Hess 1943; Belinkiy et al. 1967; Bernstein 1967). Further, the coordination between the two components has been described using the notion of 'postural synergies' (Bernstein 1967; Allum and Honegger 1993; Alexandrov et al. 1998b; Vernazza-Martin et al. 1999).

Bernstein considered synergies to be built-in combinations of motor commands to a number of joints 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 mechanical redundancy.

Postural synergies have been demonstrated in both kinematic studies (Alexandrov et al. 1998b; Vernazza-Martin et al. 1999) and in studies looking at muscle synergies (Bouisset et al. 1977, Crenna et al. 1987, Allum and Honegger 1993, Sabatini 2002, Holdefer and Miller 2002). However, the concept of synergy lacks a clear, unambiguous definition (Latash 1999). Further, identification of such muscle synergies, based on muscle activation levels (electromyogram, EMG), has been an elusive issue.

Recently, the notion of synergies has been defined operationally following the traditions set by Gelfand and Tsetlin (Gelfand and Tsetlin 1966). By definition, synergies are task-specific groups of elements, which stabilize particular performance variables. A computational approach to the identification and analysis of synergies has been suggested, termed the uncontrolled manifold (UCM) hypothesis (Scholz and Schoner 1999; reviewed in Latash et al. 2002b). The hypothesis assumes that the controller (the central nervous system, CNS) acts in the state space of control variables and selects in this space a manifold corresponding to a value of a performance variable, which needs to be stabilized. If several attempts at a task are analyzed, variance in the state 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 mechanical variables (kinematic variables such as joint angles and kinetic variables such as force and moment; Scholz and Schoner 1999; Scholz et al. 2000; Scholz et al. 2002; Latash et al. 2002a) . In this dissertation, we intend to extend the use of this method to identification and analysis of muscle synergies using a more physiological variable, level of muscle activation as reflected in EMG signals.

Steps in UCM analysis for a particular task will be discussed in detail with examples in Chapter 5. A brief summary is given below:

1. Identification of independent control variables (ICVs): These are the control variables that are presumed to be independently manipulated by the CNS to stabilize particular performance variables.

2. Identification of relations between the ICVs with selected performance variables. We will refer to a matrix reflecting these relations as the Jacobian of the system. Selection of a set of particular performance variables will be referred to as the formulation of a control hypothesis, i.e. a hypothesis about a presumed aspect of performance, which is supposed to be stabilized by a synergy.
3. UCM Analysis: A manifold (UCM) corresponding to a value of a selected performance variable is determined. Several attempts at a task are analyzed and the variance, computed across tasks is partitioned into two components, one within the manifold and the other, orthogonal to it. The former is supposed to be significantly larger than the latter.

One of the main advantages of the UCM approach is the ability to perform analysis with respect to different control hypotheses. This allows us to quantify the degree of stabilization of different performance variables thus discovering the purpose of an alleged synergy. The method potentially allows also to track the emergence and changes in synergies with practice as well as quantify synergies in atypical populations including patients with neurological disorders.

Outline of dissertation

In the next chapter (Chapter 2), literature is reviewed in relevant areas of postural control, the notion of synergies and the UCM approach. Topics under postural control will include literature pertaining to the control of quiet stance, postural reactions to perturbations and anticipatory postural adjustments (APAs). The role of sensory information in control of posture will be presented. This will be followed by a chapter (Chapter 3) in which we introduce the main research questions addressed in this dissertation. Chapters 4, 5, 6 and 7 describe specific experiments. Each will have its own introduction, methods, results and discussion sections. Chapters 4 and 5 describe

experiments on the use of the UCM approach to identify postural muscle synergies under stable support conditions. Chapter 6 contains a report on an experiment investigating the role of different types of touch on postural sway. In Chapter 7, details of the experiment conducted to study the effects of postural instability (mechanical and sensory) on formation and co-variation of M-modes is presented.

Chapter 2

LITERATURE REVIEW

In this chapter, we will review literature pertaining to postural control. The following areas of research within postural control will be reviewed: a) postural sway during quiet standing, b) preprogrammed reactions in response to external perturbations, c) anticipatory postural adjustments (APAs) in preparation of an expected self-generated perturbation, d) postural synergies and e) the uncontrolled manifold hypothesis. Particular emphasis will be laid on the importance of sensory information for postural control. In the section on postural synergies, we will examine the various approaches in the literature pertaining to identification of synergies, paying particular attention to postural muscle synergies.

Postural sway during quiet stance

When a person is instructed to stand as quietly as possible in a spot, there is always some persistent fluctuation in their posture, which is called sway. Postural sway is commonly measured using a force platform, which registers the ground reaction forces from the supporting surface under the subject's feet. An index used to quantify postural sway is displacement of the center of pressure or COP, which is the point of application of the ground reaction forces on the body. In perfectly static conditions, the position of the COP and the center of mass, COM (projected to the base of support) coincide with each other. In normal upright quiet stance with eyes open, the COP migrates approximately 0.4 cm in the anterior posterior (AP) direction and 0.18 cm in the medial

lateral (ML) direction (Winter et al. 1998). COM displacements are smaller. A number of measures in the time and frequency domain can be extracted from the COP trajectories and have been evaluated for their reliability and validity in both healthy subjects and special populations (see Goldie et al. 1989; Duarte and Zatsiorsky 1999).

The migration of the COP in the AP direction is under the control of the ankle muscles (dorsiflexors and plantarflexors), while COP migration in the ML direction is under the control of the hip abductors and adductors (Winter et al. 1996). The magnitude of postural sway is modified by the shape and size of the base of support. For example, during tandem stance (when one foot is placed in front of the other) an increase in ML sway is seen, whereas during duck-stance (heel-to-heel, feet rotated outward with bent knees) AP sway is increased (Winter et al. 1996).

Postural sway is also influenced by muscle stiffness and sensory information such as vision, vestibular information and proprioceptive information. These will be discussed in the sub-sections below:

Role of muscle stiffness

Muscle stiffness is an ill-defined term in motor control (Latash and Zatsiorsky 1993), which usually refers to the generation of muscle force against stretch and is assumed to be proportional to the magnitude of stretch up to a certain length and at a given level of muscle activation. Muscle stiffness is believed to play an important role in postural control during quiet stance (Fitzpatrick et al. 1992b; Magnusson et al. 1994; Bloem et al. 1995; Winter et al. 1998; Gatev et al. 1999; Morasso and Schieppati 1999).

According to some authors, ankle muscle stiffness alone is sufficient to maintain an upright posture (Fitzpatrick et al. 1992b; Winter et al. 1998). Fitzpatrick et al (Fitzpatrick et al. 1992b) found a linear relationship between ankle torque and ankle angle under imperceptibly small postural perturbations. The applied perturbations resulted in sway similar in magnitude and velocity to sway during quiet stance. Depending on the intentional set (instruction to stand either ‘as quiet as possible’ or ‘at

ease') ankle stiffness was adequate to remain upright. These results were supported by a study by Winter et al (Winter et al. 1998). They assumed that muscles act as springs to cause the COP to move in phase with the COM as the body sways about a desired position. Using an inverted pendulum model, they calculated the undamped natural frequency and the effective stiffness of the system from the spectrum of the COP-COM error signal. They showed that restoring forces act at a close to zero delay, such that other sources of information were either below threshold (vestibular and proprioceptive) or induce no changes in stiffness (visual information) suggesting that ankle stiffness alone was sufficient to maintain normal upright stance.

Morasso and Shieppati (Morasso and Schieppati 1999) criticized the results of Winter et al. Their calculations based on a different method showed that muscle stiffness values are too low to maintain vertical posture and other sources of information (such as pressure receptors of the foot and muscle receptors) can contribute to postural control during quiet stance. However, it is important to note that the two groups defined stiffness differently. This may lead to the differences of opinion on the role of muscle stiffness in postural control (Latash and Zatsiorsky 1993).

Role of afferent information

Sensory information has an important role in maintaining postural equilibrium. The roles of visual, vestibular and proprioceptive information have been extensively studied (Roll et al. 1980; Dijkstra et al. 1994a; Fitzpatrick and McCloskey 1994; Kuo et al. 1998). More recently, the role of cutaneous information from the soles of the feet and from the fingers has also been emphasized (Jeka and Lackner 1994; Jeka 1997; Kavounoudias et al. 1998; Rabin et al. 1999). The effects of different types of afferent information on descriptors of postural sway, such as total sway area, ranges, length, velocity or standard deviation of COP trajectories (Murray et al. 1975; Diener et al. 1984) have commonly been used.

Visual information

Visual information is one of the most important sources of information for postural control and under conditions of altered information from other sensory sources, subjects are able to almost completely compensate for the loss of that information by 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, the visual surround has been manipulated using the 'moving room paradigm'. In this paradigm, the visual surround is manipulated either by actually moving the room or by altering the display in front of the subject that mimics motion of the visual surround (Schoner 1991; Dijkstra et al. 1994a; Dijkstra et al. 1994b). These experiments show the strong influence of visual information. For example, when the visual surround accelerates towards the subject, it is perceived as a forward sway and this is accompanied by an actual backward sway of the body.

Vestibular information

Galvanic stimulation of the vestibular organ behind the ear leads to changes in the firing rate of peripheral vestibular afferents. Depending on the position of the subject's head (Hlavacka et al. 1995; Hlavacka et al. 1996) and the polarity of the current (Coats and Stoltz 1969), subjects show a body lean in a particular direction.

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 rotated to the right, a displacement in the posterior direction is observed (Hlavacka and Njiokikjien 1985).

An increase in the amplitude of vestibular stimulation leads to an approximately linear increase in 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 sinusoidal sway patterns at low frequencies (Petersen et al. 1995). When visual

information is available, it suppresses the effect of vestibular stimulation causing lateral body sway only in the lower frequency range (0.2 – 0.3 Hz; Petersen et al. 1994).

Muscle spindle information

Muscle-tendon vibration causes an excitation of muscle spindles (Ia afferents) and causes a tonic contraction of the muscle that is stimulated. This is called the tonic vibration reflex. There is a linear correspondence between the muscle spindle discharge and the stimulus at frequencies below 100 Hz (Lackner and Levine 1979). The contraction starts a few seconds after the beginning of the vibration, increases gradually and then stays at a relatively constant level until the stimulus is turned off.

Muscle vibration also produces segmental and postural kinesthetic illusions (Lackner and Levine 1979; Calvin-Figuiere et al. 1999). The CNS interprets the activity in the muscle spindle endings as a sign that the muscle is lengthening and in the absence of other sensory information (visual or haptic), this generates the illusory perception of a new joint position corresponding to increased muscle length (Eklund and Hagbarth 1967; Eklund 1969). When the tendon of a postural muscle, such as the Achilles tendon is vibrated, 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, which could result in a fall (vibration induced falling, VIF). This effect is especially strong when the eyes are closed (Nakagawa et al. 1993). Under ‘unstable’ circumstances, when there is decreased base of support, 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 vibration (Lackner and Levine 1979; Feldman and Latash 1982; Latash 1995). For instance, switching from segmental to 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).

Cutaneous information

A ‘light touch’ by a fingertip at mechanically non-supportive force levels (< 1 N) greatly attenuates postural sway during quiet stance (Holden et al. 1994; Jeka and Lackner 1994). Postural sway is not further reduced at higher force levels. The index finger with its high 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). In the tandem Romberg position (feet placed behind one another) and with eyes open, correlation between changes in applied forces and COP displacement has been found (Jeka and Lackner 1994). The effect of touch is seen even in blind individuals and those with vestibular loss and 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 relationship is in phase at frequencies below 0.4 Hz while there is a phase lag at higher frequencies (Jeka et al. 1998).

Rabin et al (Rabin et al. 1999) investigated the directional specificity of touch contact. They showed that finger touch was more effective in reducing sway in the plane of greatest sway, that is a finger contact in the frontal plane shows a reduction in sway in the AP direction and contact in the sagittal plane shows a reduction in the ML direction. This suggests that fingertip contact provides information both about the amplitude and direction of sway.

Riley at al (Riley et al. 1999) investigated if it is the cutaneous information from the fingertip that plays the primary role in reducing sway or it is the implicit task of keeping the finger at a fixed position that plays the larger role. In their study, subjects either touched a hanging curtain as a mere result of extending the forearm or were instructed to minimize the force and movement at the point of contact. Only under the latter instruction did the subjects show a decrease in the 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 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 the position of the touch surface were manipulated. They could account for the sensory integration of visual and cutaneous information within a linear additive model. In a recent study, Lackner et al (Lackner et al. 2000) looked at the relationship between cutaneous and muscle spindle information. Subjects stood in the Romberg position while their peroneus longus and brevis tendons were vibrated. They stood either 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.

Recently, vibration to the sole of the foot has shown to induce COP shift in the opposite direction of the stimulation (Kavounoudias et al. 1998). The authors suggest that the vibration stimulus is similar to increased pressure on the sole of the foot and this provides information about the orientation of the body.

All the above information points to the importance of the different sources of afferent information and the complex interactions between them.

Theories on control of quiet stance

Several models have been proposed to describe COP migration during quiet stance. A few of them are discussed below.

Winters et al (Winter et al. 1998; Winter et al. 2001) explain the control of balance based on stiffness of ankle plantar and dorsiflexors and hip abductor and adductor muscles (for control in the sagittal and frontal plane respectively). They modeled the human body as an inverted pendulum. They showed that the COP-COM error signal is proportional to the horizontal acceleration of the COM 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 muscle and thereby reduces the burden on the CNS.

There has been some criticism of this idea of stiffness control of balance. Morasso and Schieppati (Morasso and Schieppati 1999; Morasso and Sanguineti 2002) state that muscle stiffness alone is not enough to keep the body upright. Other sources of information, such as pressure receptors in the foot and muscle receptors can actively contribute to the control of quiet stance. However, as discussed in the section on 'muscle stiffness', this disagreement may arise partly from the different definitions of muscle stiffness. More recently, Loram and Lakie (Loram and Lakie 2002), suggest that the 'inverted pendulum' moves from one resting equilibrium position to another, as any single resting equilibrium position is unstable. Besides intrinsic mechanical stiffness of ankle muscles, this is achieved by a biphasic 'throw and catch' pattern of anticipatory ankle torque.

There have been several criticisms of the inverted pendulum model. In addition to the doubts raised about the adequacy of muscle stiffness in maintaining upright posture, the assumption that only motion at the ankle is of importance has also been criticized (Day et al. 1993; Kuo and Zajac 1993; Accornero et al. 1997; Aramaki et al. 2001). Also, the model assumes a fixed reference point for stabilization of posture. Several studies have pointed at a moving reference point (Gurfinkel et al. 1995; Accornero et al. 1997; Zatsiorsky and Duarte 1999).

Another theory examining quiet stance posture is that of Collins and De Luca (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 (< 1 s), an open-loop control mechanism is called to act and in the long-term there is a closed-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 was 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 (visual, vestibular and somatosensory) 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'.

A more recent theory on control of quiet stance was introduced by Zatsiorsky and Duarte (Zatsiorsky and Duarte 1999; Zatsiorsky and Duarte 2000): the rambling-trembling hypothesis. According to this approach, the body does not oscillate about a fixed equilibrium point, but the reference frame is moving. Zatsiorsky and Duarte proposed an idea of an 'instant equilibrium point' when the sum of all horizontal forces equals zero and the body is at an instantaneous equilibrium. The trajectory of the instant equilibrium point is called the rambling trajectory and the deviation of the COP from the rambling trajectory is called the trembling trajectory. The trembling trajectory is a reflection of the restoring forces to counteract deviations from the rambling trajectory and the restoration is believed to be primarily through the inherent stiffness of ankle muscles.

The above discussion has been limited to the control of posture during quiet stance or under minimal perturbations. However, in daily life, we have to maintain posture against stronger perturbations of different nature. As indicated in the Introduction, perturbations may be from two sources: external or internal. Examples of external perturbations are being pushed in a crowd or being accelerated backward, when a stationary bus suddenly moves. These are countered by preprogrammed reactions and later, voluntary corrections and are discussed in the next sub-section. Internal perturbations are generated by subjects themselves, when they perform movements such as catching or releasing an object, making a fast arm movement, or lifting a leg to take a step. Since these perturbations are expected, the body prepares for them with anticipatory postural adjustments (APAs).

Preprogrammed reactions to external perturbations

The human body has several lines of defense against unexpected external perturbations such as a push. These include both passive resistance as well as actively generated responses. In the order of latency, the various responses are: 1) Passive elasticity or 'stiffness' of muscles and tendons which oppose perturbing forces. 2) Stretch reflexes at a latency of 35-60 ms. These responses have a phasic component (a short-lasting, strong contraction) if there is a fast change in the muscle length and a tonic component (steady-state contraction) if the muscle is slowly stretched. The first two responses are usually sufficient to maintain balance during quiet stance. 3) Preprogrammed reactions act at the latency of 50-100 ms and are the first responses to larger perturbations. Preprogrammed reactions (also called automatic postural responses or corrective/compensatory reactions) are combinations of muscle activation in response to specific perturbations which are different from simple reflexes in that they can be modified by instruction to the subject and their magnitude is independent of muscle length (Latash 1993).

The nature of preprogrammed reactions under a variety of mechanical perturbations and the contributions of various sources of sensory information have been extensively studied (Nashner 1976; Nashner and Woollacott 1979; Nashner et al. 1989; Horak et al. 1990; Horak et al. 1994) and are briefly reviewed below.

Response to mechanical perturbations: ankle and hip strategies

Nashner (Nashner 1976) developed a special force platform, which could translate in the AP and ML directions and also rotate forward or backward about the axis passing through the ankle joints. His group studied the responses of leg and trunk muscles to these platform perturbations and identified particular 'postural strategies' depending on the direction of perturbation and the size of the base of support.

In young healthy subjects, in response to a slow forward translation of the platform on a firm support surface longer than the foot, the body swayed backward and there was an increase in the background activity of the ventral muscles (tibialis anterior, rectus femoris and rectus abdominus). On the other hand, in response to a backward translation of the platform, the body swayed forward and there was an increase in the background activity of the dorsal muscles (soleus, biceps femoris and erector spinae). These responses occurred at a delay of about 80 ms and occurred in a distal to proximal order. This pattern of muscle activation and the accompanying kinematics have been called 'ankle strategy' (Horak and Nashner 1986).

When healthy subjects stand on a support surface that is short or is translated quickly or when elderly individuals stand on longer support surfaces, the order of recruitment of muscles is reversed to proximal to distal, called 'hip strategy'(Horak and Nashner 1986; Woollacott and Shumway-Cook 1990). This strategy helps to reduce the excursion of the COM.

The ankle and hip strategies have been viewed as postural synergies. Although there are an infinite number of combinations of muscle activation patterns and joint positions, which may produce stable upright stance, use of a few combinations such as the 'ankle strategy' and the 'hip strategy' simplifies this problem. Muscle synergies are discussed in further detail under the section 'Postural synergies'.

The simplistic and strict dichotomy between ankle and hip strategies has been disputed (Macpherson 1991). More than one joint at a time are usually involved in postural responses. The hip and ankle strategies are defined at the level of kinematics and provide limited information about the organization of these responses at the level of muscle activity (Bardy et al. 1999).

Role of afferent information

Several studies have investigated the role of various sources of afferent information in scaling of preprogrammed reactions (Allum and Pfaltz 1985; Dietz et al.

1992; Fitzpatrick and McCloskey 1994; Allum et al. 1998). The relative contribution of somatosensory and vestibular sources of information was studied by translating or rotating the supporting surface of sitting subjects (Forssberg and Hirschfeld 1994). Since the kinematics of the body remained the same in both cases, it was suggested that somatosensory information from backward tilting of the pelvis triggered the preprogrammed reaction. The role of the vestibular system in establishing an internal frame for verticality and modifying postural reactions and the final equilibrium position has also been shown (Inglis et al. 1995). The importance of proprioceptive information was demonstrated in studies on patients with neuropathy who showed delays in postural reactions as compared to normal subjects (Inglis et al. 1994; Bloem et al. 2000). It has also been suggested that the Golgi tendon organs have an important role to play in maintaining upright stance (Dietz 1993; Dietz 1998).

Somatosensory and vestibular information have been shown to be important in the selection of the appropriate postural response. Somatosensory loss results in a pronounced hip strategy when standing on a shortened base of support while vestibular impairment results in a persistent use of ankle strategy even on a shortened base of support (Horak et al. 1990).

Preprogrammed reactions can be modified by a predictable perturbation and by habituation to a repeated perturbation in standing subjects (Horak et al. 1989). These effects are not seen in sitting subjects (Zedka et al. 1998).

Anticipatory postural adjustments during voluntary movements

Voluntary movements, especially large amplitude and quick movements by large body parts can disturb postural equilibrium. There are two main reasons for this. 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, compensating at least partially for the upcoming perturbation by shifting the center of gravity in the direction opposite 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 a fall (Friedli et al. 1984; Ramos and Stark 1990). Ramos and Stark (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 countered by anticipatory muscle activity.

APAs were first observed by Belenkiy et al (Belinkiy et al. 1967) who reported that during arm raising in a standing position, the leg muscles involved in postural control are activated some 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 and trunk while standing (Belinkiy et al. 1967; Cordo and Nashner 1982; Breniere and Do 1986; Mouchnino et al. 1991), forearm loading and unloading (Hugon et al. 1982; Dufosse et al. 1985; Johansson and Magnusson 1989; Lacquaniti and Maioli 1989; Paulignan et al. 1989; Aruin and Latash 1995a; Bennis et al. 1996), 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).

APAs are commonly quantified by using EMG signals, body segment kinematics and displacements of the COP

The importance of motor action

Earlier it was believed that APAs are only generated when expected movements are performed by large body parts and not when the movement is produced by a smaller

effector such as a 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; Aruin and Latash 1995b; Scholz and Latash 1998; Diedrichsen et al. 2003). More recent studies have shown that APAs can be generated not only by small movements, such as that of a finger (the magnitude of APAs are however smaller) but also in the absence of movements. In their study, Aruin and Latash (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 finger movement was enough to trigger APAs. Later, Shiratori and Latash (Shiratori and Latash 2001) showed that when a standing subject is required to catch a load without any movement, visual information about the falling load without any overt action was sufficient to trigger APAs.

Coordination between movement and posture

It has been suggested that all movements that humans perform consist of two components: one directed at the explicit motor task (‘focal’ movement) and the other directed at regulation of posture (Bernstein 1967). There are two theories presently prevalent on the coordination of these two components. According to one theory, the control of posture and the focal movement separate processes (Massion 1992; Massion et al. 1999). The other view is that both processes are components of a single central control process (Latash 1993; Aruin and Latash 1995a; Toussaint et al. 1997; Latash 1998).

Factors that modulate APAs

The generation of APAs is affected by three main factors: expected direction and magnitude of perturbation, characteristics of voluntary movements associated with the perturbation, and current postural task (for e.g. stability conditions; Aruin et al. 1998). Modulation of APAs under time pressure in simple reaction time (SRT) and choice reaction time (CRT) tasks has also been studied. It has been shown that under SRT conditions, the interval between APAs and the focal movement is shortened and the APAs may become sub-optimal (Cordo and Nashner 1982; Horak et al. 1984; Brown and Frank 1987; Benvenuti et al. 1997; De Wolf et al. 1998; Nougier et al. 1999; Dietz et al. 2000). In CRT conditions APA onsets are similar to that in self-paced conditions (Slijper et al. 2002a).

Modulation of APAs with stability conditions

As suggested in the Introduction, postural instability may be introduced from two sources: mechanical and sensory. Most studies have focused on the former and it has been shown that the current postural task i.e. mechanical stability conditions can modify APAs (Friedli et al. 1984; Nardone and Schieppati 1988; Gantchev and Dimitrova 1996; Aruin et al. 1998). APAs in arm raising tasks have been studied by changing the size of the base of support (Friedli et al. 1984; Gantchev and Dimitrova 1996; Aruin et al. 1998). It has been found that in ‘very stable’ conditions, the requirement of APAs to stabilize posture is reduced. For instance, when subjects supported themselves by leaning against a wall during an arm flexion movement, APAs decreased in leg and trunk muscles (Friedli et al. 1984). Similar attenuation of APAs was also observed in other tasks such as standing on tiptoes or on the heels when holding on to a handle for support (Nardone and Schieppati 1988).

In other studies, researchers looked at APAs under ‘less stable’ conditions such as standing on a platform fitted below with a narrow beam or a small sphere of different

diameters (Gantchev and Dimitrova 1996; Aruin et al. 1998) or in single-leg stance (Nouillot et al. 1992). Under all these conditions the 'safe area' within which the COM can move without the subject falling is reduced. A decrease in APAs was observed during arm (Aruin et al. 1998) and leg (Nouillot et al. 1992) movements under conditions of decreased support. Further, the decrease in APAs was more pronounced in the direction of instability (Aruin et al. 1998). It has been hypothesized that APAs themselves may be viewed as perturbations, which may be sufficient to move the COP outside the decreased area of support (Aruin et al. 1998).

We can thus conclude that APAs decrease under 'very stable' as well as 'unstable' conditions.

The effect of reduced plantar support on APAs associated with flexion of the lower leg has also been studied (Do and Gilles 1992). It was found that reducing the support under the flexing leg (and not the supporting leg) lead to a scaling down of the APA magnitude. The authors suggested that knowledge of stability conditions and/or reduced sensory information has a role in the modulation of APAs.

Other types of mechanical perturbations to posture, not related to the size of the base of support have been studied. Reduced information from load receptors of the leg during underwater standing leads to a decrease in APAs (Dietz and Colombo 1996). A study of bilateral arm raising while standing on roller skates (Shiratori and Latash 2000) has shown that APAs are reduced in the lower leg muscles but not in the trunk muscles.

APAs are also influenced by sensory manipulations. The addition of a light touch during quiet stance has been shown to reduce postural sway (Holden et al. 1994; Jeka and Lackner 1994) and also results in decreased APAs in leg and trunk muscles during a unilateral arm raising task. Additional support in the form of a hand grasp does not cause any further changes in the APAs (Slijper and Latash 2000). APAs are also modulated by vibration to the Achilles tendon. It has been shown that there is an increase in APAs in some of the postural muscles in response to Achilles tendon vibration (Slijper and Latash 2002)

Thus we can see a modulation in anticipatory activity in postural muscles in response to different types of instability.

APAs associated with arm movement and load release while standing

In this dissertation, two types of tasks associated with APAs will be studied, namely, fast arm movements and load release from a hand/hands of extended arm(s) while standing. During fast arm movements, the moving limb generates forces and torques that disturb equilibrium. On the other hand, when a load is released from the hand, quick changes in the COM position lead to postural disturbance. Qualitatively different types of APAs accompany these two types of perturbations.

First, we will discuss APAs associated with fast arm movements, which have been extensively studied. During a quick shoulder flexion (extension) movement, from a relaxed position to about 45 degrees), an increase in the activity of dorsal (ventral) leg and trunk muscles is observed. The onset of these changes is observed 150 to 100 ms prior to the onset of the anterior (posterior) deltoid muscle activity (Massion 1992). APA patterns depend upon the direction of perturbation (Aruin and Latash 1995a), velocity of arm movement (Lee et al. 1987) and magnitude of inertial load added to the forearm (Zattara and Bouisset 1986; Bouisset and Zattara 1988). The above EMG changes are accompanied by shifts in COP (about 5 mm) in the posterior direction prior to shoulder flexion and in the anterior direction prior to shoulder extension, creating a moment in a direction opposite to the moment induced by the arm movement (Aruin and Latash 1995a). Further, minimal changes in ankle, knee and hip angles have been observed prior to the arm movement (Aruin and Latash 1995a).

Proximal and distal muscles seem to play different roles in the control of posture during APAs (Shiratori and Latash 2000). While proximal muscles provide the general pattern countering expected perturbations in the AP direction, the distal muscles deal with asymmetric perturbations, such as in unilateral arm raising.

Loading and unloading perturbations have been used to study abrupt changes in body (or segment) mass distribution in sitting and standing subjects (Lacquaniti and Maioli 1989; Paulignan et al. 1989; Aruin and Latash 1996; Bennis et al. 1996). When a standing person releases a load in front of the body, dorsal muscles show a decrease in activity, which may be accompanied by an increase in the activity of ventral muscles

(Aruin and Latash 1996). The APAs depend upon the magnitude of the perturbation and are accompanied by shifts of the COP in the posterior direction prior to unloading (Aruin and Latash 1996).

Impairments of APAs after brain lesions

Since APAs occur prior to the onset of focal movement and joint displacements before the onset of the perturbation are negligible, it has been assumed that feedback mechanisms such as spinal reflexes have a minimal role to play in the generation of APAs. This has been supported by a study on a deafferented individual, who showed normal APA patterns (Forget and Lamarre 1995). Patients having lesions to certain brain structures such as the supplementary motor area (SMA) have shown impairment in the generation of APAs, while the performance of focal movements was relatively unaffected (Viallet et al. 1992) favoring central control involving two parallel processes.

In patients suffering from Parkinson's disease APAs were observed in only about 5 % of subjects (Bazalgette et al. 1987). Contrary to these results, other studies have shown relatively well-preserved APAs in Parkinson's patients (Dick et al. 1986; Latash et al. 1995; Aruin et al. 1996; Rogers 1996). It has been suggested patients with Parkinson's disease have deficits in APAs that are quantitative rather than qualitative (Aruin et al. 1996).

Patients suffering from stroke have decreased or delayed APAs with respect to healthy individuals (Horak et al. 1984; Garland et al. 1997; Hedmann et al. 1997). In paretic muscles, the modulation of APAs with the direction of the perturbation is decreased or shows atypical patterns (Slijper et al. 2002b).

Massion et al (Massion et al. 1999) tested patients with hemiparesis and Parkinson's disease during a bimanual load-lifting task. They proposed a model of coordination between control of posture and focal movement. According to this model, the contralateral motor cortex controls the focal movement, while the ipsilateral motor cortex controls the postural response. These signals are combined at the level of the

brainstem and/or the spinal cord ('anticipatory network') under the influence of the SMA and the basal ganglia setting gate and gain values. Further, based on the impaired acquisition of APAs in patients with Parkinson's disease and hemiparesis from capsular lesions, the motor cortex, premotor area, SMA and basal ganglia are assumed to play an important role in the acquisition of APAs (Massion et al. 1989; Viallet et al. 1992; Massion et al. 1999).

Synergies

The term synergy is widely used in motor control literature often with different meanings by different people.

In a general sense, 'synergy' means 'working together'. Hughlings Jackson (Hughlings Jackson 1889) was probably the first to introduce the idea that muscles are controlled in groups and not independently although he did not use the term synergy. He believed that '… the central nervous system know nothing about muscles, it knows only movements'.

The Russian scientist, Nikolai Bernstein (Bernstein 1967) emphasized that synergies are a way of solving the 'degrees of freedom problem'. Humans usually have many more independently controlled variables (degrees of freedom) than the number of independent parameters describing a task. As a result, the CNS is posed with the problem of choosing one solution from an infinite number of possible solutions. Bernstein described 4 levels in a hierarchically organized motor system: 1) Level A- Level of tone, 2) Level B- Level of muscular-articular links, 3) Level C- Level of space and 4) Level D- Level of actions

Level B or the level of muscular-articular link is the level of synergies. The higher levels (C and D) are where voluntary decisions and planning of sequences of movements are made. However, the 'lower' Level B is where the movement plans are executed using synergies.

According to Lee (Lee 1984), a goal-directed interpretation of a 'neuromotor synergy' is a set of muscles acting together to produce a desired effect. In contrast, a morphological interpretation emphasizes the importance of temporal, spatial or scaling relations in phenomenological action patterns. She also proposed that in addition to solving the degrees of freedom problem, synergies are also needed to decrease the number of iterations required to compute e.g. trajectory of reaching. This allows for low-level adjustment of output without executive knowledge and synergies are elements in automatic as well as intentional actions.

It should be noted that the term synergy was also used by Sherrington, but with a different meaning. He referred to different muscles performing essentially the same action (e.g. elbow flexion by biceps and brachialis) as synergists.

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

1. The internal structure of a unit is more complex than its interaction with the environment.
2. Part of a structural unit cannot itself be a structural unit for the same tasks.
3. Parts of a structural unit that do not work with respect to a task either are eliminated (Principal of economy) or find their own places within the task (Principal of abundance; allows for flexibility)

They also proposed the 'Principle of minimal interaction', which they described at two levels: 1) At the level of interaction among elements (local)- 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)- 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).

In line with Gelfand's ideas on synergy (which emphasize error compensations) and principle of abundance (rather than redundancy of DOFs), the "uncontrolled manifold" (UCM) hypothesis has recently been proposed (Scholz and Schoner 1999;

reviewed in Latash et al. 2002b). According to this hypothesis, when a controller of a multi-element system wants to stabilize a particular value of a performance variable, it selects a subspace within the state space of the elements, such that within the subspace, the desired value of the variable is constant. This subspace is the uncontrolled manifold. The UCM hypothesis is discussed in greater detail in a separate section at the end of this chapter.

Postural synergies

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 kinematic synergies as well as muscle synergies.

Kinematic postural synergies

Alexandrov et al. (Alexandrov et al. 1998a) studied axial synergies during upper trunk bending. They found that forward and backward trunk-bending movements were accompanied by opposite movement of the lower body segments, such that the projection of the COM remained within the base of support. They performed principal component analysis (PCA) on the hip, knee and ankle joint angles during a movement or along a trial and found that there was a strong correlation between the three angles. The first principal component (PC1) accounted for 98-99 % of total variance indicating a strong central command controlling the time course as well as amplitude of movement across joints. The ratio between the hip, knee and ankle joints did not vary much with change in amplitude and velocity of movement and this ensured that the COM projection always fell within the base of support.

The study was extended (Vernazza-Martin et al. 1999) to trunk bending with loads. It was found that PC1 accounted for 98-99 % of the variance, irrespective of whether the trunk bending was done with or without a load.

Abe et al. (Abe and Yamada 2001) studied the frequency of arm swinging on postural co-ordination patterns. They found that above the natural frequency of the arm there is an ankle-shoulder in-phase pattern, where as at frequencies below the natural frequency of the arm, there is a hip-shoulder in-phase pattern.

Postural muscle synergies

In an experiment by Cordo and Nashner (Cordo and Nashner 1982), subjects were either pushed or pulled by a stiff handle they held on to or were instructed to push or pull rapidly on the handle (rapid arm movements). Postural muscle EMGs were recorded. Subjects either showed postural reactions in response to the handle or platform perturbations or showed anticipatory postural activities (APA) prior to the focal movement, in case of voluntary push or pull. They found that postural synergies were similar in APAs and postural reactions, since in both cases

- There was distal to proximal activation of muscles
- There was similar ratio of activity of hamstring to gastrocnemius
- Muscle responses could be elicited from either the leg muscles or the arm muscles (when arm was supported and platform perturbations were performed)

This idea that muscle synergies are fixed was challenged by Macpherson (Macpherson 1991), who suggested that synergies are flexible, since she noticed that synergies depend on biomechanical constraints such as direction of perturbation. Changes in synergies as a result of change in support surface were also reported (Horak and Nashner 1986). As described earlier in the section on ‘Preprogrammed reactions’, ‘ankle strategy’ is observed when there is a normal support surface and a ‘hip strategy’ is observed when there is a short support surface. Pedotti et al (Pedotti et al. 1989) also found differences in trained and untrained subject’s APAs during backward trunk bending when on a narrow base of support. Hwang et al (Hwang and Abraham 2001)

examined the recruitment strategy of irradiated knee muscles and prime movers (ankle muscles) during isokinetic ankle movements and determined the co-activation to be speed-dependent.

Most of the above studies on muscle synergies have used analysis of the latency or magnitude of EMG bursts to define synergies.

Statistical techniques used in the analysis of synergies

Various statistical techniques have been used in the study of synergies and they are summarized below.

Cross-correlations

This method is used to estimate the degree to which two series (for example, muscle EMGs) are correlated. Abe et al (Abe and Yamada 2001) performed cross-correlations between the motions of shoulder and hip joints as well as ankle and hip joints at different frequencies of arm swinging. They found that there was a coupling between shoulder and hip joint motion during low frequency swinging and a tight coupling between hip and ankle joint during high frequency swinging. De Luca and colleagues (De Luca and Erim 2002) used this technique on the mean firing rates of motor units of two synergistic muscles. They found high cross-correlations indicating a common drive to these muscles implying that the CNS considers these muscles as a functional unit.

Ratio of EMG between functionally related pairs

This method was used by Nashner (Nashner 1977) to demonstrate the synergistic relationship between the gastrocnemius and hamstring (G-H) as well as tibialis anterior

and quadriceps (TA-Q). They found that the ratio between these muscle pairs remains the same when the subject is exposed to platform translations and rotations. They interpreted their findings as indicative of a pre-programmed response under different stimulations to maintain upright stance.

Correlation and regression

Bouisset et al (Bouisset et al. 1977) correlated the integrated EMG activities of three agonist muscles- biceps, brachialis and brachioradialis. They found that under conditions of different inertias and velocities of elbow flexion, there was high correlation between the integrated EMGs of any two of the three muscles, suggesting a stable synergy between the agonists. Crenna (Crenna et al. 1987) used regression analysis on the latencies of activation (or inhibition) of postural muscles in a trunk-bending task. Significant regression lines indicated closely related EMG events.

Principal component analysis and Factor analysis

Principal component analysis and factor analysis are concerned with explaining the variance-covariance structure of a set of variables through a few linear combinations of the original variables. The objectives are data reduction and interpretation.

If a data set has p variables and n observations, and most of the variability of these variables can be expressed by a smaller number of new variables, k, or the principal components, then the original p variables can now be replaced by a smaller number of k variables. If **X** is a random vector of original variables, then the *i*th principal component, PC_i is given by $PC_i = \mathbf{e}_i^{'}\mathbf{X}$ where **e** (eigenvector) contains the coefficients for the principal components (i = 1, 2, …,p). The coefficients of PC1 are chosen so as to make its variance as large as possible. Coefficients of PC2 are chosen to make the variance of the combined variable as large as possible, subject to the restriction that PC1 and PC2 are uncorrelated and so on (Harris 2001; Johnson and Wichern 2002b). If the cumulative variance

explained by PC1 to PCk is satisfactorily large, the remaining PCs can be ignored. Sometimes, the principal components may not be easily interpretable, so one can perform rotations on the components, however the rotated components may explain different amounts of variance.

The essential purpose of factor analysis is to describe the covariance relationships among variables in terms of a few underlying, but unobservable, random quantities called factors. Factor analysis can be considered an extension of PCA, but it is a more elaborate model that allows for explicit separation of variance into variance unique to a factor or specific factors and shared variance or common factors (Johnson and Wichern 2002b).

Principal component analysis has been used to quantify both kinematic and muscle synergies. Alexandrov et al (Alexandrov et al. 1998b) and Vernazza-Martin and colleagues (Vernazza-Martin et al. 1999) used this method to describe the relationship between hip, knee and ankle joint changes during a trial in an upper trunk-bending task. They found that the first PC could explain 98-99 % of the variance, indicating a strong coupling between the movements at these joints by the CNS.

Factor analysis has also been used to study neuro-muscular synergies (Kutch and Buchanan 2001; Holdefer and Miller 2002; Sabatini 2002). In the Sabatini study, factor analysis was applied to within trial EMG signals from various arm muscles involved in an upper arm task involving reaching, grasping and retrieval in a horizontal plane. He found that two types of muscle synergies were seen in subjects and interpreted this as indicative of different feed-forward motor commands in trajectory planning in the two groups. Kutch and Buchanan (Kutch and Buchanan 2001) also performed a principal component analysis on EMG of eight arm muscles, but during an isometric task. They found that the first two components explained 98% of total variance. According to them, the first component corresponded to the joint torque generated and the second component to the sum of EMG signals from all eight muscles.

Cluster analysis

This method has not been used much in movement science, but can be used as a first step to analyze data before using confirmatory procedures. This is a rather primitive, exploratory technique, which can be used to find the number of underlying dimensions in a data set based upon certain measures of similarity, such as correlation. In hierarchical clustering methods, for example, groupings are done either on the basis of successive mergers of successive divisions based upon some measure of similarity. The hierarchical and k-means procedures have been used to cluster neurons of similar function (Holdefer and Miller 2002).

The uncontrolled manifold hypothesis

One of the central problems in motor control is the so-called degrees of freedom problem (DOF problem; also called motor redundancy problem or Bernstein problem), which was first described by Bernstein (Bernstein 1967). He astutely observed that during repetitions of functional tasks each repetition of a movement involves unique motor patterns (joint rotations and muscle activation patterns), however the spatial aspects of the required movement are more reproducible. This pattern gives rise to a commonly seen feature in human movements, motor variability. Motor variability can be used as a window to understand the central organization of the system, which produces voluntary movements.

Gelfand and Tsetlin (Gelfand and Tsetlin 1966) described a structural unit as a task-specific organization of elements such that, if an element introduces an error into the common output, other elements change their contributions to minimize that error and no corrective action is required from the controller (cf. Principal of minimal interaction; also see section on ‘Synergies’). Systems that function according to this principle and

demonstrate error compensation among elements will be referred to as synergies in this dissertation.

Most theories of human movement, have previously attempted to solve the motor redundancy problem by selecting an optimal solution based on some specific criteria (Cole and Abbs 1986; Cruse et al. 1990; Viviani and Flash 1995; Okadome and Honda 1999; Rosenbaum et al. 1999; Binding et al. 2000; Schwartz and Moran 2000 for reviews see Sief-Naraghi and Winters 1990; Latash 1993). These theories try to eliminate DOF in attempting to choose a single optimal solution. Recently, the principle of abundance has been proposed (Gelfand and Latash 1998). According to this principal, no DOFs are eliminated or frozen. All DOFs or elements participate in a task assuring flexibility and stability of performance. Stability of a system is its capacity to return to a given state after a (phasic) perturbation has driven the system way from that state. Thus, stability is a prerequisite to the realization of a motor goal. Differential stability of variables may be a feature that differentiates the primary variables of control of the CNS during a task from secondary variables.

Experimentally, stability can be assessed by the variability of the corresponding variable in time (Scholz and Kelso 1989) or reproducibility of that variable from trial to trial (Schoner 1990). Such analysis of variability is used in the uncontrolled manifold approach to define synergies. The UCM hypothesis assumes that when a controller of a multi-element system wants to stabilize a particular value of a performance variable, it selects a sub-space within a state space of elements, such that within the subspace, the desired value of the variable is constant. This subspace is called the uncontrolled manifold (UCM). Once the UCM is chosen, the controller selectively restricts variability of solutions that do not lead to desired values of the important control variable while making use of the abundant solutions available to it, allowing a range of solutions, which allow the task goal to be met. Thus, the controller allows elements to show high variability as long as the desired value of the performance variable is met.

This approach makes it possible to formally address the following questions: 1) how to distinguish a synergy from a non-synergy 2) how to quantify the ‘strength’ of a synergy 3) how to test if a synergy contributes to a task and 4) how to test if a new synergy has been developed for a task? (Latash et al. 2002b)

This hypothesis has been used to study a number of kinematic (joint angles) and kinetic (finger forces and moments) variables (Scholz and Schoner 1999; Scholz et al. 2000; Latash et al. 2001; Domkin et al. 2002; Latash et al. 2002a).

Kinematic studies using the UCM approach

Whole body kinematics was studied in a sit-to-stand task (Scholz and Schoner 1999; Scholz et al. 2001; Reisman et al. 2002). The joint configurations observed at each point in normalized time were analyzed with respect to trial-to-trial variability. The variability of joint configurations across trials was decomposed into components that did not affect (within the UCM) and that did affect (orthogonal to the UCM) the values of variables such as position of the COM. It was found that the position of the COM in the sagittal plane and linear momentum of COM (Reisman et al. 2002) was selectively stabilized. The horizontal head position and the position of the hand were controlled less stably, while vertical head position appears to be no more stabilized than joint motions (Scholz and Schoner 1999). This effect was even more pronounced under difficult perceptual conditions (eyes closed, short support surface) (Scholz et al. 2001). This provides evidence for the hypothesis that under challenging task constraints increased variability is selectively directed into task-irrelevant degrees of freedom.

Study of 3D kinematics of the arm in a quick-draw pistol-shooting task (Scholz et al. 2000) revealed that orientation of the pistol was selectively stabilized throughout the whole movement, whereas pistol position and center of mass of the arm were only stabilized in the early phase of the movement. The UCM approach has also been used to study unimanual and bimanual pointing tasks (Domkin et al. 2002; Tseng et al. 2002). For unimanual pointing, the path of the hand and path of the COM of the arm were found to be selectively stabilized (Tseng et al. 2002). In the bimanual task (Domkin et al. 2002), one hand held a target and the other a pointer. Subjects were asked to move the pointer towards the target. In this task, the vectorial distance between the target and the pointer tip was selectively stabilized. This effect was greater after a period of practice. Thus, the

UCM hypothesis allows quantitative assessment of the degree of stabilization of selected performance variables and provides information on changes in the structure of a multijoint synergy that may not be reflected in its overall performance.

Multi-finger force production studies using the UCM approach

When a person is instructed to produce force with one finger of a hand, other fingers show involuntary force production, a phenomenon called enslaving (Zatsiorsky et al. 1998). So, UCM analysis is done on another set of independent variables, 'modes' (Latash et al. 2001; Latash et al. 2002a; Scholz et al. 2002). These studies showed that in tasks requiring subjects to produce a certain amount of force (cyclic and ramp force production) with two, three or four fingers, subjects selectively stabilized total force only at high force levels, whereas total moment was stabilized throughout the cycle.

In all the above studies, the UCM framework has been used at the level of mechanical variables. It is our aim in this dissertation, to extend the use of this method to a more physiological variable, namely muscle activation patterns recorded by electromyography (EMG). The first step in this process will be to identify independent control variables (ICVs; see section on 'Postural synergies' in Chapter 1). We propose to do this by using principal component analysis (PCA) on integrated EMGs of muscles across multiple trials. We will refer to these ICVs as muscle-modes or M-modes. We will then relate these M-modes to an important performance variable, COP (Baratto et al. 2002; Collins and De Luca 1993; Winter et al. 1998; Zatsiorsky and Duarte 2000) and compute the Jacobian of the system. Finally, a UCM will be computed based on average across tasks shift in COP and UCM analysis will be performed on repetitions of the task, by decomposing variance in magnitudes of M-modes into two components, one along the UCM (V_{UCM}) and the other orthogonal to it (V_{ORT}). We expect $V_{UCM} > V_{ORT}$ per degree of freedom, if the M-modes co-vary to stabilize COP shifts. Further, we would like to verify if the muscle synergies are similar or different for shifts in the COP in opposite

directions (COP shift to the front of back). Next, we would like to use this method to test if the same or different M-modes and synergies are used under different conditions of stability and additional sensory information or support.

Chapter 3

FORMULATION OF RESEARCH PROBLEMS

In this chapter, the main issues and research questions of this dissertation are presented. These questions will be addressed in Chapters 4-7 of the dissertation.

Postural muscle synergies

The UCM hypothesis assumes that the controller (the central nervous system, CNS) acts in a state space of independent control variables (ICVs) and selects in this space a manifold corresponding to a value of a performance variable, which needs to be stabilized. When analyzing muscle synergies from EMG signals, it is important to realize that muscles are not independently controlled (Hughlings Jackson 1889), but are controlled in groups. In order to perform UCM analysis on independent control variables in the muscle space, the first task is to verify if it is possible to identify such ICVs. We will refer to these as M-modes.

First group of research questions

1. Is it possible to identify M-modes in a subject for a particular task?
2. Are these M-modes robust across tasks and subjects?

To identify M-modes for a particular task in a subject, we will perform principal component analysis on the integrated EMG indices of recorded muscles across several repetitions of the task. If this analysis gives a small number of components that can explain a reasonably high amount of the total variance of all the muscles, we can say that it is possible to identify M-modes in a subject for a particular task. Next, we will compute the cosines between corresponding PC vectors within a subject for different tasks and within the same task for different subjects. If this analysis reveals high values of cosines (nearly collinear vectors), then we will conclude that M-modes are similar across tasks and subjects.

If it is possible to identify such M-modes, then we can proceed to the next step of UCM analysis, namely relating the M-modes with an important performance variable. Position of the center of pressure (COP) can be regarded as such a variable based on previous literature (Baratto et al. 2002; Collins and De Luca 1993; Winter et al. 1998; Zatsiorsky and Duarte 2000). We hypothesize that the magnitude of the COP shift would be stabilized not by a fixed, optimal combination of the M-modes but by co-variations of the magnitudes of M-modes across trials at the same task.

Once we have a Jacobian relating the changes in magnitudes of M-modes with shifts of the COP, we can perform the UCM analysis by partitioning the variance in the space of M-modes into a component within the UCM and the other one orthogonal to it. If the component within the UCM is greater than the orthogonal component per degree of freedom, then our hypothesis is confirmed.

Second group of research questions

1. Can postural control be described as a process within a relatively low-dimensional space (M-mode space)?
2. Can we confirm the control hypothesis on stabilization of COP shift by co-variations of the magnitudes of M-modes?

3. Is the same synergy used for shifts of the COP in different directions, namely forward and backward?

To answer these questions, we would first need to repeat the process of identifying M-modes as described for the previous group of questions. After that, we need to compute the Jacobian of the system relating the changes in magnitudes of M-modes to COP shift. Then, a manifold corresponding to average (across trials) COP shift should be computed and the variance in the M-mode space should be partitioned into its components along this manifold and perpendicular to it. If $V_{UCM} > V_{ORT}$ per degree of freedom, we can conclude that the M-modes co-vary to stabilize the COP shift. This will answer both questions 1 and 2. In order to answer question 3, we should use two different tasks in Step 2 (see section on 'Postural synergies' in Introduction), when the Jacobian is identified. These tasks should be associated with COP shifts to the front and back respectively, giving two Jacobians, which could then be used in the UCM analysis in Step 3. If $V_{UCM} > V_{ORT}$ only when the Jacobian with COP shift in the same direction as the task in Step 3, then there are different synergies for shifts of the COP forward and backward.

Once we verify that the framework of the UCM hypothesis can be used to identify muscle synergies with the above experiments, we would like to extend the use of this approach to see if such multi-muscle synergies are modified by factors such as postural stability. Before doing that we plan to perform an experiment examining the role of touch in postural sway.

Postural stability: effects of touch

A number of studies have investigated the role of sensory information on the control of vertical posture. Some of these have looked particularly at the role of cutaneous information from the finger in decreasing postural sway (Holden et al. 1994;

Jeka 1997). However, it is not clear if there is something special about finger contact with respect to its effect on sway. Further, it is not apparent what feature of the touch is actually responsible for the effects seen.

Third group of research questions

1. Is it active touch by the subject or availability of a stable external reference point that is important for sway reduction?
2. Is the effect of touch to different body parts quantitatively similar despite the differences in the density of sensory receptors and their ability to discriminate sensory stimuli?
3. How is postural sway modulated by change in the point of contact with respect to the plane of greatest sway? This has been investigated in only one study.
4. Does the effect of touch depend on the stability of the touched surface and how? There is conflicting evidence about this in the literature.

To answer question 1, we will compare different indices of sway under two conditions: finger touch to a stable external surface and clasp of the fingertip in a clip fixed to an external frame. If the latter results in larger decrease in sway indices, then a stable reference point is more important. To answer question 2, we will compare the effects of finger touch to a stable surface to touch to the head and neck, which have a lower density of sensory receptors. To investigate the role of direction of touch on reduction in sway, we will compare the effects of finger touch to the front of the body to finger touch to the side of the body. Finally, to examine the role of stability of the touched surface, we will compare finger touch to a stable external point to touch to a handle that is free to move in the AP and ML directions. In the latter case, if there is a significant reduction in sway, it shows that availability of a stable external reference alone is not the only important factor in reducing sway.

Relating postural muscle synergies to postural stability

If it is possible to identify synergies using the UCM approach as indicated by second set of questions above, it would be useful to extend this approach to understand if postural instability could modify these synergies.

Fourth group of research questions

1. Are similar M-modes used in conditions of postural instability as in stable conditions?
2. Are the M-modes used in conditions of postural instability modified by a light finger touch to a stable support or hand grasp?
3. In a task when an arm can contribute to stabilization of the vertical posture, do two groups of M-modes exist, one across the lower limb and trunk muscles and the other across the arm muscles? Alternatively, are muscles grouped into common M-modes across effectors?
4. Can we confirm a control hypothesis about stabilization of COP shift by co-variations of the magnitudes of M-modes under stable and unstable conditions and with an addition of finger touch? If so, are the multi-muscle synergies that are identified similar across these three conditions?

To answer questions 1-3, we will perform an experiment where we will ask subjects to release a load while standing on 1) a stable surface without touch and 2) an unstable board without additional touch, 3) an unstable board with a light touch to a stable support and 4) an unstable board with a grasp to a handle. We will compare M-modes computed at each of these conditions across tasks and subjects. If the M-modes are dissimilar across tasks we will conclude that there is an effect of stability or additional hand support on organization of M-modes. Further, examination of muscle

groups within the M-modes for these tasks will help us answer the third question. When the hand is grasping a handle, since the arm has a role in postural stabilization, we expect these muscles to be grouped together with other postural muscles.

Finally, we will repeat UCM analysis as described under the second set of questions under conditions of stability, instability and instability with finger touch to see if the M-modes co-vary to stabilize COP shift. If yes, then we will also examine if the same or different synergies are used in these three conditions.

Chapter 4

MUSCLE SYNERGIES DURING SHIFTS OF THE CENTER OF PRESSURE BY STANDING PERSONS: IDENTIFICATION OF MUSCLE MODES.

Introduction

The notion of muscle synergies is commonly used in both basic and clinical research including studies of control of vertical posture (Bouisset et al. 1977, Crenna et al. 1987, Allum and Honegger 1993, Sabatini 2002, Holdefer and Miller 2002). However, identification of such muscle synergies, based on experimentally recorded signals reflecting muscle activation levels (electromyogram, EMG), has been an elusive issue.

Previous studies identified muscle synergies by examining the correlations between indices of activation patterns of pairs of muscles at a given time (Bouisset et al. 1977, De Luca and Erim 2002) or the order of recruitment within a muscle group (Crenna et al. 1987). Different statistical methods have also been used to identify multi-muscle synergies, including multiple regression (Yoshida et al. 2002), factor analysis (Sabatini 2002), principal component analysis (Kutch and Buchanan 2001, Holdefer and Miller 2002), and cluster analysis (Holdefer and Miller 2002). In all these studies, synergies were defined as correlated changes in certain performance variables, kinematic, kinetic, or electromyographic. We would like to suggest a different approach that uses analysis of performance variables to discover relations among control variables that we view as more relevant to analysis of muscle synergies.

The approach we advocate follows the traditions set by Gelfand and Tsetlin (Gelfand and Tsetlin 1966). By definition, synergies are task-specific groups of elements, which stabilize particular performance variables. Depending on the level of analysis, a muscle may be viewed as an element of a multi-muscle synergy or as a synergy

composed of motor units as elements. A computational approach to the identification and analysis of synergies has been suggested, termed the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999; reviewed in Latash et al. 2002). The UCM hypothesis assumes that the controller (the central nervous system, CNS) acts in a state space of control variables and selects in this space a manifold corresponding to a value or a time profile of a performance variable, which needs to be stabilized. By doing this, the controller selectively limits variability of control variables in directions that lead to changes in the selected performance variable, while it allows higher variability in other directions. If several attempts at a task are analyzed, variance in the state space orthogonal to such a manifold is expected to be reduced as compared to the variance within the manifold.

The UCM-hypothesis is formulated in terms of hypothetical control variables. In experiments, however, performance variables are measured. A set of measured performance variables may not be equivalent to a hypothetical set of control variables. For example, in multi-finger force production tasks, forces of individual fingers are not independent because of the phenomenon of enslaving (Kilbreath and Gandevia 1994, Zatsiorsky et al. 1998; Zatsiorsky et al. 2000). Therefore, analysis of multi-finger synergies within the UCM framework was performed using another set of variables, force modes, which represent hypothetical independent variables manipulated by the brain for such tasks (Latash et al. 2001; Zatsiorsky et al. 2002a; Zatsiorsky et al. 2002b). The number of force modes was assumed to be equal to the number of explicitly involved fingers, while changes in the gain of a force mode were assumed to induce changes in forces produced by all the fingers of the hand.

Since Hughlings Jackson (Hughlings Jackson 1889), it has been assumed that the brain does not control individual muscles independently but unites them in groups. In other words, there are likely to be fewer control variables than muscles. Hence, any analysis of multi-muscle synergies should begin with identification of jointly activated muscle groups that are formed for particular tasks and can be seen across variations in task parameters. We are going to address such hypothetical control variables as muscle modes (M-modes) and assume that the CNS manipulates gain factors at the M-modes.

Note that the number of M-modes is expected to be significantly smaller than the number of muscles whose activity is recorded within a particular experiment.

The main purpose of the current study has been to identify M-modes in postural muscles, during tasks that involve shifts of the center of pressure (COP). Two types of tasks were selected that required a COP shift as an implicit or an explicit component. The former represented effects of anticipatory postural adjustments (APAs; reviewed in Massion 1992) to a self-triggered unloading, while the latter was produced by a voluntary body sway. We tried to answer the following specific questions:

1. Is it possible to identify M-modes in a subject for a particular task?
2. Are M-modes robust across tasks and subjects?

Methods

Subjects

Nine healthy male subjects of mean age 29.1 yr. (± 3.8 SD), mean weight 69.7 kg (± 7.8 SD) and mean height 175.6 cm (± 11.3 SD), without any known neurological or motor disorder, participated in the experiment. All subjects except one were right-handed based on their preferential hand use during eating and writing. The subjects gave written informed consent according to the procedure approved by the Office for Regulatory Compliance of the Pennsylvania State University.

Apparatus

A force platform (AMTI, OR-6) was used to record the moment around a frontal axis (M_y), and the vertical component of the reaction force (F_z). An oscilloscope (Tektronics TDS 210) showed the time pattern of M_y to the subject and the experimenter. A uni-directional accelerometer (Sensotec) was taped to the dorsal aspect of the subject's hand, just under the metacarpophalangeal joint of the middle finger. The axis of sensitivity of the accelerometer was directed along the required motion. Disposable self adhesive electrodes (3M) were used to record the surface EMG activity of the following eleven leg and trunk muscles: tibialis anterior (TA), lateral head of gastrocnemius (GL), medial head of gastrocnemius (GM), soleus (SOL), vastus lateralis (VL), vastus medialis (VM), rectus femoris (RF), biceps femoris (BF), semi-tendinosus (ST), rectus abdominis (RA) and erector spinae (ES), see Figure 1. The electrodes were always placed on the left side of the subject's body on the muscle bellies, with their centers approximately three centimeters apart.

Signals from the electrodes were amplified (× 3000) and band-pass filtered (60-500 Hz). Data were recorded at a sampling frequency of 1000 Hz with a 12-bit resolution. A Gateway 450 MHz PC with customized software based on the LabView-4 package was used to control the experiment and collect the data.

In some conditions, subjects held a load (20 × 20 × 10 cm) between their hands, by pressing on the sides of the load or via a pulley system (Figure 1). The load could either be heavy (3 kg) or light (2.3 kg); on average, this mass was approximately 4% (heavy) or 3% (light) of the subject's body mass.

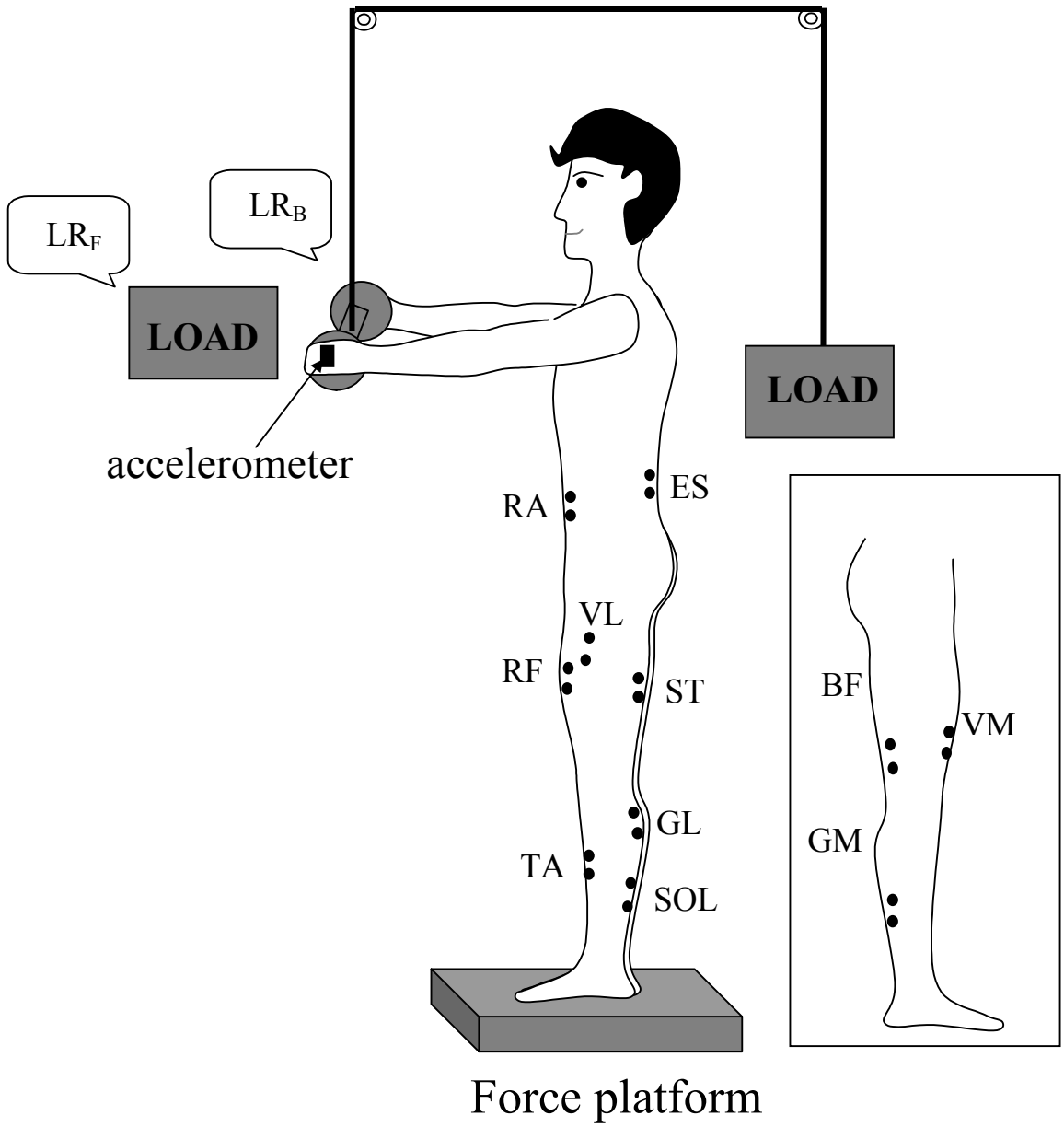

Figure 1: The experimental setup. Subjects stood on a force platform. In trials when subjects were required to release the load in front, the load was held directly in the hands (LR_F) and when the load was to be released behind the subject, the subject held a handle, which was connected to the load through the pulley system (LR_B). Location of the EMG electrodes is also shown. The insert shows position of electrodes placed on the medial side of the leg. GL: lateral head of gastrocnemius, GM: medial head of gastrocnemius, SOL: soleus, BF: biceps femoris, ST: semi-tendinosus, ES: erector spinae, TA: tibialis anterior, VL: vastus lateralis, VM: vastus medialis, RF: rectus femoris and RA: rectus abdominis.

Procedure

Two types of tasks were used, both associated with shifts of the COP. One group of tasks associated with APAs leading to a COP shift required the subjects to release a load from extended arms (Aruin and Latash 1996). The other task required the subjects to voluntarily shift their COP using visual feedback provided by the oscilloscope.

Load release (LR) task

In the initial position, subjects stood on the force platform with their feet side-by-side, at hip-width. This position was marked on the platform and was reproduced across trials. In trials where the load was released in front of the subject, the subjects pressed on the sides of the load with extended hands (Figure 1). When the load was to be released at the back, the subject pressed on the sides of the horizontal handle, which in turn was attached to the load through the pulley system (Figure 1). The LR task was performed with the heavy as well as with the light load in both directions. Subjects were instructed to release the load with a quick, small amplitude, bilateral shoulder abduction movement.

Voluntary sway (VS) task

The initial position was the same as in the LR task, except that the subjects' hands were now hanging loosely by their sides. The subjects were required to quickly move their body towards the toes. Subjects were asked to monitor their M_y shift on the oscilloscope and to keep the amplitude of M_y shift consistent across trials. The required M_y shift corresponded to a COP shift of about 1-2 cm.

In all there were 5 conditions: 1) Releasing the heavy load behind the subject (LR_{BH}), 2) Releasing the light load behind the subject (LR_{BL}), 3) Releasing the heavy

load in front of the subject (LR_{FH}), 4) Releasing the light load in front of the subject (LR_{FL}) and 5) Quick voluntary shift of the COP towards the toes (voluntary sway, VS).

For each trial, data were collected over 3 s. Subjects were instructed to stand as quietly as possible in the initial position before the beginning of the trial. The subjects heard a computer generated beep 500 ms after data collection had begun, which indicated to them that they could initiate the required action. Subjects were reminded not to initiate their actions immediately after the beep, but to wait for about a second.

The order of the conditions was pseudo-randomized across subjects. They performed 50 repetitions at each condition. Usually, 50 trials were presented as two sets of 25 trials each with a rest period of 6 seconds between trials and a rest period of two minutes between the sets. In a few subjects, some series of 50 trials were broken into 3-4 sets of about 15 trials each. Sufficient rest periods were given between sets of trials, such that fatigue was never an issue. Prior to each condition, three practice trials were given.

In addition to the above conditions, two control trials were performed: The subject was asked to hold a load of 5.3 kg in front of the body and behind the body (through the pulley system) for 5 s.

Data processing

All signals were processed off-line, filtered with a 50-Hz low-pass, fourth order, zero-lag Butterworth filter using LabView 4. All EMG signals were rectified. Individual LR trials were viewed on a monitor screen and aligned according to the first change in the signal of the accelerometer (movement initiation) that could be identified by visual inspection at an optimal resolution. This moment will be referred to as “time zero” (t_0). VS trials were aligned by the first visible shift of M_y.

Changes in the background muscle activity associated with the early phase of the COP shift were quantified as follows. In the LR trials, rectified EMG signals were integrated from 100 ms prior to t_0 to t_0 ($\int$EMG). In these trials, M_y shift started, on average, 80 ms prior to t_0 (cf. Aruin and Latash 1995). Since VS tasks were aligned by

the earliest M_y shift, to have comparable intervals of EMG integration across tasks, EMG were integrated from –20 ms to +80 ms with respect to t_0 in the VS task. Figure 2 illustrates typical patterns of M_y shifts as well as activity of SOL during a LR_{BH} trial and a VS trial (in this particular illustration, the earliest My shift was likely produced by the action of other muscles, not shown in the Figure). The upper graph shows signal from the accelerometer that was used to align the LR trial (the next two graphs). The lower two graphs (VS trial) are shifted in time with respect to the upper ones by 80 ms such that the windows of EMG integration (shown by vertical lines) coincide. These integrals were corrected by subtracting integrated activity from –500 to –450 ms prior to t_0 multiplied by two - the baseline EMG activity, $\int EMG_{bl}$.

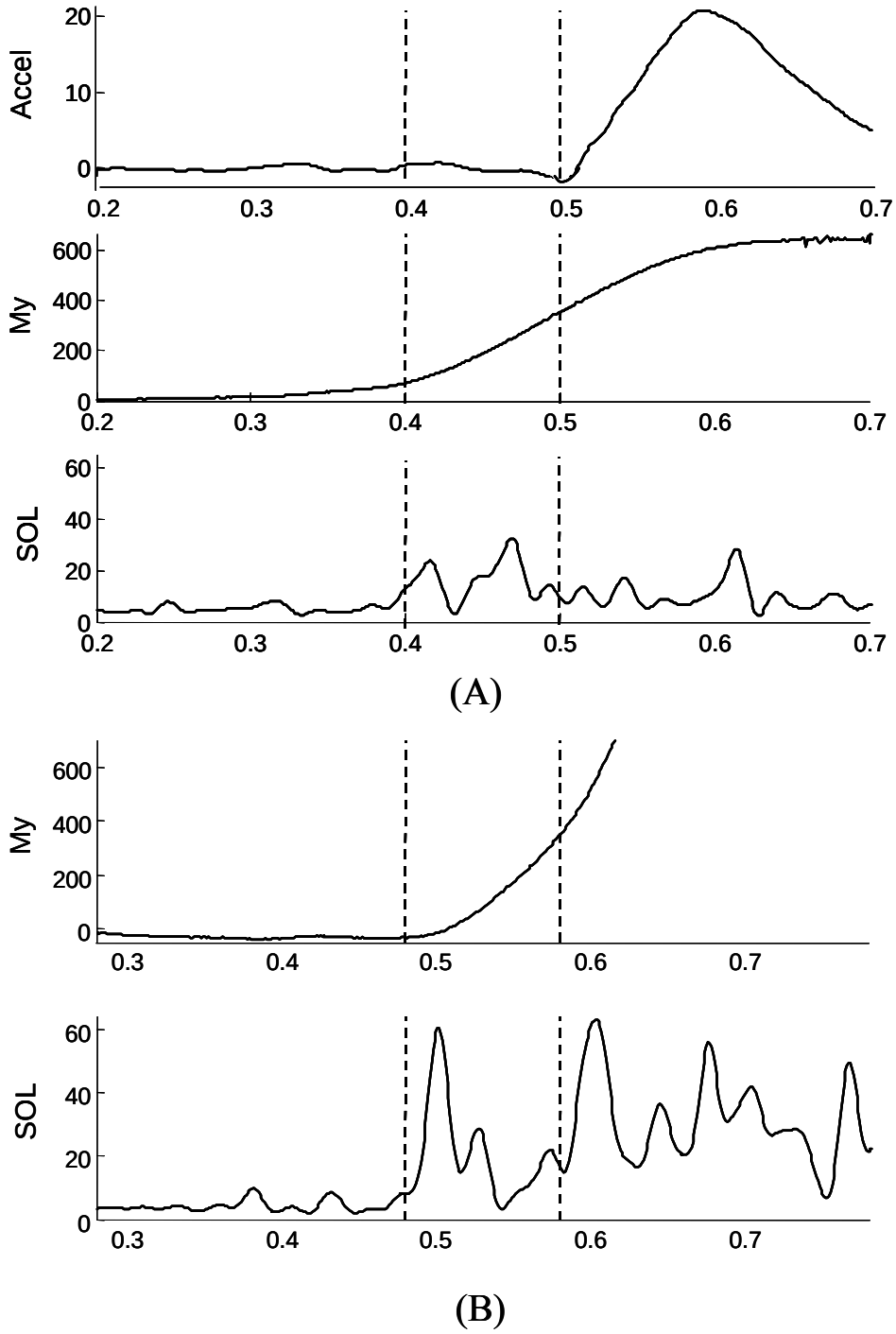

Figure 2: (A) The top three graphs show signals from the accelerometer (Accel), moment in the sagittal plane, M_y and EMG of soleus (SOL) during task LR_{BH} performed by a typical subject. (B) Time series of M_y and EMG of SOL during the VS task performed by the same subject. In both panels, the vertical dashed lines show the interval of EMG integration. Note the time shift in panel (B).

$$\int \mathrm{EMG}_{\mathrm{LR}} = \int_{-100}^{t_0} \mathrm{EMG}\, dt - 2\int_{-500}^{-450} \mathrm{EMG}_{\mathrm{bl}}\, dt \quad \textbf{(1A)}$$

$$\int \mathrm{EMG}_{\mathrm{VS}} = \int_{-20}^{+80} \mathrm{EMG}\, dt - 2\int_{-500}^{-450} \mathrm{EMG}_{\mathrm{bl}}\, dt \quad \textbf{(1B)}$$

In order to compare the ∫EMG indices across muscles and subjects, we normalized them by the integrals of EMGs collected in the control trials as follows: ∫EMG indices for dorsal (ventral) muscles were divided by integrals of EMG over 100 ms, $\int \mathrm{EMG}_{\mathrm{control}}$, during holding the load in front of (behind) the body:

$$e = \int \mathrm{EMG}_{\mathrm{LR/VS}} / \int \mathrm{EMG}_{\mathrm{control}} \quad \textbf{(2)}$$

Finally, all the experimental data are represented by components $e_{m,t,s,n}$, where $m = 1, \ldots, M$, $M = 11$ is the number of muscles; $t = 1, \ldots, T$, $T = 5$ is the number of tasks; $s = 1, \ldots, S$, $S = 9$ is the number of subjects, $n = 1, \ldots, N$, $N = 50$ is the number of trials (repetitions) in each task and subject.

Statistics

Standard statistical methods were used. Data are mostly presented as means and standard errors.

Principal component analysis

For a particular task t, in each subject s, we have e data matrices $\mathbf{D}_{t,s}$ with the size 50×11 (50 rows corresponding to repetitions and 11 columns corresponding to muscles). The matrix $\mathbf{C}_{t,s}$ of correlations between the e's was subjected to PCA, using procedures

from Statistica 6.0 (StatSoft, Inc.). The correlations were computed among the columns. The factor analysis module with principal component extraction was employed.

For each task and subject, the obtained eigen-values $\{\lambda_{i,t,s}$; where, $i = 1, 2, 3$; $t = 1,2,..,5$; $s = 1, 2, \ldots,9$) and PCs (vectors $\mathbf{p}_{i,t,s}$) of the matrix $\mathbf{C}_{t,s}$ were then considered. The first three PCs explain on average 60% of the variance in the data. Within each task and subject, the first three PCs contained several muscles with significantly high loadings each (over ± 0.5; Hair et al. 1995). The remaining PC's commonly included only one muscle with a high loading. Besides, examination of the scree plot revealed a bend at or about the third PC (see Fig. 4 in Results). Hence, only the first three PCs were analyzed.

In order to verify that the results from PC analysis were robust and not dependent on the specific muscles in the data, we selected a few sets of data to repeat the analysis after excluding one muscle. Different muscles were excluded one at a time and the analysis was repeated. We found that removal of a muscle did not significantly alter the PC results, suggesting that the analysis was robust. This will not be discussed further.

Cluster analysis

Cluster analysis is a technique used to group objects on the basis of similarities or distances (dissimilarities) (Johnson and Wichern 2002a). No assumptions are made regarding the number of groups or the group structure. Cluster analysis on the PC vectors computed for the different tasks and subjects was performed using the SPSS package. To form the data for the analysis, we took the first three PCs for each subject and task, i.e., $\mathbf{p}_{1,t,s}$, $\mathbf{p}_{2,t,s}$, and $\mathbf{p}_{3,t,s}$. These sets of PCs were pooled across tasks for each subject (which gave 15 vectors) or across subjects for each task (which gave 27 vectors). Pearson's correlation coefficients between muscle EMGs were used as a measure of similarity. The closest muscles from the perspective of this criterion were grouped in clusters. The agglomerative hierarchical method of clustering was employed. This method begins with as many clusters as objects, in this case eleven muscles. The most similar muscles are grouped first and these initial groups are then merged further based on their similarity (correlation). Finally, all groups are fused into a single cluster. When analyzing the

results of cluster analysis, one usually proceeds from one cluster to higher number of clusters in order to interpret the data reasonably.

Statistical verification of similarity of PCs across tasks and subjects

In order to test the assumption that the PCs are similar across tasks and subjects, we introduced a concept of a central vector. By definition, the central vector is a PC vector for which the sum of squared distances between it and the remaining vectors in the sample is minimal. With regard to this property, the central vector is analogous to the mean vector. Note that direct averaging of the vectors is impossible. Using the central vectors selected among the actual PC vectors avoids this problem. This procedure leads to the identification of three central vectors for each comparison; the three vectors are not necessarily orthogonal because they can belong to different subjects or different tasks.

Since we consider three main PCs, we select central vectors from the sets of the first, second, and third PCs separately. During the analysis, central vectors for each subject over all tasks $\{\overline{\mathbf{p}}_i(\mathrm{s})\}$, and for each task over all subjects $\{\overline{\mathbf{p}}_i(\mathrm{t})\}$ were identified. In the above expressions the horizontal line above $\mathbf{p}$ signifies selecting of a central vector; $i = 1, 2, 3$. We hypothesized that: (1) For each subject, a PC vector $\mathbf{p}_i$ is collinear to a central vector $\{\overline{\mathbf{p}}_i(\mathrm{s})\}$ if $i = j$, and orthogonal to $\{\overline{\mathbf{p}}_i(\mathrm{s})\}$ if $i \neq j$ (where $i, j = 1, 2, 3$); and (2) for each task, a PC vector $\mathbf{p}_i$ is collinear to the central vector $\{\overline{\mathbf{p}}_i(\mathrm{t})\}$ if $i = j$, and orthogonal to $\{\overline{\mathbf{p}}_i(\mathrm{t})\}$ if $i \neq j$.

Absolute values of cosines between 11-dimensional PC vectors were used as a measure of similarity. Cosines of angles between each $\overline{\mathbf{p}}_i$, ($i = 1, 2, 3$) for a selected task and $\mathbf{p}_i$ of each subject in each task were calculated and transformed into z-scores using Fisher's z-transformation. Further, these values were averaged either across subjects or across tasks for the following analyses of variance.

ANOVAs were run on the z-scores computed for each $\overline{\mathbf{p}}_i$ separately. Since cosines were computed between a selected $\overline{\mathbf{p}}_i$ and individual $\mathbf{p}_{i,t,s}$, factors included PC ($\overline{\mathbf{p}}$) (three

levels; i = 1, 2, 3), TASK (five levels, t = 1, 2, .., 5) and SUBJECT (9 levels, s = 1, 2, …, 9). Two sets of two-way repeated measure ANOVAs (PC, TASK and PC, SUBJECT) were run for each $\overline{\mathbf{p}}_i$ separately after averaging over the third factor.

Results

General EMG Patterns

When a subject stood and held a load in front of the body, there was increased background activity of dorsal muscles (GL, GM, SOL, BF, ST, and ES). Prior to load release, a drop in this activity was typically seen, commonly accompanied by bursts of activity in the ventral muscles (TA, RA, VL, VM, and RF). When a subject stood and held a load behind the body, increased background activity of ventral muscles was seen. Prior to load release, this activity dropped, and there were commonly EMG bursts in the dorsal muscles. Panels A and B of Figure 3 illustrate typical EMG patterns in a representative subject for LR trials. Early EMG changes (APAs) were variable across subjects; some subjects did not show clear bursts or episodes of EMG suppression in some muscles. In the voluntary sway (VS) trials, an early anterior shift of the COP was usually accompanied by a drop in the background activity of ventral muscles and bursts of activity in dorsal muscles. Figure 3C shows typical EMG patterns that accompanied VS. These EMG patterns also varied across subjects.

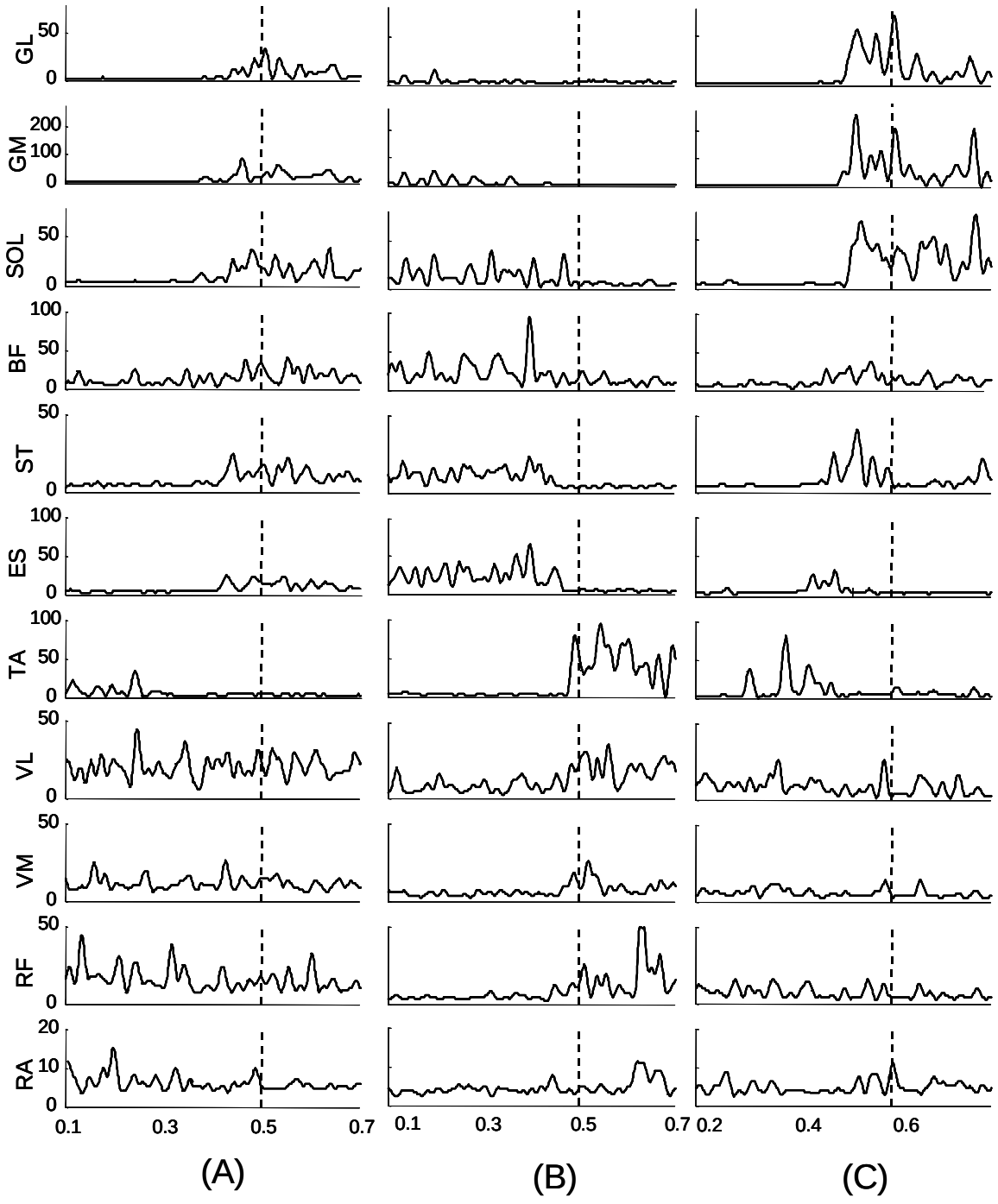

Figure 3: EMG activity in the eleven postural muscles during tasks involving load release in the back (LR_{BH}; A), load release in the front (LR_{FH}; B), and volunatry sway (VS; C) for a typical subject. Vertical dashed lines correspond to time zero, t_0. EMG was integrated over the 100 ms interval before t_0. For other abbreviations see Figure 1.

Principal Component Analysis

The *e* indices for all muscles from the 50 repetitions of each task by a subject were subjected to a PCA. In all, 44 PCA were performed (5 tasks x 9 subjects; subject 9 did not perform the LR_{FH} task). Figure 4 shows a typical scree plot. Note the sharp decrease in the amount of variance explained (< 10%) by components after PC3.

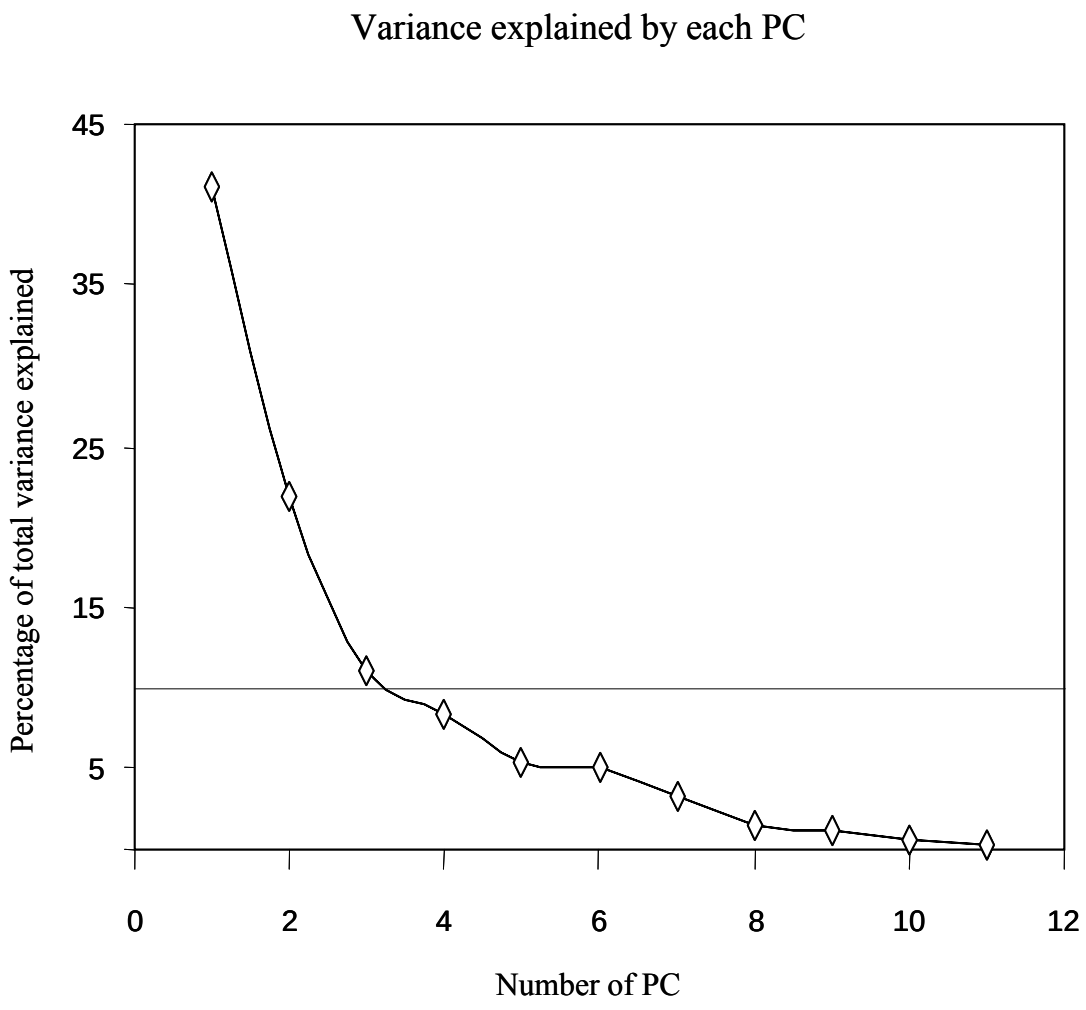

Figure 4: A scree plot: Percentage of variance corresponding to each PC for a typical subject who performed the voluntary sway task, VS. The horizontal line indicates 10 % of the total variance.

Across all the analyses, we found that components from PC4 onwards not only explained little variance, but these components also had at most one muscle with significant loading, and were poorly reproducible across subjects and tasks. There were three consistent PCs accounting on average for about 60% (± 5%) of the total variance. The average amount of variance explained by PC1 was 30% (± 4%), by PC2 was 18% (± 2%) and by PC3 was 12% (± 1%) across all subjects and tasks.

Table 1 shows the loadings of all the muscles on the three PCs for a representative subject in task LR_{BH}. The significant loadings are in bold. Table 2 shows how many times a muscle loaded significantly on a given PC across all the 44 PCAs. Note that the dorsal muscles (GL, GM, SOL, BF, ST and ES) predominantly loaded significantly on PC1 and the quadriceps muscle group (VL, VM, RF) on PC2. TA loaded on PC2 and also on PC3. RA was mostly seen in PC3, but often did not load significantly on any of the three PCs. Based on these results we can say that muscles with significantly high loadings in the three PCs were:

- PC1: GL, GM, SOL, BF, ST, ES – "push-back M-mode"
- PC2: VL or VM, RF, TA – "push-forward M-mode"
- PC3: *TA*, RA, *VM, GL* – "mixed M-mode"

The groups are named based on the general effect of the changes in muscle activity within a group on induced displacement of the center of mass. The muscles indicated in *italics* in the third group, did not show up consistently in the PC3, but were sometimes in one of the other M-modes. In general, the composition of significantly loaded muscles in PC3 was most variable across subjects.

Muscle	PC1 push-back	PC2 push-forward	PC3 mixed
TA	0.48	-0.02	**0.60**
GL	**0.57**	0.02	**0.66**
GM	**0.86**	0.01	-0.15
SOL	**0.65**	0.21	0.46
VL	-0.08	**-0.86**	-0.02
VM	-0.05	**-0.76**	0.14
RF	-0.08	**-0.86**	0.18
BF	**0.59**	-0.08	**-0.53**
ST	**0.74**	-0.27	-0.33
RA	0.06	0.21	-0.33
ES	**0.51**	-0.18	-0.47

Table1: Results of PCA in a typical subject. Typical sets of loading factors for one typical subject who performed the task of releasing the heavy load behind the body. Loadings over 0.5 are shown in bold.

Muscle	*M-mode*		
	push-back	*push-forward*	*mixed*
TA	8	**15**	**12**
GL	**31**	5	5
GM	**41**	0	1
SOL	**36**	3	2
VL	0	**33**	1
VM	4	**29**	6
RF	0	**31**	4
BF	**27**	7	9
ST	**33**	4	5
RA	1	7	**13**
ES	**24**	2	**10**

Table 2: The number of times a muscle is seen as part of an M-mode. Bold numbers show muscles that were significantly loaded in at least 10 cases.

Cluster analysis

Two sets of cluster analyses were run on the PC vectors:

- Clustering muscles for each task across PCs in all subjects; and
- Clustering muscles for each subject across PCs in all tasks.

We found similar muscle groups for clustering by task and by subject. In both cases, there were two broad clusters of dorsal and ventral muscles (corresponding to the "push-back" and "push-forward" M-mode; see Tables 1 and 2). Dendrograms of the results of cluster analysis for Task VS and a typical subject respectively are shown in Figure 5. Within the two broad 'back' and 'forward' M-modes, "sub-M-modes" can also be seen: those uniting the heads of the triceps surae (GL, GM, SOL), the heads of the quadriceps (VL, VM, RF), and the heads of hamstrings (BF, ST) together with ES.

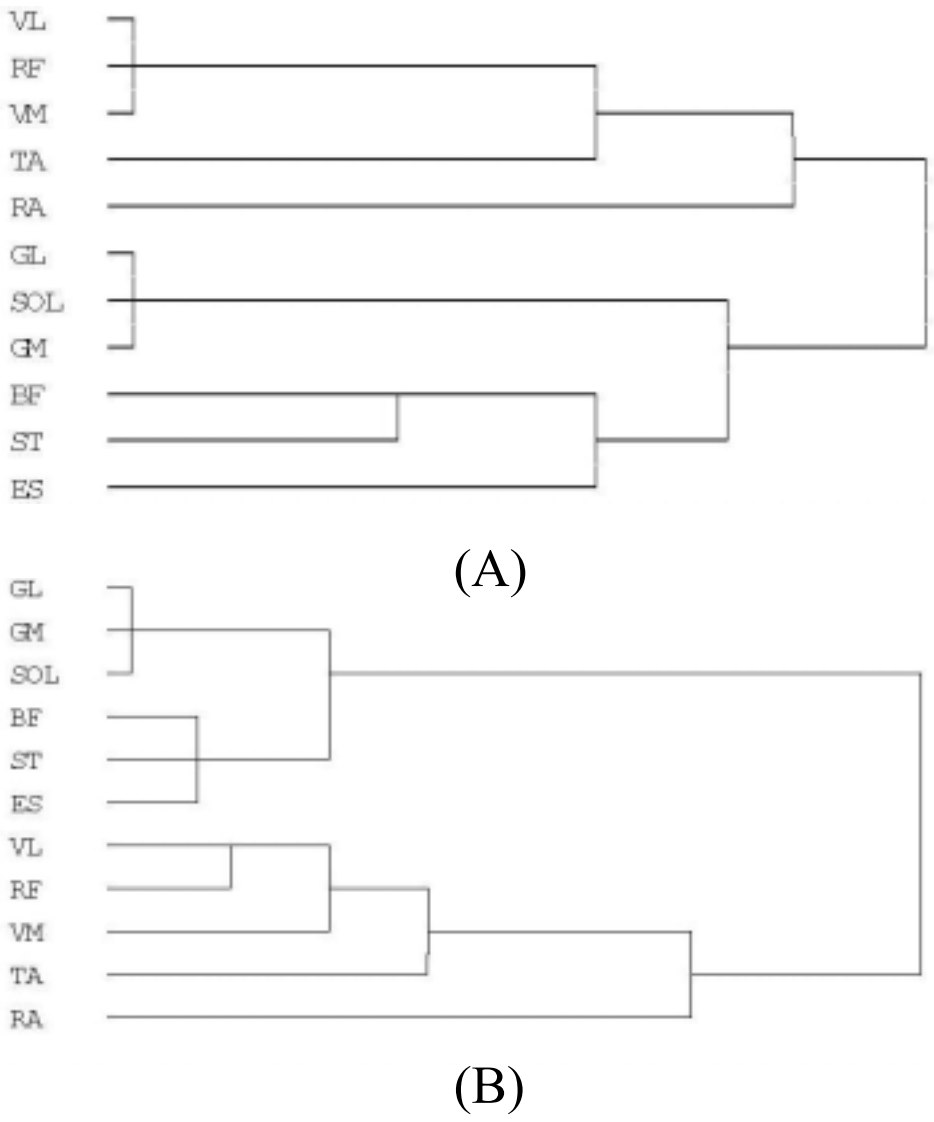

Figure 5: (A) A dendrogram shows clustering of muscles across all tasks for a typical subject. (B) A dendrogram shows clustering of muscles across all subjects for the voluntary sway task, VS. For other abbreviations see Figure 1.

Statistical verification of similarity of PCs across tasks and subjects

Absolute values of cosines between the PC vectors were used as a measure of similarity. Cosines between central vectors, $\overline{\mathbf{p}}_i$ and each individual PC ($\mathbf{p}_{i,t,s}$) were computed and compared across both tasks and subjects (see Methods for details). For further comparisons, cosine values were transformed into z-scores. Panel A of Figure 6 shows the mean z-scores of cosines of individual PCs with $\{\overline{\mathbf{p}}_i(\mathrm{t})\}$ computed over all PC_1, PC_2, and PC_3 separately for different tasks and averaged across subjects. Panel B of Figure 6 shows similarly organized data computed separately for different subjects and averaged across tasks. In both panels, z-scores for comparisons of a $\overline{\mathbf{p}}_i$ (i = 1, 2, 3) with individual $\mathbf{p}_j$ (j = 1, 2, 3) were higher for $j = i$ as compared to comparisons with $j \neq i$. This was particularly pronounced for the first $\overline{\mathbf{p}}$ (the first sets of columns in each panel).

These observations have been supported by two-way repeated measures ANOVAs. ANOVA-1 (PC and TASK) showed main effects of PC for $\overline{\mathbf{p}}_1$ and $\overline{\mathbf{p}}_3$ ($F_{(2, 8)} > 122$; $p < 0.001$). The p-value for $\overline{\mathbf{p}}_2$ was just above the level of significance ($p = 0.067$). There was a main effect of TASK ($F_{(4, 16)} > 4.2$; $p < 0.01$) and a significant interaction between PC and TASK ($F_{(8, 32)} > 2.9$; $p < 0.01$). The interaction reflected the fact that, for $\overline{\mathbf{p}}_1$ and $\overline{\mathbf{p}}_3$, all tasks showed similar results, while for $\overline{\mathbf{p}}_2$, only tasks LR_{BH} and VS showed significantly higher z-scores for comparisons with individual $\mathbf{p}_2$ than with $\mathbf{p}_1$ and $\mathbf{p}_3$.

ANOVA-2 (PC and SUBJECTS) showed main effects of PC for all $\overline{\mathbf{p}}$ ($F_{(2, 16)} > 13.3$; $p < 0.001$). There was a main effect of SUBJECT for $\overline{\mathbf{p}}_1$ and $\overline{\mathbf{p}}_3$ ($F_{(8, 64)} > 2.26$; $p < 0.05$) and a close to significant effect for $\overline{\mathbf{p}}_2$ ($p = 0.079$). There was also a significant interaction between PC and SUBJECT ($F > 1.8_{(16, 128)}$; $p < 0.03$) reflecting subject-specific behavior of z-scores.

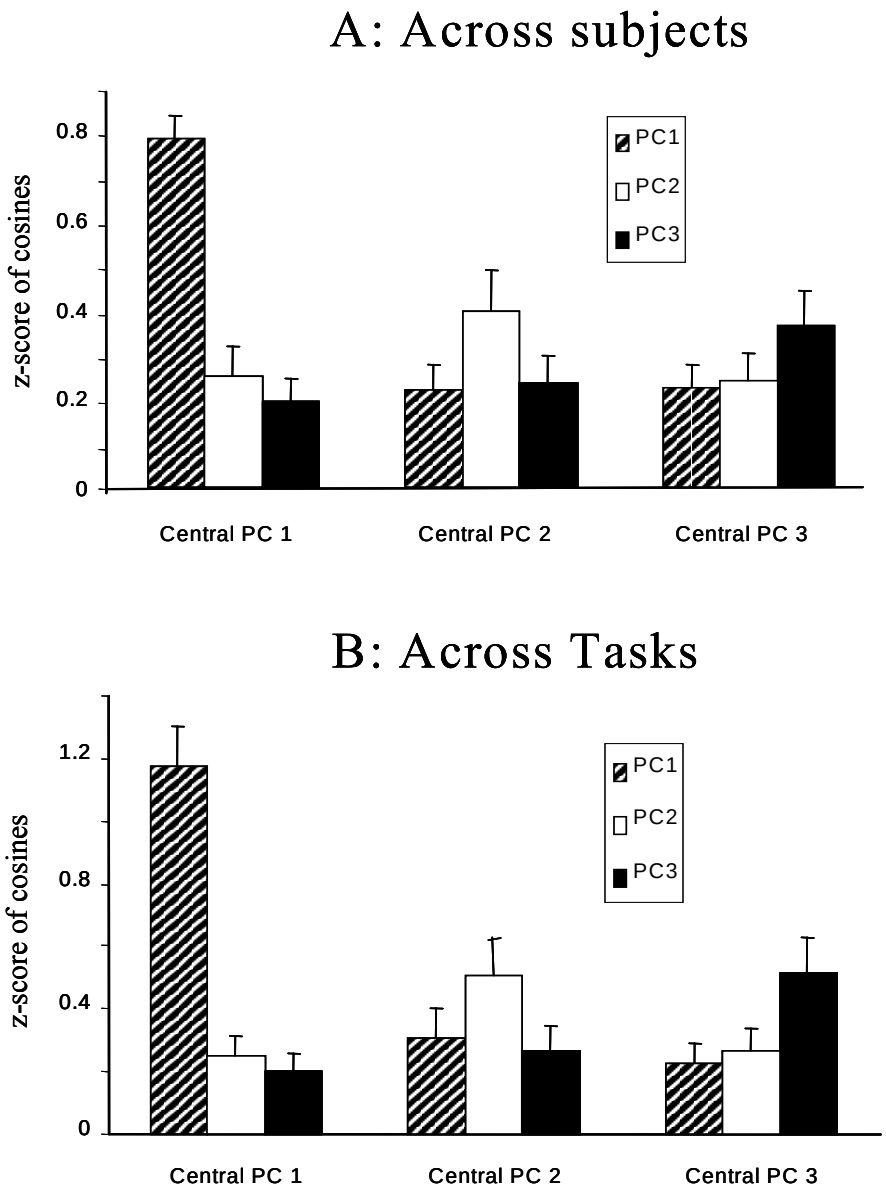

Figure 6: z-scores of cosines between a central vector, $\bar{\mathbf{p}}_i$ and each principal component vector, PC_i averaged across subjects (A) and averaged across tasks (B) with standard error bars. Note that the z-scores are highest between a PC and the central vector of the same number.

Discussion

Our findings show that indices of muscle activity (integrated EMG) associated with an early shift of the COP can be described with a few principal components (PCs). We view this observation as supporting our main hypothesis (see the Introduction) that the CNS uses a few central variables to adjust activity of the many postural muscles contributing to the production of a desired COP shift. In other words, the CNS uses a lower-dimensional space of control variables to produce changes in a higher-dimensional space of muscle activation.

The directions of vectors of PCs in the muscle space were similar across subjects and across tasks as confirmed by both the cluster analysis and the analysis of cosines between pairs of PCs (particularly for $\mathbf{p}_1$). We used two types of analysis to demonstrate the robustness of the result. This general finding emerged despite the fact that the tasks were rather dissimilar and involved both explicit (voluntary sway, VS) and implicit COP shifts associated with anticipatory postural adjustments (APAs, see Massion 1992) prior to releasing a load held in the hands of the extended arms. Moreover, the load release tasks could require early shifts of the COP in opposite directions depending on whether the load was held in front of the body or behind the body (using the pulley system). We do not want to claim that such M-modes represent multi-muscle synergies. By definition, synergies are supposed to stabilize particular functionally important performance variables (see the Introduction), while the M-modes represent multi-muscle units that decrease the number of control variables manipulated by the controller but they are not specific to a particular performance variable. The controller is expected to unite the control variables into a synergy with a functional purpose. Hence, we view this study as only the first step along the road to identification of multi-muscle synergies (see section 4.3).

Postural synergies

Many studies of postural control have invoked the notion of postural synergies following the traditions set by Bernstein (Bernstein 1967). This notion has been used rather loosely implying a co-variation of EMG or kinematic indices over the time course of a postural adjustment or across several repetitions of a task with a postural component. In particular, short-latency reactions of standing subjects to an unexpected rotation or translation of the force platform have been described using the notions of the ankle strategy and of the hip strategy (Horak and Nashner 1986; Horak et al. 1990) implying two postural synergies used predominantly by subjects during slow translations of the force plate (the ankle strategy) and during fast translations (the hip strategy). The hip strategy also dominated in elderly subjects. However, more complex patterns of adjustments have also been described including a "multi-link strategy" (Allum et al. 1989).

As mentioned in the Introduction, we view synergies as task-specific relations among control variables, not among performance variables. The current study identifies such potential control variables, M-modes, for postural tasks associated with COP shifts. However, it does not yet address issues of possible coordinated changes of M-modes across trials, i.e. M-mode synergies (see section 4.3). We would like to note that the M-modes identified in our study do not allow direct analogies with the ankle and hip strategies. Each of the three M-modes involved muscles spanning several joints. Their mechanical effects can be described in terms of their overall action on the center of mass of the body, at least for the first two M-modes, as reflected in their names, “push-back” and “push-forward”. However, we failed to find separation of muscles into groups acting predominantly at the ankle joint or at the hip joint.

This latter observation may be specific to the tasks our subjects performed. At least, they are compatible with muscle activation patterns described for APAs. During APAs, changes in the background muscle activity are commonly seen in muscles crossing all the major leg and trunk joints, and these changes do not allow to single out a

joint or a subset of joints to support the notions of the ankle or hip synergies (Aruin and Latash 1995); although see Alexandrov et al. 2000).

Different computational approaches to synergies

In the Introduction, we mentioned several methods used to study muscle synergies (loosely defined, as mentioned in the previous section). Bouisset et al (Bouisset et al. 1977) studied correlations among indices of integrated EMG activity of biceps brachii, brachialis and brachioradialis during elbow flexion movements at various velocities and against different inertial loads. They found significant correlations across all conditions, which they interpreted as signs of stability of a synergy among elbow flexors during different tasks. Crenna et al (Crenna et al. 1987) performed regression analysis on the activation time of pairs of postural muscles during a trunk-bending task and discussed synergies in terms of timing of EMG recruitment. Yoshida et al (Yoshida et al. 2002) used multiple regression to estimate torque vector directions of individual muscles from the shoulder torque and EMG of several shoulder muscles.

More recently, multi-variate statistical techniques have been used to study multi-muscle synergies. These include factor analysis, PCA, and cluster analysis. Sabatini (Sabatini 2002) used factor analysis on six shoulder muscle EMGs during a reaching and grasping task. He described three factors labeled ‘forward transport’, ‘backward transport’ and ‘shoulder support’. Further, he found in different subjects, two different groupings of muscles interpreted as two different neuro-muscular synergies. In the study by Kutch and Buchanan (Kutch and Buchanan 2001), PCA was applied to EMGs of eight elbow muscles during an isometric flexion/extension task at a fixed joint position. Much of the variance in the data could be explained by two PCs; the first PC could be related to the net torque produced while the second PC covaried with the sum of EMG signals from all muscles. Holdefer and Miller (Holdefer and Miller 2002) studied ‘functional muscle synergies’ in monkeys by recording discharge patterns of neurons in the primary motor cortex as well as EMGs in arm and hand muscles. They performed PCA to reduce the

muscle space to three components and further, cluster analysis revealed groups of neurons clustered together with particular groups of muscles.

PCA has also been used to identify kinematic synergies (Alexandrov et al. 1998b; Vernazza-Martin et al. 1999). In these studies, PCA was applied to joint angles of hip, knee and ankle during a trunk-bending task. The authors found that the first PC accounted for close to 99% of the variance, indicating that there was a fixed ratio between changes in these joint angles, which helped to keep the center of gravity of the body within the support surface.

As mentioned earlier, we do not view PC analysis as an adequate tool to identify multi-muscle synergies, mostly because it operates with performance variables such as levels of muscle activation, which are unlikely to have a one-to-one correspondence to hypothetical variables at the level of control (Hughlings Jackson 1889). Muscle groups identified in this way represent groups of peripheral elements, whose activity is presumably scaled with the help of a single control variable, an M-mode. As such, PC analysis can be used to identify M-modes, as done in our study, while identification of M-mode synergies requires the next step considered in the next section.

Setting the stage for UCM analysis

According to the UCM hypotheses, when the CNS controls a multi-element task, it defines a subspace within the space of control variables where a particular value or a time series of a performance variable is stabilized by a properly organized co-variation of the control variables. Since Hughlings Jackson (Hughlings Jackson 1889), researchers agree that muscles are not controlled by the CNS independently. Hence, one cannot associate changes in EMGs of individual muscles with changes in control variables, and correlated changes in EMGs of several muscles cannot be viewed as a control synergy. Therefore, the first step before the UCM method could be used, is to identify a set of control variables that are presumably used by the CNS to control a large group of muscles for a set of tasks. We have decided to focus on a group of postural tasks

associated with shifts of the COP. For this group of tasks, PC analysis was used to reduce the original set of eleven muscle variables to three variables (M-modes), which we view as control variables manipulated by the CNS.

Our experiments have also allowed to select tasks which are characterized by more stable M-modes (VS and LR_{BH}) to be used in future experiments to identify subject-specific M-modes. Further, we plan to use multiple regression to map gains of M-modes onto shifts of the COP in the anterior-posterior direction, i.e. define a matrix transforming the three-dimensional control space into the one-dimensional space of COP shifts or shifts in other variables that can be hypothetically controlled during postural tasks, such as the trajectory of the center of mass or the trajectory of the head (cf. Scholz and Schöner1999). Ultimately, one will be able to use the UCM analysis, i.e. to compare variance components in the space of control variables that lead and do not lead to changes in a particular performance variable (see Latash et al. 2002 for review). We hope that this line of research will make it possible to use the operational definition of multi-element synergies suggested by the UCM hypothesis to identify multi-muscle synergies and test their relations to particular tasks.

Chapter 5

MUSCLE SYNERGIES DURING SHIFTS OF THE CENTER OF PRESSURE BY STANDING PERSONS

Introduction

Since Hughlings Jackson (Hughlings Jackson 1889), it has been recognized that the central nervous system (CNS) does not control muscles independently, but unites them in groups. Bernstein (Bernstein 1967) proposed that the CNS uses muscle synergies as a means of solving the 'motor redundancy' problem. Gelfand and Tsetlin (Gelfand and Tsetlin 1966) viewed muscle synergies as a particular example of structural units, which are task-specific ensembles of elements within a neuromotor system. In the previous chapter we discussed the use of the terms muscle synergy (Bouisset et al. 1977, Crenna et al. 1987, Massion, Gurfinkel et al 1992, Allum and Honegger 1993, Sabatini 2002, Holdefer and Miller 2002), postural synergy or postural strategy (Horak and Nashner 1986; Horak et al. 1990, Allum et al. 1989) and kinematic synergy (Alexandrov et al. 1998b; Vernazza-Martin et al. 1999).

We also introduced a new approach to the identification and analysis of synergies, namely the uncontrolled manifold (UCM) approach (Scholz and Schoner 1999; reviewed in Latash et al. 2002). In this chapter, we will use this approach to identify multi-muscle synergies.

To perform the UCM analysis for a particular task, one needs to move through the following steps:

(1) Identification of independent control variables (ICV): These are the control variables that are independently manipulated by the CNS to stabilize performance variables. For example, in multi-finger force production studies, individual finger forces

cannot be considered independent because of the phenomenon of enslaving (Kilbreath and Gandevia 1994, Zatsiorsky et al. 1998; Zatsiorsky et al. 2000). Hence, UCM analysis of finger coordination in such tasks has been based on a different set of variables, force modes, defined in a special experimental series (Scholz et al. 2002). Force modes are the hypothetical independent control variables whereas the actual measured forces of each finger depend on a command to this finger (its force mode), as well as on commands to other fingers.

(2) Identification of relations between the ICV with a selected performance variable (the Jacobian of the system): This stage of analysis starts with the formulation of a control hypothesis, i.e. a hypothesis about a particular performance variable, which is supposed to be stabilized by a synergy. For example, in earlier kinematic studies, features of the trajectory of the endpoint of a kinematic chain were assumed to be stabilized, and the Jacobian was defined by the geometry of the moving effector (Scholz and Schöner 1999). In multi-finger force production experiments, the control hypotheses assumed that the total force (or total moment) produced by a set of fingers was stabilized, and the Jacobian linked its changes to changes in force modes (Scholz et al. 2002).

(3) UCM Analysis: A manifold (UCM) corresponding to a value of the performance variable is determined. Several attempts at a task are analyzed and the variance, computed across tasks is partitioned into two components, one within the manifold and the other, orthogonal to it. The former is supposed to be significantly larger than the latter. In multi-finger force production studies (Scholz et al. 2002), force profiles of individual fingers were recorded and subjected to such an analysis across trials at different phases of the task.

Previous studies using the UCM approach (Scholz and Schöner 1999; Scholz et al. 2000; Scholz et al. 2002) were done at the level of mechanical variables, such as joint angles and finger forces. With this experiment, our aim is to expand the use of this approach to a ‘more physiological’ variable, EMG, to identify muscle synergies associated with postural tasks.

We are going to move through the above three steps using the notion of muscle modes (M-modes) (Krishnamoorthy et al. in press-a, also Chapter 4), which are jointly activated muscle groups that are formed for particular tasks and can be een across

variations in task parameters. M-modes are assumed to be orthogonal dimensions in the control space such that a control signal can be represented as a vector in the M-mode space. Further, we introduce a control hypothesis that the CNS arranges co-variations among changes in magnitudes of M-modes to stabilize a certain task-specific center of pressure (COP) shift. This hypothesis is based on a body of literature that views coordinates of COP as an important variable for postural control (Collins and De Luca 1993; Winter et al. 1998; Zatsiorsky and Duarte 2000; Baratto et al. 2002). Muscle synergies are defined as co-variations of control variables (M-modes) that stabilize a particular value of COP shift.

In the present study, regression techniques are used to relate variations in the magnitude of the M-modes to variations in the COP shift. Finally, we compute a UCM in the M-mode space corresponding to a certain average (across trials) shift of the COP and compare variances per degree of freedom within the UCM (V_{UCM}) and orthogonal (V_{ORT}) to the UCM.

We hypothesized that the magnitude of the COP shift would be stabilized not by a fixed, optimal combination of the M-modes but by co-variations of the changes in magnitudes of M-modes across trials at the same task. If this hypothesis is confirmed, i.e. the variance within the corresponding UCM is significantly higher than variance orthogonal to the UCM ($V_{UCM} > V_{ORT}$), the following conclusions can be made: (1) the control hypothesis on stabilization of COP shift by co-variations of the magnitudes of M-modes is confirmed; (2) postural control can be described as a process of organizing task-specific synergies as combinations of elements (M-modes) in a relatively low-dimensional space; and (3) the UCM approach can be used to identify muscle synergies based on EMG indices.

A priori, we could not predict whether similar or different combinations of M-modes (synergies) would be used for forward and backward COP shifts. Thus, another goal of the study was to use the UCM method to verify if a single synergy or two different synergies are used in tasks that require COP shifts in different directions.

Methods

Subjects

Eight unpaid healthy subjects, four male and four female, of mean age 29 yr. (± 4.5 SD), mean weight 60.63 kg (± 7.2 SD) and mean height 1.68m (± 0.1 SD) without any known neurological or motor disorder, participated in the experiment. All subjects were right-handed based on their preferential hand use during eating and writing. The subjects gave written informed consent according to the procedure approved by the Office for Regulatory Compliance of the Pennsylvania State University.

Apparatus

A force platform (AMTI, OR-6) was used to record the moment around a frontal axis (M_y), and the vertical component of the reaction force (F_z). An oscilloscope (Tektronics TDS 210) showed the time pattern of M_y to the subject and the experimenter. A uni-directional accelerometer (Sensotec) was taped to the dorsal aspect of the subject's hand, just under the metacarpophalangeal joint of the middle finger or the thumb, depending on the task. The axis of sensitivity of the accelerometer was directed along the required motion. Disposable self adhesive electrodes (3M) were used to record the surface EMG activity of the following eleven leg and trunk muscles: tibialis anterior (TA), gastrocnemius lateralis (GL), gastrocnemius medialis (GM), soleus (SOL), vastus lateralis (VL), vastus medialis (VM), rectus femoris (RF), biceps femoris (BF), semitendinosus (ST), rectus abdominis (RA) and erector spinae (ES) (see Figure 1, Chapter 4). The electrodes were always placed on the left side of the subject's body on the muscle bellies, with their centers approximately three centimeters apart. Signals from the electrodes were amplified (× 3000) and band-pass filtered (60-500 Hz). Data were

recorded at a sampling frequency of 1000 Hz with a 12-bit resolution. A Gateway 450 MHz PC with customized software based on the LabView-4 package was used to control the experiment and collect the data.

In some conditions, the subject held a load (20 × 20 × 10 cm) between his/ her hands, by pressing on the sides of the load or via a pulley system (Figure 1, Chapter 4).

Procedure

One group of tasks was associated with anticipatory postural adjustments (APAs, for review see Massion 1992) and involved COP shifts as an implicit component. These tasks required the subject to release a load (LR) from extended arms (Aruin and Latash 1996) or to perform a fast bilateral arm movement (Belen'kii et al. 1967). The other group of tasks explicitly required the subject to voluntarily shift his/ her COP (VS) using visual feedback provided by the oscilloscope (Danion et al. 1999).

Load release (LR) task

In the initial position, the subject stood on the force platform with his/ her feet side-by-side, at hip width. This position was marked on the platform and was reproduced across trials. In trials where the 3 kg load was released in front of the subject (LR_F), the subject pressed on the sides of the load with extended hands. When the same load was to be released at the back (LR_B), the subject pressed on the sides of the horizontal handle, which in turn was attached to the load through the pulley system (Figure 1, Chapter4). In another condition, the subject was asked to drop a variable load at the back (LR_{BV}), with the load mass ranging from 2 kg to 7 kg (3% -11.5% of subject's body mass, on average) in increments of 0.5 kg. Subjects were instructed to release the load with a quick, small amplitude, bilateral shoulder abduction movement.

Arm movement (AM) task

The initial position was the same as in the LR task, except that the subject's hands were now hanging loosely by his/her side. Subjects were asked to perform a fast, bilateral arm flexion movement (AM_F) or bilateral arm extension movement (AM_B) over a nominal distance of 40°. However, subjects were allowed to select a comfortable distance and reproduce it.

Voluntary sway (VS) task

The initial position was the same as in the AM task. The subject was required to move his/ her body weight towards the toes (VS_F) or the heels (VS_B). In different trials they were asked to produce this movement at different speeds, self-selected by the subjects. Subjects watched the oscilloscope, which showed them the current value of M_y. The initial position of the subject was marked on the oscilloscope. The required M_y shift was also marked and was approximately 10 Nm, which corresponded to a COP shift of about 1-2 cm depending on the subject's body weight.

For each trial, data were collected over 3 s. Subjects were instructed to stand as quietly as possible in the initial position before the beginning of the trial. The subjects heard a computer generated beep 500 ms after data collection had begun, which indicated to them that they could initiate the required action. Subjects were reminded not to initiate their actions immediately after the beep, but to wait for about a second.

The order of the conditions was pseudo-randomized across subjects. A rest period of 6 seconds between trials and a rest period of two minutes between two conditions was given. Sufficient rest periods (about a minute) were given between sets of trials, such that fatigue was never an issue. Prior to each condition, two practice trials were given.

Different variations of the three tasks were used at different steps of analysis (Steps 1, 2 and 3 described in the Introduction). In all there were seven series of experiments:

Step 1: Identification of M-modes.

Series 1: Releasing the 3 kg load behind the subject (LR_B): 50 trials (two sets of 25); This particular task was selected based on results from our previous study (Krishnamoorthy et al. in press-a), as leading to the most reproducible M-modes across subjects.

Step 2: Computation of the Jacobian matrix.

Three series of experiments were selected to analyze the relations between changes in magnitudes of M-modes and the corresponding COP shifts, i.e. to define the Jacobian matrix:

Series 2: Releasing different loads (2 kg to 7 kg in increments of 0.5 kg) behind the subject (LR_{BV}): 2 repetitions with each load for a total of 22 trials;

Series 3: Shift of COP voluntarily towards the toes at varying speeds (VS_F), 22 trials; and

Series 4: Shift of COP voluntarily towards the heel at varying speeds (VS_B), 22 trials (Only seven subjects performed this task);

First, we used the load release task as for the identification of M-modes, but with varying weights, LR_{BV}. In this series, forward COP shifts were an implicit task component; they occurred prior to the release of the load and were associated with APAs. Second, we used a task associated with explicit COP shifts in the same direction, forward (VS_F). Third, voluntary sway backwards (VS_B) was used to check if relations between COP shifts and magnitudes of M-modes were direction-specific.

Step 3: UCM analysis.

At this step, we used a set of tasks associated with APAs leading to COP shifts.

Series 5: Releasing the 3 kg load in front of the subject (LR_F): 25 trials (This condition was more fatiguing than the LR_B because the subject acted against the combined weight of the arms and the load. Hence, the series were split into two sets of 15 and 10 trials);

Series 6: Fast arm movement forward (AM_F): 25 trials; and

Series 7: Fast arm movement backward (AM_B): 25 trials.

In addition, two control trials were performed: The subject was asked to hold a load of 5.3 kg in front of the body and behind the body (through the pulley system) for 5 s. These data were used for EMG normalization as described in the next subsection.

Data processing

All signals were processed off-line, filtered with a 50 Hz low-pass, fourth order, zero-lag Butterworth filter using LabView 4. All EMG signals were rectified. Individual LR and AM trials were viewed on a monitor screen and aligned according to the first change in the signal of the accelerometer (movement initiation) that could be identified by visual inspection at optimal resolution. This moment will be referred to as "time zero" (t_0). VS trials were aligned by the first visible shift of M_y.

Changes in the background muscle activity associated with the early phase of the COP shift were quantified as follows. In the LR and AM trials, rectified EMG signals were integrated from 100 ms prior to t_0 to t_0 ($\int$EMG). In these trials, M_y shift started, on average, 80 ms prior to t_0 (cf. Aruin and Latash 1995). Since VS trials were aligned by the earliest M_y shift, to have comparable intervals of EMG integration across tasks, EMG were integrated from –20 ms to +80 ms with respect to t_0 in the VS task (Krishnamoorthy et al. in press-a). These integrals were corrected by subtracting integrated activity from –500 to –450 ms prior to t_0 multiplied by two (the baseline EMG activity, $\int EMG_{bl}$).

$$\Delta I\mathrm{EMG}_{\mathrm{LR,AM}} = \int_{-100}^{t_0} \mathrm{EMG}\,dt - 2\int_{-500}^{-450} \mathrm{EMG}_{\mathrm{bl}}\,dt \qquad \textbf{(3A)}$$

$$\Delta I\mathrm{EMG}_{\mathrm{VS}} = \int_{-20}^{+80} \mathrm{EMG}\,dt - 2\int_{-500}^{-450} \mathrm{EMG}_{\mathrm{bl}}\,dt \qquad \textbf{(3B)}$$

In order to compare the ΔIEMG indices across muscles and subjects, we normalized them by the integrals of EMGs collected in the control trials as follows: ΔIEMG indices for dorsal (ventral) muscles were divided by integrals of EMG over 100

ms in the middle of the control trial, $IEMG_{control}$, during holding the load in front of (behind) the body:

$$\Delta IEMG_{norm} = \Delta IEMG_{LR,AM,VS} / IEMG_{control} \quad \textbf{(4)}$$

Coordinates of the center of pressure (COP) in the anterior-posterior directions were calculated using the following approximation:

$$COP = M_Y / F_Z \quad \textbf{(5A)}$$

COP shift corresponding to the EMG activity calculated above, was computed as follows:

$$\Delta COP = \frac{M_{Y1}}{F_{Z1}} - \frac{M_{Y2}}{F_{Z2}} \quad \textbf{(5B)}$$

where, M_{y1}/ F_{z1} was computed at time, t_0 + 50 ms and M_{y2}/ F_{z2} is the average COP position between -150 ms and -100 ms with respect to t_0 (50 ms prior to the period of EMG integration).

Statistics

Standard statistical methods were used. Data are mostly presented as means and standard errors.

Step 1: Defining M-modes using Principal Component Analysis (PCA)

For the LR_B series, in each subject, we have $\Delta IEMG_{norm}$ data matrices with the size 50×11 (50 rows corresponding to repetitions and 11 columns corresponding to muscles). The correlation matrix between the $\Delta IEMG_{norm}$ was subjected to PCA, using procedures from Statistica 6.0 (StatSoft, Inc.). The correlations were computed among

the columns. The factor analysis module with principal component extraction was employed.

For each subject, the obtained eigen-values and PCs of the matrix were then considered. Based on the percentage of total variance accounted by individual PCs (see later) and on analysis of the scree plots, only the first three PCs (M-modes) were selected for further analysis. The eigenvectors of the three PCs were used in further data processing.

Step 2: Defining the Jacobian using multiple regression

Linear relations between changes in the M-modes magnitudes and the COP shifts were assumed and the corresponding multiple regression equations computed. The coefficients of the regression equations were arranged in a matrix that is in essence a Jacobian matrix, **J**. Series 2, 3 and 4 were used to generate linear estimates of the Jacobians. The columns of the **J** are coefficients relating changes in magnitude of M-modes (ΔMMMs) to COP shift. Three tasks (LR_{BV}, VS_B, VS_F) were used to define three separate Jacobians ($\mathbf{J}_{LRBV}$, $\mathbf{J}_{VSB}$, and $\mathbf{J}_{VSF}$). This was done to check whether the Jacobians were task-specific and/or COP direction specific.

$\Delta IEMG_{norm}$ data (22 x 11) for each of the series (LR_{BV}, VS_F and VS_B) were multiplied with the eigenvectors (11 x 3) obtained at Step 1 and further summed up to yield three ΔMMMs (22 x 3) for each trial. A multiple regression analysis was then performed using these ΔMMMs as the independent variables and the corresponding ΔCOP shift as the dependent variable (see Step 2, Procedure). Optimal sets of coefficients were defined for each subject and for each of the three series using:

$$\Delta COP = k_1 \Delta MMM_1 + k_2 \Delta MMM_2 + k_3 \Delta MMM_3 \quad \textbf{(6)}$$

$$\mathbf{J} = [\boldsymbol{k}_1 \boldsymbol{k}_2 \boldsymbol{k}_3] \quad \textbf{(7)}$$

With this approach, the Jacobian matrices are reduced to (3×1) vectors.

Step 3: UCM Analysis

For each trial of series 5, 6 and 7, $\Delta IEMG_{norm}$ were computed and transformed into ΔMMMs as in Step 2. The hypothesis that ΔCOP is stabilized, accounts for one DOF (d=1). The space of ΔMMMs has dimensionality n = 3. Thus, the system is redundant with respect to the task of stabilizing ΔCOP. The mean contribution of each M-mode to ΔCOP was calculated. Since the model relating ΔMMMs to ΔCOP is linear, the mean values were subtracted from each computed value and the residuals were further analyzed as follows.

The uncontrolled manifold represents combinations of M-modes that are consistent with a stable value of ΔCOP. The UCM is calculated as the null space of the Jacobian matrix. The null space of **J** is the set of all vector solutions **x** of the system of equations **Jx=0**. The null space is spanned by the basis vectors, $\boldsymbol{\varepsilon}_i$, which have two degrees of freedom. The vector of individual mean-free ΔMMMs was resolved into its projection onto the null space:

$$\underline{f}_{UCM} = \sum_{i=1}^{n-d} (\underline{\varepsilon}_i^T \cdot (\Delta\text{MMM}))\underline{\varepsilon}_i . \qquad \textbf{(8A)}$$

and component orthogonal to the null space:

$$\underline{f}_{ORT} = (\Delta\text{MMM}) - \underline{f}_{UCM} \qquad \textbf{(8B)}$$

The amount of variance per DOF within the UCM is:

$$\sigma_{UCM}^2 = \sum_{trials} f_{UCM}^2 /((n-d)N_{trials}) \qquad \textbf{(9A)}$$

and orthogonal to the UCM is:

$$\sigma_{ORT}^2 = \sum_{trials} f_{ORT}^2 /(dN_{trials}) \qquad \textbf{(9B)}$$

We used the Wilcoxon signed rank test to compare if there was a significant difference between V_{UCM} and V_{ORT} across subjects. A non-parametric test was used because of the relatively small sample size and high variability across subjects.

Results

General EMG Patterns

When a subject stood and held a load in front of the body, there was increased background activity of dorsal muscles (GL, GM, SOL, BF, ST, and ES). Prior to load release, a drop in this activity was typically seen, commonly accompanied by bursts of activity in the ventral muscles (TA, RA, VL, VM, and RF). Conversely, prior to load release behind the body, the background activity in ventral muscles typically dropped, and there could be EMG bursts in the dorsal muscles. Figure 7A illustrates typical EMG patterns in a representative subject for a LR_B trial.

Fast arm movements forward AM_F (backwards, AM_B), were preceded by an increase in the background activity of ventral (dorsal) muscles accompanied by a decrease in the activity of dorsal (ventral) muscles. Figure 7C illustrates typical EMG patterns in a representative subject for an AM_F trial. Early EMG changes (APAs) were variable across subjects; some subjects did not show clear bursts or episodes of EMG suppression in some muscles.

In trials involving voluntary sway forward (VS_F), a drop in the background activity of ventral muscles and bursts of activity in dorsal muscles usually accompanied an early anterior shift of the COP. In the VS_B trials, there was an increase in the background activity of ventral muscles and a drop in the activity of dorsal muscles. Figure 7B shows typical EMG patterns during a VS_F trial. These EMG patterns also varied across subjects.

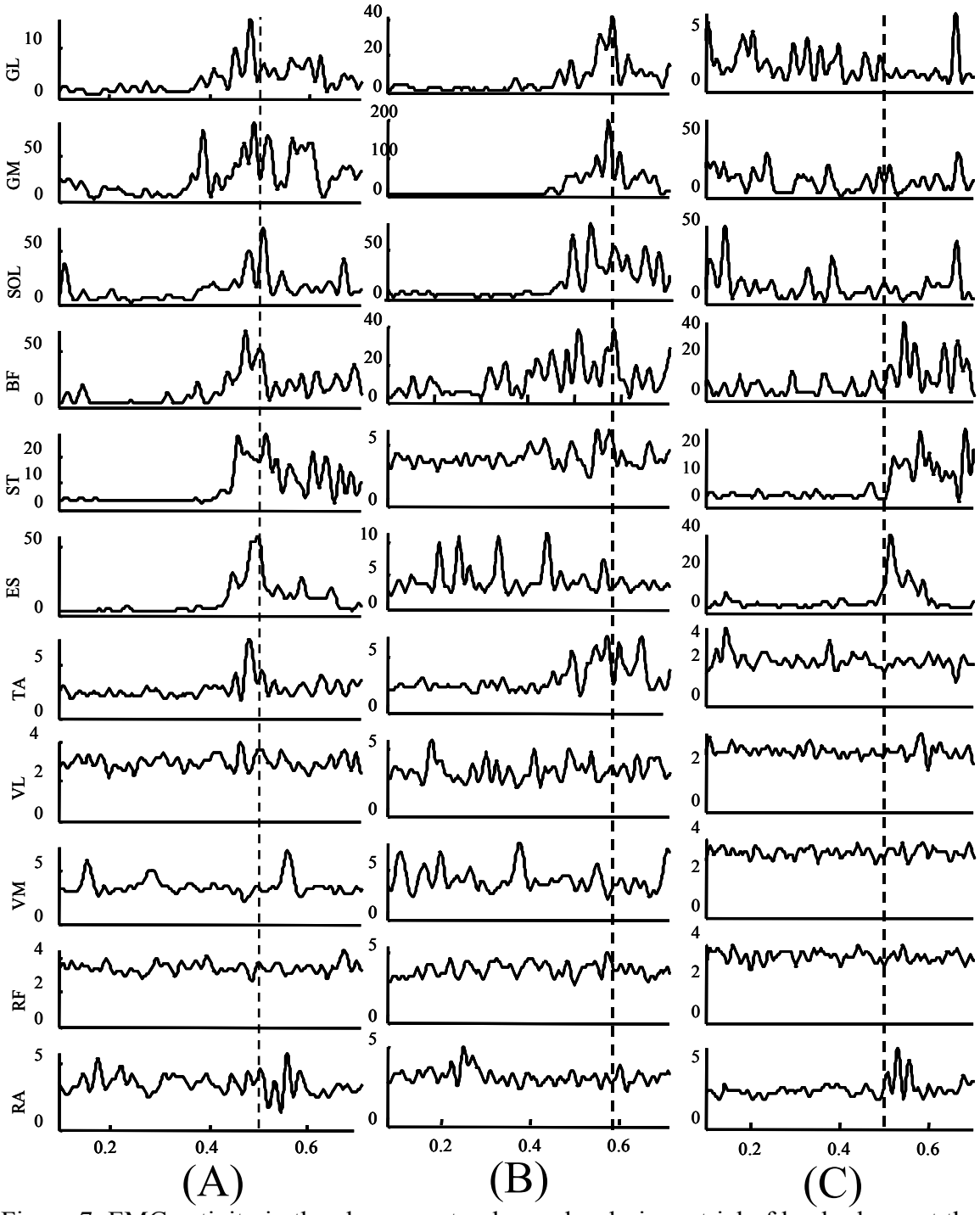

Figure 7: EMG activity in the eleven postural muscles during a trial of load release at the back, LR_B (A), voluntary sway forward, VS_F (B) and arm movement forward, AM_F (C) for a typical subject. Vertical dashed lines correspond to time zero, t_0. EMG was integrated over the 100 ms interval before t_0 for the LR and AM tasks and from –20 to +80 ms with respect to t_0 for the VS task. GL: lateral head of gastrocnemius, GM: medial head of gastrocnemius, SOL: soleus, BF: biceps femoris, ST: semi-tendinosus, ES: erector spinae, TA: tibialis anterior, VL: vastus lateralis, VM: vastus medialis, RF: rectus femoris and RA: rectus abdominis.

Identification of M-modes: Results of PCA

The indices of integrated muscle activity associated with an early shift of the COP (ΔIEMG indices, see the Methods) for all muscles were measured in each trial of Series-1 that involved 50 repetitions of LR_B task. These were normalized by the integrated muscle activity during control trials ($\Delta IEMG_{norm}$ indices). The $\Delta IEMG_{norm}$ indices for each subject were subjected to a PCA. Consistent with the previous study (Krishnamoorthy et al. in press-a; see Chapter 4), across all subjects, we found that principal components from PC4 onwards not only explained little variance in the $\Delta IEMG_{norm}$ space, but these components also had at most one muscle with significant loading, and were poorly reproducible across subjects. There were three consistent PCs accounting on average for about 62% (± 1%) of the total variance. The average amount of variance explained by PC1 was 32% (± 1%), by PC2 was 17% (± 1%) and by PC3 was 12% (± 0.5%) across all subjects. Table 3 shows the loadings of all the muscles on the three PCs for a representative subject in the LR_B condition. The significant loadings (loadings above ± 0.5; see Hair et al. 1995) are in bold. Muscles typically seen in the three PCs were:

- PC1: GL, GM, SOL, BF, ST, ES – "push-back M-mode" or M1-mode.
- PC2: VL and/or VM, RF, TA – "push-forward M-mode" or M2-mode.
- PC3: *TA*, RA, *VM, GL* – "mixed M-mode" or M3-mode.

The groups are named based on the general effect of the changes in muscle activity in a group on COP displacement. The muscles indicated in *italics* in the third synergy, did not show up consistently in the PC indicated, but were sometimes in one of the other M-modes.

Muscle	M1-mode (push-back)	M2-mode (push-forward)	M3-mode (mixed)
TA	-0.27	0.05	**-0.73**
GL	**0.66**	-0.22	0.36
GM	**0.81**	0.05	0.04
SOL	**0.75**	-0.08	0.11
VL	0.07	**0.77**	0.08
VM	0.29	**0.69**	0.02
RF	-0.25	**0.65**	-0.01
BF	**0.81**	0.20	0.06
ST	**0.79**	0.14	-0.31
RA	-0.31	0.22	**0.69**
ES	**0.74**	-0.05	-0.43

Table 3: Results of PCA in a representative subject. TA – tibialis anterior; GL – gastrocnemius lateralis; GM – gastrocnemius medialis; SOL – soleus; VL – vastus lateralis; VM – vastus medialis; RF – rectus femoris; ST – semitendinosus; BF – biceps femoris; RA – rectus abdominis; and ES – erector spinae.

Identifying the Jacobians: Results of multiple regression procedure

To identify the relations between changes in the magnitudes of the three M-modes (MMMs) and associated COP shifts (ΔCOP), we used series 2, 3, and 4. In these series, the subjects were asked to produce sets of trials, which induced early COP shifts of different magnitude. Three series were used to identify three possible sets of coefficients between MMMs and ΔCOP (three Jacobians), one associated with an implicit early COP shift forward (LR_{BV}), the second associated with an explicit COP shift forward (VS_F), and the third associated with an explicit COP shift backwards (VS_B).

Table 4 presents a summary of the regression coefficients for the three conditions for all subjects. Note that the three Jacobians ($\mathbf{J}_{LRBV}$, $\mathbf{J}_{VSB}$, and $\mathbf{J}_{VSF}$) vary significantly in

the magnitudes of coefficients. Numbers in bold in Table 2 are significant predictors of ΔCOP. In general, M1-mode was a significant predictor in series LR_{BV} and VS_F. M2-mode was a significant predictor in LR_{BV} and VS_B, although only in some of the subjects. M3-mode was a significant predictor in VS_B and rarely in LR_{BV} and VS_F. The three M-modes accounted for 79% (± 6%) of the total variance in ΔCOP for the LR_{BV} series, 85% (± 3%) of the total variance in ΔCOP for the VS_B series and 88% (± 3%) of the total variance in ΔCOP for the VS_F series.

	Subject	k_1	k_2	k_3
LR_{BV}	s1	**5.24**	**-3.14**	1.45
	s2	**-9.90**	**-14.25**	6.06
	s3	**-8.85**	**-10.58**	2.69
	s4	**-7.45**	**-10.02**	5.35
	s5	**8.21**	**14.56**	-7.38
	s6	**8.93**	-5.14	-4.56
	s7	**-10.15**	-1.42	**-14.40**
	s8	**-6.24**	**-4.54**	**12.78**
VS_B	s1	0.64	1.17	**3.93**
	s3	6.57	-7.86	**16.64**
	s4	7.51	-0.93	10.44
	s5	**14.19**	4.82	17.04
	s6	**13.31**	**11.34**	**-32.24**
	s7	**14.94**	-1.49	1.30
	s8	-1.32	**-1.97**	**20.66**
VS_F	s1	9.18	-0.58	-0.50
	s2	**-21.98**	-4.53	-11.86
	s3	**-22.28**	-10.53	**-24.20**
	s4	**-20.74**	1.77	19.17
	s5	**11.72**	4.73	-1.19
	s6	**30.73**	-2.35	6.23
	s7	-7.61	-9.49	7.97
	s8	**-21.44**	**-12.00**	13.54

Table 4: Regression coefficients between ΔMMMs and ΔCOP. The coefficients were computed for each subject based on each of the three tasks, LR_{BV} – load release in the back of the trunk with varying weights, VS_B – voluntary sway backwards, and VS_F – voluntary sway forward (numbers in bold are significant predictors of ΔCOP)

We also used these data to confirm the results of identification of M-modes described in the previous section. To do this, variance in the space of integrated EMG indices was partitioned into components within the space of M-modes and orthogonal to that space. Then, each variance component was divided by the number of DOFs in each of the two subspaces. On average, variance per DOF in the M-mode space was twice as high as orthogonal to the M-mode space. Each subject showed higher variance per DOF within the M-mode space in each of the three tests; this difference was statistically significant ($p < 0.01$) as confirmed by Wilcoxon signed-rank tests.

UCM analysis

Data from three series (series-5, -6, and -7 in the Methods) were used to perform analysis of the structure of variability in the space of M-modes. These series were associated with implicit early shifts of the COP during APAs. One of them involved an action similar to that used to identify M-modes and their relations to ΔCOP, namely releasing the load held in front of the body (LR_F). The other two series involved a completely different action, fast bilateral arm movement forward (AM_F) or backwards (AM_B). Total variance in the M-mode space across repetitions was partitioned into two components, one of which (V_{UCM}) was within an uncontrolled manifold (UCM) computed using one of the Jacobians defined at the previous step, while the other one (V_{ORT}) was orthogonal to the UCM.

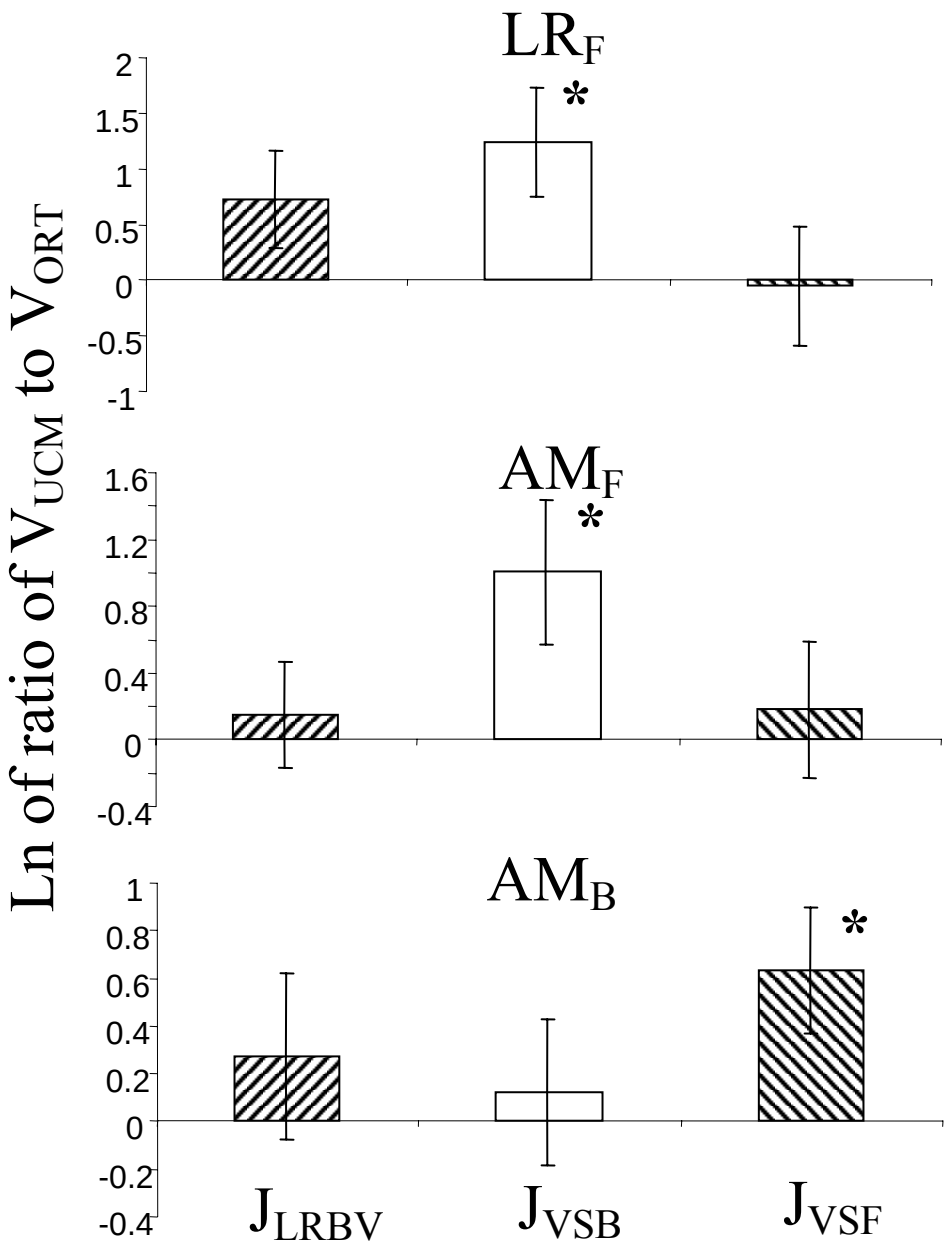

Figure 8: Results of UCM analysis across subjects for the series load release in the front, LR_F, arm movement forward, AM_F and arm movement backward, AM_B. The bars represent ratio of V_{UCM} to V_{ORT} after natural log transformation. The bars with upward slanted lines are results from using different Jacobians, $\mathbf{J}_{LRBV}$, the unfilled bars from $\mathbf{J}_{VSB}$ and the bars with downward slanted lines from $\mathbf{J}_{VSF}$.

Figure 8 shows the log-transformed ratios of V_{UCM} to V_{ORT} averaged across subjects with standard error bars, for each of the three series LR_F, AM_F and AM_B, using each of the Jacobians, $\mathbf{J}_{LRBV}$, $\mathbf{J}_{VSB}$, $\mathbf{J}_{VSF}$. The top, middle and bottom panels show results for the LR_F, AM_F and AM_B series respectively. The bars with upward slanted lines in all three panels are results of using the Jacobian from the LR_{BV} condition ($\mathbf{J}_{LRBV}$). The middle bars in all panels are results from using $\mathbf{J}_{VSB}$ and the bars with downward slanted lines are results from using $\mathbf{J}_{VSF}$.

V_{UCM} is significantly higher than V_{ORT} if the log-transformed ratio of the two is significantly different for zero. Relatively high average values of the ratio were observed when data from series associated with an early shift of the COP forward (backwards) were processed using Jacobians computed also based on series with an early COP shift forward (backwards). However, these values were not different from zero when data from a series associated with a COP shift in a certain direction were processed using a Jacobian from a series with an early COP shift in the opposite direction. In particular, Wilcoxon tests have confirmed that the ratio was significantly higher than zero when the data from the LR_F and AM_F series were processed using $\mathbf{J}_{VSB}$ and when the data from the AM_B series were processed using $\mathbf{J}_{VSF}$. The ratios were not significantly different from zero when the other combinations of series and Jacobians were used.

Discussion

The main purpose of this study has been to explore the possibility of identification of muscle synergies in a postural task using the framework offered by the uncontrolled manifold hypothesis (Scholz and Schöner 1999; Latash et al. 2002b). One of the major advantages of the UCM-hypothesis is that it allows testing different control hypotheses, i.e. hypotheses on variables that may or may not be selectively stabilized by the coordinated activity of a set of motor elements forming a motor synergy. Earlier studies

have shown that analysis of the structure of variability within the UCM-hypothesis is indeed able to distinguish among competing control hypotheses using studies of kinematic and kinetic variables (Scholz and Schöner 1999; Scholz et al. 2000; Latash et al. 2001; Latash et al. 2002a; Latash et al. 2002b; Scholz et al. 2002). However, as mentioned in the Introduction, applying the UCM-hypothesis to EMG signals is far from being trivial because of the several necessary steps that need to be taken to partition the variance in the space of muscle activation patterns (EMG space) into components that affect and do not affect a hypothesized performance variable.

We selected for this study a set of postural tasks partly based on our previous experience with such tasks (Aruin and Latash 1995a; Shiratori and Latash 2000) and partly because maintenance of the vertical posture has commonly been associated with the generation of adequate patterns of shifts of the center of pressure (Collins and De Luca 1993; Winter et al. 1998; Zatsiorsky and Duarte 2000; Baratto et al. 2002). Note that the control hypothesis that patterns of activation of postural muscles are organized to stabilize a particular pattern of the COP shift is not the only possible one. Other performance variables can be considered such as position of the center of mass of the body (cf. Gollhofer et al. 1989; Vernazza et al. 1996) or position of the head (cf. Pozzo et al. 1990; Simoneau et al. 1992; Ledebt et al. 1995).

Within the current study, however, we tested only one control hypothesis, namely that the CNS organizes co-variations of control variables to stabilize a COP shift. Within the selected time window of 100 ms, actual displacements of the joints and of the center of mass are very small and cannot be assessed with sufficient accuracy. On the other hand, we wanted to limit our analysis to a small time window that has typically been used in APA studies (Massion 1992). This is a limitation to be overcome in future.

Using the UCM approach to identify postural synergies

In our previous experiment (Krishnamoorthy et al. in press-a; see Chapter 4), we showed that indices of muscle activity (integrated EMG) associated with an early shift of

the COP could be described with a few principal components. This approach is somewhat similar to attempts at identifying motor synergies using PCA applied to kinematic or kinetic data (Alexandrov et al. 1998a; Alexandrov et al. 1998b; Vernazza-Martin et al. 1999; Sabatini 2002). We interpreted the presence of a few reproducible PCs as evidence that the CNS uses a few central variables ("muscle modes" or M-modes) to adjust activity of the many postural muscles contributing to the production of a desired COP shift. Further, the directions of vectors of PCs in the muscle space were similar across subjects and across tasks. This was not a trivial finding, since the tasks varied not only in the direction of required COP shift (anterior or posterior) and magnitude of perturbation (releasing a heavy or light load), but the tasks also involved either an explicit (voluntary sway, VS) COP shift or implicit COP shift associated with anticipatory postural adjustments (APAs, see Massion 1992) prior to releasing a load held in the hands of extended arms.

We did not interpret M-modes as multi-muscle synergies. This contrasts with other recent work that employed statistical procedures similar to PCA to identify groups of muscles employed in the performance of functional tasks (Bizzi et al. 2002; Tresch, Saltiel and Bizzi 1999). Those investigators have characterized the identified muscle groupings as synergies that are used as basic building blocks in the construction of functional postures or movements. Instead, we prefer to characterize such muscle groupings as control modes and view identification of M-modes as only the first step along the road to identification of multi-muscle synergies, namely the step of identification of a set of independent central variables that are organized into synergies by the CNS. Another important result from that study has been the identification of a task associated with most reproducible M-modes across subjects, namely load release in the back of the body. We used this result to select the first series to identify M-modes in the present study. Figure 9 illustrates the idea of control using a set of M-modes. The controller is assumed to define magnitudes of the three M-modes ultimately resulting in changed levels of activation of all the postural muscles. According to our control hypothesis, changes in magnitudes of the M-modes co-varied to preserve a particular value of COP shift.

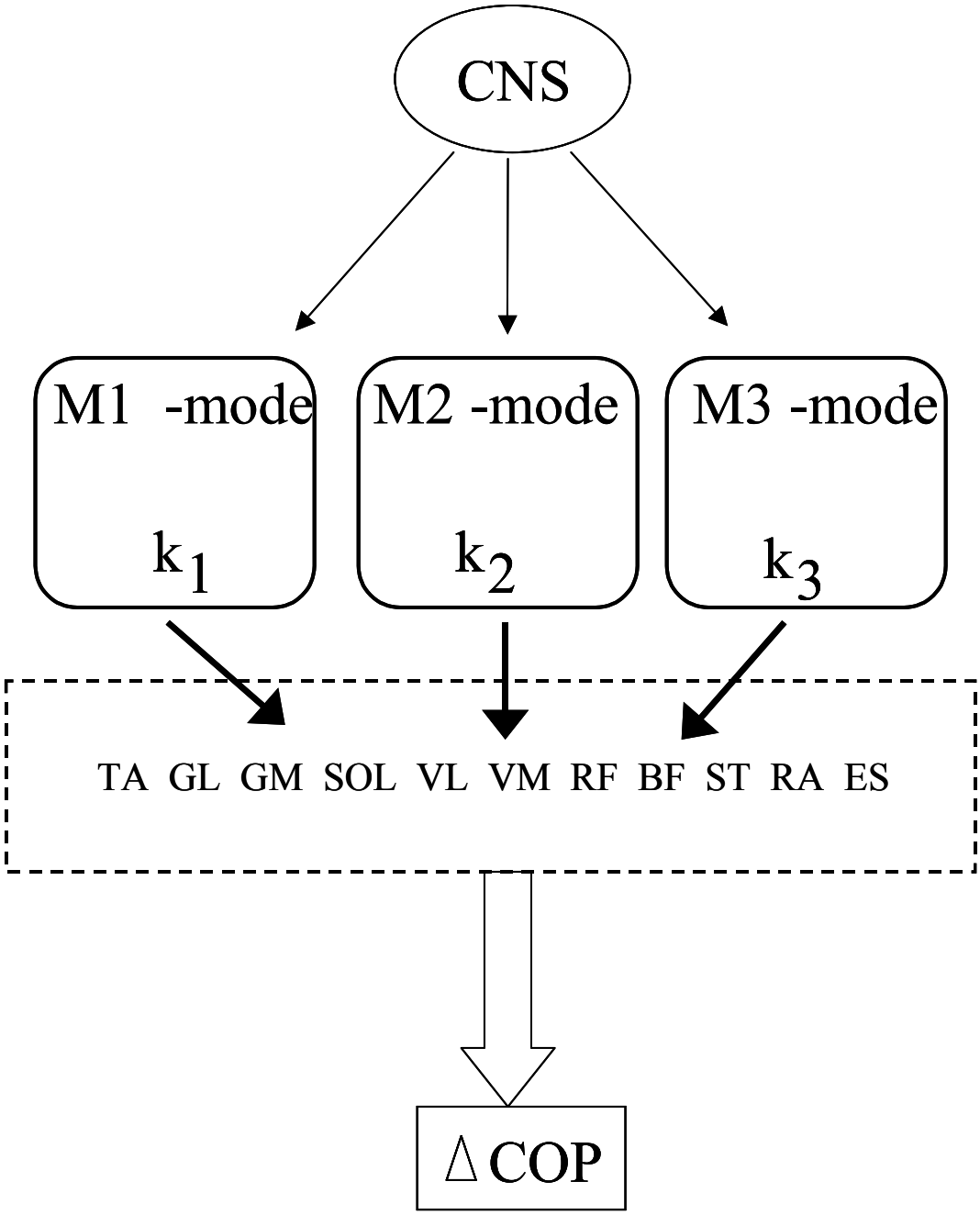

Figure 9: A scheme illustrating idea of control using a set of M-modes. The controller defines magnitudes of the three M-modes resulting in changed levels of activation of all the postural muscles, which preserve a particular value of COP shift. Abbreviations for muscles are the same as in Figure 7.

Further analysis in the M-mode space was directed at computing a null-space (UCM) of the Jacobian linking variations of magnitudes of M-modes to COP shifts. This null-space provides a linear estimate of a manifold in the space of M-modes, the values of which stabilize a particular value of COP shift. Variance in the M-mode space obtained in Step 3 experiments was then projected onto this UCM and orthogonal to it. We found that the variance along the UCM was significantly higher than orthogonal to it for the tasks LR_F, AM_F and AM_B when analysis was based on the Jacobians computed using series associated with COP shifts in the same direction. Thus, we can conclude that there is a multi-M-mode synergy, which selectively stabilizes the desired magnitude of the COP shift in these conditions. In other words, the gains at the M-modes co-varied across trials in such a way that the effects of their variation on the COP shift compensated (partly) for each other.

Two separate postural synergies

We purposefully used different tasks at different steps of the study. The differences among the tasks were two-fold. First, COP shift could be an explicit (voluntary sway) or implicit (APA) task component. Second, it could be directed forward or backwards. Because of the natural limitation on the number of trials that could be performed by a subject within one session, we could not do a complete crossover design. However, one result suggests that two different M-mode synergies are used to stabilize the displacement of the COP in different directions. The use of different Jacobians defined in the three different series at Step 2 (see the Introduction) yielded different results when the UCM analysis was performed. Note that the tasks LR_{BV} and VS_F required an anterior early shift of the COP, while VS_B required an early posterior COP shift. In the main experiment, the tasks LR_F and AM_F were accompanied by an early posterior COP shift, whereas AM_B was accompanied by an anterior COP shift (see Table 3).

When the UCM analysis (Step 3) was done using the Jacobian from a task (Step 2) requiring COP shift in the same direction at both Steps, V_{UCM} was significantly higher than V_{ORT} (except when the Jacobian from the LR_{BV} task was used, which never showed significant results). However, there were no differences in the two variance components when early COP shifts at Steps 2 and 3 were in opposite directions. One may conclude, therefore, that even though the same M-modes were being used, their gains were adjusted differently to perform COP shifts in the anterior and in the posterior directions.

We would like to note that such tasks as voluntary sway forward and backwards and fast arm movements forward and backwards started from similar postures and, as such, may be assumed to be associated with similar levels of the background postural muscle activity. Hence, we have assumed that the control system acted about the same initial operating point and the differences in the Jacobians and outcomes of the UCM analysis were related to the required different directions of the COP shift. Note that the load release tasks are associated with significantly different background levels of postural muscle activity. This may be a reason why using the Jacobian defined in the load release task did not show significant UCM effects. This observation suggests that our assumption of linear relations between COP shifts and magnitudes of the M-modes may be correct only locally, about a given operating point in the M-mode space, but may be violated significantly if the operating point changes.

During quiet comfortable standing, the COP falls just in front of the ankle joint (Winter et al. 1998). As a result, there is a larger ‘safe’ area for COP shift within the base of support in the anterior direction as compared to its shift backwards. Therefore, a posterior COP shift may be perceived as potentially more destabilizing and a different strategy of muscular interactions may be used to produce it as compared to a forward COP shift. Note that different postural strategies have been described for tasks that differed in conditions of postural stability (Horak and Nashner 1986; Szturm and Fallang 1998). These observations are compatible with our conclusion on the two synergies used to produce anterior and posterior COP shifts.

M-modes and postural synergies

As was mentioned in the Introduction, the term postural synergy has been used by a number of researchers, usually to mean co-variation of EMGs or kinematic indices over several trials of postural tasks. In particular, terms such as ankle strategy, hip strategy (Horak and Nashner 1986; Horak et al. 1990), or multi-link strategies (Allum et al. 1989) have been used implying different postural synergies. We have now shown that even though patterns of activity of peripheral elements (muscles) may co-vary, making it possible to identify M-modes, this co-variation falls short of proving stabilization of an important performance variable. Indeed, the M-modes may then be manipulated differently in a task-specific fashion, resulting in at least two different synergies. This adds support to our general view that muscle synergies are not merely a set of muscles that 'work together', but a set of central variables that show task-specific co-variations to stabilize significant performance variables.

Variance explained my M-modes

The amount of variance explained by the three M-modes was on average only 62%. That is, the three modes explain only about two-thirds of the total variance. However, when the changes in magnitudes of three M-modes were related to the magnitude of shift of the COP, the M-modes accounted for between 79% and 88% of the variance of shift in the COP. Thus, even though the M-modes that were retained from the principal component analysis explain only explained two-thirds of the variance in the muscle space, they explained most of the variance in the shift of the COP. This suggests that the three M-modes retained are most relevant to the shift of the COP and the remaining variance in the muscle space (PCs 4 to 11) possibly explain little variance in the shift of the COP.

UCM analysis of ankle muscles

In our analysis of muscle synergies, we have directly related in a cause-effect manner a physiological variable, that is muscle activity or EMG to a more global performance variable, that is shift of the COP. It has been suggested that stiffness of the ankle muscles (plantar flexors) causes shifts of the COP in quiet stance (Winter et al. 1998). To verify if the ankle muscles are primarily responsible for shift of the COP, we performed PCA and UCM analyses on changes in the levels of activation of the ankle muscles alone, ignoring effects of other postural muscles.

PCA was performed on the integrated EMG indices of the ankle muscles (TA, GL, GM and SOL). Two PCs were retained that explained on average 83.4 % (± 2.1 %) of the total variance. The dorsal muscles (GL, GM and SOL) always loaded significantly on the first component and the ventral muscle, TA on the second component. Table 5 shows the results of PCA for a representative subject.

Muscle	PC 1	PC 2
TA	-0.14	**0.96**
GL	**0.81**	0.43
GM	**0.92**	-0.14
SOL	**0.93**	-0.09

Table 5: Results of PCA on ankle muscles for a representative subject. Loadings about ±0.5 are indicted in bold. Abbreviations for muscles are the same as in Table 3.

Following all the steps in UCM analysis, just as done previously for the 11 postural muscles, we repeated the analysis for only the four ankle muscles. For the three tasks (LR_F, AM_F and AM_B), UCM analysis was performed using the Jacobians from tasks

VS_B (for LR_F and AM_F) and VS_B (for AM_B). Ratio of V_{UCM} to V_{ORT} was computed. The Wilcoxon test failed to reveal a significant UCM effect across subjects ($p > 0.09$).

These results suggest that changes in the ankle muscle activity alone cannot account for the COP shift in our experiment. The ankle torque is likely produced by the combined effect of muscle activity from all the postural muscles.

Chapter 6

EFFECTS OF DIFFERENT TYPES OF LIGHT TOUCH ON POSTURAL SWAY

Introduction

Recent studies have drawn attention to the effects of "light touch" on the stabilization of upright posture. In particular, contact of the index finger to a stationary surface, at mechanically inefficient force levels, has been shown to decrease indices of postural sway by up to 50 % (Holden et al. 1994; Jeka and Lackner 1994; Jeka and Lackner 1995). The authors observed, in particular, a drop in sway when touching a slippery surface and emphasized the importance of active touch for the sway reduction effects. In further studies it has been shown that movement of the touched surface is able to entrain postural sway (Jeka et al. 1997; Jeka et al. 1998b). These findings have been interpreted as suggesting that an external point of contact provides a reference frame with respect to which vertical posture is stabilized (cf. "reference vertical" in (Gurfinkel et al. 1995)).

Riley and his colleagues (Riley et al. 1999) suggested that the implicit task of stabilizing the kinematic chain of an arm to keep the fingertip at a fixed position could lead to decreased postural sway. In their study, subjects either touched a hanging curtain as a mere result of extending the forearm or were instructed to minimize the force and movement at the point of contact. Only under the latter instruction did the subjects showed a decrease in the 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 subjects were not required to

minimize applied forces or remain in contact with the touched surface. The results of the two studies (Rogers et al. 2001) suggest that besides the nature of contact (active or passive) also the location of touch on the body might play a role in the efficacy of the touch.

The study by Rogers and his colleagues (2001) also investigated the effects of the stability of the touch pad in external space. The touch pad was either at a fixed position, moved in phase with the postural sway, or moved in a random fashion. Only when the touch pad was stable in external space, a significant reduction in the postural sway was observed (Reginella et al. 1999). These conclusions have been recently challenged by the group of Lackner (Lackner et al. 2001) who have shown that when subjects touched a flexible filament with their index finger, a significant reduction in sway was observed dependent on the buckling force of the filament. Even when the filament was highly flexible, a significant reduction of postural sway was observed.

Another factor that has been shown to modulate the effects of a light touch is the location of the touch with respect to the plane of greatest sway. In a study by (Rabin et al. 1999) subjects stood in the tandem Romberg position or in a 'duckstance' (feet turned outwards) with finger contact at the side or in front of the body. The effects of the light touch were greater when the finger was positioned in the plane of greater sway.

In summary, the above studies present conflicting and/or incomplete information on the role of at least four factors in the reduction of postural sway by light touch. First, it is unclear whether active touch by the subject or availability of a stable external reference point is important for sway reduction. Second, it is unclear whether effects of touch to different body parts are quantitatively similar despite the differences in the density of sensory receptors and their ability to discriminate sensory stimuli. Third, modulation of the effects of touch with the position of the contact point in relation to the plane of greatest sway has been investigated in only one study. And fourth, there is conflicting evidence on how the effects of touch depend on the stability of the touched surface.

We would like to suggest a hypothesis that the central nervous system (CNS) can use afferent information on a stable reference point and/or transient forces at the point of contact with an external object to stabilize posture. Hence, the availability of a stable reference point and active touch are sufficient but not necessary factors for sway

reduction effects. Following a number of researchers (Collins and De Luca 1993; Riccio and Stoffregen 1993; Riley et al. 1997), we view sway as an active process. One of its purposes is to locate the instantaneous position of the projection of the center of mass within the area of support, in particular with respect to its proximity to the edge of the support area (safety margin). In the presence of contact of a body part with an external object (besides the obvious contact of the feet with the ground), slowly-adapting receptors continuously supply information on the location of the point of contact. Spontaneous deviations of the trunk from the vertical lead to modulation of contact forces even if the external object is unstable. This leads to tissue deformation and activation of fast-adapting cutaneous and subcutaneous sensory endings. The information from either source reduces uncertainty in the location of the center of mass and can indirectly lead to a reduction in sway. Within this general scheme we studied four controversial issues related to the efficacy of touch contact for the modulation of postural sway.

To address the first issue we compared finger touch to a stable pad with placing the tip of the index finger into a clip fixed to an external stand. If the stability of a reference point plays a crucial role, the clip is expected to have larger effects on sway reduction than finger touch. If active control of finger position on the pad were most important, free finger touch could be expected to lead to stronger sway reduction than placing the finger into the clip.

To address the second issue, we compared the effects of touch to the index finger with touch to the head and the neck. These areas have different sensory resolutions and sensitivities to normal and lateral deformation (Johansson et al. 1980; Gardner 1988). Besides, touch to the head or neck provides direct information on possible deviations of the trunk from the vertical, while touch to the finger needs to be combined with proprioceptive information on the kinematic chain linking the finger to the trunk. More direct relevance of touch to the head or neck to changes in the trunk orientation allows us to expect its higher efficacy in sway reduction despite the disadvantage in sensory resolution.

The role of the location of touch with respect to the direction of greatest sway was investigated by having subjects touch a pad in front of the body or at the side.

The ability of subjects to show sway reduction during contact with an unstable object was studied to address the fourth controversy. We investigated changes in postural sway in subjects holding a load in the extended arm through a pulley system and without the pulley system. When a subject simply holds a load in the hand, inertial forces and moments emerge between the hand and the load during sway. According to our hypothesis, these forces could be by themselves sufficient to provide relevant information and induce a reduction in sway. Contact through the pulley system can be viewed as providing an unstable reference point in addition to the inertial forces. The cable connecting the load to the pulley exerts forces deviating from the vertical when the handle moves away from its neutral position. We studied whether information resulting from these horizontal force components could lead to sway reduction and whether additional finger touch would be able to lead to further reduction in sway.

Methods

The study consisted of two experiments testing the effects of a light touch on postural stabilization. The experiments were always run on different days, less than 2 weeks apart. In addition, a control experiment was run studying the contact forces between body parts and touch pads in different conditions.

Subjects

Eight healthy subjects, four males and four females, mean weight 68.3 kg (± 15.3 SD) and mean age 25.1 yr. (±3.7 SD), without any known neurological or motor disorder, participated in Experiment 1. Six subjects, three males and three females, took part in Experiment 2. Two subjects took part in both Experiments. All subjects were right-

handed. The subjects gave written informed consent according to the procedure approved by the Office for Regulatory Compliance of the Pennsylvania State University.

Experiment 1

A force platform (AMTI, OR-6) was used to record two moments, around a sagittal axis (M_x) and around a frontal axis (M_y), and the vertical component of the reaction force (F_z). Also horizontal forces in both anterior-posterior (Fx) and medio-lateral (Fy) directions were recorded. A force sensor (208A02, PCB Piezoelectronics, Inc., Depew, NY) with a small protruding touch pad (0.9×0.9 cm) was mounted on a rigid stand. Due to the limitation in the number of channels, we only recorded forces normal to the touch surface. An oscilloscope (Tektronics TDS 210) showed the applied force level to the experimenter. Force data were monitored online and the experimenter made sure that the forces were always under 1N. The height, position, and orientation of the touch pad could be adjusted to accommodate for the differences in subject's height and the different experimental conditions. The touch pad could be replaced with a metal clip that clasped the fingertip. The clip pinched the fingertip with forces of up to 14 N applied to the dorsal and palmar surfaces of the finger tip; net forces applied by the clip to the touch pad continued to be under 1N. Force platform data were recorded at the sampling frequency of 100 Hz with a 12-bit resolution. A Mac-IIci computer with customized software based on the LabView-2 package was used to control the experiment and collect the data. The data were analyzed off-line with customized software based on the LabView-4 package and Matlab 5.3.

The total number of trials had to be limited, so as not to cause fatigue. As a result we were unable to implement a full crossover design within one experiment that would manipulate all factors such as body part which touches an external pad, location of the point of touch with respect to the body, and presence or absence of the clip. The experiment tested the effects of two main factors on postural sway: VISION (subjects stood either with their eyes open or closed) and TOUCH, which had the following levels:

1. No touch;
2. Finger touch in front of the body (FTF);
3. Finger touch at the side of the body (FTS);
4. Touch to the side of the head (HT);
5. Touch to the side of the neck (NT); and
6. Fingertip in the clip in front of the body (FC).

The order of the conditions was pseudo-randomized across subjects. In the initial position, the subject stood on the platform, with the feet placed at hip-width, side-by-side. Foot position was marked and monitored during the entire experiment. The left side of the body was used to apply the different touches. The right arm was loosely hanging along the body during all conditions (Figure 10).

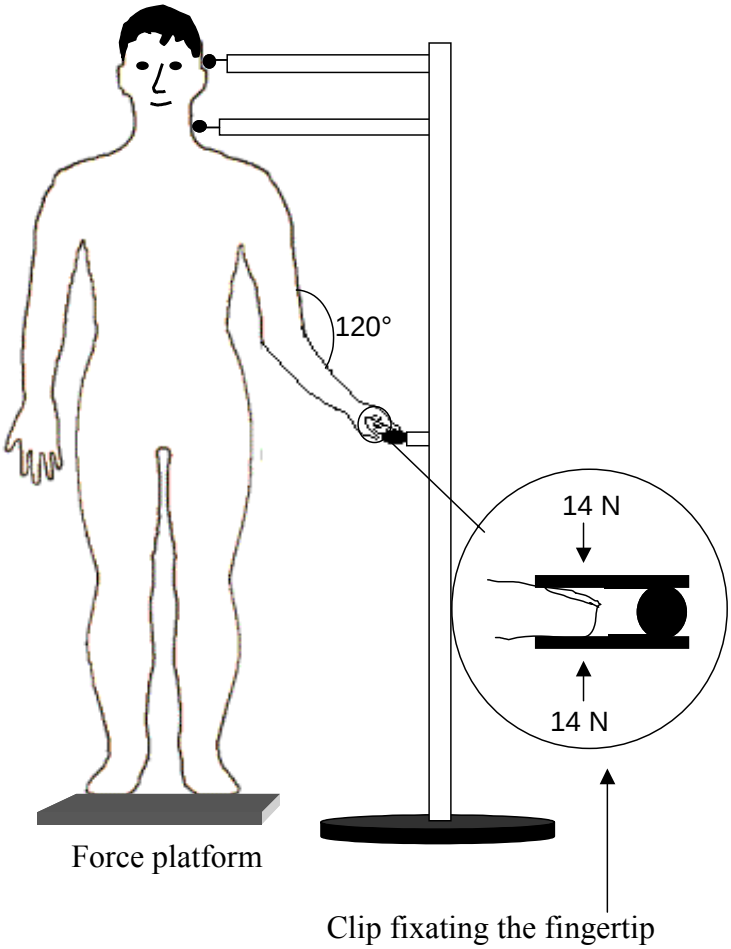

Figure 10: Subjects stood on the force platform. In some trials, the left index finger touched a touch pad with a built in force sensor or was placed in a clip in front of the subject (see insert in Figure10). The finger touch could be at the side of the subject (shown) or in front of the subject (not shown in Figure 10). A touch to the head (temple) or the side of the neck was provided using a stand next to the subject.

The position of the fingertip during conditions with finger touch or clip contact in the front was similar. The upper arm was oriented along the body while the forearm was held horizontal (elbow angle at 90°). With a finger touch at the side, the touch pad was at elbow height and placed in the frontal plane of the body at such a distance from the trunk that the elbow angle was approximately 120°. The touch to the head was applied at the os temporale, pars squamosa (temple). The touch to the neck was applied over the sternocleidomastoid muscle at the level of C4.

At a computer-generated tone, the subjects were asked to maintain contact with the touch pad with forces of less than 1N and stand as quiet as possible for 30 s. Two trials were recorded for each condition, and a pause of 10 s was given between trials. The rest periods between conditions were about one minute. Fatigue was never an issue. Prior to each series subjects performed one practice trial. The subject was asked to look at the oscilloscope and apply less than 1N of force, which was marked on the screen. After they were able to stand quiet and apply less than 1N of force, data collection started. One of the experimenters monitored the applied forces during the trials. If at any moment in time, more than 1N was applied, the trial was rejected and repeated. Across all subjects this happened only 6 times, while commonly forces were well below the threshold of 1N.

Control experiment

To ensure that forces in all three directions were under 1N in the different touch conditions, we ran an additional series of trials for the five touch conditions (FTF, FTS, HT, NT, and FC) using a 6-dimensional force/moment transducer (ATI Nano-17). Three subjects who participated in Experiment 1 took part in this series. Force platform data were not recorded for technical reasons. All other details were as in Experiment 1.

Experiment 2

Six subjects were tested under four conditions (Figure 11):

- Holding a standard load (3 kg mass) by the handle attached directly to the load with the right hand, no contact to the touch pad by the left hand;
- Holding the load by the handle attached directly to the load with the right hand, the index finger of the left hand touched the touch pad;
- Holding the same handle attached to the load via the pulley system, no contact to the touch pad by the left hand; and
- Holding the same handle attached to the load via the pulley system, while the index finger of the left hand touched the touch pad.

All trials were performed with eyes closed. Other details were as in Experiment 1.

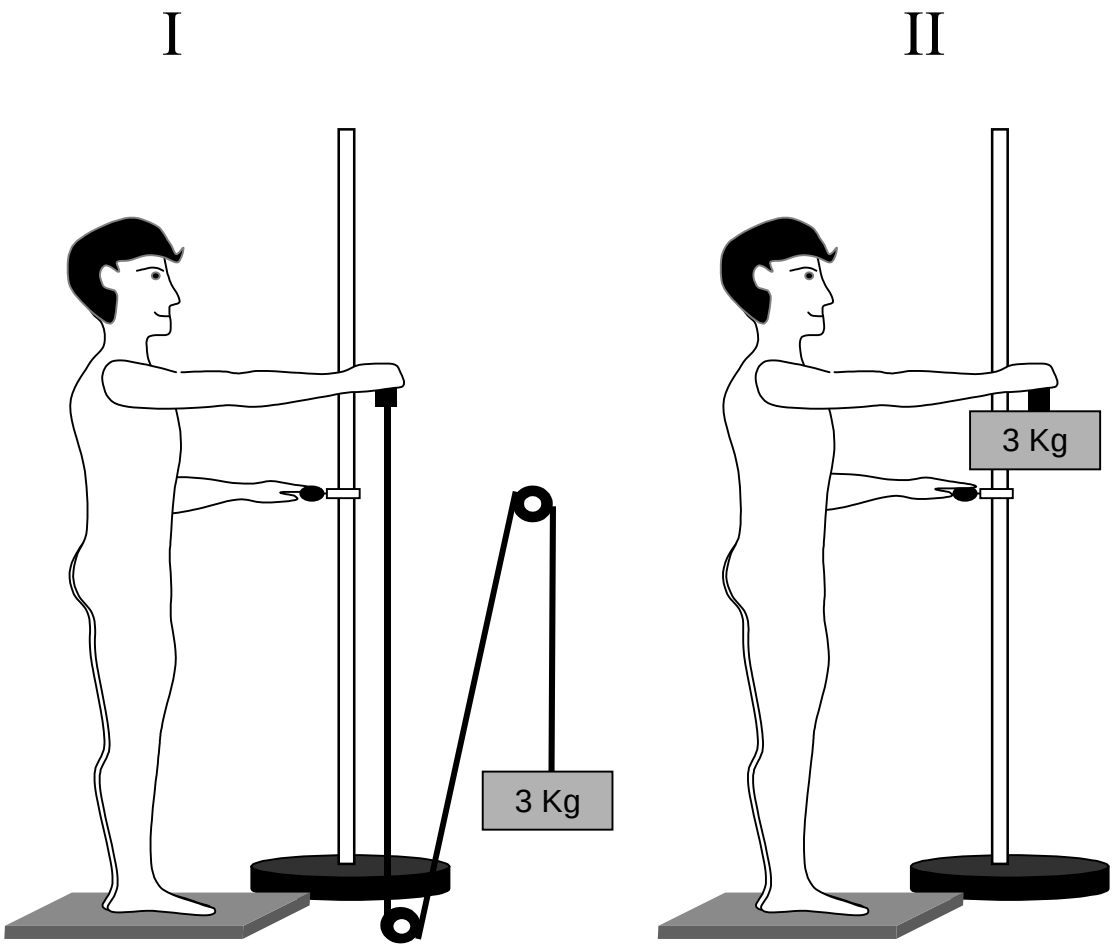

Figure 11: In Experiment-2, subjects were required to release the load that was either suspended through a pulley system (I) or was held freely in the right hand (II). The effect of a light touch by the left hand index finger was tested.

Data processing

All signals were processed off-line, filtered with a 20-Hz low-pass, fourth order, zero-lag Butterworth filter using Matlab 5.3. The first and the last second of the data were

discarded from further analysis. Horizontal displacements of the center of pressure (COP) in medio-lateral (COPy) and anterior-posterior directions (COPx) were calculated according to the following approximation: $COPx,y = My,x / Fz$

To quantify COP displacement during quiet standing, we computed the root mean square (RMSx,y) and the averaged velocity (VELx,y) in both anterior-posterior (x) and medio-lateral (y) directions. Furthermore, we calculated the area of COP migration (M-Area) by fitting an ellipse to the data, using principal component analysis such that 85% of the data were included. The data from the two trials in each of the conditions were averaged.

Statistics

Statistical methods, for Experiment 1, included repeated measures analysis of variance (ANOVA). To determine the effects of VISION and TOUCH, we performed a two way ANOVA in which all touch conditions (no touch, FTF, FTS, HT, NT and FC) were pooled. To test specific differences between pairs of conditions Tukey's Honest Significant Difference (HSD) tests were used. We also performed planned comparisons to test the effect of direction of touch with respect to the plane of greatest sway (FTS vs. FTF) as well as to compare the effects of touch by the finger to the touch pad in front of the body with the effects when the finger tip was in the clip (FTF vs. FC).

In Experiment 2 we used a repeated measures ANOVA with TOUCH (no touch and finger touch) and PULLEY (the load suspended with and without the pulley) as factors. Tukey's HSD tests were used as post-hocs.

Results

Control Experiment: Forces applied to the touch pad

Normal force applied at the touch surface was always well below 1N (average 0.1 ± 0.2 N across all touch conditions). The control experiment (see Methods) revealed that not only the normal forces, but also the shear forces were always below 1N. In particular, average force in the antero-posterior direction was 0.15 ± 0.24 N across all touch conditions while average force in the medio-lateral direction was 0.05 ± 0.08 N across all touch conditions. Table 6 shows the average forces in the three directions for each of the five touch conditions. Note the higher forces for the clip condition compared to all the other touch conditions, while the contact forces during touch to the head and to the neck tended to be the lowest. One-way repeated measures ANOVA with the factor TOUCH has shown a main effect for forces in each of the three directions, anterior-posterior, medio-lateral, and vertical ($F_{(4,8)} > 7.5$; $p < 0.01$). Post-hoc tests revealed no differences among touch to the head, to the neck, and to the finger tip (HT, NT, FTF, and FTS), while using the clip resulted in significantly higher forces, although, always under 1 N.

	Force (N) for different touch conditions				
DIRECTION	FTF	FTS	HT	NT	FC
AP	0.08 ± 0.06	0.05 ± 0.05	0.04 ± 0.04	0.02 ± 0.03	0.47 ± 0.12
ML	0.03 ± 0.02	0.09 ± 0.09	0.03 ± 0.02	0.01 ± 0.01	0.16 ± 0.09
VERTICAL	0.05 ± 0.06	0.07 ± 0.04	0.06 ± 0.01	0.02 ± 0.09	0.32 ± 0.21

Table 6: Average forces with standard deviations in different conditions are shown in Newtons. AP – anterior-posterior, ML – medio-lateral, FTF – finger touch in front of the body, FTS – finger touch at the side of the body, HT – touch to the head, NT – touch to the neck, FC – finger in the clip.

Experiment 1: The effects of vision and site of touch

During quiet standing, subjects demonstrated spontaneous changes in the position of COP in both anterior-posterior (COPx) and medio-lateral (COPy) directions. The top panel of Figure 12 shows a COPx time series, for a typical subject standing unsupported, with eyes open, while the left bottom panel shows the COP migration in the plane of the force plate. When the subject closed his or her eyes, the COP trajectory demonstrated larger variations (the middle panel and the right bottom panel of Figure 12).

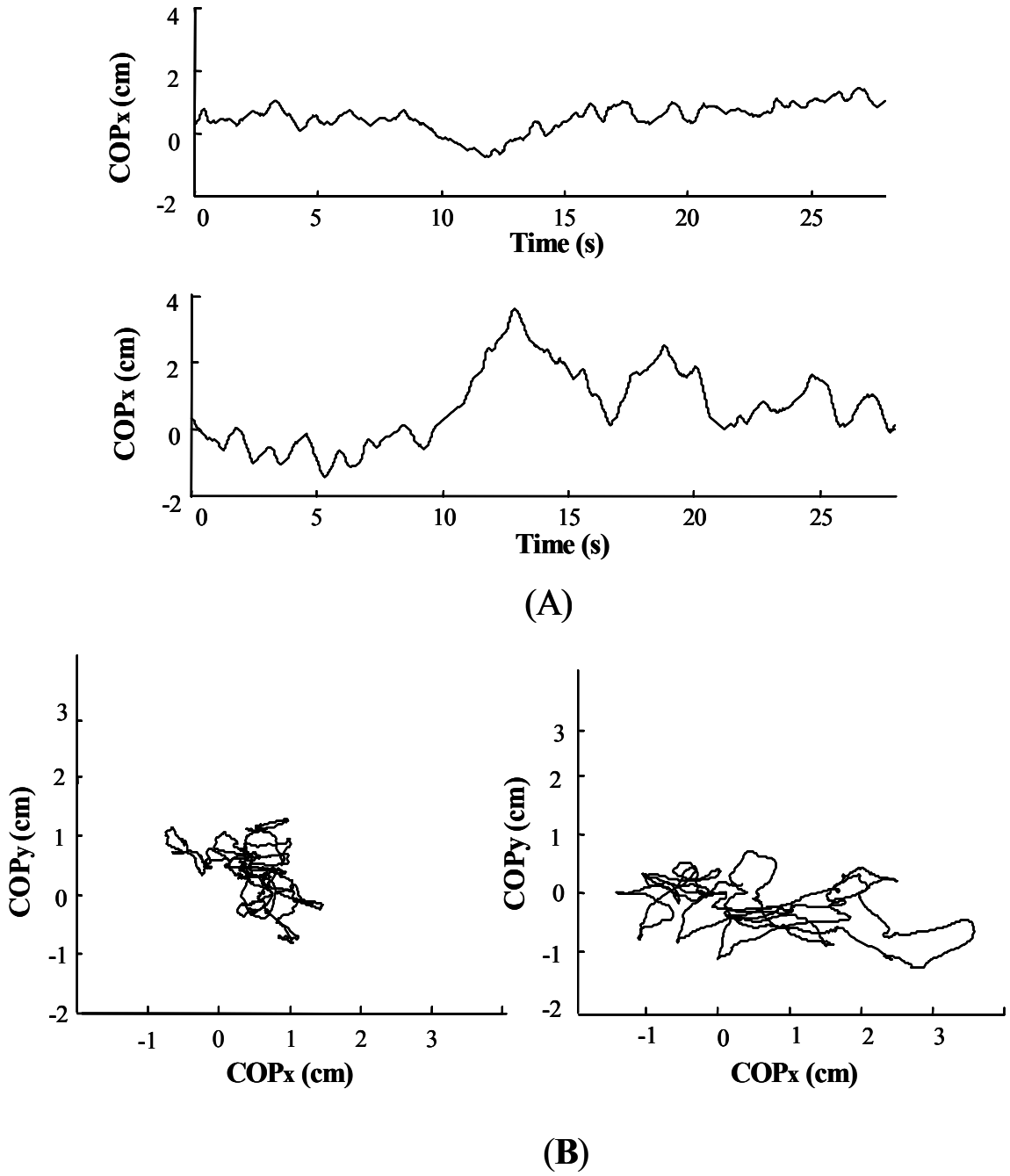

Figure 12: The top panels show time series of COPx of a representative subject standing quietly (no touch) for 28 second with eyes open and eyes closed. The bottom panels show the medio-lateral (COPy) and anterior-posterior (COPx) COP displacements. Note the increased displacements under the eyes closed condition.

There was an increase in all indices of postural sway when the subjects closed their eyes. These effects were supported by two-way repeated measures ANOVAs (VISION × TOUCH). In particular, M-Area increased significantly by nearly 50% ($F_{(1,7)} = 5.71$; $p < 0.05$). RMS and VEL of COP increased significantly across all touch conditions, except for RMS of COPx, where the p-value did not reach the level of significance ($p < 0.08$). No significant interactions between VISION and TOUCH were found.

A light touch to any part of the body reduced postural sway as reflected by all indices of COP migration. Figure 13 shows data averaged across subjects for M-area, RMSx, RMSy, VELx and VELy for unsupported conditions (No touch) and also during touch to the head (HT), to the neck (NT), to the finger at body side (FTS), and to the finger in front of the body (FTF). In general, HT and NT were more effective in decreasing indices of COP than FTS and had stronger or similar effects as compared to those of FTF. These results were supported by main effects of TOUCH for each of the indices shown in Figure 13 within the two-way, VISION × TOUCH, repeated measures ANOVAs ($F_{(5,35)} > 6.34$; $p < 0.001$). Tukey's HSD tests comparing the "No touch" condition with each of the 5 touch conditions showed significant differences for all touch conditions and all indices ($p < 0.05$, shown by * in Figure 12), except for the FTS condition for RMSx, VELx and VELy and for the FTF condition for VELy ($0.1 > p > 0.05$). There were no differences between the effects of HT and NT ($p > 0.9$). Significant differences between FTS and other touch conditions are shown by crosses.

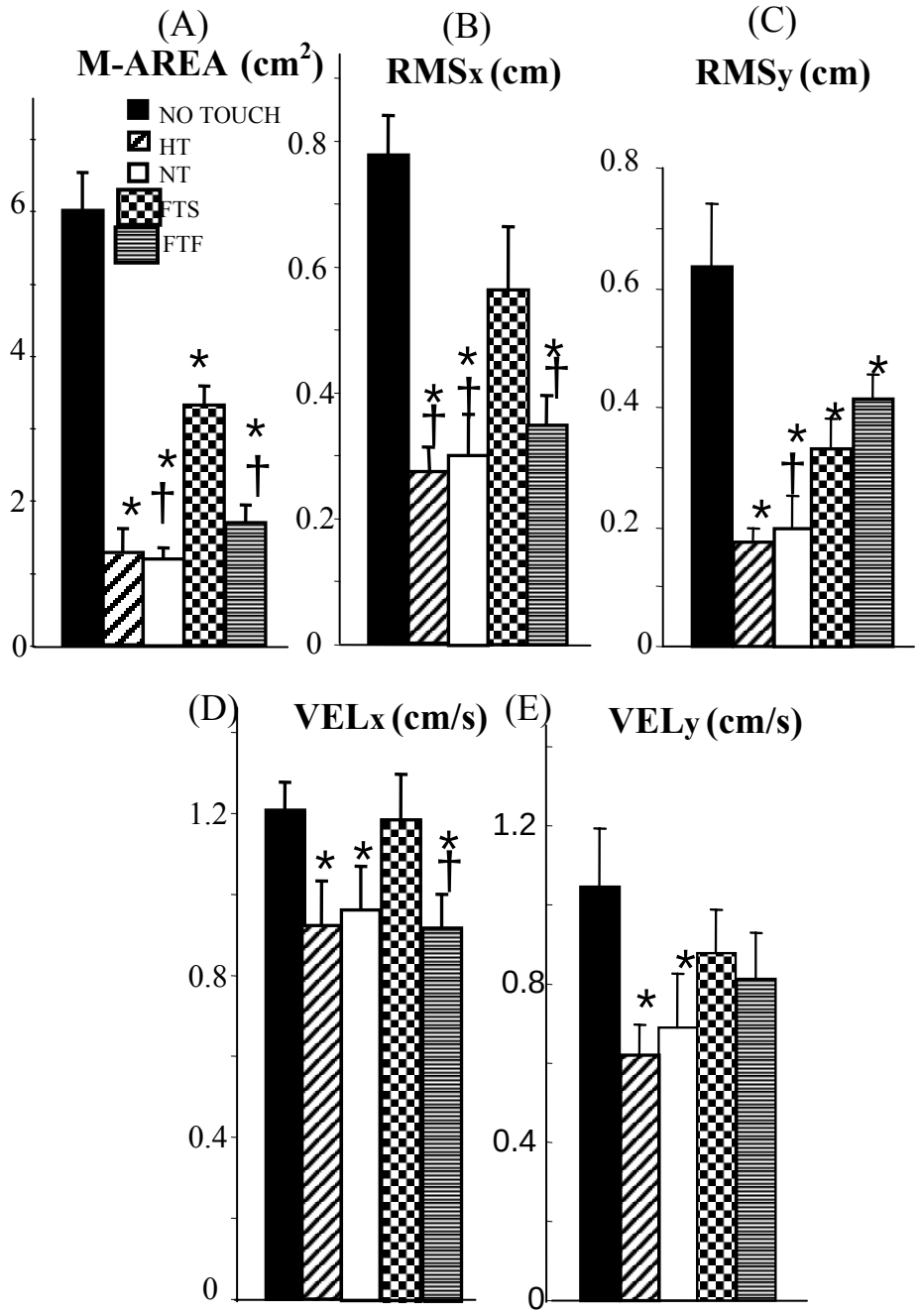

Figure 13: Area (M-area) (a), Root mean square in anterior-posterior direction (RMSx) (b), Root mean square in medio-lateral direction (RMSy) (c), Velocity in anterior-posterior direction (VELx) (d) and Velocity in medio-lateral direction (VELy) (e) of COP trajectory, averaged across all subjects during standing with eyes closed. Note that contact to the head (HT) and neck (NT) was more efficient in reducing indices of sway than finger touch. Standard error bars are shown. † Significant difference between finger touch at the side of the body (FTS) and other touch conditions ($p < 0.05$). * Significant difference between no touch and touch conditions ($p < 0.05$). FTF – finger touch in front of the body.

Experiment 1: The effects of the type of finger contact

Index finger touch reduced indices of postural sway when the finger was touching the pad in front of the body, both with and without the clip on the tip of the finger. Using the clip on the index finger tip increased the effectiveness of finger touch, producing a greater decrease across the indices of sway. This effect was statistically significant for M-Area (see Figure 14A) and VELx (Figure 14B) as demonstrated by the planned comparisons between the FTF and FC conditions in a two-way VISION × TOUCH ANOVA ($F_{(1,7)} > 6.8$; $p < 0.05$). In particular, using the clip produced a 19.6 % greater decrease in M-area of COP as compared to finger touch without the clip. VELx dropped 18% more in the FC condition as compared to the FTF condition.

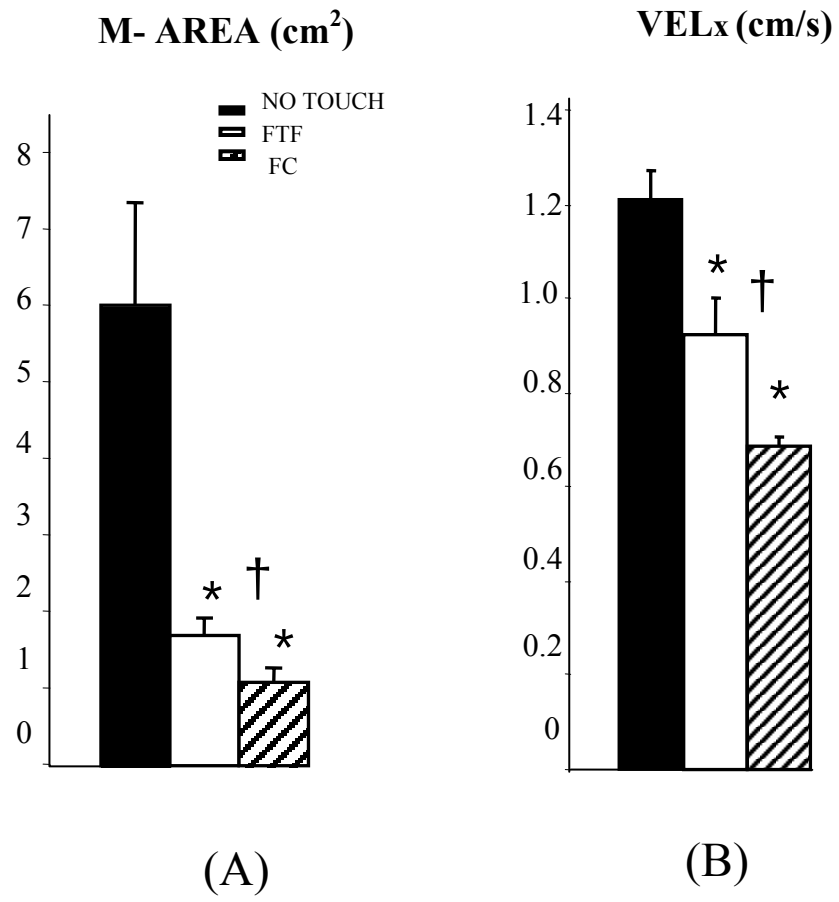

Figure 14: COP area **(A)** and VELx **(B)** changes induced by finger touch at the front of the body and by placing the tip of the finger into the clip, averaged across all subjects during standing with eyes closed. Note that placing the finger into the clip was more efficient in reducing sway than a touch in the front. Standard error bars are shown. † Significant difference between touch and clip contact. * Significant difference between no touch and touch conditions (all, $p < 0.05$).

Experiment 1: The effects of the direction of finger contact

Manipulations of the point of finger contact showed significantly larger effects on characteristics of the sway when the finger touched the pad in front of the body as

compared to touching it at the side of the body. In particular, COP showed a larger drop in M-area, RMSx and VELx for the touch in front of the body. This was supported by two-way repeated measures VISION × TOUCH ANOVA (see Figure 14; planned comparison between FTF and FTS conditions, $F_{(1,7)} > 5.8$; $p < 0.05$).

Experiment 2: Effects of stable and unstable contact on indices of sway

In this experiment (Figure 11 in the Methods), the subjects held a 3 kg load in the extended arm either directly by the handle attached to the load or through the pulley system, which connected the load to the handle. The index finger of the other hand could either touch the touch pad or have no contact.

Overall, additional touch led to a decrease in postural sway. Figure 15 illustrates the results for RMSx and VELx values averaged across all subjects. Both RMSx and VELx of COP significantly decreased with finger touch as confirmed by main effects of TOUCH in two-way repeated measures PULLEY × TOUCH ANOVA ($F_{(1,5)} > 9.24$; $p < 0.05$). These effects depended, however, on how the load was held. When the load was freely held by one hand, a significant reduction in the sway was observed with additional touch. When the load was held through the pulley system, no significant reduction was observed. A significant interaction between PULLEY and TOUCH for VELx and RMSx ($F_{(1,5)} > 10.23$; $p < 0.05$) confirmed these differences. Tukey HSD test on the interaction showed that RMSx and VELx were significantly higher when subjects held the load freely with no touch compared to holding the load either freely or through the pulley, but with touch ($p < 0.05$). VELx also showed a main effect of PULLEY reflecting a decrease in the postural sway when the load was held through the pulley as compared to the same load freely held ($F_{(1,5)} = 9.86$; $p < 0.05$). No significant modulation of sway indices in the medio-lateral direction was found.

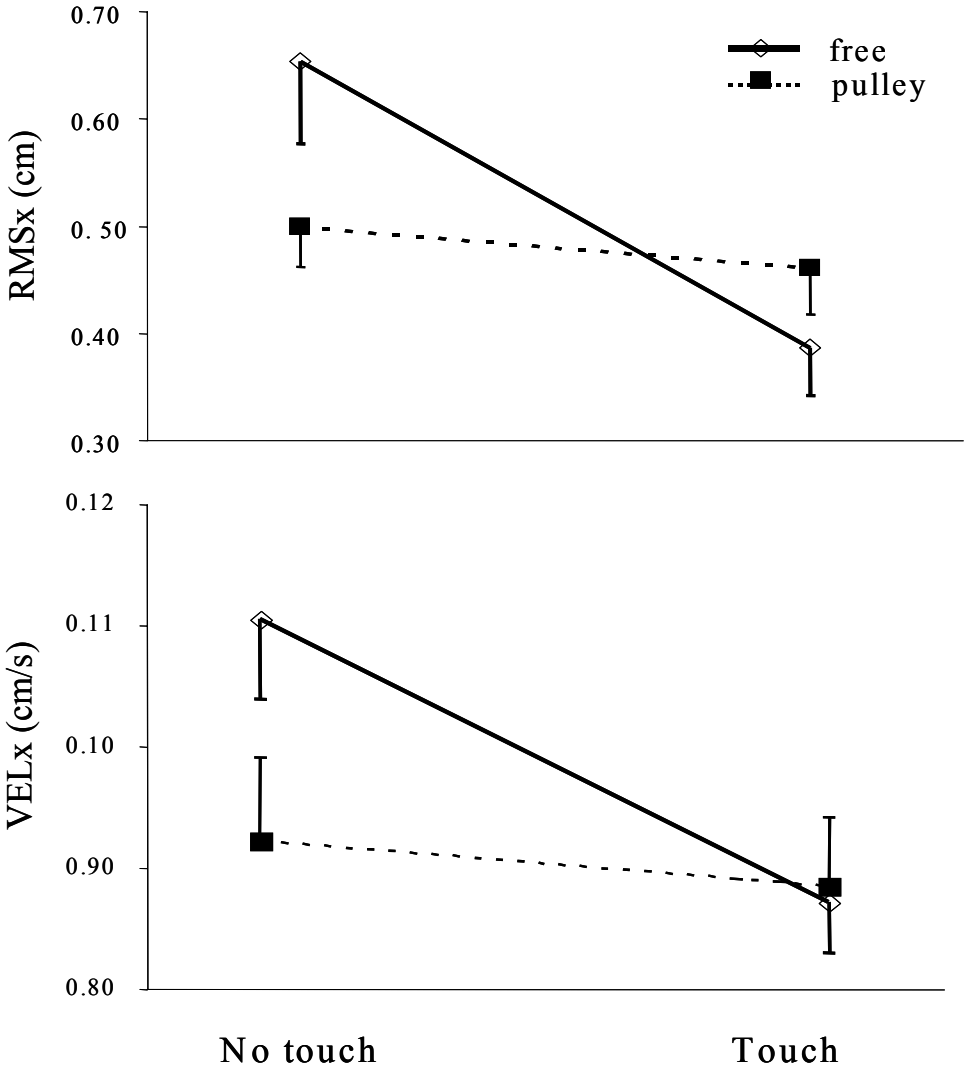

Figure 15: Subjects held a load in the right arm. The load was either suspended through the pulley system (pulley: dashed line, open symbols) or held freely (free: solid line, filled symbols). The top panel shows RMSx of COP displacement, while the bottom panel shows velocity of COP in the anterior-poterior direction (VELx). Additional touch by the left index finger in front of the body (Touch on the X-axis) led to a decrease in both indices of the sway. However, this decrease was significant only when the load was held without the pulley.

Discussion

In the Introduction we have suggested a general scheme of possible interactions between sensory information related to touch and postural sway and brought up four issues that have been addressed in the study. The two experiments produced the following major relevant findings, related to the four controversial issues:

1. Providing a stable reference point for the finger using a clip was more effective in reducing sway as compared to the effects of active finger touch to the touch pad;
2. Light touch to the side of the head or of the neck was more efficient in reducing postural sway as compared to finger touch at the side of the body and similar in the effects of finger touch in front of the body;
3. Finger touch in front of the body was more efficient than finger touch at the side.
4. Holding the load in front of the body did not change postural sway; adding a finger touch by the other hand to a stationary pad led to a decrease in the sway.
5. Holding the load through the pulley system reduced postural sway qualitatively similarly to the effects of a light finger touch to the pad.

Light touch: Providing a reference point or stabilizing a kinematic chain?

Two opinions have been expressed on possible reasons for the postural stabilizing effects of light touch. A number of studies have suggested that an external point of contact provides a reference frame with respect to which vertical posture is stabilized (Jeka et al. 1997; Jeka et al. 1998a; Lackner et al. 2001; Rogers et al. 2001). In contrast, Riley and his colleagues (Riley et al. 1999) have suggested that the implicit task of keeping the fingertip at a fixed position is associated with stabilization of the kinematic chain connecting the fingertip to the trunk and, consequently, leads to reduced postural sway. Their interpretation emphasizes the role of active touch rather than availability of a fixed reference point for the reduction in postural sway (also see Jeka and Lackner 1995).

In our experiments, postural sway decreased significantly more when the fingertip was placed into a relatively strong clip as compared to a free light touch to a stationary pad. We would like to emphasize that, while the forces exerted by the clip on the dorsal and palmar surfaces of the finger tip were relatively high (up to 14 N), the net forces between the finger with the clip and the stationary touch pad were always under 1 N. Only these forces, comparable to those used in other studies of the effects of light touch (e.g., Jeka and Lackner, 1994, 1995), could be used to stabilize the body mechanically. When the finger was in the clip, the subject did not need to stabilize the kinematic chain to keep the position of the fingertip unchanged during postural sway. The external reference point provided by the clip was highly stable and did not depend on the sway. These results support the view that providing a fixed reference point is crucial for sway reduction while facing a task of stabilizing the fingertip in space is not. However, findings in our second experiment have suggested that having a fixed reference point is also not necessary, and postural sway can be reduced based on information on sway-related changes in contact forces with an external object, which moves with the hand.

Two sources of sensory information for postural stabilization

As suggested in the Introduction, two sources of sensory information can play a role in the reduction of the postural sway with touch. First, slowly-adapting receptors provide information on the location of the point of contact. Second, both slowly- and fast-adapting receptors can be activated by sway-associated deformation of the skin and subcutaneous tissues. Experiments with the clip have suggested that the first source of information, related to providing a stable reference point, could lead to strong sway reduction. On the other hand, the results of Experiment 2 with holding the load show that sensory information related to changes in forces at the point of contact can by itself induce postural stabilization effects even in the absence of a fixed reference point.

When a standing person holds a handle directly attached to a load, postural sway leads to small deviations of the body and to small deviations of the hand holding the load

in the extrinsic system of coordinates. These deviations are associated with transient inertial forces and moments between the hand and the load, which can be detected by sensory endings in the hand (and/or in more proximal segments of the arm) and be used by the CNS for postural stabilization. Postural sway is a slow process and is associated with small body displacements. Typical displacements of the center of mass during sway are of the order of 0.2 cm (leading to shoulder displacements of about 0.25 cm) while their typical frequency is about 0.3 Hz (e.g., Kingma et al. 1995; Zatsiorsky and King 1998). If one views sway as a sine process, peak acceleration of the shoulder (and the hand) can be expected to be about $0.08*10^{-2}$ m/s^2. If one holds the load of 3 kg in the hand, associated peak inertial forces are expected to be of the order of 0.02 N.

When the same load is attached to the handle via a pulley system (as shown in Figure 11), hand displacement is associated with a change in the direction of the force transmitted by the cord to the handle. This leads to a horizontal force component that tends to move the handle with the hand towards the original equilibrium position. For the load of 3 kg, a displacement of the hand of 0.25 cm and the distance from the hand to the pulley of 0.7 m, these forces could be expected to be of the order of 0.12 N, i.e. they are substantially higher than the inertial forces and of a similar magnitude or slightly lower than contact forces during a light finger touch to a stationary pad (see Table 6 and Jeka and Lackner, 1994). In a sense, these forces are similar to those that emerged in experiments by the group of Lackner (Lackner et al. 2001) when subjects touched a flexible filament, since these forces are proportional to deviation of the end effector from a reference point defined by the position of the pulley or by the position of the fixed end of the filament.

We can conclude that sensory signals providing information on a fixed reference point and those informing on changes in contact forces can each potentially lead to a decrease in sway. However, a hierarchy of their effects can be expected. Holding the load with directly attached handle did not result in decreased sway. Apparently, the very small inertial forces associated with the sway were insufficient to provide adequate sensory information in the absence of a fixed reference point. Note that these forces were likely of the same order of magnitude as those measured in the control experiments during touch to the neck and to the head (Table 6), which were very effective in reducing the sway.

Hence, having a fixed reference point leads to decreased sway even if the modulation of contact forces is small.

Holding the same load via the pulley system was likely associated with larger changes in contact forces, which resulted in a large sway decrease, such that an additional finger touch to the pad lead only to a small, non-significant further drop in sway indices (Figure 15). Holding the 3 kg load via the pulley system can hardly be associated with active touch or with providing a fixed reference point in space. We conclude, therefore, that, if modulation of contact forces is large enough, availability of a fixed reference point may not be necessary for sway reduction.

The importance of what is touched and where

An interaction between the two sources of information was also indirectly addressed in experiments with touch to different body parts. Touch to the head/neck and finger touch differed in several aspects. On the one hand, finger skin is known for its high spatial resolution and sensitivity (Weinstein 1968) allowing one to expect finger touch to be more efficient. However, during finger touch, in order to use information from the fingertip, an accurate perception of the joint configuration in the hand and arm is essential. On the other hand, head/neck touch provides information more relevant to trunk position being at the rostral end of the kinematic chain of the body.

If sway is viewed as a pendulum like motion at the ankle joints, tissue deformation induced by the sway at different body parts depends on the distance between the ankle joints and the body part or its point of contact with the trunk. In particular, assuming that the configuration of an arm does not change, deformation of fingertip tissue depends on the distance from the ankle to the shoulder joint, not on the actual location of the fingertip in space. The distances from the ankle joints to the shoulders, to the neck, and to the trunk are only slightly different from each other (by 10% to 15%) and are not expected to lead to major differences in the magnitude of tissue deformation. We actually observed smaller magnitudes of contact forces in the head touch and neck touch

conditions as compared to finger touch conditions (Table 6). In contrast, some indices of postural sway decreased under touch to the neck or head nearly twice as much as under finger touch (e.g., RMSy in Figure 13). Touch to the side of the head/neck was more efficient in reducing sway as compared to finger touch at the side of the body. This finding supports the hypothesis formulated in the Introduction that sensory information more directly related to trunk orientation with respect to the vertical is potentially more efficient for postural stabilization.

Finger touch in front of the body had higher effects on postural sway as compared to finger touch at the side of the body, confirming the report by Rabin et al. (Rabin et al. 1999). These differences were interpreted by Rabin et al. using a simple model of the arm as a rigid link with a compliant element. However, the complex actual arm configuration during touch probably requires a much more detailed biomechanical analysis to link postural sway to force changes at the point of contact.

Particular importance of transient shear forces at the point of contact

Several of our observations suggest that information on the location of the reference point could have come mainly from receptors sensitive to shear forces at the point of contact. In particular, touch to the side of the head or the side of the neck was more effective than finger touch at the side of the body. A potentially important difference among the touch locations is the resolution of cutaneous information (Johansson et al. 1980; Gardner 1988). Both the glabrous skin at the fingertip and the hairy skin have high directional sensitivity (Vallbo et al. 1995; Olausson et al. 2000). However the two types of skin differ in the types of receptors they carry. While the glabrous skin at the tip of the fingers contains a dense network of fast-adapting sensory endings with small receptive fields, including in particular Merkel disks (Johansson et al. 1980; Gardner 1988), hairy skin is primarily infused with receptors sensitive to lateral tension (Norrsell and Olausson 1994; Norrsell et al. 2001) making them particularly sensitive to changes in shear forces.

Our observations of the effects of touch to the head and neck contrast those of Lackner and his colleagues (Lackner et al. 2001). In that study, a touch to the forehead or nose was only half as effective as finger touch in reducing postural sway. Note, however, that touch used in the experiments by the group of Lackner likely lead to modulation of the normal force at the point of contact with the dominating anterior-posterior sway while touch to the side of the head/neck in our experiments led to modulation of shear forces. The mentioned high sensitivity of the receptors in the hairy skin to lateral tension allows one to expect the modulation of shear forces to be more efficient in postural stabilization as compared to modulation of normal forces. In line with our results are those of Norrsell and colleagues (Norrsell et al. 2001). This study compared touch to the forearm with finger touch and found similar degrees of reduction in the postural sway.

Concluding comments

The results of the present series of studies on the effects of light touch on postural sway demonstrate the amazing versatility of the system for postural stabilization, which can use information from different sensory sources related to different mechanical interactions with external objects. It seems that no single source of sensory information and no single associated motor task is necessary while many of them may be sufficient for reduction of postural sway with touch. Even a modulation of contact forces produced by horizontal force components during holding a load via a pulley has proven to be sufficient. Our results emphasize the importance of an interaction between two sources of haptic sensory signals associated with touch, one related to providing a fixed reference point in space, and the other related to transient force changes at the point of contact induced by actual sway. The system of postural stabilization can couple itself to either of these two sources of sensory information.

Chapter 7

MUSCLE SYNERGIES DURING SHIFTS OF THE CENTER OF PRESSURE BY STANDING PERSONS: EFFECT OF INSTABILITY AND ADDITIONAL SUPPORT

Introduction

In previous studies (Chapters 4 and 5), we have shown that the framework of the UCM-hypothesis can be used to identify muscle synergies in postural tasks. In Chapter 6, we tested the effects of different types of touch on postural sway. In this chapter, we present two experiments, which test the effects of support instability, finger touch and grasp on the formation and co-variation of M-modes. Recollect that M-modes are the independent control variables consisiting of a failry consistent group of muscle activity.

In Chapter 5, a control hypothesis that the CNS co-varies magnitudes of muscle-modes (M-modes) to stabilize a certain task-specific COP shift was confirmed for three tasks (load release in the front, LR_F; fast arm movement to the front and back, AM_F and AM_B) performed by subjects standing on a stable horizontal surface. Further, separate M-mode synergies were identified for forward and backward COP shifts.

When using the UCM approach, the first step is to identify independent control variables (ICVs), which we assume the CNS manipulates in order to stabilize particular performance variables. In the above experiment, these ICVs, which were referred to as M-modes, were identified in a number of subjects for various tasks requiring COP shifts as an implicit or an explicit component (see Chapters 4 and 5). Tasks that required COP shifts as an implicit component were associated with anticipatory postural adjustments (APAs). M-modes did not vary significantly across tasks and subjects (see Chapter 4),

indicating that muscles were organized in similar groups for various postural tasks. All the tasks in the above experiment were performed under stable conditions. In other words, no mechanical or sensory manipulations were imposed.

It is known that APAs are modulated with changes in postural stability. APAs decrease under 'very stable' as well as 'unstable' conditions (Friedli et al. 1984; Nardone and Schieppati 1988; Gantchev and Dimitrova 1996; Aruin et al. 1998). APAs in arm raising tasks have been studied during changes in the size of the base of support (Friedli et al. 1984; Gantchev and Dimitrova 1996; Aruin et al. 1998). It has been suggested that in 'very stable' conditions, the requirement of APAs to stabilize posture is reduced. For instance, when subjects supported themselves by leaning against a wall during an arm flexion movement, APAs decreased in leg and trunk muscles (Friedli et al. 1984). Similar attenuation of APAs was also observed in other tasks such as standing on tiptoes or on the heels when holding on to a handle for support (Nardone and Schieppati 1988).

In other studies, researchers looked at APAs under 'less stable' conditions such as standing on a platform fitted below with a narrow beam or a small sphere of different diameters (Gantchev and Dimitrova 1996; Aruin et al. 1998) or in single-leg stance (Nouillot et al. 1992). Under all these conditions the 'safe area' within which the COP and COM can move without the subject falling is reduced. A decrease in APAs was observed during arm (Aruin et al. 1998) and leg (Nouillot et al. 1992) movements under conditions of decreased support. Further, the decrease in APAs was more pronounced in the direction of instability (Aruin et al. 1998). It has been hypothesized that APAs themselves may be viewed as perturbations, which may be sufficient to move the COP outside the decreased area of support (Aruin et al. 1998).

APAs are also influenced by sensory manipulations. The addition of a light touch during quiet stance has been shown to reduce postural sway (Holden et al. 1994; Jeka and Lackner 1994) and also results in decreased APAs in leg and trunk muscles during a unilateral arm raising task (Slijper and Latash 2000). In the latter study, additional support in the form of a hand grasp did not cause any further changes in the APAs.

In the present study, we investigated the effects of postural instability and availability of additional hand support on the formation and co-variation of M-modes. Specifically, we were interested in the following questions:

1. Are similar M-modes used in conditions of postural instability as in stable conditions?
2. Are the M-modes used in conditions of postural instability modified by a light finger touch to a stable surface or hand grasp to a stable support?
3. In a task when an arm can contribute to stabilization of the vertical posture, do two groups of M-modes exist, one across the lower limb and trunk muscles and the other across the arm muscles? Alternatively, are muscles grouped into common M-modes across effectors?

To answer the first two questions we compared the M-modes obtained while performing a load release task under four stability conditions: 1) standing on a stable support surface, on the force plate; 2) standing on an unstable support surface, that is on a wooden board with a narrow beam glued to its bottom leading to instability in the anterior-posterior direction (AP instability); 3) standing on an unstable support surface with a light touch to a stable surface and 4) standing on an unstable support surface with additional support in the form of a grasp to a handle placed at a comfortable height. Comparison between the first two conditions can help answer the first question and comparison between the later three conditions can help answer the second question. Since the task requirements are different across conditions, with or without an additional requirement of balancing on the unstable board or with or without additional sensory information (light touch) or additional support (grasp), the M-modes in the different conditions may be expected to differ. Alternatively, it is possible that the same M-modes are used, and only their gains are modulated differently in different conditions to stabilize shifts in the COP.

In a task where subjects are asked to stand on an unstable surface and provided with additional hand support, hand muscles may be used in postural stabilization (cf. APAs in hand muscles during loading/unloading Dufosse et al. 1985; Paulignan et al. 1989; Forget and Lamarre 1995; Biryukova et al. 1999 and arm raising Slijper and Latash 2000). We defined M-modes in this task to answer question 3, that is, to verify if arm, leg, and trunk muscles form common M-modes or if they are grouped separately.

When subjects are allowed a light finger touch in unstable conditions, APAs in the leg and trunk muscles decrease in unstable conditions as compared to stable

conditions in an arm raising task, while there are no comparable changes in APAs seen in arm muscles (Slijper and Latash 2000). In the same study, it was shown that an additional grasp by a hand leads to no further changes in APAs in the leg and trunk muscles, but there is a significant increase in the APAs seen in arm muscles. Hence, it is possible that there may be two groups of M-modes, one uniting the lower limb and trunk muscles and the other uniting arm muscles. On the other hand, when the arm muscles contribute to postural stabilization in the task where hand grasp is available, one can expect to see common M-modes uniting muscles across effectors.

Another aim of this study was to understand how the interaction between M-modes is influenced by factors such as support stability and availability of a finger touch. We used the UCM method to see if the M-modes work together as a synergy to stabilize COP shifts under three different conditions: standing on a stable surface with no touch, standing on an unstable surface with no touch and standing on an unstable surface with a light touch. In particular, we attempted to answer the following question:

4. Can we confirm a control hypothesis about stabilization of COP shift by co-variations of the magnitudes of M-modes under stable and unstable conditions with no touch and in unstable conditions with the addition of a light finger touch? If so, are the M-mode synergies similar across these three conditions?

To answer these questions we included a condition of fast, unilateral arm extension movement to different degrees of extension (associated with different COP shifts) to compute the Jacobian relating the M-modes to COP shifts (similar to varying weights of loads in the load release task, described in detail in Chapter 5). Another task, voluntary sway to the front at different speeds, was also used to compute a Jacobian. Both these tasks were performed under 3 conditions: stable, unstable and unstable with a finger touch. Finally, unilateral arm raising tasks to a nominal distance under these three conditions were included and UCM analysis was performed on this task. We expect different synergies (patterns of M-mode co-variations) to be used in the three conditions because of the different stability requirements in the three tasks.

Methods

Subjects

Twelve healthy right-handed subjects, without any known neurological or motor disorder, participated in the experiment. Of these, 6 were males and the remaining were females, with the mean age 31.1 yr. (± 9.3 SD), mean weight 64.4 kg (± 8.8 SD) and mean height 169.3 cm (± 7.1 SD). The subjects gave written informed consent according to the procedure approved by the Office for Regulatory Compliance of the Pennsylvania State University.

Apparatus

A force platform (AMTI, OR-6) was used to record the moment around a frontal axis (M_y), the vertical component of the reaction force (F_Z) and the horizontal component in AP direction (F_X). An oscilloscope (Tektronics TDS 210) showed the time pattern of M_y to the subject and the experimenter. A uni-directional accelerometer (Sensotec) was taped to the handle attached to the load or over the dorsal aspect of the hand, depending on the task such that the axis of sensitivity of the accelerometer was directed along the required motion. Disposable self-adhesive electrodes (3M) were used to record the surface EMG activity of the following leg and trunk muscles: tibialis anterior (TA), soleus (SOL), medial head gastrocnemius (GM), rectus femoris (RF), vastus lateralis (VL), biceps femoris (BF), rectus abdominis (RA) and erector spinae (ES) (as in Figure 1, Chapter 4). Electrodes were also placed on the following upper limb muscles: anterior deltoid (AD), posterior deltoid (PD), biceps brachii (BB), long head of triceps brachii (TB), wrist flexors (flexor carpi radialis, WF) and wrist extensors (extensor carpi ulnaris, WE). The electrodes were placed on the left side of the subject's body on the muscle

bellies, with their centers approximately three centimeters apart. Data were recorded at a sampling frequency of 1000 Hz with a 12-bit resolution. A Gateway 450 MHz PC with customized software based on the LabView-4 package was used to control the experiment and collect the data.

In some conditions, the subject held a load (20 × 20 × 10 cm) of 3 kg mass behind them with the right hand through a handle connected to a pulley system (see Figure 16). In some trials, subjects stood on a wooden board of the same dimensions as the force plate, but fitted with a narrow beam on the undersurface (5.5 cm wide and 6.4 cm in height). This board was placed over the force plate and caused instability in the AP direction. In trials involving finger touch or grasp, subjects were asked to lightly touch their left index fingertip to a stable support (with less than 1 N force) or grasp a metal handle, which was fixed by a vise placed in front of and slightly to the left of the subject's midline.

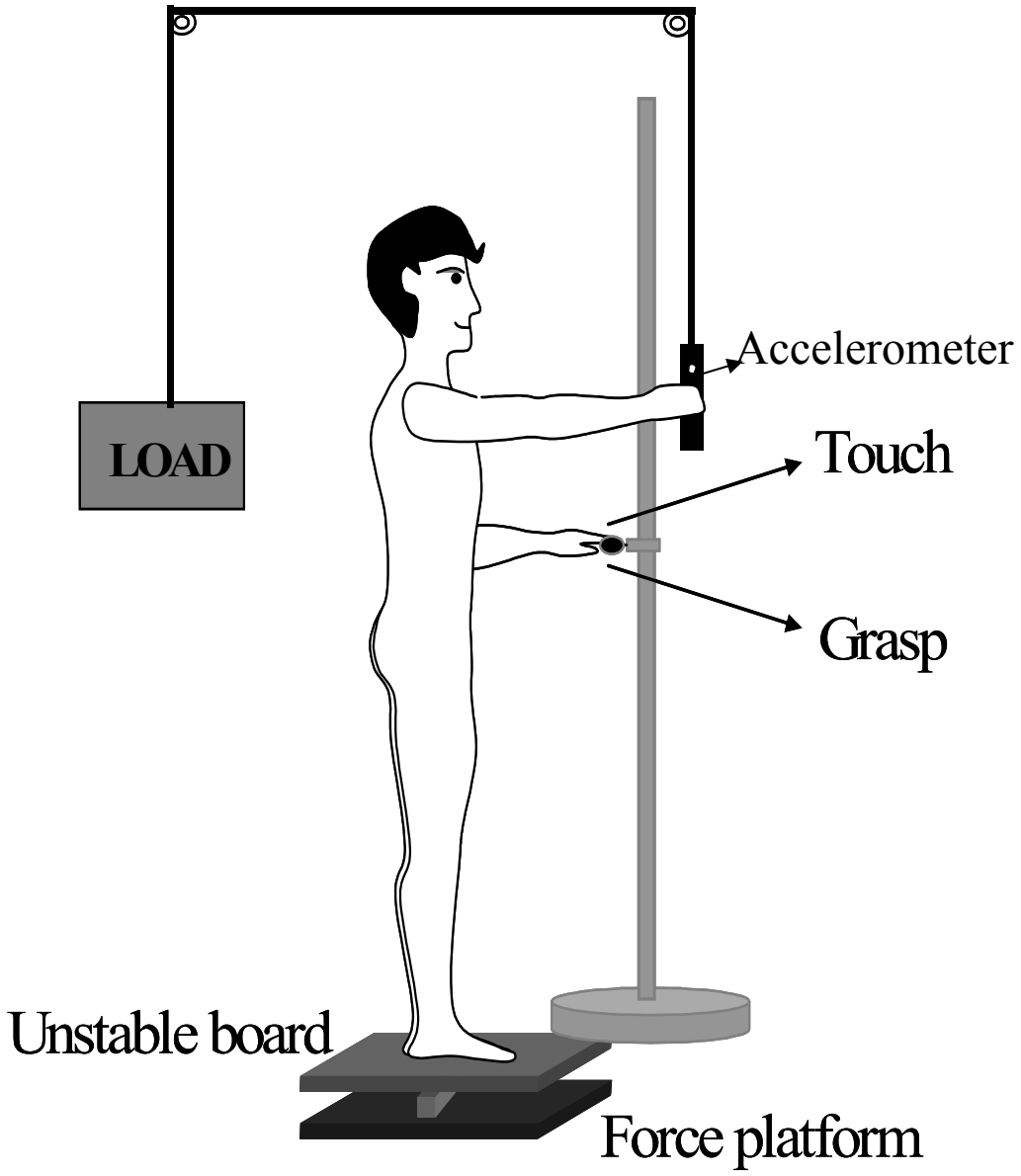

Figure 16: The experimental set-up for the load release task. Subjects stood either on the force platform or on an unstable board placed on the force platform. In some trials the left index finger touched a touch pad with a built in force sensor ($LR_{UN,T}$) or grasped a handle ($LR_{UN,G}$) in front of the subject. With their right hand, subjects held a handle attached to the load through a pulley system.

Procedure

This experiment was designed to study the effects of support surface stability and availability of additional hand support on the organization of M-modes and muscle synergies.

Similar to Chapter 5, three types of tasks were used in this experiment. Two tasks were associated with anticipatory postural adjustments (APAs, for review see Massion 1992) and involved COP shifts as an implicit component. These tasks required the subject to release a load from extended arms (cf. Aruin and Latash 1996) or to perform a fast unilateral arm movement (cf. Belen'kii et al. 1967). The third task required the subject to explicitly (voluntarily) shift his/ her COP using visual feedback provided by the oscilloscope (cf. Danion et al. 1999).

Load release (LR) at the back

This particular task was selected based on results from our previous study (see Chapter 4), as leading to the most reproducible M-modes across subjects. In the initial position, the subject stood on the force platform (or unstable board) with his/her feet side-by-side, at hip width. To keep the initial position similar across conditions, subjects were instructed to keep the left forearm horizontal such that the elbow was at 90º-flexion and the upper arm was vertical by the side of the body. The right arm was flexed at 90º-shoulder angle with elbow extension to hold the handle connected to the load through the pulley system. The position of the feet was marked on the platform and was reproduced across trials. Subjects were asked to release the 3 kg load at the back with a quick opening motion of the hand, releasing the handle. The load release task was performed in four different series under different conditions of stability and additional support (see below).

Voluntary sway (VS) forward

The initial position of the subject was the same as in the LR task, except the right hand was placed by the side of the subject. The moment, M_y at the initial position of the subject was marked on the oscilloscope, and the subject was asked to occupy this position prior to each trial. The subject was instructed to move his/her body weight towards their toes. In different trials, the subjects were asked to produce this movement at different self-selected speeds. Subjects were asked to watch the oscilloscope, which showed them the current value of M_y. The required M_y shift was also marked on the screen of the oscilloscope (approximately 10 Nm, which corresponds to a COP shift of about 1-2 cm depending on the subject's body weight).

Arm movement (AM) to the back

The initial position was the same as in the VS task. Subjects were asked to perform a fast, unilateral arm extension movement with the right arm. This action leads to an initial COP shift forward, i.e. in the same direction as in the LR and VS tasks. In one set of trials, the subjects were asked to perform this movement over a nominal distance of 40°. In another set (see below), the subjects were asked to vary the distance through which they extended their arm, thus varying the magnitude of COP shift in each trial.

For each trial, data was collected over 3 s. Subjects were instructed to stand as quietly as possible in the initial position before the beginning of the trial. The subject heard a computer generated beep 500 ms after data collection began, which indicated that he or she should initiate the required action. Subjects were reminded not to initiate their actions immediately after the beep, but to wait for about a second.

The order of the conditions was pseudo-randomized across subjects. A rest period of 6 seconds between trials and a rest period of two minutes between two conditions was given. Sufficient rest periods (about a minute) were given between sets of trials, such that fatigue was not an issue. Prior to each condition, two practice trials were given.

In all there were thirteen series, which were performed in two separate experiments to avoid fatigue. In the first session (Experiment 1), we identified M-modes in different stability conditions. Data from this experiment were used to address questions 1-3 presented in the Introduction. Experiment 2 was performed in a separate session within a few weeks on ten of the subjects and included a series of experimental tasks to identify the Jacobian and to perform UCM analysis. We assumed that M-modes were robust within a subject and would not change much between the two sessions. To verify this, we repeated one of the series from the first experiment on four of the subjects in the second session. We used M-modes from Experiment 1 to perform UCM analysis on data from Experiment 2 to answer question 4 in the Introduction.

Experiment 1: Analysis of M-modes

Step 1: Identification of M-modes.

Series 1: Load release at the back when standing on the stable surface, with no additional support (LR_{ST}): 60 trials (three sets of 20);

Series 2: Load release at the back, when standing on the unstable surface (wooden board), with no additional support (LR_{UN}): 60 trials (three sets of 20);

Series 3: Load release at the back, when standing on the unstable surface, with light finger touch to a touch pad ($LR_{UN,T}$): 60 trials (three sets of 20);

Force applied by the finger to the touch pad was monitored to ensure that the force never exceeded 1N. Trials where forces greater than 1N were recorded were discarded from further analysis. On average about two trials per subject were discarded.

Series 4: Load release at the back, when standing on the unstable surface, with additional support (grasp to a handle, $LR_{UN,G}$): 60 trials (three sets of 20);

Subjects were asked to grasp the metal handle with their left hand. The handle was positioned such that the subject was able to grasp the handle comfortably with the elbow at 90º and the upper arm vertical. Force applied to the handle was not controlled and subjects were free to apply as much force to the handle as they wanted.

In Series 1 and 2, subjects were asked always to keep their left arm flexed as in Series 3 and 4. In all the above series a 3kg mass load was released.

Experiment 2: Analysis of multi-M-mode synergies

Step 2: Computation of the Jacobian matrix.

Series 5: Fast right arm extension movement (JAM_{ST}) over varying distances self-selected by the subjects, while standing on the stable surface with no touch: 20 trials;

Series 6: Fast right arm extension movement (JAM_{UN}) over varying distances self-selected by the subjects, while standing on the unstable surface with no touch: 20 trials;

Series 7: Fast right arm extension movement ($JAM_{UN,T}$) to varying distances self-selected by the subjects, while standing on the unstable surface with light touch (< 1 N force): 20 trials;

Series 8: Voluntary sway forward at different speeds (JVS_{ST}) while standing on a stable surface with no touch: 20 trials;

Series 9: Voluntary sway forward at different speeds (JVS_{UN}) while standing on the unstable surface with no touch: 20 trials;

Series 10: Voluntary sway forward at different speeds ($JVS_{UN,T}$) while standing on the unstable surface with light touch (< 1 N force): 20 trials.

Step 3: UCM analysis.

Series 11: Right arm extension over the nominal distance of about 40° while standing on stable surface with no touch (AM_{ST}): 25 trials.

Series 12: Right arm extension over the nominal distance of about 40° while standing on the unstable surface with no touch (AM_{UN}): 25 trials.

Series 13: Right arm extension over the nominal distance of about 40° while standing on the unstable surface with light touch (< 1 N force) ($AM_{UN,T}$): 25 trials.

Four out of the ten subjects that participated in Experiment 2 also repeated the LR_{ST} series that they had performed in Experiment 1.

In addition, in Experiment 2, two control trials were performed: The subject was asked to hold a load of 5 kg in front of the body and behind the body (through the pulley system) for 5 s. These data were used for EMG normalization for leg and trunk muscles as described in the next subsection.

Data processing

Processing of signals involved filtering, aligning, rectifying and integrating EMG signals, which was done in the same way as in Chapter 5 (see sub-section in Methods, Chapter 5). APAs were also computed in the same manner as before as integrated EMG activity in the 100 ms period before initiation of action (time zero; t_0) after subtracting background activity.

For Experiment 2, in order to compare the integrated EMG indices (∫EMG) across muscles and subjects, we normalized them by the integrals of EMGs collected in the control trials as follows: ∫EMG indices for dorsal (ventral) muscles were divided by integrals of EMG over 100 ms in the middle of the control trial, $\int EMG_{control}$, during holding the load in front of (behind) the body:

$$IEMG = \int \mathrm{EMG}_{\mathrm{JVS,JAM,AM}} / \int \mathrm{EMG}_{\mathrm{control}} \quad \textbf{(10)}$$

Coordinates of the center of pressure (COP) and shifts in the COP were computed in the same way as in Chapter 5 (see sub-section on Data processing in Methods, Chapter 5). However, we now made a correction to take into account the moment produced by the horizontal force, F_X due to the height of the unstable board (6.4 cm) above the force plate. This moment was calculated as follows:

$$M = Fx * 0.064 \quad \textbf{(11)}$$

The COP position was corrected by subtracting M from M_Y in Equation 5A (Chapter 5),

$$COP_{corr} = (M_Y - M) / F_Z \quad \textbf{(12)}$$

Shifts of the COP were computed in the same way as earlier (refer to Equation 5B in Chapter 5).

Statistics

Statistical techniques that will be used to identify and compare M-modes in Experiment 1 will be described first, followed by steps in UCM analysis for Experiment 2.

Experiment 1

Step 1: Defining M-modes using Principal Component Analysis (PCA)

For the LR_{ST}, LR_{UN}, $LR_{UN,T}$ and $LR_{UN,G}$ series, in each subject, we have IEMG data matrices with the size 60×14 (60 rows corresponding to repetitions and 14 columns corresponding to muscles). For the LR_{ST}, LR_{UN} and $LR_{UN,T}$ series we were interested in the correlations among the eight leg and trunk muscles. The correlation matrix (8×8) between the IEMGs was subjected to PCA, using procedures from Statistica 6.0 (StatSoft, Inc.). The factor analysis module with principal component extraction was employed. For the $LR_{UN,G}$ series, we were interested in the correlations among the leg and trunk muscles separately, among arm muscles separately, and among muscles of the leg, trunk and arm combined together. Therefore, PCA was performed on the 8×8 correlation matrix of leg and trunk IEMGs, 6×6 correlation matrix of arm IEMGs and 14×14 correlation matrix of leg and trunk and arm IEMGs

For each subject and each task, the obtained eigen-values and PCs of the matrices were then considered. Based on the percentage of total variance accounted by individual PCs and on analysis of the scree plots, only the first three PCs (M-modes) were selected for further analysis of the leg and trunk muscles.

Analysis of similarity of leg and trunk M-modes across tasks

PCA on the IEMG data of leg and trunk muscles revealed predominantly two types of M-modes: reciprocal patterns and co-contraction patterns (see Results for details). In order to compare if the M-modes were similar or different for the three tasks

described in Step 1, we first tabulated the Modes qualitatively as corresponding to reciprocal or co-contraction muscle patterns. We then performed a Friedman's test to verify if there was a difference in the occurrence of co-contraction patterns among the three tasks.

To test the similarity between the conditions, we performed another qualitative comparison. For each subject and for each condition, we named the three PCs by the type of M-mode (push-back M-mode, push-forward M-mode, co-contraction M-mode at hip, knee or ankle; see Results for details). Next, we computed the number of mismatches in the types of M-modes between the LR_{ST} condition and the other conditions. Since there were five types of possible M-modes and only three PCs were retained, there is a maximum of 2 mismatches possible and the number of mismatches by chance is 1.2.

Experiment 2

M-modes identified in Experiment 1 from LR_{ST}, LR_{UN} and $LR_{UN,T}$ were used in further analysis.

Step 2: Defining the Jacobian using multiple regression

Linear relations between changes in the M-modes magnitudes and the COP shifts were assumed and the corresponding multiple regression equations were computed. The coefficients of the regression equations formed a Jacobian matrix, **J**. Series 5-10 were used to generate linear estimates of the Jacobians. The columns of **J** are coefficients relating changes in magnitude of M-modes (MMMs) to COP shift.

IEMG data from these series were multiplied with the eigenvectors obtained at Step 1 (Experiment 1) and further summed up to yield three MMMs for each trial. A multiple regression analysis was performed using these MMMs as the independent variables and the corresponding ΔCOP shift as the dependent variable (see also Step 2, Procedure in Chapter 5). Optimal sets of coefficients were defined for each subject using Equations 6 and 7 (see Chapter 5).

Step 3: UCM Analysis

For each trial of series 11-13, IEMG were computed and transformed into MMMs as in Step 2. The hypothesis that ΔCOP is stabilized, accounts for one degree of freedom (DOF). The space of MMMs has dimensionality n = 3. Thus, the system is redundant with respect to the task of stabilizing ΔCOP. The mean contribution of each M-mode to ΔCOP was calculated. Since the model relating MMMs to ΔCOP is linear, the mean values were subtracted from each computed value and the residuals were further analyzed as before (see Chapter 5). We used the Wilcoxon signed rank test to compare if there is a significant difference between V_{UCM} and V_{ORT} across subjects.

Comparison of M-modes across tasks

In performing the above UCM analysis, one of our assumptions is that M-modes are the same for the three tasks (LR, AM and VS), used in different stages of analysis (Chapter 4). In order to test this assumption, we performed PCA on the IEMG indices of the JAM and JVS tasks used to compute the Jacobian. We then performed a Friedman's test on the number of co-contraction patterns obtained in each stability condition (ST, UN and UN,T). Note that the power of the PCA on the data from the JAM and JVS tasks is limited because the number of repetitions in this case is only twenty, unlike the LR tasks where subjects performed sixty repetitions. However, the number of trials for these conditions was limited to avoid fatigue among the subjects.

To support the results of the Friedman's test, we performed a comparison of the number of mismatches of M-modes for the three tasks (LR, VS and AM in each of the stability conditions (ST, UN and UN,T). This comparison is similar to that described for the comparison for the LR tasks across different stability conditions in Experiment 1.

Results

General EMG patterns

Subjects performed the same tasks in these experiments as those in Chapter 5. The resulting EMG patterns are similar to those described under the Results section of Chapter 5. In general, all three tasks (load release at the back, fast arm extension movement and voluntary sway forward) were accompanied by an increase in the background activity in dorsal muscles prior to action. This was sometimes accompanied by a decrease in the activity of ventral muscles. The same qualitative picture was seen under all the stability conditions. Figure 17 shows the EMG of the leg and trunk muscles for three tasks (load release at the back, LR_{UN}; voluntary sway forward, VS_{UN} and arm extension movement, AM_{UN}) under the unstable condition in a representative subject. Note that in all three tasks there is an increase in dorsal muscle (GM, SOL, BF, ES) activity, accompanied sometimes by a decrease in ventral muscle (TA, VL, RF and RA) activity prior to initiation of action (at time, t_0).

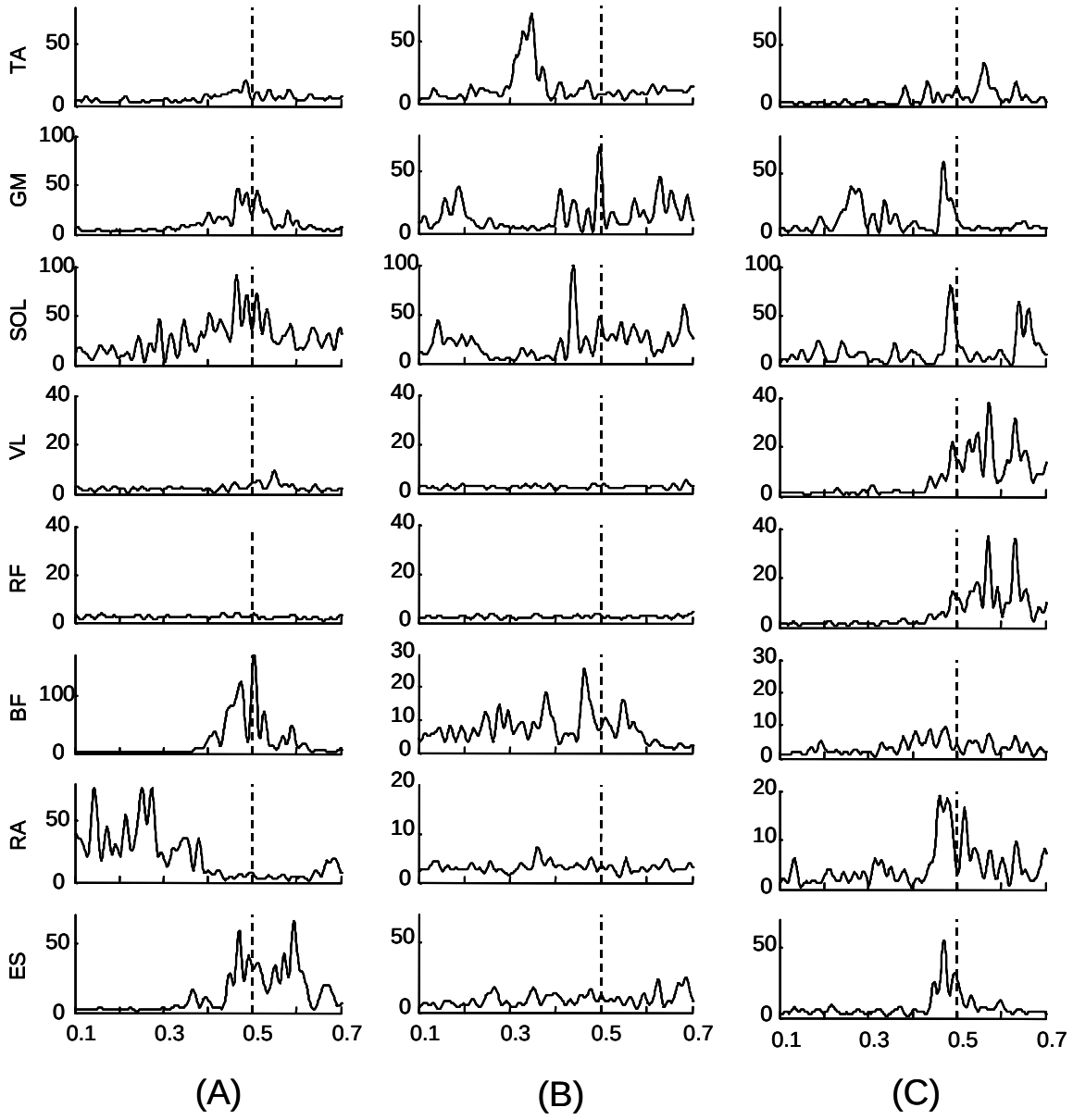

Figure 17: General EMG patterns during different tasks (A: LR_{UN}, B: VS_{UN}, C: AM_{UN}) under the unstable condition. Vertical dashed lines correspond to time zero, t_0. EMG was integrated over the 100 ms interval before t_0. Note the increase in the activity of dorsal muscles, accompanied sometimes by a decrease in the activity of ventral muscles. (TA: tibialis anterior, GM: medial head of gastrocnemius, SOL: soleus, VL: vastus lateralis, RF: rectus femoris, BF: biceps femoris, RA: rectus abdominus, ES: erector spinae.)

Results from Experiment 1

1. Results of PCA

Results of PCA on leg and trunk muscles

The IEMG indices of leg and trunk muscles associated with an early shift of the COP of each subject for the four series (LR_{ST}, LR_{UN} and $LR_{UN,T}$ and $LR_{UN,G}$) in Experiment 1, were subjected to a PCA. Consistent with the previous studies (Chapters 4 and 5), we retained three PCs. Principal components from PC4 onwards explained little variance and had at most one muscle load significantly on them. The first three PCs accounted for an average of 68.5 % (± 1.9 %) variance across all subjects. The average variance explained by each of the first three PCs were 32.2 % (± 1.9 %) by PC1, 20.9 % (± 0.8 %) by PC2 and 15.4 % (± 0.6 %) by PC3.

Across all subjects and series, we found five types of PCs (M-modes) based on muscles that load significantly on them. Loadings above ± 0.5 were considered significant (Hair et al. 1995). These five types of M-modes (basic M-modes) could be grouped into two patterns: reciprocal and co-contraction patterns. The five basic M-modes and the muscles typically seen in them were:

Reciprocal patterns:

- Push-back (GM, SOL, BF, ES)
- Push-forward (TA, VL, RF, RA)

Modes were named as reciprocal when at least two muscles from either the dorsal or ventral groups loaded significantly on a mode. For example, if GM and BF loaded significantly on a PC, we called that a Push-back M-mode.

Co-contraction patterns:

- Co-contraction at the ankle (TA, GM and/or SOL)
- Co-contraction at the knee (VL and/or RF, BF)
- Co-contraction at the hip (RA, ES)

In the case of the ankle and the knee when at least two of three antagonist muscles (for example, TA and SOL) loaded significantly on a PC, we called that a co-contraction pattern.

In each individual subject and series, the three PCs that were retained could be any combination of the 5 basic PCs. Tables 7A and 7B are results of PCA for the LR_{ST} and $LR_{UN,G}$ series for a representative subject. Note the predominance of co-contraction patterns in the $LR_{UN,G}$ series.

Muscle	Mode 1	Mode 2	Mode 3
TA	-0.39	**-0.71**	-0.05
GM	**0.83**	-0.01	0.27
SOL	**0.82**	-0.11	0.03
VL	-0.29	**-0.74**	0.08
RF	0.38	**-0.74**	-0.03
BF	0.13	-0.36	0.45
RA	0.46	-0.13	**-0.64**
ES	0.01	-0.12	**-0.66**

Table 7A: Results of PCA in a representative subject for the LR_{ST} series. Loadings over 0.5 are shown in bold. Note that in this subject two modes show reciprocal patterns (mode 1: push back; mode 2: push forward) and one mode shows a co-contraction pattern (mode 3: hip co-contraction) TA: tibialis anterior, GM: medial head of gastrocnemius, SOL: soleus, VL: vastus lateralis, RF: rectus femoris, BF: biceps femoris, RA: rectus abdominus, ES: erector spinae.

Muscle	Mode 1	Mode 2	Mode 3
TA	0.02	**0.64**	-0.35
GM	0.16	**0.70**	0.02
SOL	-0.25	**0.72**	0.07
VL	**0.91**	-0.05	0.13
RF	**0.70**	0.41	0.25
BF	**0.61**	0.34	0.12
RA	-0.15	-0.04	**0.80**
ES	0.30	-0.02	**0.74**

Table 7B: Results of PCA in a representative subject for the $LR_{UN,G}$ series. Loadings over 0.5 are shown in bold. Note that in this subject all three modes show co-contraction patterns (mode 1: knee co-contraction, mode 2: ankle co-contraction and mode 3: hip co-contraction). Abbreviation of muscles is the same as in Table 7A.

Results of PCA when arm muscles are included in PCA

We expect the arm muscles to play a role in postural stabilization in the $LR_{UN,G}$ series (Slijper and Latash 2000). In order to test if there would be common M-modes across effectors, we ran a PCA on the correlation matrix of IEMG indices of all the leg, trunk and arm muscles pooled together (14×14 matrix). Across subjects, we retained 4 PCs, which explained 65.4 % (± 1.7 %) of the total variance. Among the twelve subjects, eight showed an M-mode uniting the hip and shoulder muscles (RA, ES, AD, PD or at least three of the four muscles). Further, ten subjects also showed wrist muscle co-contraction. Ankle and/or knee muscle co-contraction was seen in nine subjects. Table 8 shows the results of PCA of all 14 muscles from a typical subject for the $LR_{UN,G}$ series.

Muscle	Mode 1	Mode 2	Mode 3	Mode 4
TA	0.03	**0.78**	0.23	-0.13
GM	0.06	**0.84**	0.14	0.05
SOL	-0.13	**0.82**	-0.13	-0.05
VL	-0.17	-0.07	-0.04	**0.62**
RF	0.07	-0.03	0.00	**0.84**
BF	-0.37	0.30	-0.28	0.30
RA	**0.91**	-0.09	0.10	-0.12
ES	**0.91**	0.02	0.05	-0.03
AD	**0.94**	-0.12	0.04	-0.04
PD	**0.86**	0.08	0.01	-0.13
BB	-0.02	0.02	**0.80**	-0.23
TB	**0.73**	0.03	0.28	0.10
WF	0.22	-0.01	**0.82**	0.03
WE	0.12	0.25	**0.84**	0.11

Table 8: Results of PCA of all leg, trunk and arm muscles in a representative subject in the $LR_{UN,G}$ series in Experiment 1. Loadings over 0.5 are shown in bold. Note that this subject shows co-contraction patterns at the hip, shoulder (mode 1), ankle (mode 2) and wrist (mode 3). AD: anterior head of deltoid, PD: posterior head of deltoid, BB: biceps barchii, TB: triceps brachii, WF: wrist flexor, WE: wrist extensor. Abbreviation of other muscles is the same as in Table 7A.

To further test the correlations among arm muscles, we performed a separate PCA on the correlation matrix of IEMG indices of arm muscles only (6×6 matrix). We retained 3 PCs, which explained 75.9 % (± 2.1 %) of the total variance. Seven out of 12 subjects showed co-contraction patterns at the shoulder and wrist and reciprocal patterns at the elbow. Of the remaining five, three subjects showed co-contraction patterns only at the shoulder and one only at the wrist. Table 9 shows the results of PCA of the arm muscles from a typical subject for the $LR_{UN,G}$ series.

Muscle	Mode 1	Mode 2	Mode 3
AD	-0.02	**0.85**	-0.01
PD	0.43	**0.57**	-0.44
BB	0.28	**-0.60**	-0.10
TB	0.24	0.06	**0.87**
WF	**0.77**	-0.20	0.03
WE	**0.77**	0.02	0.25

Table 9: Results of PCA for arm muscles in a representative subject in the $LR_{UN,G}$ series in Experiment 1. Loadings over 0.5 are shown in bold. Note that this subject shows co-contraction patterns at the shoulder (mode 2), wrist (mode 1) and reciprocal patterns at the elbow (mode 2/3). Abbreviation of muscles is the same as in Table 8.

2. Results of Friedman's test

In order to answer questions 1 and 2 posed in the Introduction, we compared the M-modes obtained for the four series (LR_{ST}, LR_{UN} and $LR_{UN,T}$ and $LR_{UN,G}$) in Experiment 1. To do this, we first classified the M-modes into reciprocal or co-contraction patterns. We then calculated the number of times the co-contraction patterns were identified in each of the four series for each subject. We used these data to perform a Friedman's test with the factor: number of times the co-contraction pattern occurred and levels: LR_{ST}, $LR_{UN,}$ $LR_{UN,T}$ and $LR_{UN,G}$. The results showed a significant difference among the four series ($N = 12$, $df = 3$, $p < 0.01$). Further examination revealed that the number of times the co-contraction patterns occurred in the $LR_{UN,G}$ series was significantly higher than in the other three series (see Figure 18). Note that the maximum number of times the co-contraction pattern could be seen per subject, per condition was three, when all the M-modes showed co-contraction patterns (at the hip, knee and ankle). There was no significant difference among the LR_{ST}, LR_{UN} and $LR_{UN,T}$ series.

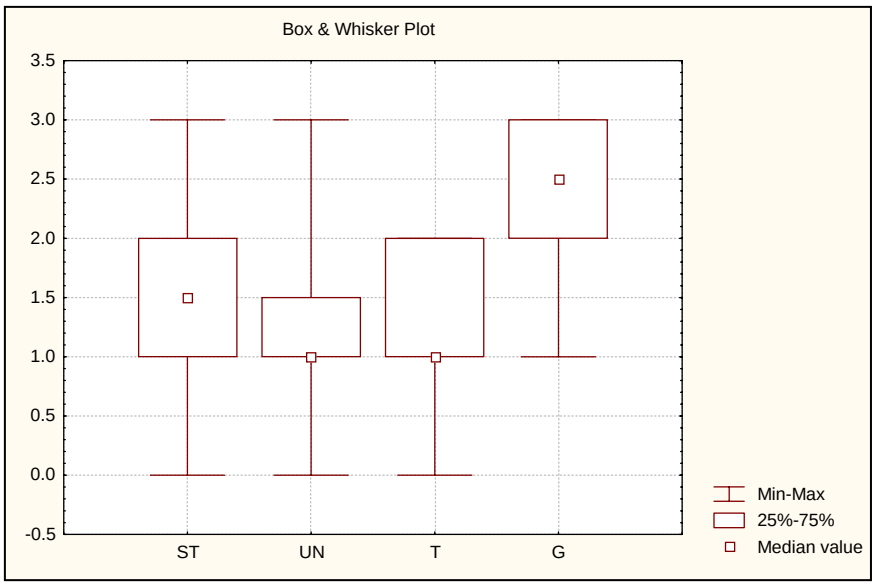

Figure 18: Plot showing the total range (Min-Max), the 25%-75% range, and the median for the number of times the co-contraction patterns were seen across subjects. The maximum number of times the co-contraction pattern could be seen per subject was three. Conditions, ST: stable, UN: unstable, T: unstable with light touch and G: unstable with grasp. Note that the co-contraction pattern is seen more often in the grasp condition.

Further, on comparing the number of mismatches between the LR_{ST} and the other three conditions, we found that on average the number of mismatches of M-modes between the LR_{ST}, LR_{UN} and $LR_{UN,T}$ conditions was less than 1 (0.88). However, the number of mismatches between the LR_{ST} and the $LR_{UN,G}$ conditions was 1.1, which is close to the number of mismatches expected by chance, 1.2. This finding adds supports our above findings based on the analysis on frequency of occurrence of co-contraction patterns.

Results from Experiment 2

1. Results of multiple regression

The relation between changes in the magnitudes of M-modes (MMMs) and the associated COP shifts (ΔCOP) was computed using multiple regression. This was done using data from series 5-10. In these series, subjects were asked to produce sets of trials, which induced early COP shifts of different magnitudes either by varying the degree of arm extension in the JAM task or by varying the speed of shift of COP in the voluntary sway, JVS task. These two tasks were performed under three stability conditions (ST, UN and UN,T). Six sets of coefficients (six Jacobians) were computed.

Variance in the magnitudes of the three M-modes accounted for 33.7 % (± 4.4 %) of the variance in ΔCOP for the JAM_{ST} series, 22.9 % (± 4.4 %) for the JAM_{UN} series, 37.4 % (± 5.8 %) for the $JAM_{UN,T}$ series, 55.2 % (± 6.5 %) for the JVS_{ST} series, 53.9 % (± 6.6 %) for the JVS_{UN} series and 64.3 % (± 5.6 %) for the $JVS_{UN,T}$ series.

Jacobian	Subject	k1	k2	k3	Jacobian	Subject	k1	k2	k3
JVS_{ST}	s1	1.16	5.18	3.75	JAM_{ST}	s1	0.57	-1.13	-1.09
	s2	1.64	-0.89	0.27		s2	0.73	0.19	-0.36
	s3	-0.73	**1.15**	1.52		s3	0.33	-1.44	1.43
	s4	**7.55**	**5.40**	0.50		s4	0.62	0.00	0.07
	s5	-1.19	**9.36**	-5.38		s5	0.62	2.72	**13.18**
	s6	**2.52**	-0.74	9.48		s6	0.68	0.81	-5.98
	s7	**1.99**	-0.57	-1.56		s7	0.57	0.49	-0.96
	s8	0.89	0.28	-0.89		s8	**-3.30**	0.10	**10.90**
	s9	**2.03**	2.30	1.01		s9	1.06	-0.35	0.13
	s10	0.27	**2.09**	0.49		s10	0.40	0.52	-0.15
JVS_{UN}	s1	2.71	**1.59**	1.46	JAM_{UN}	s1	1.10	-0.09	2.22
	s2	0.41	0.32	-0.64		s2	**2.36**	-1.66	-0.06
	s3	-0.27	**1.57**	2.16		s3	-0.34	1.13	1.42
	s4	1.69	1.35	-1.35		s4	0.34	-0.89	**-1.36**
	s5	**3.67**	0.50	**2.14**		s5	0.16	0.57	0.54
	s6	**7.99**	**-8.49**	-4.22		s6	2.71	-3.88	-1.51
	s7	-0.48	**6.29**	-2.13		s7	0.63	-0.47	0.29
	s8	**-0.98**	0.27	0.55		s8	**-0.68**	-0.06	**-5.94**
	s9	0.67	**1.21**	-1.29		s9	0.29	0.53	-0.68
	s10	-1.16	1.29	-0.84		s10	-0.33	**0.54**	-0.16
$JVS_{UN,T}$	s1	**1.85**	-3.16	-2.30	$AM_{UN,T}$	s1	0.93	**-4.56**	-1.19
	s2	**1.31**	**-1.41**	**3.17**		s2	**1.74**	-0.28	0.25
	s3	0.02	**1.19**	0.41		s3	-0.15	**0.92**	1.30
	s4	**2.63**	-0.37	2.00		s4	0.21	0.63	**-1.38**
	s5	-0.13	0.13	**4.67**		s5	0.91	-0.15	1.27
	s6	**2.67**	-0.55	2.75		s6	2.97	0.40	**-6.03**
	s7	-4.63	2.13	1.53		s7	0.12	0.38	-0.24
	s8	0.04	**0.95**	0.04		s8	**-1.17**	**0.83**	**1.89**
	s9	0.01	**2.11**	-0.67		s9	-0.54	**1.02**	-0.54
	s10	**4.36**	1.90	**1.56**		s10	-0.17	-0.04	-0.44

Table 10: Regression coefficients between ΔMMMs and ΔCOP. The coefficients were computed for each subject based on each of the two tasks, Voluntary sway (JVS) and arm extension movement (JAM) under three stability conditions; stable: ST, unstable: UN and unstable with light touch: UN,T (numbers in bold are significant predictors of ΔCOP).

2. Results of UCM analysis

UCM analysis was performed on data from series 11-13 from Experiment 2. In these series, subjects were asked to perform arm extension movements, the same task as one of those used to compute the Jacobian. The total variance in the M-mode space across repetitions was partitioned into two components, one of which was within the UCM and the other was orthogonal to the UCM. This was done using one of the Jacobians defined in the previous step. Three sets of UCM analysis were performed under the three stability conditions (ST, UN and UN, T).

The ratio of V_{UCM} to V_{ORT} was computed and Wilcoxon test was used to see if this ratio was significantly different from unity. A high ratio (significantly higher than unity) would indicate that the M-modes co-varied to stabilize a particular value of the COP shift. However, we found that none of the ratios except one (UCM analysis on AM_T series using Jacobian, J_{VSU}, $p = 0.02$) was significantly higher than unity ($p > 0.05$).

Comparison of M-modes between Experiment 1 and 2

Of the 10 subjects that participated in Experiment 2, four repeated the LR_{ST} series that they performed in the Experiment 1. This was done to compare the M-modes obtained in the two sessions for possible differences. There was an average of 0.75 mismatches between the modes at the two sessions. Tables 11A and 11B are results of PCA from the two experiments for the LR_{ST} series from a representative subject. The results show only minor qualitative differences. In the second table a clear co-contraction pattern at the hip is seen, whereas in the first table, the muscle RA has a loading slightly below the 0.5 cut-off and hence a hip-co-contraction pattern is not seen.

Muscle	Mode 1	Mode 2	Mode 3
TA	0.14	0.02	0.32
GM	**0.83**	0.29	0.36
SOL	**0.76**	0.35	0.42
VL	0.21	**-0.79**	0.37
RF	0.00	**-0.86**	0.37
BF	**0.62**	-0.04	-0.42
RA	0.30	-0.41	-0.41
ES	**0.65**	-0.32	**-0.54**

Table 11A: Results of PCA in a representative subject for the LR_{ST} series from Experiment 1. Loadings over 0.5 are shown in bold. Note that in this subject two modes show reciprocal patterns (mode 1: push back; mode 2: push forward) and the third mode has only one significantly loaded muscle (ES). Abbreviations of muscles are the same as in Table 7A.

Muscle	Mode 1	Mode 2	Mode 3
TA	0.45	-0.27	0.04
GM	**0.89**	0.02	0.16
SOL	**0.69**	0.20	-0.21
VL	0.20	0.03	**0.89**
RF	-0.01	0.13	**0.91**
BF	**0.67**	0.03	0.24
RA	-0.11	**0.86**	0.14
ES	0.16	**0.86**	0.03

Table 11B: Results of PCA in a representative subject for the LR_{ST} series from Experiment 2. Loadings over 0.5 are shown in bold. Note that in this subject two modes show reciprocal patterns (mode 1: push back; mode 3: push forward) and the third mode shows a co-contraction pattern (mode 2: hip co-contraction). Abbreviations of muscles are the same as in Table 7A.

Results of Friedman's test on different tasks in a stability condition

In order to verify our assumption that M-modes for the three tasks used in the experiment (LR, AM and VS) are the same, we ran a PCA on the series used to compute the Jacobian. As in the LR task described previously, 3 components were retained. The three PCs explained on average 73.7 % (± 2.3 %) of the total variance in the JAM and JVS tasks.

The M-modes were classified as reciprocal or co-contraction type and a Friedman's test was performed separately for each of the stability conditions (ST, UN and UN, T) using the number of times co-contraction occurred as the dependent variable; the factor TASK had three levels (LR, JAM and JVS). The results showed no significant differences among the three tasks in the number of times the co-contraction patterns occurred ($p > 0.3$).

We analyzed the mismatches of M-modes between the LR, VS and AM conditions to support the above analysis. On average the number of mismatches for the ST and UN conditions was only 0.73, which is well below the number of mismatches expected by chance (1.2). However, for the third stability condition, UN,T, even though the Friedman's test did not reveal any differences in the number of occurrences of co-contraction patterns, the number of mismatches was relatively high at 1.1.

Discussion

The main purpose of this study has been to examine the organization of M-modes and muscle synergies under different conditions of postural stability. We used PCA to identify M-modes in the different conditions in Experiment 1. In the second experiment, we used the framework of the UCM hypothesis to test the hypothesis that these M-modes co-varied to stabilize shifts of the COP.

We examined the effects of support instability, availability of a light touch as well as support in the form of grasp to a stable external support on the organization of muscles into M-modes and M-modes into synergies. We found two groups of M-modes: reciprocal and co-contraction patterns. Different combinations of these were used under different stability conditions for the load release task. While the reciprocal and co-contraction patterns were used equally often in stable and unstable conditions with no touch, as well as in the unstable condition with the light touch, the co-contraction patterns were more predominant in the grasp condition. Further, in the grasp condition, M-modes were found that united muscles across effectors, particularly across the hip and shoulder muscles.

UCM analysis on the M-modes did not reveal significant M-mode synergies. Possible reasons for this are discussed in the sub-section 'UCM analysis and multi-muscle synergies'.

The "Menu" of M-modes

In previous studies, we identified three M-modes of postural muscles, which were reproduced across different postural tasks and across subjects when the subjects stood on the stable surface (Chapters 4 and 5). In the present study, we manipulated the stability of the support surface, availability of additional sensory information in the form of a light touch, as well as availability of additional support in the form of grasp to a stable support. We found that subjects chose three M-modes from a set (a "menu") of five M-modes. Different combinations of these M-modes could be selected for a particular stability condition by different subjects. Based on this, we now propose a new scheme of control using M-modes, which is a modification of the scheme presented in Chapter 5 (see Figure 9). The new scheme is presented in Figure 19. The basic idea remains the same as before. That is, the controller is assumed to define magnitudes of three M-modes, resulting in changed levels of activation of postural muscles. However, unlike the scheme presented

earlier, where the three M-modes were fixed, in the present scheme, the controller chooses three M-modes from an available menu of five modes.

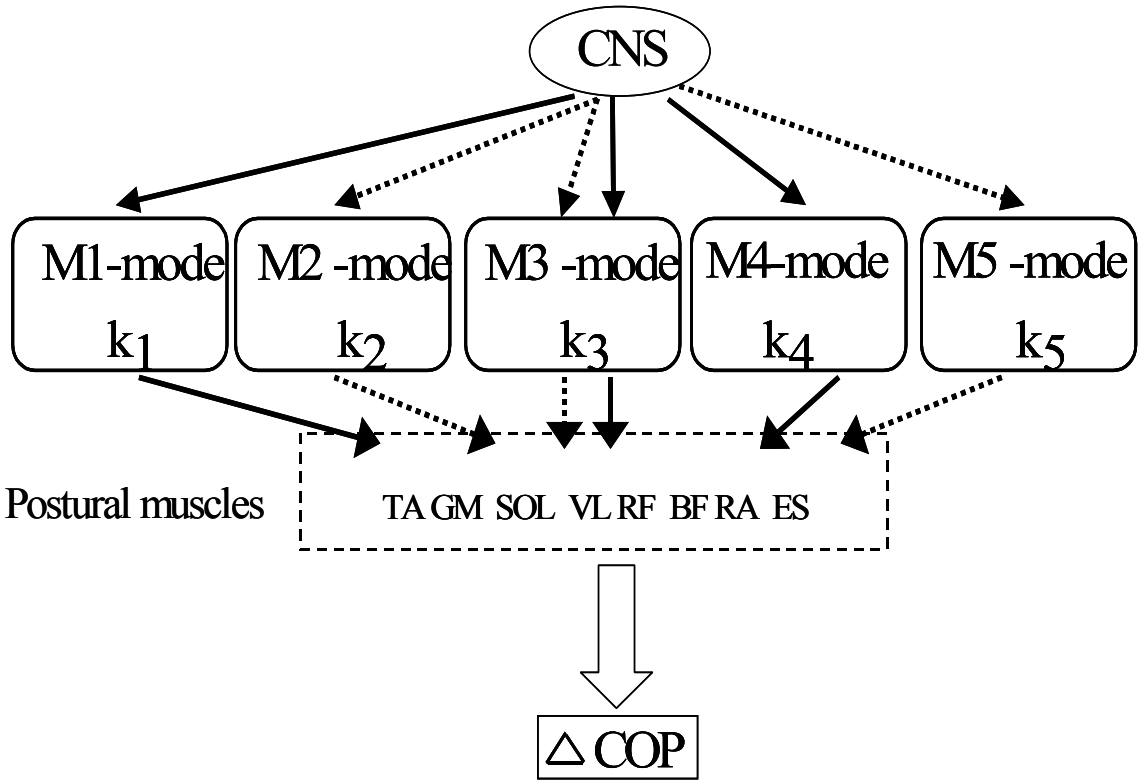

Figure 19: A scheme illustrating postural control using sets of M-modes. The controller chooses three M-modes from a menu of five available modes and defines the magnitudes of these M-modes, which results in changed levels of activation of all postural muscles leading to a particular magnitude of the COP shift.

Reciprocal and Co-contraction patterns

In the previous experiments (Chapters 4 & 5), we identified three M-modes that we referred to as push-back, push-forward and mixed modes, based on their effects on the COM of the subject. As described in the Results section as well as under the sub-section

'The "Menu" of M-modes' above, in this experiment we found five types of M-modes across subjects and stability conditions. Among these, there are two M-modes that showed reciprocal patterns of muscle activity, as all the muscles that loaded significantly on these modes are either dorsal muscles or ventral muscles across joints. On the other hand, co-contraction patterns of mode had antagonist muscles at the same joint load significantly on them. These patterns were not observed in purely stable support surface conditions of the previous experiments. However, in the present study, the co-contraction patterns occurred as frequently as the reciprocal patterns under all conditions except the grasp condition when the co-contraction patterns predominated (see Figure 18). Subjects showed co-contraction patterns at the hip, knee and ankle joints. In addition, co-contraction patterns were dominant in the arm as well, particularly at the shoulder and the wrist.

Co-contraction patterns of anticipatory postural adjustments and of postural reactions to perturbations have been described in earlier studies. In particular, persons with Down syndrome tend to show co-contraction APA patterns in conditions when persons without Down syndrome show reciprocal patterns (Aruin and Almeida 1997). Elderly and persons with neurological disorders have been described to display atypical co-contraction patterns of postural reactions to unexpected perturbations (Woollacott et al. 1988; Woollacott and Burtner 1996). Such findings have been interpreted as reflections of adaptive neural strategies to tasks that are perceived as potentially destabilizing and not fully predictable (cf. Latash and Anson 1996). In our earlier experiments, all series were performed during normal standing, without any instability, and we did not observe co-contraction patterns. In the current series, subjects started to show co-contraction patterns even during standing without instability. We interpret this as a consequence of a general increase in the difficulty of the tasks that involved perturbing actions while standing on the unstable board. Note that APAs during standing on an unstable board may themselves be sources of postural perturbations if the COP moves outside the area of support (Aruin et al. 1998). Because of the unavoidable postural sway, which increases during standing on an unstable board (Latash et al. 2003), the subjects could not use standard, optimal COP shifts, even in preparation to a standard, self-triggered unloading. Apparently, one method of preparing to a postural perturbation

without a major COP shift is “stiffening” the main postural joints by using co-contraction patterns.

The co-contraction patterns are joint specific and thus reminiscent of the ankle and hip strategies (Horak and Nashner 1986). However, pure ankle and hip strategies were described in response to support surface (platform) perturbations and corresponded to an increase in the activity in either the dorsal or ventral muscles depending on the direction of a perturbation, but rarely simultaneous activation of both. In contrast, the co-contraction patterns observed in this study involved simultaneous unidirectional changes in the activity of agonist-antagonist muscle pairs prior to a self-induced perturbation.

Modes across effectors

As mentioned in previous sections, subjects commonly showed co-contraction patterns at the hip, knee and ankle joints in the grasp condition. One of the questions that we posed in the introduction was: Would there be separate M-modes for leg/ trunk muscles and for the arm muscles? PCA on all the leg, trunk and arm muscles pooled together was performed and revealed co-contraction at the hip, knee, ankle, shoulder and wrist muscles. Commonly, the hip and shoulder muscles loaded together significantly on a mode, showing that M-modes could unite muscles across effectors. Reciprocal patterns were only seen at the elbow joint. Similar M-modes in the arm muscles were also seen when separate PCA on the arm muscles alone was preformed; namely co-contraction patterns at the shoulder and wrist and a reciprocal patterns at the elbow.

These patterns suggest that there could be two possible ways to shift the COP in the grasp condition. First, it is possible that even though most of the agonist-antagonist pairs show co-contraction patterns, the two muscle groups may not be activated to the same extent. If one of the groups were more active than the other, this could lead to a shift of the COP in that direction. Another possibility is that while all the other joints are stiffened by co-contraction of muscles, the reciprocal activity at the elbow joint is primarily responsible for shifts of the COP. This latter possibility is corroborated by the

fact that co-contraction patterns were seen significantly more frequently in the grasp condition than during standing on the unstable board without any support or with the touch.

Postural muscle activity: effects of touch/ grasp

In the study described in Chapter 6, we found a decrease in postural sway following finger touch (as well as touch to the head and neck). The reduction in sway was due to an interaction between two sources of haptic sensory signals associated with touch, one related to providing a fixed reference point in space, and the other related to transient force changes at the point of contact induced by actual sway.

These findings taken together with the results of the current study, support the general idea that with the addition of touch, the reference position of posture is more accurately available than without touch. This leads to a decrease in the error of estimation of the reference position and a larger 'safe zone' is available around this reference position within which the center of mass can move (Slijper 2001).

In the grasp condition, we found co-contraction patterns predominant at all the joints of the leg, trunk and arm except for the elbow joint. These results support the findings of Slijper and Latash (Slijper and Latash 2000), who performed an analysis of APAs across muscles for an arm flexion task based on the equilibrium point hypothesis. They used the idea of the R and C indices to reflect changes in the reciprocal and co-contraction (r and c) central commands. They found that the C-index showed a significant modulation in the leg and trunk muscle pairs with the addition of grasp, while the R-index remained relatively invariant. On the other hand, the arm muscles showed an increase in the C-index at the wrist and elbow.

UCM analysis and multi-muscle synergies

In our previous experiment (Chapter 5), we demonstrated that there are multi-M-mode synergies that selectively stabilize shifts of the center of pressure when the support surface is stable. One of the aims of the present study was to verify if there are such multi-M-mode synergies in different conditions of postural stability and, if there are, whether the same synergies are used across conditions. Unlike the earlier experiment, in this study we failed to find the presence of significant M-mode synergies. Let us discuss possible causes of this outcome.

One possible reason for this is that there are no pre-existent muscle synergies that are adequate to form APAs in conditions of instability. In the previous experiment, tasks were performed under stable standing conditions. Experience in performing postural tasks under stable conditions in daily life can be expected to lead to the development of muscle synergies that stabilize shifts of the COP. However, most daily activities do not involve balancing on a board with a reduced support area as imposed in the current experiment. Lack of experience in performing tasks under unstable conditions may result in poorly coordinated activity of postural muscles in these tasks. This could be a reason for our failure to detect multi-M-mode synergies. It is not possible to verify this hypothesis within this experiment, but a future study could be planned where subjects can be trained in tasks performed under unstable conditions. Post-training, if subjects show significant synergies, this hypothesis would be supported.

There could however be other reasons that are methodological, that could at least partly explain the failure to find synergies in this study. Possible sources of error in computations at each step of the UCM analysis are feasible. First, we made an assumption that M-modes are relatively stable based on results from previous experiments (Chapters 4 and 5). We attempted to verify this assumption by repeating one of the conditions (LR_{ST}) from Experiment 1in the second experiment. While the qualitative differences appeared to be minor, there were quantitative differences, which could have influenced the results. In other words, subjects could have used somewhat differently organized M-modes on the two days when the two Experiments were run.

A second possible source of error is that the task used to identify the M-modes, namely load release, has a different initial operating point (background EMG activity) from the tasks used to compute the Jacobian as well as perform the UCM analysis, that is, arm movements and voluntary sway. In the case of the load release task, there is a high background activity in the ventral muscles while holding the load at the back and a relatively low background activity in the dorsal muscles. On the other hand, both the arm movement and voluntary sway tasks started from essentially a quiet stance posture where the background activity in the dorsal muscles is expected to be slightly higher than that in the ventral muscles. Different tasks in the three different steps of UCM analysis were chosen to verify robustness of the method. However, this could also be a drawback because of the different operating points in the two sets of tasks. Note that all our analyses are run under an assumption of linear relations between changes in the M-mode magnitudes and COP shifts. This may be true if all tasks are performed starting from similar operating points (in the muscle space). Changes in the operating point, however, could violate the assumption of linearity and lead to the negative outcome.

We attempted to verify this by computing the M-modes for the tasks used to compute the Jacobian in Step 2, that is the arm movement and voluntary sway tasks. Note that using PCA to compute M-modes for these tasks has less power than that used in the load release task, because of the fewer number of trials (twenty). However, the fact that the three PCs retained explained on average 73.7% of the total variance, suggests that the results are reliable based on results from the LR tasks where 68.5 % of the total variance was explained by the three PCs. We performed a Friedman's test to compare the number of times the co-contraction pattern appeared in these three tasks for each of the stability conditions (ST, UN and UN,T). The results showed no significant differences across the three tasks. This suggests that even though the operating points were different for these tasks, the M-modes were similar. However, the statistical power of this test is limited.

A third possible reason for the lack of multi-M-mode synergies is that the Jacobians computed were inaccurate. The Jacobians explained on average only 44.6 % (± 7.1 %) of the variance in ΔCOP. The Jacobian from the three JAM series accounted for even less, that is, 31.3 % (± 5.1 %) of the variance in ΔCOP. In the previous experiment, when we found significant synergies, the percentage of variance explained was above

80%. This suggests that there was a weak relation between the M-modes and ΔCOP. This weak relation may be due to either of the reasons explored in the preceding paragraphs, namely inaccurate M-modes or different operating points of the tasks used to compute the M-modes and the Jacobians.

In conclusion, we would like to emphasize a potentially important difference between this series of studies and earlier applications of the UCM-method to analyze kinematic and kinetic variables (reviewed in Latash et al. 2002). Earlier studies focused on co-variations in control variables that were expected to preserve a particular value of a performance variable, for example covariations of joint angles to preserve a position of the endpoint in space (cf. Scholz et al. 2001). Our current analysis looks at *changes* in control variables (M-modes) that preserve a *change* in a performance variable (ΔCOP). This is a non-trivial extension of the method since COP shifts can generally speaking begin from somewhat different initial positions, although we tried to make sure that initial postures of our subjects were similar across trials.

The drawbacks of this study need to be overcome in future before one can answer question 4 posed in the Introduction. One needs to make sure that adequate M-modes and Jacobians are used, keeping in mind the operating points of the tasks. A separate study on learning of tasks in unstable stability conditions could be performed to study the development of novel synergies.

Chapter 8

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; Holdefer and Miller 2002; 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 define the term synergy operationally and to present an approach to identify and analyze muscle synergies.

Following the traditions of Gelfand and Tsetlin (Gelfand and Tsetlin 1966), we defined synergies as task-specific groups of control variables, which stabilize particular performance variables. Next, we presented a computational method of identifying and analyzing muscle synergies, based on the framework of the uncontrolled manifold or UCM hypothesis (Scholz and Schoner 1999; reviewed in Latash et al. 2002b). UCM analysis was performed on postural muscle EMG signals during different types of postural tasks.

In Chapters 4 and 5, we presented the steps in the UCM analysis and tested the method on subjects while they performed various postural tasks during standing on a stable support surface. In Chapter 6, we studied the effects of light touch on postural sway. In Chapter 7, we used the method developed in Chapters 4 and 5 to study the effects of different types of postural instability on the organization of muscle synergies.

The UCM approach and muscle synergies

The UCM approach provides a toolbox to analyze synergies. The first step in using this approach is to identify independent control variables (CVs), which we believe the controller manipulates. The second step is to relate small changes in these control variables to shifts in an important performance variable that is hypothesized to be stabilized by the system. Finally, the UCM analysis is performed on multiple repetitions of a task in the space of the CVs.

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; Domkin et al. 2002; Latash et al. 2002a), the first two steps were relatively straightforward. However, in the case of analysis of muscle synergies, these two steps were a challenge. First, we believe that muscles are not independently controlled but are united in groups (Hughlings Jackson 1889), so we had to develop a method to identify control variables (M-modes) that are used to scale in parallel the activity of muscles within such groups. This was done using PCA (Krishnamoorthy et al. in press-a; Krishnamoorthy et al. in press-b, also Chapters 4 and 5). Second, the relationship between changes in the magnitudes of M-modes and shifts of the COP had to be computed. Note that these two variables have different units of measurement (microvolts and millimeters). This was done using multiple regression analysis (Krishnamoorthy et al. in press-b, also Chapter 5).

In Chapter 4, we have shown that it is possible to identify M-modes using PCA. Further, these M-modes were similar across subjects for a variety of postural tasks under stable conditions. These tasks included explicit as well as implicit shifts of the COP produced by APAs. The tasks also varied in the direction as well as magnitude of COP shift. But across all these conditions the compositions of the M-modes were similar.

In Chapter 5, UCM analysis was performed in the M-mode space for a variety of postural tasks that involved APAs and explicit voluntary COP shifts (voluntary sway). We have demonstrated that the M-modes co-varied to stabilize a particular value of a

COP shift. In other words, the existence of M-mode synergies has been demonstrated. Further, there were different M-mode synergies for COP shifts forward and backward.

Effects of various stability conditions of postural sway and muscle synergies

In Chapters 6 and 7 we looked at the effects of mechanical and sensory manipulations on postural sway and postural muscle activity. In Chapter 6, we looked at the effects of sensory manipulations, namely different types of touch on postural sway. We showed that postural sway is reduced to the same extent by the availability of touch to the finger, head and neck. The reduction in sway was due to an interaction between two sources of haptic sensory signals associated with touch, one related to providing a fixed reference point in space, and the other related to transient force changes at the point of contact induced by actual sway.

In Chapter 7, we used the UCM approach to study muscle activity under conditions of support surface instability as well as conditions where additional sensory/ mechanical information was available in the form of a light touch or grasp to a stable handle. While we were unable to find M-mode synergies that stabilized a particular value of the COP under the different stability conditions, we found that there was a “menu” of five M-modes from which the system chooses three modes for a given task.

Scheme of control

In Chapter 7, we present a scheme of control using M-modes (Figure 19, Chapter 7). The basic idea of this scheme is that there is a “menu” of five possible M-modes from

which the controller chooses three for a given postural task. The number of possible M-modes (five) is smaller than the total number of postural muscles recorded (eight in Chapter 7 and eleven in Chapters 4 and 5). The controller defines the magnitudes of the three M-modes by changing the gains at each of the modes. This results in changed levels of activation of the postural muscles, which determines the magnitude and direction of shift of the COP.

It has been suggested that changes in the ankle plantar flexor activity are primarily responsible for modification of the stiffness at the ankle joint (Winter et al. 1998), which is thought to be responsible for shifts of the COP in quiet stance. We performed UCM analysis on the ankle muscles (Chapter 5) and found no significant ankle M-mode synergies that would stabilize the COP, indicating that shifts of the COP in postural tasks are the result of the combined action of a number of postural muscles spanning all major leg/trunk joints.

Direction for future research

The studies performed as part of this dissertation have left a few unanswered questions and also raised several new and interesting questions, which could be answered by future experiments. Some of these are addressed below.

A few unanswered questions remained in the last study in this dissertation, which were enumerated in Chapter 7. It was not clear if the lack of M-mode synergies in that study were due to methodological problems or if there are actually no pre-existing M-mode synergies for the conditions studied. Additionally, it is possible that subjects use different combinations of M-modes (different sets of three from the menu of five) in different trials/ conditions. One needs to keep these issues in mind while interpreting the results of the study. Some of these questions can be answered by performing two sets of experiments to address two separate issues.

First, it is important to address all the methodological shortcomings of the study presented in Chapter 7. In that study, we looked at four different stability conditions in all. As a result, we were limited by the number of trials and types of tasks that could be used to perform analysis. Some of the tasks used had different operating points (background EMG activity). In a new study, it might be prudent to study just the unstable condition alone with no additional touch or grasp (these conditions could be addressed in separate experiments). This would allow us to increase the number of trials per step of analysis and use tasks where the operating point is the same for the different steps of analysis. Secondly, all data for different steps of analysis should be collected in a single session.

Next, we could address separately the question whether there are pre-existing M-mode synergies for the unstable condition, since this is not a common situation in everyday life. We could design a learning study where subjects are taught to perform postural tasks on an unstable board. UCM analysis could be performed before and after they learn the tasks. If there are no M-mode synergies pre-learning, but synergies do appear post-learning, it would support the idea that the failure to find synergies in Chapter 7, may be primarily because they did not exist. There could also be changes in the M-modes themselves or in the Jacobians.

The UCM approach could be a very good tool to track the development of new synergies and could potentially have a number of applications to study learning. This approach could also be used to study the evolution of synergies over the course of lifetime. Specifically, synergies in children in the process of their natural development and in elderly in the process of their natural deterioration could be examined.

One of the main advantages of the UCM approach is that it allows us to simultaneously test a number of hypotheses. In this dissertation, we studied only one performance variable, namely COP coordinate. There are other potentially important variables in the control of posture such as position of the center of mass of the body (cf. Gollhofer et al. 1989; Vernazza et al. 1996) or position of the head (cf. Pozzo et al. 1990; Simoneau et al. 1992; Ledebt et al. 1995). Control hypotheses related to selective stabilization of these variables could be studied in future experiments.

Another interesting application of the methods developed in this dissertation, would be to study abnormal synergies in patients suffering from neurological problems, such as stroke or cerebral palsy. These populations are known to have atypical movement and postural patterns and poor muscle coordination. The UCM approach could be used to address the source of these apparent problems. Some interesting questions that one could address are: 1) Do these patients form different control variables (M-modes) from healthy controls? 2) Are the abnormal synergies observed in these patients due to altered relationships between control variables and performance variables (a different Jacobian from controls)? or 3). Are there differences in the patterns of co-variation among control variables?

In this dissertation, all analyses were performed over a small time interval (100 ms) before the initiation of action. In other words, a single snapshot over the realization of a task was taken as representative of the hypothetical M-mode synergies. One more direction this research could take in the future is to apply the UCM method to analyze patterns of M-mode co-variation during the time course of a postural or movement task.

In our experiments, we studied various postural tasks in standing persons. However, M-modes and their co-variations could be studied in a number of other postural tasks. For example, postural adjustments within a limb to a self-performed loading/ unloading (Dufosse et al. 1985; Aruin and Latash 1995a; Shiratori and Latash 2000) could be studied. One could also use other motor tasks, such as isometric force production by a limb.

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