AFTER-EFFECTS OF STANCE OR STEPPING ON AN INCLINED SURFACE: ADAPTIVE PLASTICITY IN THE CENTRAL ESTIMATE OF POSTURAL VERTICAL

by

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ABSTRACT

Postural control is a complex sensorimotor task that involves establishing a reference, or a set point, for postural orientation and regulating equilibrium about this set point. How the nervous system determines a preferred postural orientation and adapts the postural set point when environmental conditions change is only partially understood. This dissertation investigated how changes in surface inclination affected postural orientation in healthy human subjects. A previously unreported leaning after-effect that follows a period of stance on an inclined surface is investigated and characterized and the underlying mechanism for the post-incline lean is explored. Inclination of the support surface alters the relative relationship between the geometry of the support surface and the direction of gravity, enabling investigation of the relative contributions of surface-related and gravity-related sensory information to postural orientation.

The first study investigated how direction (toes-up, toes-down, lateral), amplitude (2.5-10°), and duration (0.5-5 min) of surface inclination affect post-incline leaning. Postural alignment (center of mass (CoM), body segment and joint angles), center of pressure (CoP), and trunk and leg EMG activity were measured before, during, and after subjects stood on an inclined surface. After standing on an inclined surface, blindfolded subjects leaned with a direction and magnitude that maintained the relative alignment of their trunks to the surface as if they still stood on the incline. Leaning persisted for up to 4 minutes, with exponential decay toward upright. The amplitude of leaning in the trunk and head increased linearly as the amplitude of surface inclination increased. Ankle angle, CoP, CoM, and tonic EMG levels showed less systematic effects, suggesting that

the mechanism responsible for the lean acts mainly on orientation of global, kinematic variables.

The second study showed that adaptive after-effects in ankle muscle spindles or segmental reflexes are not the main cause of post-incline leaning. When the legs were prevented from leaning in the post-incline period, the trunk still leaned. When subjects stepped-in-place while on the incline so that ankle muscle length and force were not held constant during adaptation to the incline, the post-incline lean still occurred.

Not all healthy subjects showed a postural lean after standing on an incline. The third study reports a continuum of post-incline postural effects in 51 healthy subjects. At one extreme, subjects leaned forward after they stood on an inclined surface, with an average trunk lean near 5°. The lean persisted from a few seconds for up to 4 minutes. At the other extreme, subjects did not lean in the post-incline period, but instead, stayed aligned near upright with respect to gravity. Subjects were highly consistent in their post-incline postural behaviors upon repeated testing over days to months and across different directions of surface inclination. The results of this study suggest that healthy subjects differ in their preferential weighting or dependence on different frames of reference frame for their postural orientation. Leaners appear to depend more heavily on kinematic information related to support surface geometry, while non-leaners depend more on kinetic information related to gravity and forces.

Chapter 1: Introduction

Healthy humans have little difficulty adapting their posture and locomotion to a wide variety of support surface configurations, such as standing on a hill or walking down a theatre aisle. The seemingly simple task of adjusting to changes in surface conditions is a complex postural control task for the nervous system. The support surface provides the point of interface between the body and the physical world. The support surface is not only the physical platform against which the body can exert force to change or to correct postural alignment, but the support surface also provides a reference frame that the nervous system can use to determine the current state of the body's orientation (Gurfinkel et al. 1995a; Ivanenko et al. 1997, 1999; Mergner et al. 1998, 2002b; Riccio and Stoffregen 1988; Stoffregen and Riccio 1988). Postural mechanisms involved in adapting to changes in surface configuration are not fully understood. This dissertation is aimed at understanding how the control of postural orientation adapts to changes in support surface inclination.

During stance on a horizontal support surface with eyes closed, posture is typically oriented in parallel with gravity-vertical and perpendicular to the surface. Under this condition, it is difficult to determine whether postural orientation is being controlled with respect to gravity, the surface, or both. When the surface is inclined, the perpendicular relationship between the surface and gravitational vertical is altered, allowing investigation of relative contributions of surface- and gravity-related sensory information for postural orientation. The studies reported in Chapters 2-4 investigated how blindfolded subjects adapt their postural orientation to changes in surface inclination in order to examine how support surface geometry is used as a reference for estimating the direction of upright, or vertical, for postural orientation. A leaning after-effect occurred when the support surface returned from an inclined to a horizontal position. Chapter 4 reports that individual healthy subjects were consistent in their post-incline postural responses when tested days to months apart, but that subjects varied from one another in terms of whether or not the post-incline leaning occurred and in the magnitude and duration of the lean. In subjects who leaned, postural alignment returned from a leaned to a near upright posture exponentially, with a decay time constant greater than 20 seconds (range 20- 69 s) in 27 out of 51 subjects. Thus, approximately half of the subjects leaned for 1 to 4 minutes.

The post-incline lean maintained the relative body-to-surface alignment as if subjects were still standing on the inclined surface. This suggests that the nervous system had learned a new estimate of the direction of postural upright based on the experience of standing on the incline and only gradually recalibrated this estimate for congruence between gravity- and surface-vertical for postural orientation. The post-incline lean effect has not been previously reported in the literature, but resembles other examples of gradual sensorimotor adaptation when the environmental conditions suddenly change. The three studies that comprise this dissertation: 1) characterized how different features of the incline condition affected the direction, magnitude, and duration of the post-incline lean in order to determine what factors contribute to the post-incline lean and which postural orientation variables are adaptively modified by the changes in surface inclination; 2) investigated whether the post-incline lean could be explained by a peripheral or segmental mechanism affecting ankle muscle activity; and 3) determined the frequency and consistency of the post-incline lean to gain insight into differences in preferred postural orientation strategies among healthy individuals .

Postural Orientation

The task of postural orientation involves two components: orientation of body segments relative to one another and orientation of the whole body with respect to the environment (Horak and Macpherson 1996; Massion et al. 1994, 1998). Although the necessity of maintaining equilibrium imposes constraints on the postural orientation system, the number of possible postural configurations with which one can maintain balance remains large. Despite a wide range of possible postural configurations, subjects tend to adopt habitual postures that are characteristic of the individual and are slow to change (Gurfinkel et al. 1995a; Lestienne and Gurfinkel 1988). This suggests that the postural orientation system has determined an optimal, preferred posture. Lestienne and Gurfinkel (1988) have suggested that the central control of posture includes two systems. The first system is a 'conservative' system, which sets or establishes the reference posture, or the set point, that the nervous system tries to maintain, and which operates on a relatively slow time scale. The second system is a fast acting 'operative' system, which acts to stabilize the body and return the body to the established set point when fast transient changes occur. This postural set point established by the conservative system can be updated, or adapted, when conditions change, such as when astronauts are exposed to microgravity environments for prolonged periods (Baroni et al. 1999; Clement et al. 1984; Lestienne and Gurfinkel 1988, Massion et al. 1997). The studies presented in

Chapters 2, 3, and 4 show that standing on an inclined surface affects the set point for postural upright with respect to the support surface and demonstrates slow, exponential return of the set point to the habitual posture across minutes when the surface returns to the horizontal condition.

While evidence suggests that postural orientation and equilibrium may be separately regulated, the two tasks mutually constrain one another. For example, when the postural orientation set point has been altered by galvanic vestibular stimulation, equilibrium responses to surface translations are altered in magnitude and latency to return the body to the new postural orientation (Hlavacka et al. 1999; Horak and Hlavacka 2002). Whatever alignment the postural orientation system is trying to achieve, equilibrium requirements must be satisfied if the postural alignment is to be successfully maintained. When the surface is inclined, both postural orientation and equilibrium are affected and must adjust to the altered conditions. This investigation will focus on how *postural orientation* is regulated with respect to the surface and gravity when the surface is inclined, taking into account that there is a limit to the degree that the body can stay aligned perpendicular to the inclined surface and continue to remain balanced.

Control of human upright standing posture is a complex sensorimotor task that involves multisensory integration and regulation of a large number of muscles to control alignment of a multi-segmented body with a high center of mass over a small base of support (Horak and Macpherson 1996; Mergner et al. 1998, 2002b; Peterka 2002; Winter 1995). The nervous system must solve a number of problems to achieve upright postural alignment. First, the nervous system must solve the problem of coordination of the multi-segmented body moving in a gravitational environment, which involves controlling a large number of variables such as muscle forces and motor neuron recruitment, while taking into account the physical forces that act on the body as it moves. Second, the nervous system needs sensory information to estimate the current state of body segments with respect to the environment and needs to integrate multimodal sensory information to solve the sensory ambiguity of distinguishing between movement of the body in the world versus movement of the world around the body. Third, the nervous system needs a reference frame, or a stable coordinate system, against which to judge the relative movement of body. Lastly, the nervous system needs a way to flexibly alter how control is organized in order to successfully and optimally adapt to altered environmental conditions, task goals, and individual changes such as growth, fatigue, disease and learning. A change in surface inclination affects the postural dynamics that must be controlled and alters the meaning of somatosensory information regarding body orientation with respect to the support surface.

Coordination of a multi-segmented body for postural orientation

To achieve upright, stable stance, the nervous system must solve the problem of controlling a multi-segmented body in the physical environment that involves counteracting and even exploiting gravitational and interactive forces (Kuo and Zajak, 1993a, 1993b). When muscular forces are applied to correct alignment of body segments, the movement generated depends on a number of factors including the initial muscle length, the relative position of the body segments to one another as well as to the line of gravitational forces, and reactive forces exerted against the support surface. Thus, the nervous system must take into account potentially destabilizing interactive and gravitational forces that will occur throughout the kinematic chain as the motion occurs. Forces generated against the support surface ultimately determine the displacement and the equilibrium of the center of mass and are the means by which changes in postural orientation are achieved (Macpherson 1988, 1994a, 1994b). Support surface inclination alters the biomechanical constraints, and thus the postural dynamics, of the postural orientation task. The way in which forces are generated and coordinated must be modified in order to keep the same body orientation relative to gravity-vertical as when standing on an inclined surface. Limited studies exist of human postural orientation on a statically inclined surface. A recent study showed that humans standing on a toes-up inclined surface with eyes open adopt similar head and trunk in space alignment (near gravity-vertical) as when standing on a horizontal surface (Leroux et al. 2002). Studies of cats on inclined surfaces have shown that the legs stay oriented near gravity-vertical and the trunk stays parallel to the support surface (Lacquaniti et al. 1984, 1990). When vision is not available and the surface is rotated very slowly (0.04 °/s) to only 1° of surface tilt, a quasi-static condition, human subjects stay aligned to the surface rather than to gravity, showing that postural orientation is not always organized to stay upright relative to gravity, but that it may be also orientated with respect to the support surface (Gurfinkel et al. 1995a). None of the studies of stance on an inclined surface or very slowly rotating surface have reported how postural alignment is affected when returning to stance on a horizontal surface (after-effects). Chapters 2, 3, and 4 investigate how postural orientation is affected both during and after a period of stance on an incline surface.

To maintain a particular postural alignment, the nervous system must control several linked body segments through timely, organized activation of a large number of muscles and an even larger number of motor neurons, upon which sensory inputs converge. This problem has been referred to as the 'degrees of freedom problem' by Bernstein, who has suggested that the nervous system must have a way to simplify control of movement and may do this by regulating a select, small number of high level, global variables (Bernstein 1967; Turvey et al. 1992). An important question in the field of postural control research is determining which postural variables are the main controlled variables (Horak and Macpherson 1996; Lacquaniti and Maioli 1994; Massion et al. 1994, 1997; Macpherson 1988, 1994a; Nashner and McCollum 1985). Two variables that have been suggested to be main posture control variables are trunk alignment (Baroni et al. 1999; Fung and Macpherson 1995; Gurfinkel et al. 1981, 1995a) and the projection of the body's center of mass (CoM) within the support base (Gurfinkel et al. 1992; Horak et al. 1986; Massion et al. 1994, 1995). Chapter 2 investigates which postural variables undergo systematic adaptive change when the direction and amplitude of support surface inclination are varied.

Sensory contributions to postural orientation

Control of postural orientation is achieved through multisensory integration, including contributions from somatosensory, visual, vestibular, and graviceptor systems (Horak and Macpherson 1996; Mergner et al. 1998, 2003). How different sources of sensory information are integrated to solve postural orientation and equilibrium tasks is not completely understood and is an important, ongoing area of posture control research

(Mergner et al. 1998, 2002a, 2002b, 2003; Peterka 2002; Oie et al. 2002; van der Kooij 1999).

The somatosensory system includes several different types of sensory receptors, each of which encodes unique information about either movement or about haptic, or touch contact with the environment. Muscle spindles, which detect stretch and stretch velocity of muscles, are important in the perception and in the regulation of body orientation that is used to control postural orientation (Eklund 1972; Gurfinkel and Levik 1991; Roll et al. 1989b). Tendon vibration preferentially stimulates muscle spindles (Burke et al. 1976; Roll et al. 1982, 1989a). Subjects lean in a direction-specific manner when postural muscles are vibrated, including even eye muscles, suggesting that muscle spindle information contributes to a central representation of the whole body, kinematic alignment in space (Eklund 1972; Hlavacka et al. 1995; Quoniam et al. 1990; Roll et al. 1989b, 1991; Wierzbicka et al. 1998). If the hand is in light contact with a stable object in the environment, then cutaneous mechanoreceptors in the hand can also contribute information about kinematic parameters of body orientation. Slow movement of a lightly touched object causes the body to sway in a way that keeps the body aligned to the object (Jeka et al. 1997, 1998). In addition, light fingertip contact with a stable object reduces postural sway in subjects with distal peripheral neuropathy (Dickstein et al. 2001), in subjects with bilateral vestibular loss (Creath et al. 2002, Lackner et al. 1999), and even in healthy subjects with eyes closed (Holden et al. 1994).

Information about load and forces acting on the body are important for providing the nervous system with information about the projection of the CoM relative to the support base (Dietz et al. 1992, 1998; Massion 1994). The importance of load information for postural control has been shown via underwater experiments, which reduce the gravity forces acting on the muscles due to buoyancy (Horstmann and Dietz 1990), and via experiments that reduce or increase load on the body (Dietz et al. 1992). Load-related information has been shown to affect the amplitude of postural responses to perturbation (Dietz et al. 1992; Horstmann and Dietz 1990). Golgi tendon organs provide information about load or tension and could be one contributor to how the nervous system determines the distribution of load on the body (Dietz et al. 1992; Duysens et al. 2000). Sensory receptors underneath the feet are also believed to provide graviceptive, or gravity-related, information about the projection of the whole body CoM within the support base. The location of the CoP, derived from the integration of somatosensory receptor systems under the foot, could provide information for orientation of the whole body CoM as long as the movements are slow and body configuration is not drastically altered. Vibration of regions of the foot sole has been shown to elicit directionally-specific body leans (Kavounoudias et al. 1998, 1999, 2001), supporting the idea that foot-sole information is important for postural orientation. Anesthetizing the foot by an ischemic cuff at the ankle causes instability and decreases the distance of voluntary lean (Hayashi et al. 1988). Further evidence that pressure forces under the foot may be important for controlling postural orientation is based on the finding that the direction of lean induced by ankle tendon vibration depends on whether the current location of the CoM projection on the support base is forward or backward of the habitual CoM projection location (Gurfinkel et al. 1992). An additional source of sensory information about body orientation with respect to gravity is the truncal graviceptive system, related to distribution of fluids in the body and kidney (Mittelstaedt 1996, 1998, 1999).

The vestibular system provides the nervous system with information about head alignment and acceleration with respect to gravity. When combined with neck and trunk somatosensory information, vestibular information can provide the nervous system with information about trunk orientation (Mergner et al. 1998, 2003). Galvanic vestibular stimulation causes a whole body lean that is dependent on the position of the head relative to the trunk (Hlavacka et al. 1985, 1995; Lund and Broberg 1983; Nashner and Wolfson 1974), suggesting vestibular information provides the nervous system with information about alignment of the whole body relative to the gravity-vertical. Otoliths, which are sensitive to head static tilt and head linear acceleration, might be expected to be particularly important for determining how the body is aligned with respect to gravity forces. However, subjects make large errors in postural vertical when underwater, a condition in which otoliths can still receive gravity information, but somatosensory feedback is altered by the buoyant forces acting on the body (Nelson 1968; Massion et al. 1995). Further, bilateral vestibular loss subjects can align their bodies to gravity vertical as well as healthy subjects (Bringoux et al. 2002), suggesting that somatosensory information is more important than vestibular information for determining postural vertical. Vestibular information appears to be particularly important for postural control when support surface conditions change, suggesting it is important for interpreting somatosensory information related to the relationship between the body and the support surface (Creath et al. 2002; Maurer et al. 2000; Mergner and Rosenmeier 1998). When the support surface is solid, horizontal, and large enough, well-compensated subjects with profound bilateral vestibular loss stand with postural alignment and stability that cannot be distinguished from healthy subjects (Black et al. 1983; Nashner et al. 1982), but when the support surface is tilting (Allum et al. 1985, Creath et al. 2002; Maurer et al. 2000), compliant (Black et al. 1983; Nashner et al. 1982), or inclined (Kluzik et al. 2002) these subjects are more unstable, sometimes to the point of loss of balance.

The visual surround also influences postural orientation. Slow motion of the visual surround causes leaning in the direction of visual flow (Bles and deWit 1976; Dichgans et al. 1972; Lee and Lishman 1975; Lestienne et al. 1977; Reason et al. 1981; van Asten et al. 1988). Sinusoidal motion of the visual surround causes postural sway that tracks the movement of the visual surround (Dijkstra et al. 1994; Oie et al. 2002; Peterka and Benolken 1995). Eye closure has an effect on postural stability in many, but not all, individuals (Chiari et al. 2000; Collins and DeLuca 1995; Lacour et al. 1997).

The problems of sensor ambiguity and sensory redundancy

No single sensory system, alone, can determine whether the body is moving with respect to the world or whether the world is moving with respect to the body. For example, when standing upright, if the ankle angle dorsiflexes, ankle muscle spindle information alone cannot be used to distinguish between forward lean of the body and inclination of the support surface with the body remaining upright. If ankle joint information is combined with otolith or visual information about head tilt, then the ambiguity can be resolved and a determination of body versus support surface movement can be made. The availability of varied sources of information about different aspects of how the body segments are oriented with respect to the environment and to one another enables the nervous system to solve the sensory ambiguity problem and to determine the direction of postural upright.

How sensory information is integrated for postural orientation is only partially understood. When subjects stand on a stable, horizontal, surface with eyes open, they could be relying on any one or more of the different sensory systems for establishing the set point for and controlling postural orientation. While the different sensory systems may appear to be redundant under quiet stance conditions, each sensory system provides unique and important information to the postural control system and each system has a different ideal frequency operating range (Mergner and Rosenmeier 1998). Which sensory system is preferentially relied upon has been shown to depend on environmental conditions (Fitzpatrick et al. 1994a; Ivanenko et al. 1999; Oie et al. 2002; Peterka 2002; Welgampola and Colebatch 2001). A recent model of posture control proposed by Mergner and colleagues suggests that when the support surface is stable, the nervous system relies predominantly on proprioceptive information about the relative alignment of the body to the support surface (Mergner et al. 1998, 2002b). This hypothesis is supported by evidence showing that the proprioceptive threshold for body sway is lower than other sensory systems (Teasdale et al. 1999) and that proprioceptive information alone is sufficient to stabilize the body in upright stance (Black et al. 1983; Nashner et al. 1982; Fitzpatrick et al. 1994b; Macpherson and Inglis 1993). Mergner's model further suggests that vestibular information becomes critical when the surface tilts relative to gravity and experimental evidence supports the idea that sensory weighting shifts from somatosensory to vestibular information when the surface is tilting (Creath et al. 2002; Maurer et al. 2000; Mergner et al. 1998, 2002b). Weighting of vestibular information also increases when somatosensory information is reduced through cooling the soles of the feet (Magnusson et al. 1990). How the nervous system adjusts the relative weighting of sensory information when the surface changes to a maintained, static inclined condition is unknown. The studies in this dissertation investigated how maintained surface inclination affects the relative weighting between somatosensory information about body orientation with respect to the support surface and vestibular and graviceptor sensory information about body orientation with respect to gravity.

Reference frames for postural orientation and verticality

How does the nervous system determine the direction of upright or postural vertical, the typical orientation adopted during stance and gait in humans? This is the main question addressed by this dissertation. Vertical is a relative term that can only be interpreted with respect to a specific reference or coordinate frame, such as the direction of the force of gravity or the direction of the objects in visual surround, such as door frames and window edges (Berthoz 1991; Gibson 1952; Mittelstaedt 1998). While the nervous system has several different sensory systems that could provide information about body alignment, individual sensors can only provide relative information, for example, how much the muscle has stretched relative to the prior position or how much the head has tilted relative to the prior position. A reference frame is necessary to interpret sensory information for determining how the body is aligned with respect to the environment.

Several different reference frames could contribute to the centrally determined postural upright or postural vertical. Postural lean has been shown to be induced by very slow rotation of the support surface (Creath et al. 2002; Gurfinkel et al. 1981,1995a;

Walsh 1973), slow movement of a lightly touched object that is perceived as stationary (Jeka et al. 1997, 1998), galvanic vestibular stimulation which is hypothesized to alter the perceived direction of the force of gravity (Hlavacka et al. 1985, 1995; Lund and Broberg 1983; Nashner and Wolfson 1974), or motion of the visual surround (Bles and DeWit 1976; Dichgans et al. 1972; Lee and Lishman 1975; Lestienne et al. 1977; Reason et al. 1981; van Asten et al. 1988). Which of these reference frames dominates postural orientation when the surface is stable and the eyes are open remains unclear. When the support surface changes from a horizontal to inclined position, the direction of upright based on somatosensory information related to the body-to-support-surface relationship will not match the direction of upright with respect to gravity information. If the body is to stay upright with respect to gravity, the nervous system could decrease the relative weighting given to somatosensory input for orientation information (Creath et al. 2002; Maurer et al. 2000; Peterka 2002) or the nervous system could recalibrate the way it interprets somatosensory information for determining postural orientation (Lackner et al. 1981, 2000; van der Kooij et al. 1999). Sensory information about alignment of the body with respect to gravity could be used to recalibrate support-surface related somatosensory information. Chapters 2, 3, and 4 describes a postural after-effect of stance on an inclined surface that suggests somatosensory information about postural upright with respect to the support surface undergoes gradual recalibration when surface inclination changes.

Terminology for different types of reference frames varies in the literature. The terms allocentric, or extrinsic reference frames, and egocentric, or intrinsic reference frames, have been used to divide different types of reference frames into two broad categories (Berthoz 1991; Paillard 1991). Allocentric, or extrinsic, reference frames are based on extrinsic or external cues based on the structure of the environment and include reference frames based upon information from vision or through somatosensory contact with surfaces. Intrinsic reference frames are based on gravito-inertial cues such as otolith information and somatosensory and visceral graviceptor information.

More than one reference frame and more than one vertical

How does the brain determine the direction of vertical? Gravity-vertical is the benchmark against which experiments test how accurately subjects are able to estimate the direction of vertical (Mittelstaedt 1998; Young 1984). The question of how human subjects integrate sensory information in order to determine the direction of vertical has been well studied both in the neurophysiology literature as well as the psychology literature. Evidence shows that the brain constructs more than one vertical, based on different combinations of sensory information, including the subjective visual vertical, the subjective postural vertical, and actual postural vertical (Anastasopoulis et al. 1999; Bisdorff et al. 1996b; Bronstein 1999; Perennou et al. 2002; Young 1984). Subjective visual vertical refers to the ability to align a luminous rod to 'vertical' in the dark or a rod to an all white background (Bischoff 1974; Mittelstaedt 1983, 1999). Subjective visual vertical has been shown to depend not only on visual information, but also on otolith information. For example, head tilt significantly alters accuracy of the subjective visual vertical (Bischoff 1974; Mittelstaedt 1983, 1999). In addition, subjects with unilateral vestibular loss have impaired accuracy of subjective visual vertical that persists past the time when many other effects of the vestibular loss have been compensated (Tabak et al. 1997; Vibert et al. 1999).

The term postural vertical in the literature refers to the ability to align the body to 'vertical', while the subject is seated and strapped into a chair that can be tilted with a remote control device, with testing done in the dark (Bisdorff et al. 1996a; Bringoux et al. 2002; Bronstein 1999; Clark and Graybiel 1964, 1965). Humans are quite accurate at aligning their bodies near the gravitational vertical, with mean errors reported at 1.7° (Anastasopoulis et al. 1999). When visual information is not available and subjects are asked to align their bodies to gravity-vertical, the postural alignment of subjects who have vestibular loss is not significantly different from postural alignment of healthy subjects, suggesting that somatosensory information, not otolith information, is the dominant sensory input for estimating postural vertical (Bisdorff et al. 1996a; Bringoux et al. 2002; Bronstein 1999; Clark and Graybiel 1965). The importance of somatosensory over vestibular information for aligning the body to vertical is also supported by the finding that humans show large errors in aligning their bodies to vertical (Nelson 1968) or horizontal (Jarchow et al. 1999) when underwater, a condition in which somatosensory, especially pressure-related, information about upright is diminished because of buoyancy. Bias can be introduced into the direction of perceived postural vertical by changing the pattern of somatosensory input on the body (Bisdorff et al. 1996a). When seated subjects were passively roll-tilted sinusoidally with a biased offset of 5° to 15° off-vertical, the perceived postural vertical corresponded to the offset rather than to gravity-vertical in both healthy and bilateral vestibular loss subjects. The subjective postural vertical or horizontal can be dissociated from the subjective visual vertical, showing that these two forms of vertical can be based on different combinations of sensory information and are separately represented by the nervous system (Anastasopoulis et al. 1999; Bronstein 1999; Jarchow et al. 1999; Mast et al. 1996).

The actual, physical postural vertical, or postural upright, is defined as the postural alignment that a freely sitting or standing subject actively assumes. The group of studies in this dissertation investigated the influence of surface inclination on actual postural vertical in standing subjects. The actual postural vertical has been tested under various environmental conditions that include microgravity (Baroni et al. 1999; Clement et al. 1984, 1988; Lestienne and Gurfinkel 1988; Massion et al. 1997), underwater (Massion et al. 1995), and altered visual conditions (Bles and deWit 1976; Dichgans et al. 1972; Lee and Lishman; Lestienne et al. 1977; Reason et al. 1981; van Asten et al. 1988). When exposed to microgravity, astronauts whose feet were strapped to the floor and whose eyes were closed, initially leaned their trunks far forward, but gradually, over a time course of weeks to months, assumed a postural alignment that was similar to when standing on earth, showing that the nervous system slowly adapted how it interpreted somatosensory and otolith information for establishing postural orientation when gravity conditions changed (Clement et al. 1984, 1988; Lestienne and Gurfinkel 1988, Massion et al. 1997). When subjects tried to stand while underwater, with their feet strapped to a support, subjects also leaned their trunks forward (Massion et al. 1995). Because load-related sensory information is reduced due to buoyancy forces and otolith information is still available underwater, this leaning is taken as evidence of the importance of somatosensory information for establishing a postural orientation reference. In contrast to the effects of altering somatosensory information with microgravity or underwater conditions, static tilt of the visual surround affected postural alignment only slightly (Bles and deWit 1976; Witkin 1949). However, in standing subjects, circular motion of the focal visual surround induced lateral leans (Dichgans et al. 1972) and anterior-posterior motion of the peripheral or the whole visual surround induced anterior-posterior leans (Lestienne et al. 1977; Reason et al. 1981; Lee and Lishman 1975). The availability of more than one reference frame for establishing postural orientation provides the nervous system with flexibility for adapting to altered conditions.

While the ability to use more than one reference frame has many advantages in terms of adaptability, it also raises a question. How does the brain select a reference frame or combine reference frames for determining postural upright when conditions are stable and when several different reference frames could provide accurate and reliable information about body alignment with respect to the true vertical? Healthy subjects have been shown to differ from one another in how they weight sensory information when more than one reference frame is available (Lacour et al. 1997; Witkin and Asch 1948; Young et al.1996). For example, individuals vary in the degree to which they weight information about the visual background for postural stability (Chiari et al. 2000; Collins and Deluca 1995; Cremieux and Mesure 1994; Golomer et al. 1999; Isableau et al. 1997; Lacour et al. 1997) and for the perception of visual vertical (Asch and Witkin 1948; Witkin and Asch 1948). Responsiveness to tendon vibration on posture and movement is also variable across individuals, suggesting that subjects may differ in the degree to which they weight proprioceptive information for postural orientation (Eklund and Hagbarth 1966; Gurfinkel et al. 1995b; Gurfinkel et al. 1998; Ivanenko et al. 2000). Past experience and training have been shown to contribute to individual differences in preferred reference frames or sensory weighting (Bringoux et al. 2000; Golomer et al. 1999; Mouchnino et al. 1992; Perrin et al. 2002). For example, gymnasts show less dependence on somatosensory information than non-trained subjects for aligning the body to vertical, as measured by ability to bring the body to vertical when placed in a body cast that minimizes somatosensory information about forces or body segment alignment with respect to a supporting surface (Bringoux et al. 2000). Chapter 4 reports how the post-incline lean varies across a large group of healthy adults. Chapter 4 also reports the consistency of post-incline leaning or non-leaning within individual subjects across time and across direction of incline. The difference in the extent of post-incline leaning effects across subjects may reflect differences in each subject's preferred sensory reference frame for postural orientation.

Studies in humans (Hlavacka et al. 1995, 1996; Kavounoudias et al. 2001) and fish (Schöne 1984; von Holst 1973) show that more than one reference frame can simultaneously influence the adopted postural alignment. In fish, postural orientation depends simultaneously on the direction of light and on the availability of otolithic information (von Holst 1973). In humans, when both tendon vibration and galvanic stimulation are applied, the direction of the lean appears to depend on a vectorial summation of the estimated vertical based on the two source of sensory information (Hlavacka et al. 1995, 1996). When standing on a stable, horizontal surface with eyes closed, it is difficult to determine if subjects are relying primarily on the support surface and/or gravity for a postural reference because the task of standing is well learned and the reference frames provide congruent information. When the surface changes alignment from horizontal to inclined or from inclined to horizontal, a sensory conflict is created between upright based on the orientation of the support surface and upright based on the direction of gravity. Will the body align to the support surface or to gravity or some orientation that takes into account both references?

Sensory conflict when reference frames are altered

When the surface changes orientation from horizontal to inclined, a postural set point based on a horizontal surface will no longer match a postural set point based on the direction of gravity and forces acting on the body. A sensory conflict will exist. If subjects stay aligned to the inclined surface, they will lean with respect to gravity, an inefficient and potentially unstable posture. A possible solution for addressing the problem of a set point that no longer provides an optimal estimate of vertical is to switch to, or increase the relative weighting of, a different reference frame (Black et al. 1983; Nashner et al. 1982; Oie et al. 2002; Peterka 2002). For example, when the surface is inclined, the nervous system could increase weighting of gravity-related sensory information and decrease weighting of surface-related sensory information. Several studies have shown that subjects decrease their reliance on somatosensory information related to the support surface (Ivanenko et al. 1999; Peterka 2002), and increase their reliance on vestibular information (Creath et al. 2002; Maurer et al. 2000; Peterka 2002; Welgampola and Colebatch 2001) or visual information (Bles and deWit 1976; Lee and Lishman 1975) when the surface is unstable. How the relative weighting between gravity and surface related sensory information is affected under static, maintained changes in surface inclination have not been reported. This dissertation investigated how a maintained change in surface inclination affects postural orientation and the relative weighting between support-surface-related and gravity-related sensory information.

A second possible solution to the problem of an altered reference frame is to adapt or recalibrate the set point based on that reference frame. In other words, the nervous system could recalibrate the relationship between sensory information and motor output (Lackner et al. 1981, 2000; Lestienne and Gurfinkel 1988; Melvill Jones and Mandl 1983; Rieser et al. 1995; Thach et al. 1992). This solution involves an adaptive process that gradually shapes or optimizes the set point for the new, constant environmental condition. If humans rely on the support surface as a reference frame for postural orientation when it is stationary, as has been suggested in posture control models (Mergner et al. 1998, 2002b), then when the support surface's static orientation changes from horizontal to inclined or inclined to horizontal, subjects would need to adjust, or adapt, the surface-referenced set point for postural upright in order to maintain reliance on a support surface reference frame. One might predict that when the surface moves from an inclined to a horizontal position, that subjects would initially align their bodies to the surface as if the surface were still inclined, and then would gradually return toward upright with respect to gravity as the surface-referenced set point underwent recalibration. During very slow (0.04 °/s), small amplitude (1°) tilt of the support surface from a horizontal to an inclined position, subjects leaned away from gravity-vertical and maintained constant alignment relative to the support surface, returning to a gravity-upright posture only slowly and gradually after the surface was stationary (Gurfinkel et al. 1995a). This suggests that the surface was a relied upon orientation reference frame and that the set point for controlling postural orientation with respect to the surface underwent slow, gradual recalibration once the surface was stable. The after-effects of standing on an inclined surface that occur when the surface returns to a horizontal position have not been reported. The studies in this dissertation investigate how postural alignment changes when the surface changes from a horizontal to an inclined and an inclined to a horizontal position when vision is not available.

Internal models and sensory conflict resolution

A change in internal representation of sensory and motor dynamics relative to the external environment is a possible mechanism for resolving the conflict among reference frames by either adjusting the relative weighting among different sensory systems or by adjusting the set point estimates of postural upright (Merfeld et al. 1993, 1999; Wolpert et al. 1995; Zupan et al. 2002). Many current models of posture control include the concept of a central representation of the body and environmental sensorimotor dynamics, sometimes referred to as an internal model or as a body scheme, for explaining how the postural control system can act in a predictive manner and how adaptation to altered conditions occurs (Gurfinkel and Levik 1991; Horak and Macpherson 1996; Maioli and Poppele 1991; Mergner et al. 1998, 2002b, 2003; van der Kooij et al. 1999). The internal model not only includes representation of the body-in-space, but also involves estimation of task-dependent, stationary reference frames such as gravity and the support surface (Maioli and Poppele 1991; Merfeld et al. 1999; Mergner et al. 1998, 2002b, 2003; Zupan et al. 2002). When the reference frames used by the nervous system are unchanging, there is a constant, invariant relationship among different sensory modalities for a given body position with respect to the environment (Gibson 1952; Lackner and DiZio 2000;

Riccio and Stoffregen 1988; Stoffregen and Riccio 1988). However, when the relationship among reference frames is altered, sensory feedback will not match the predicted sensory afference, and the direction of vertical may become ambiguous (Gibson 1952). Some models suggest that when a sensory conflict occurs, an error signal between expected sensory information derived from the internal representations and the actual sensory information derived from sensory afference is used to gradually update the model to match the new sensory context (Merfeld et al. 1993; van der Kooij et al. 1999; Wolpert et al. 1995; Zupan et al. 2002). Other models suggest that the nervous system can resolve sensory conflicts from changed external conditions by reweighting relative dependence on sensory information (Black et al. 1983; Fitzpatrick et al. 1994a; Nashner et al. 1982; Oie et al. 2002; Peterka 2002).

The conflict between estimates of postural upright based on a surface- versus a gravity- reference frame could be the basis for the post-incline leaned posture that slowly and gradually returns to upright with respect to gravity. When subjects stand vertical-re-gravity on a toes-up-inclined surface, they are leaned forward with respect to the support surface compared to stance on a horizontal surface. The vertical-re-gravity alignment alters the kinematic state of the entire body, generating somatosensory feedback that does not match expected feedback for vertical posture. Thus, a change occurs in the relationship between kinematic and kinetic sensory information about postural vertical. The conflict in actual and predicted sensory information could drive a gradual change in the internal model's estimate of surface-referenced postural vertical until the actual and predicted feedback match. A new set point for surface referenced postural orientation could be learned. When the surface returns to horizontal, if subjects predominantly weight the surface-referenced postural vertical for controlling postural orientation, then the body would be predicted to align to the new surface-referenced postural orientation set point and to lean with respect to gravity-vertical. While leaning, gravity-related sensory feedback (otolith, foot pressure, GTO) would not match expected feedback for gravity-referenced vertical. As subjects align toward gravity-vertical, expected and actual proprioceptive feedback would not match. Once again, the internal model's estimate of surface-referenced postural vertical could be gradually updated until the actual and the predicted feedback were congruent. Subjects would be predicted to return toward the gravity-vertical postural orientation as the surface-referenced set point for upright was updated. A finding that subjects lean in a direction and with a magnitude that systematically depends on the direction and amplitude of surface inclination would lend support to the hypothesis that leaning occurs because of a modified postural set point for orientation of the body with respect to the support surface. This prediction was tested in Chapter 2.

Adaptation and sensorimotor after-effects

Webster's New World Dictionary defines the term adapt as 'to make suitable by changing; to adjust to new circumstances'. The term adaptation is used in the sensorimotor control literature to refer to a modification in neural processing that enables an organism to adjust and optimize its performance to changed environmental conditions, such as altered visual fields or altered surface configurations, or to a changed internal constraint (Lackner et al. 1981, 2000; Melvill Jones and Mandl 1983; Robinson 1976;

Thach et al. 1992; Young et al. 1986). When environmental conditions change, performance errors occur because central interpretation of sensory information for planning and generating movement is no longer accurately calibrated. Errors are reduced by adaptive recalibration of the relationship between sensory input and motor output.

Distinctions have been made in the literature between sensorimotor adaptation processes that involve a slow recalibration of how sensory information is integrated, and fast sensory reweighting or habituation processes (Guedry 1974; Kandel 1991; Nashner et al. 1976, 1982; Oman 1982). For example, when subjects are exposed to rapid toes-up surface rotations, an ankle extensor muscle burst that is counterproductive to keeping the body upright is triggered by stretch of ankle muscles, and this extensor burst rapidly diminishes across as few as 3 to 5 repeated trials (Nashner 1976). When stepping on a broken escalator, the initial step often feels odd. This situation has been replicated experimentally, showing that after repeated trials of stepping onto a moving platform, when returning to stepping onto a stationary platform, only the first step shows carry over of muscle activity and movement velocity appropriate for the moving sled condition (Reynolds and Bronstein 2003). When subjects are exposed to altered sensory conditions, such a compliant or unstable support surface, subjects rapidly reduce reliance on the support surface and increase reliance on visual or vestibular information (Black et al. 1983; Nashner et al. 1982; Peterka 2002).

Slower adaptation processes are believed to involve a gradual recalibration of how sensory information is integrated for planning and performing a movement. For example, when subjects first put on goggles with displacing prisms that shift the visual field, they initially make errors in throwing (Martin et al. 1996a, 1996b; Thach et al.) and pointing tasks (Baizer et al. 1999; Harris 1965; Redding and Wallace 1993), but the errors subside with practice. The displacing prisms alter the relationship between visual information and proprioceptive information, thus the predicted displacement of the arm in visual space does not match actual arm displacement. Practice gradually recalibrates the central estimate of the visual-proprioceptive relationship for moving the arm in visual space. Adaptive neural mechanisms recalibrate, or update, sensorimotor relationships so that they are more suitable for the new environmental conditions (Lackner et al. 1981, 2000; Melvill Jones and Mandl 1983). Adaptation implies that learning has occurred and the nervous system has altered how incoming sensory information is integrated to determine future movement planning (Gandolfo et al. 1996; Melvill Jones et al. 1983, 1988; Shadmehr et al. 1994, 1997a, 1997b; Thach et al. 1992). The studies in this dissertation investigate how subjects adapt their postural orientation when surface inclination changes, when a conflict occurs between predicted upright based on gravity information and predicted upright based on surface geometry. Will subjects quickly alter the relative weighting between support-surface-related somatosensory information and gravity-related vestibular information or will they slowly recalibrate how sensory information is integrated to determine postural upright?

Sensorimotor after-effects as evidence of adaptive processes

Sensorimotor after-effects have been studied to uncover neural mechanisms that underlie sensorimotor recalibration and sensorimotor memory or storage mechanisms (Baizer et al. 1999; Clower et al. 1996; Cohen et al. 1981; Earhart et al. 2002a; Lang and Bastian 1999; Li et al. 2001; Lisberger 1988; Martin et al. 1996a; Robinson 1976;

Shadmehr et al. 1994, 1997a, 1997b). Sensorimotor after-effects are persistent behavioral or perceptual effects that occur *after* a period of adaptation to a novel environmental condition, when the environmental conditions return to the original state. For example, *after* prism-displacing goggles are removed, subjects make errors in the opposite direction as when the goggles were first put on (Baizer et al. 1999; Harris 1965; Redding and Wallace 1993, 1994). Subjects need to re-adapt to the original environmental condition of no prisms. After-effects that follow altered sensorimotor conditions or altered environmental conditions have been interpreted as evidence of adaptive plasticity, or a learning effect, in how sensory information is interpreted centrally for controlling movement (Gandolfo et al. 1996; Gonshor and Melvill Jones 1980; Martin et al. 1996a, 1996b; Melvill Jones et al. 1983, 1988; Shadmehr et al. 1994, 1997a, 1997b; Thach et al. 1992). Sensorimotor after-effects can occur following a change in many different aspects of the environment, including shifts in the visual field (Baizer et al. 1999; Gonshor and Melvill Jones 1980; Harris 1965; Martin et al. 1996a, 1996b; Melvill Jones et al. 1988; Robinson 1976), changes in the force field in which the subject moves (Gandolfo et al. 1996; Konczak et al. 2003; Shadmehr et al. 1994, 1997a, 1997b), and changes in the support surface conditions (Anstis 1995; Gordon et al. 1995; Earhart et al. 2001; Hashiba 1998; Jensen et al. 1998; Weber et al. 1998). After-effects have been demonstrated in diverse behaviors that include postural alignment (Hashiba 1998; Lestienne et al. 1977; Michel et al. 2003), locomotor trajectory (Gordon et al. 1995; Earhart et al. 2001; Jürgens et al. 1999; Rieser et al. 1995; Weber et al. 1998), throwing (Martin et al. 1996a, 1996b), catching (Lang and Bastian 1998), pointing (Baizer et al. 1999; Harris et al. 1965; Redding and Wallace 1993, 1994), and the gain of reflexive eye movement produced by the vestibulo-ocular reflex (Lisberger 1988; Melvill Jones et al. 1988; Robinson 1976). Most relevant to the current study of postural alignment after stance on an inclined surface are after-effect conditions that affect postural alignment and after-effects that occur when the surface conditions are altered.

Subjects demonstrate postural after-effects following a period of exposure to a moving linear visual surround (Lestienne et al. 1977; Reason et a. 1981) and following a period of walking on a treadmill with eyes open (Hashiba 1998). When exposed to linear visual surround motion, subjects leaned in the direction of the optical flow and when the visual surround motion ceased, subjects leaned in the opposite direction for 2 to 3 minutes (Lestienne et al. 1977; Reason et al. 1981). Subjects also leaned for about a minute after a period of walking or running on a treadmill with eyes open, but not closed. Both of these postural effects occurred after a maintained change in the relationship between visual flow information and somatosensory information about body motion in space, suggesting that visual and support surface information had been recalibrated. The studies in this dissertation created a condition in which the relationship between support-surface related and gravity-related information about postural orientation was altered to investigate whether similar sensorimotor recalibration occurs.

After-effects on the perceived postural vertical have been reported to occur when subjects are passively held in a tilted position. When a subject, who was seated and strapped into a chair, was maintained in a laterally tilted position for 2 minutes, after-effects occurred in how closely the subject was able to match the perceived postural vertical to gravity-vertical (Clark and Graybiel 1964). Both healthy and vestibular loss subjects made errors that were biased in the direction of the prior tilt, suggesting a somatosensory adaptation to the tilted position. A similar somatosensory adaptation could occur when subjects stand on an inclined surface and could result in after-effects on actual postural alignment adopted by subjects in the post-incline period.

Experience-dependent after-effects have been reported to occur not only in actual postural alignment and in the subjective postural vertical, but also in the perception of orientation of the support surface. Walking (Hutton 1966) or jogging (Anstis 1995) on an inclined treadmill led to an after-effect on the ability of subjects to estimate when the support surface was horizontal. For example, after a period of jogging on a 4°-toes-up-inclined treadmill, subjects perceived a 4°-toes-up-inclined treadmill as horizontal and a horizontal treadmill as toes-down-inclined (Anstis 1995). Similar perceptual after-effects could occur after subjects stand quietly on an inclined surface.

Changes in the conditions of the support surface have been shown to affect locomotor trajectory. After a period of walking on a rotating, circular treadmill, subjects with eyes closed walked in curved trajectories when attempting to walk straight ahead in a way that suggests that subjects learned a new foot-to-trunk relative relationship, an effect called Podokinetic After-Rotation or PKAR (Gordon et al. 1995; Weber et al. 1998). Likewise, after jogging for several minutes on a treadmill, subjects with eyes closed jogged forward, backward or sideways when attempting to jog-in-place, with the direction of drift depending on the direction that subjects jogged while on the treadmill (Anstis 1995). The PKAR and the post-incline locomotor after-effects maintained a body-to-surface relationship based on the immediately prior surface conditions, suggesting that while subjects were exposed to the altered surface condition, the nervous system recalibrated how it integrated and interpreted somatosensory information for controlling orientation and movement of the body with respect to the surface. Similar after-effects of altered surface conditions might occur when subjects are exposed to a prolonged period of standing on an inclined surface. When standing on an inclined surface, subjects might learn a new body-to-surface relationship as 'postural upright', just as subjects who walked on the circular treadmill learned a new body-to-surface relationship as 'straight ahead locomotion'. When returning to stance on a horizontal surface, subjects might lean to maintain the immediately prior body-to-surface relationship. Chapters 2-4 test whether subjects lean after stance on an inclined surface.

Adaptation that results in an after-effect can generalize or transfer from one task to another if the two tasks share similar enough task goals and effectors (Earhart et al. 2001, 2002b; Martin et al 1996b; Rieser et al. 1995). For example, PKAR has been shown to generalize between walking and hopping (Earhart 2002b) and between forward and backward walking (Earhart et al. 2001). This dissertation investigated whether stepping on an inclined surface would lead to postural after-effects during quiet stance when the surface returned to a horizontal position.

Neural mechanisms responsible for after-effects

To understand the mechanisms responsible for a sensorimotor after-effect, a first step might be to determine at what level the after-effect is occurring and what variables undergo adaptive change. Is adaptation occurring at the level of sensory receptors, such as a change in sensitivity or threshold? Is adaptation occurring in the motor output, such as a change in motor neuron excitability? Or is adaptation occurring centrally, in processes that integrate sensory information and determine the relationship between combined sensory information and postural activity for postural orientation? The studies in Chapter 3 were designed to rule out that the post-incline lean is due to a peripheral sensory or segmental reflex mechanism that affects tonic activity of ankle muscles.

When subjects stand on a toes-up inclined surface, they accomplish upright body alignment with respect to gravity mainly by a large increase in ankle dorsiflexion. The altered postural configuration while on the incline affects muscle length and alters the biomechanical conditions for controlling ankle torque and for maintaining whole body CoM stability. Actively maintaining a muscle in either a lengthened or shortened position for a period of time has been shown to result in after-effects of altered muscle spindle reflex sensitivity (Enoka et al. 1980; Gregory et al. 1990), perceptual errors of limb position (Gregory et al. 1988; Wise et al. 1996), errors in force production (Hutton et al. 1984, 1987) and, most relevant to the studies in Chapter 3, altered adopted resting posture (Ghafouri et al. 1998; Gilhodes et al. 1992; Gurfinkel et al. 1989; Hagbarth and Nordin 1998; Kohnstamm 1915; Sapirstein et al. 1937). These muscle contraction after-effects could contribute to the post-incline lean.

Sustained, isometric contraction of a muscle in a shortened position can produce after-contraction effects that include involuntary muscle contraction and movement back toward the prior posture (Ghafouri et al. 1998; Gilhodes et al. 1992; Gurfinkel et al. 1989; Hagbarth and Nordin 1998; Kohnstamm 1915). Examples of after-contraction postural effects include involuntary deltoid contraction and arm rise after a period of pushing the arm against a door frame (Hagbarth and Nordin 1998), involuntary quadriceps activity and knee extension after tonic contraction of ankle dorsiflexors while supporting a weight hung from the unsupported foot (Gurfinkel et al. 1989), and involuntary upper back muscle activity with upper trunk-shoulder rotation after tonic contraction of the trapezius muscle while supporting a weighted bag hung from the shoulder (Ghafouri et al. 1998). Both peripheral muscle spindle mechanisms (Hagbarth and Nordin 1998) and central mechanisms (Gilhodes et al. 1992; Gurfinkel et al. 1989; Ghafouri et al. 1998) have been proposed to explain after-contraction effects.

Muscle spindle thixotropy is a proposed peripheral explanation for after-contraction effects (Hagbarth and Nordin 1998, Proske et al. 1993). Muscle spindle thixotropy refers to the persistence of intrafusal muscle cross-bridge linkages that form during an isometric contraction at short muscle length and persist when the muscle relaxes and lengthens, thus stiffening intrafusal fibers, stretching the compliant receptor portion of the spindle, and causing involuntary muscle contraction with return toward the prior posture (Hagbarth and Nordin, 1998; Proske et al. 1993). A thixotropic muscle spindle mechanism for the post-incline lean could be proposed for ankle dorsiflexors, which are maintained in a shortened position during stance on the incline. Aniss and colleagues (1990) have shown that when subjects stand on an inclined surface, the resting firing rate of the muscle spindles in the tibialis is maintained despite the shortened position, suggesting that fusimotor drive adjusts muscle spindle length to maintain spindle sensitivity. When the surface returns to horizontal, muscle spindle thixotropic resistance to lengthening of the tibialis muscle could keep the body aligned to the surface and forward leaned in space. The experiments in Chapter 3 tested whether conditions that are not compatible with a thixotropic mechanism would still result in a post-incline lean. In one experiment, the legs were prevented from leaning to determine whether the upper body would still lean. In a second experiment, subjects stepped while on the incline instead of standing still.

After-contraction effects have also been explained by a change in central interpretation of proprioceptive information and to a slow change in the central setting of whole body postural tonus through brainstem 'tonogenic' structures (Gurfinkel et al. 1989; Ghafouri et al. 1998). A central, as opposed to a peripheral, mechanism is supported by the findings that after-contraction effects can switch from the adapted muscle to a different muscle that was inactive during the adapting period (Ghafouri et al. 1998, Gurfinkel et al. 1989; Craske and Craske 1986) and that the direction of movement of the unintentional postural effect depends on the postural context such as standing versus sitting (Ghafouri et al. 1998) or whether vision is available (Gilhodes et al. 1992). After-contraction effects are based on a conditioning stimulus of a sustained isometric muscle contraction (Ghafouri et al. 1998; Gilhodes et al. 1992; Gurfinkel et al. 1989). Stepping-in-place, rather than standing on an incline would not involve sustained, isometric muscle contraction, but rather would involve reciprocal muscle bursting and ongoing, cyclical joint movements. To investigate whether the post-incline lean could be due to an after-contraction effect on the distribution of postural muscle tone in the post-incline period, the studies in Chapter 3 tested whether subjects would lean after stepping-in-place, rather, than standing still while on the inclined surface.

A finding that subjects lean the upper body when the legs are prevented from leaning in the post-incline period or that subjects lean after a period of stepping on an incline would be incompatible with a segmental or peripheral mechanism but would be compatible with a central mechanism for the post-incline lean. If the effect is central, we can only speculate on possible systems that could be involved. The cerebellum, with its specific cellular architecture, multiple body maps, and convergence of multimodal sensory input, has been shown to play an important role in sensorimotor adaptive recalibration that occurs on a time course of minutes to hours (Baizer et al. 1999; Earhart et al. 2002a; Lang and Bastian 1998; Lisberger 1988; Martin et al. 1996a; Nezafat et al. 2001; Robinson 1976; Thach et al. 1992). In fact, adaptation of the vestibulo-ocular reflex and throwing or pointing movement to prisms and the PKAR adaptation to a rotating treadmill does not occur or is reduced in subjects with cerebellar lesions (Baizer et al. 1999; Earhart et al. 2002; Martin et al. 1996a; Robinson 1976). Because of the synaptic organization of the cerebellum, many have suggested that internal models are in part embedded in the cerebellar circuitry (Imamizu et al. 2000; Kawato 1999; Wolpert et al. 1995). Longer-term changes related to motor learning have been shown to involve persistent changes in brainstem nuclei (Lisberger 1994) and in cortical areas (Clower et al. 1996; Li et al 2001; Shadmehr et al. 1997b, 1999). The parieto-insular cortex has been speculated to be an important region for body spatial orientation because this region receives vestibular and somatosensory and visual information and because patients with lesions in this region have a high incidence of impairment in the subjective visual vertical (Brandt et al. 1994). The actual postural vertical may involve different cortical sites, however, since subjective visual vertical has been shown to be dissociable from postural vertical (Anastasopoulis et al. 1999; Bronstein 1999; Jarchow et al. 1999; Mast et al. 1996; Perennou et al. 2002). New imaging studies of subjects who have had a stroke and as a result have Pusher's Syndrome, a postural impairment in which subjects push toward their hemiparetic side and resist aligning to gravity-vertical, suggests an area of the thalamus may be important for determining the postural vertical (Karnath et al. 2000a, 2000b; Perennou et al. 2002). The brainstem areas shown to be important for regulating postural tone, such as the dorsal tegmental field in the caudal pons (Mori et al. 1982, 1989), or the brainstem areas shown to be important in adapting locomotion to an inclined surface (Matsuyama and Drew 2000), could also be important for adapting postural orientation to altered surface conditions.

Summary

The support surface provides important reference information for controlling postural orientation. Although the support surface is typically horizontal, inclined surface conditions such as hills, curb cuts, and sloped theater aisles are common everyday experiences. This dissertation investigates how the nervous system adapts control of postural orientation when the support surface is inclined. These studies will show that many blindfolded subjects lean after stance on an inclined surface in a way that suggests an adaptive recalibration of the support-surface-referenced, central-estimate of postural upright. These studies further show that the mechanisms responsible for leaning are not due to peripheral or segmental mechanisms affecting ankle muscle activity and ankle position, but must involve a central adaptive change in how sensory information is processed. Lastly, these studies will show that healthy individuals vary in the degree to which they depend on the support surface as a frame of reference for determining postural orientation.

Chapter 2

After-effects of stance on an inclined surface:

An adaptive mechanism for postural orientation

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Abstract

We studied how blindfolded subjects adapt their standing posture to changes in surface inclination to understand how postural orientation is regulated with respect to the surface and to gravity. We selected 11 healthy subjects who showed an after-effect of leaning after standing on an inclined surface. Postural orientation was measured before, during, and after subjects stood on an incline, with postural orientation defined by global variables (body segment orientation, CoM, and CoP) and local variables (joint angles and EMG). We varied incline direction (toes-up, toes-down, lateral), amplitude (2.5-10°), and duration (0.5-5 minutes). When subjects stood on the incline, the head, trunk, and legs aligned near to gravity-vertical, similar to postural alignment during the pre-incline period. However, after only 30 seconds of stance on an incline, when returning to a horizontal surface, subjects leaned. Leaning maintained body-to-surface relative alignment as if subjects still stood on the incline, regardless of incline direction. The leaned posture returned toward upright exponentially across 1-4 minutes. As surface inclination increased, the amplitude of leaning increased. Trunk orientation was more affected by the amplitude of surface inclination than was ankle position, suggesting that global, rather than local, postural variables were affected. Unlike the slowly changing postural set point, high-frequency CoP displacement, reflecting stabilizing activity around the set point, was disturbed only transiently. Our results suggest that the body-to-support-surface geometric relationship is an important reference for the CNS internal model of postural orientation and that the postural set point can be adaptively modified when surface inclination is altered.

Introduction

Posture control is a complex sensorimotor task that involves establishing a postural reference for body orientation with respect to the external world and simultaneously regulating equilibrium (Clement et al. 1984; Gurfinkel et al. 1995a; Horak and Macpherson 1996; Lestienne and Gurfinkel 1988; Massion 1994). The postural alignment that the postural control system tries to maintain can be thought of as a reference posture, or a postural set point. How the nervous system establishes a set point for postural orientation and adapts the postural set point when environmental contexts change remains unclear. We studied how surface inclination affects postural orientation in humans with eyes closed in order to better understand how the set point is modified when support surface conditions change.

Humans typically adopt a standing posture that is near to upright with respect to gravity, but each individual adopts a unique, habitual postural alignment and set point that is thought to be represented in the nervous system via an internal body scheme or model (Lestienne and Gurfinkel 1988). The direction of postural upright is a relative term, needing a reference frame for its definition (Berthoz 1991). When the surface is stable and eyes are open, upright posture might be referenced or organized with respect to any one of several reference frames that include the direction of gravity (Dietz et al. 1992; Mittelstaedt 1998), the support surface (Gurfinkel et al. 1992, 1995a; Ivanenko et al. 1997; Kavounoudias et al. 1998; Mergner and Rosenmeier 1998), and/or the visual surround (Lee and Lishman 1975; Lestienne et al. 1977; Dichgans et al. 1972). Evidence suggests that central nervous system (CNS) selection and/or weighting of the contribution of different reference frames for establishing postural orientation depends both on the task context (Mergner et al. 1990, 2002a; Quoniam et al. 1990) and on the environmental context (Fitzpatrick et al. 1994a; Hlavacka et al. 1995; Ivanenko et al. 1999; Mergner et al. 2003; Oie et al. 2002; Peterka 2002). During stance on a horizontal surface with eyes closed, posture is typically oriented near to and slightly forward of gravity-vertical and perpendicular to the surface. Under this condition, it is difficult to determine whether postural orientation is being controlled with respect to gravity, the surface, or both. However, when the surface is inclined, the perpendicular relationship between the surface and gravitational vertical is altered, allowing us to investigate how subjects depend upon contributions of surface- and gravity-related sensory information for their postural orientation.

Recently proposed models of posture control suggest that when a subject stands quietly on a stable support surface, the nervous system regulates postural orientation by relying predominantly on a proprioceptively based postural set point that is referenced to the support surface (Mergner et al. 1998, 2002b; Peterka 2002). This hypothesis is supported by the finding that vestibular loss subjects with eyes closed are able to stand on a stable horizontal surface with postural stability that is comparable to healthy subjects (Black et al. 1983; Nashner et al. 1982). When the surface is no longer stable, but is dynamically tilting (Ivanenko et al. 1999; Maurer et al. 2000; Nashner and Wolfson 1974; Peterka 2002) or compliant (Fitzpatrick et al. 1994a; Lee and Lishman 1975), subjects decrease their reliance on somatosensory information related to the support surface and increase their reliance on visual and/or vestibular information for postural orientation, a process referred to as sensory reweighting. The present study focused on how relative weighting of somatosensory information about the relationship of the body to the support surface is affected by adaptation to stance on an inclined surface and re-adaptation to stance on a horizontal surface.

Limited studies exist of human postural orientation on a statically inclined surface. A recent study showed that when humans stood on a toes-up inclined surface with their eyes open, they adopted similar head and trunk in space alignment (near gravity-vertical) as when they stood on a horizontal surface (Leroux et al. 2002). When cats stood on inclined surfaces, they also aligned their legs near gravity-vertical, however their trunks stayed parallel to the support surface (Lacquaniti et al. 1984, 1990). When the support surface was very slowly rotated (0.04 °/s) and held at 1° of inclination, humans, with eyes closed, kept their bodies aligned to the surface rather than to gravity-vertical, taking an average of 20 seconds to return toward upright, baseline postural alignment after the surface had reached the inclined position (Gurfinkel et al. 1995a). This result suggests that the set point for postural upright can be predominantly based on the body-to-surface relationship and that this set point can be slowly recalibrated to a new set point when surface conditions change. None of the studies of stance on an inclined surface or a very slowly rotating surface have reported how the experience of standing on an inclined surface affects posture when the subjects return to stance on a horizontal surface.

Evidence from a number of studies suggests that adaptation plays a role in recalibrating the sensorimotor systems involved in dynamic tasks when conditions in the environment are altered (Lackner and DiZio 2000; Rieser et al. 1995; Weber et al. 1998). For example, after a period of walking on a rotating, circular treadmill, subjects with eyes closed walk in curved trajectories when attempting to walk straight ahead in a way that suggests learning of a new foot-to-trunk relative relationship, an effect called Podokinetic After-Rotation or PKAR (Gordon et al. 1995; Weber et al. 1998). Likewise, after jogging for several minutes on a treadmill, subjects with eyes closed jogged forward, backward or sideways when attempting to jog-in-place on a stationary surface, and the direction of drift when attempting to jog-in-place depended on whether the subject had previously jogged forward, backward or sideways when on the treadmill (Anstis 1995). These after-effects maintained the same body-to-surface relationship as adopted during the immediately prior surface conditions, suggesting that the experience with an altered surface condition caused a recalibration of how somatosensory information related to the support surface was integrated with other sensory information. We wanted to know whether similar adaptive processes might be involved in the control of the more static task of maintaining stance. If subjects learn a new body-to-surface relationship as 'postural upright' while they stand on an inclined surface, and if subjects rely predominantly on the support surface as a reference frame for postural orientation, then when the surface returns to horizontal, subjects might adopt a postural alignment that is upright with respect to the surface but leaning with respect to gravity. We investigated whether and how adaptive postural after-effects occur following a period of exposure to stance on an inclined surface when direction and magnitude of surface inclination are varied. We predicted that subjects would lean forward after stance on a toes-up inclined surface, lean backwards after stance on a toes-down inclined surface, and lean rightward after a right-side-up inclined surface. We further predicted that the amplitude of leaning in the post-incline period would depend on the amplitude of surface inclination.

Studies of sensorimotor adaptation in other tasks have shown that the duration of exposure to an adapting condition affects the decay and magnitude of after-effects, providing insight into the time required to maximally build or store the newly recalibrated sensorimotor relationship (Melvill Jones et al. 1988; Weber et al. 1998). We investigated how the duration of exposure to stance on an inclined surface affects post-incline postural alignment with respect to the surface and to gravity, predicting that longer duration periods of stance on an incline would have larger after-effects on the extent to which subjects stayed aligned with respect to the support surface.

Investigation of which postural variables are affected by changes in surface inclination may provide insight into which variables the CNS uses to regulate the complex task of postural orientation (Lacquaniti et al. 1990). Studies of cats standing on inclined surfaces suggest that the nervous system organizes postural orientation by controlling the global, kinematic variables of leg orientation and length, which cannot be sensed directly and which require multisensory integration, rather than local joint angles, which can be sensed more directly (Lacquaniti et al. 1984, 1990; Maioli and Poppele 1991). The global variable of trunk orientation with respect to the surface has been suggested to be a critical control variable because cats keep their trunks aligned to the surface when it is inclined (Lacquaniti et al. 1984, 1990) and when the length of the support base is varied (Fung and Macpherson 1994). Several studies in humans have also provided evidence that the trunk is an important postural control variable (Baroni et al. 1999; Gurfinkel et al. 1981, 1995a; Horak and Macpherson 1996). Besides kinematic variables, global kinetic variables related to postural dynamics could also be used to regulate postural orientation (Maioli and Poppele 1991; Massion 1994; Mergner et al.

2002b, 2003). For example, studies have shown that the body's center of mass (CoM) projection onto the support base is habitually maintained within a small region, well within stability limits (Gurfinkel et al. 1992, 1995a). The center of pressure (CoP), derived from the integration of somatosensory receptor systems under the foot, could provide information for orientation of the whole body CoM, as long movement is slow and body configuration is not drastically altered. Vibration of regions of the foot sole has been shown to elicit whole body leans in a directionally-specific manner (Kavounoudias, 1998). We investigated how systematic change in the amplitude of surface inclination affects global kinematic, global kinetic, and local postural variables during and after stance on an incline, in order to gain insight into which variables are important for human postural orientation with respect to the support surface.

Preliminary results of this work have been reported as abstracts (Kluzik et al. 1999, 2000).

Methods

This study investigated leaning after-effects that occur in healthy subjects after a period of standing on an inclined surface. The lean that occurred after stance on inclined surface is referred to as the post-incline lean. Three separate experiments were conducted, each varying a different characteristic of support surface inclination: duration, direction, and amplitude (Fig. 1A).

Subjects

Seven healthy subjects (5F, range 25-47, mean 37.4 ± 9.1 yrs) participated in Experiment 1 (Durations) and Experiment 2 (Directions). Seven healthy subjects (5F, range 22-49, mean 36.1 ± 10.7 yrs) participated in Experiment 3 (Amplitudes). Four subjects participated in all three experiments. Subjects were screened with a health history to ensure that they were free of musculoskeletal, neurological, or other health impairments that could affect posture or balance. Subjects were selected because they leaned for at least 1-minute after standing for 2.5-minutes on a 5°-toes-up inclined surface. Out of 25 subjects screened with the stance-on-incline pre-test, 11 showed such a long lasting lean. A comparison between the subjects who leaned and the subjects who did not lean is addressed in a separate paper. The Institutional Review Board at Oregon Health & Science University approved the Experimental Protocol and all subjects gave their informed consent prior to participation in experiments.

Experimental protocol

Figure 1A shows the trial conditions for each experiment. All trials consisted of a pre-incline period when the support surface was horizontal, a during-incline period when the surface was inclined, and a post-incline period when the surface was again horizontal. Each experiment included a standard condition of 2.5 minutes of stance on a 5°-toes-up inclined surface. Experiment 1 varied the duration of surface inclination (0.5, 1.25, 2.5 and 5 minutes), Experiment 2 varied the direction of surface inclination (toes-up, toes-down, right-side-up), and Experiment 3 varied the magnitude of surface inclination (2.5°, 5°, 7.5°, and 10°). For all experiments, trials began with a 1- to 2-minute pre-incline

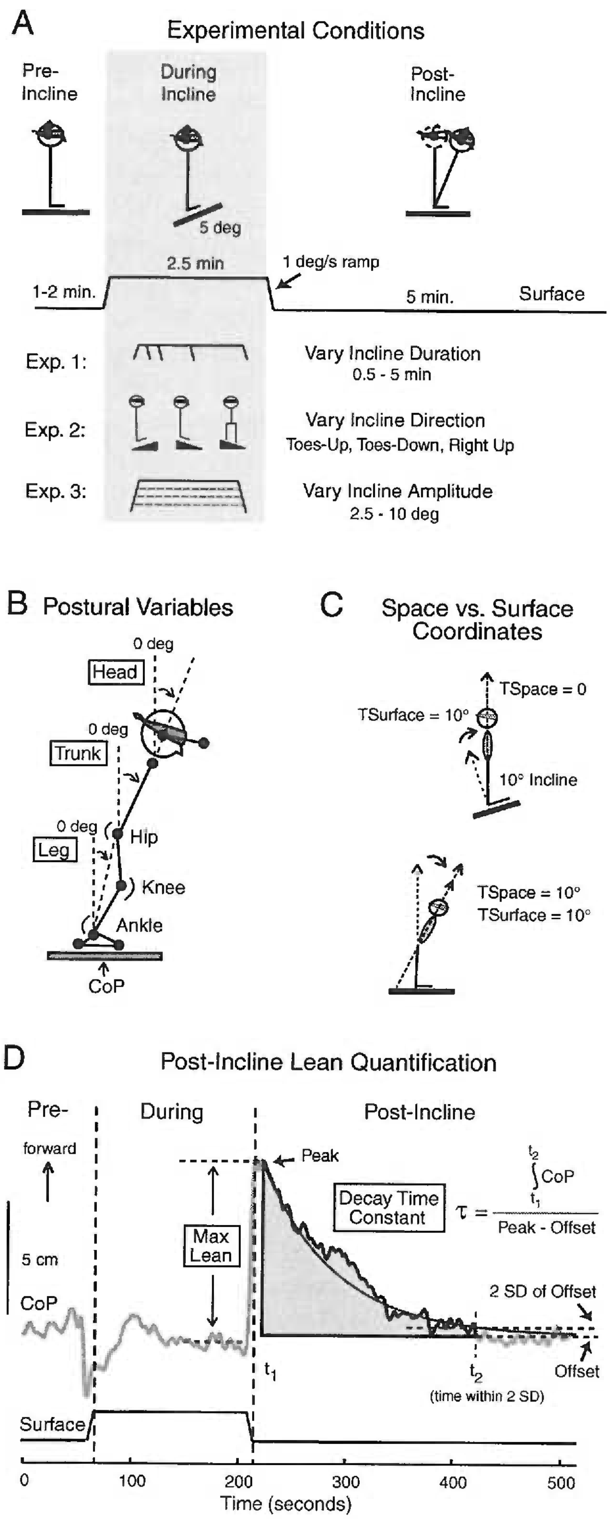

FIG. 1. Experimental protocol and dependent variables. FIG. 1A shows the standard experimental condition that was included in each experiment. The figure also shows how the standard condition was varied for the Duration, Direction and Amplitude experiments. The standard condition consisted of a 2.5-min period of stance on a 5°-toes-up inclined surface, preceded by a 1-min pre-incline period and followed by a 5-min post-incline period of stance on a horizontal surface. Gray shading indicates the period during which the surface was inclined. FIG. 1B shows the marker set-up (black circles) for Motion Analysis data capture and defines body segment angles (head, trunk, leg) and joint angles (ankle, knee, hip). Arrows indicate the positive going direction for segment angles. FIG 1C illustrates how segment angles were calculated relative to space (gravity), and to the support surface. Trunk segment relative to space (TSpace) and Trunk segment relative to the surface (TSurface) are shown. FIG. 1D illustrates how the post-incline characteristics were quantified, showing CoP data as an example. The maximum lean (Max Lean) was defined as the maximum change in amplitude between the peak displacement in the post-incline period less the mean position during the last 30 seconds of the during-incline period. The decay time constant was calculated by integrating the area under the curve from the time of the peak lean to the time when data stayed within 2 SD of the final position (offset) for at least 10 seconds

period and ended with a 5-minute post-incline period. The total length of a trial ranged from 7.5 to 15 minutes, with the length dependent on the incline-duration condition. The support surface rotated between the horizontal and inclined positions at a constant velocity of 1°/s, with the axis of rotation at approximately ankle height. Surface rotations were slow in order to avoid sharp accelerations that could trigger fast proprioceptive-triggered balance responses.

Subjects were blindfolded to eliminate visual information and wore headphones to remove auditory information that could influence postural orientation. In addition, a short story audiotape was played through the headphones in order to distract each subject's attention away from postural alignment. Subjects were instructed to: 'stand in a relaxed way; listen to the story and try not to pay attention to your posture. Do not resist any pull or tendency to lean if it occurs'. Subjects stood with head facing forward, arms crossed in front of the chest, and feet spaced a comfortable, self-selected distance apart, approximately hip width. Foot placement for each subject was kept constant across all trials. Subjects wore a safety harness that was tethered to an overhead beam to ensure safety during trials. The safety harness was adjusted so that it gave no directional/spatial cues for postural alignment. A research assistant stood near the subjects to ensure safety during the trials.

Experiment 1: Duration. Experiment 1 investigated how the duration of stance on a 5°-toes-up inclined surface affected the amplitude and the decay of the post-incline lean. Four durations were tested: 0.5-, 1.25-, 2.5-, and 5-minute periods. The period of surface inclination was preceded by a 2-minute pre-incline period and followed by a 5-minute post-incline period. For the 5-minute incline-duration, we extended the post-incline period to 10 minutes, anticipating that the duration of the after-effect might increase as the duration of stance on the incline increased. We chose an upper limit of 5 minutes for the incline-duration because, under this condition, subjects stood in one place for 17 minutes and longer time periods introduced excessive discomfort and fatigue. Subjects participated in 3 trials for each of the 4 incline-duration conditions, resulting in a total of 12 trials per subject. The duration of inclination was randomized across the 12 trials. Trials were scheduled so that an individual subject participated in no more than 1 trial per day and no more than 3 trials per week in order to avoid carry-over or learning effects.

Experiment 2: Direction. Experiment 2 varied the direction of surface inclination in order to determine whether the direction of the post-incline lean always maintained the relative body-to-surface alignment that subjects had adopted while standing on the incline. All trials consisted of 2.5 minutes of stance on a 5°-inclined surface that was preceded by a 2-minute pre-incline period and followed by a 5-minute post-incline period. Subjects participated in one trial for each of 3 incline-direction conditions, toes-up, toes-down, and right-side-up. Each trial was conducted on a separate day. Trial order was randomized.

Experiment 3: Amplitude. Experiment 3 varied the amplitude of toes-up surface inclinations (2.5°, 5°, 7.5°, and 10°) to determine if larger amplitude inclinations of the support surface would result in larger amplitude leaning in the post-incline period. All trials consisted of a 2.5-minute period of stance on a toes-up inclined surface that was preceded by a 1-minute pre-incline and followed by a 5-minute post-incline period. Each subject participated in 3 trials for each of the 4 incline-amplitude conditions, for a total of 12 trials. The 3 trials of the same incline-amplitude were conducted within one day and were scheduled at least 2 hours apart. The order in which the different amplitude conditions were presented to each subject was randomized.

Data collection and analysis

All 3 experiments used CoP data, low-pass filtered at 0.1 Hz, to obtain an overall representative measure of postural orientation. Experiment 1 (Duration) and Experiment 3 (Amplitude) measured trunk and leg segment orientation to quantify the degree to which different body segments aligned to the surface and to gravity. Experiment 3 also measured orientation of the head, shank, and whole body CoM, position of the hip, knee, and ankle joint angles, and EMG activity in the leg and trunk muscles. All data were analyzed in the sagittal plane, except for data from the right-side up incline trials of Experiment 2, which were analyzed in the frontal plane.

We quantified the strength of the post-incline lean with two main variables. We calculated the decay time constant of the return from leaned to upright postural alignment to quantify the duration of post-incline leaning. We calculated the maximum amplitude of the lean away from upright to quantify the magnitude of post-incline leaning. The decay time constant and the maximum lean were calculated for several different representative measures of postural orientation that included the CoP, the CoM, the body segments, and the joint angles. In addition to characterizing the amplitude and the decay of the post-incline lean, we also compared how postural alignment and EMG activity changed across the pre-, during-, and post-incline periods.

Center of pressure. The CoP was calculated from vertical force data recorded at 50 Hz. Forces were recorded from a single-plate force platform with 4 vertical force sensors for Experiments 1 and 2 (Duration and Direction) and from a dual-plate force platform with 8 vertical sensors for Experiment 3 (Amplitude). The CoP signal was separated into a low-frequency component (< 0.1 Hz) to assess slow changes in the CoP signal related to the postural set point, and a high frequency component (0.1 – 10 Hz) to assess the faster, corrective control around the set point (Gurfinkel 1995a, Lestienne and Gurfinkel 1988, Fransson et al. 2000). First, the low frequency CoP was extracted from the raw data with a 0.1 Hz low-pass, recursive, 2nd order Butterworth filter. The 0.1 Hz filter cut-off rate optimally preserved the slow-rate peaks and valleys of the CoP with minimal distortion, while still eliminating the fast fluctuations of stabilizing postural corrections. Next, we extracted the high frequency component of the CoP by low-pass filtering the raw data at 10 Hz with a recursive, 2nd order Butterworth filter, and then subtracting the low frequency component.

Kinematics. The orientation of the body segments, the position of the joint angles, and the location of the whole body CoM were determined from position data and trigonometric relationships. Position data were sampled at 10 Hz. The derived variables of segment orientation and joint angles were low-pass filtered at 0.1 Hz to characterize slow changes in postural orientation.

For Experiment 1 (Duration), we calculated trunk and leg segment orientation. The trunk was defined as the segment between the hip and the shoulder and the leg was defined as the segment between the ankle and the hip. The positions of the hips and shoulders were measured with lightweight metal rods that were attached to the subject at shoulder or hip height on one end and attached to a potentiometer on the other end.

For Experiment 3 (Amplitude), we calculated the orientation of the head, trunk, leg, shank and whole body CoM and the position of the hip, knee, and ankle joint angles. To determine segment and joint angles, we used a 4-camera motion analysis system (Motion Analysis, Santa Rosa, CA) to record 8 reflective markers placed on the left side of the body (Fig. 1B). Body segments were defined as follows: 1) head segment: forehead to external auditory meatus, with the forehead marker placed on a 5.5 cm extender to increase the length of the head segment, 2) trunk segment: hip to shoulder; 3) leg segment: ankle to hip; and 4) shank segment: ankle to knee. Orientation of each body segment in the sagittal plane was calculated with respect to gravity (space) and with respect to the support surface. Segment-re-space orientation was defined with respect to gravity-vertical, with '0' representing vertical and positive angles representing forward lean (Fig. 1B). Segment-re-surface orientation was defined as the angle between the body segment and the surface, with '0' representing the mean segment-to-surface position during the baseline period and positive angles representing forward lean (Fig. 1C).

Ankle, knee and hip angles were calculated based on the location of 3 markers, with the middle marker placed approximately at the axis of joint motion (Fig. 1B). The ankle angle was calculated using knee-ankle-toe markers, the knee angle was calculated using hip-knee-ankle markers, and the hip angle was calculated using shoulder-hip-knee markers. Hip and knee flexion and ankle dorsiflexion were defined as positive-going into the more acute direction, from a '0' based on the subject's mean postural alignment during the pre-incline period.

Whole body CoM location in the sagittal plane was calculated as a weighted sum of the CoM location of individual body segments using a 5-segment model (head, trunk-arms, thighs, shanks, feet) of a subject standing with arms crossed in front of the chest. The mass of individual body segments was estimated using anthropometric measures and methods proposed by Vaughn and colleagues (1991) and Chandler and colleagues (1975). Ratios for calculating location of CoM as percentage of the segment length are from Dempster (Winter 1990). Symmetry was assumed for left and right lower extremity alignment. CoM data are reported as angular changes with respect to the ankle joint.

EMG. We recorded surface EMG of 7 representative ankle, knee and lower trunk muscles in order to determine whether the post-incline lean was due to an attempt to maintain the immediately prior level of muscle activity or whether EMG activity resembled EMG changes that occur during after-contraction effects. Bipolar silver-silver electrodes were place 1.5 to 2 cm apart on each of the following muscles on the left side of the body: soleus, medial gastrocnemius, anterior tibialis, medial hamstrings, quadriceps (rectus femoris), paraspinals (iliac crest level), and rectus abdominis. Prior to sampling, raw EMG was amplified 100 X near the electrodes, band-pass filtered between 70-2000 Hz, amplified again between 20-100X, adjusted for each muscle, and rectified.

The smoothed, rectified EMG signal was then sampled at 240 Hz and smoothed with a low-pass cut-off of 100 Hz.

Decay time constant. To quantify the duration of the post-incline lean, we modeled the data as a first order exponential and calculated the decay time constant for the return from a leaned to an upright postural alignment. The decay time constant was calculated with a method previously used by Cohen and colleagues (1977) to find the dominant decay time constant of optokinetic after-nystagmus. We chose this method rather than curve fitting using single exponential equation because the decay for some subjects was more complex than a single exponential function. The method of calculating the decay time constant, illustrated in Fig. 1D, divides the area under the data trajectory by the peak lean: *Tau = Area/(Peak-Offset)*. *Peak* is defined as the peak displacement that occurs after the surface rotates to a new position relative to the final offset position. The *Offset* is defined as the mean position during the last 30 seconds of the post-incline period. The *Area* was calculated by integrating from the time of *Peak* lean to the time when the data returned to within 2 SD of the *Offset* for at least 10 consecutive seconds. The *Offset* was subtracted from the CoP time series prior to integration. The method of calculating the decay time constant was modified for trials when subjects leaned with near constant amplitude for several seconds before they began to return toward baseline postural alignment. We refer to the prolonged holding of the maximally leaned position as a plateau. When a plateau occurred, the end of the plateau period defined the decay onset and the start of integration.

Maximum lean. To quantify the amplitude of the post-incline lean, we calculated the maximum lean, defined as the peak displacement in the post-incline period with respect to the mean position during the last 30 seconds of stance on the incline surface (Fig. 1D). We waited until 5 seconds after the surface rotated to a new position before identifying the peak displacement because we were interested in the reference position subjects were trying to hold rather than transient body movements made to compensate for instability imposed by the surface rotation. The maximum lean was calculated for CoP, CoM, and body segment angles (head, trunk, leg, shank). For Experiments 1 and 2 (Duration and Direction), the maximum lean for CoP data was normalized as a percentage of maximum voluntary lean: *Maximum Lean CoP = (Peak - Baseline)/(Peak Voluntary Lean – Baseline) x 100.* For Experiment 3 (Amplitude), the maximum lean for CoP data was normalized as a percentage of foot length: *Maximum Lean CoP = 100 x (Peak-Baseline)/(Foot Length).*

Stability around the postural set point. In order to quantify stability around the postural set point, we calculated the RMS and mean velocity of the high frequency component of the CoP (0.1–10 Hz). RMS and mean velocity were calculated for consecutive 15-second epochs during the pre-, during-, and post-incline periods to identify the time when stability around the postural set point returned to pre-incline values after the surface rotated to a new orientation.

Mean postural alignment. To compare how changes in surface conditions, from horizontal to inclined and from inclined to horizontal, affected postural orientation, we calculated the mean position at 5 different times during each trial: 1) pre-incline period; 2) beginning of the during-incline period; 3) end of the during-incline period; 4) beginning of the post-incline period and 5) end of the post-incline period. Mean position was calculated across 15-second time periods, except for the pre-incline period, for which mean position was calculated across a 30-second time period.

Statistical analysis. Statistical analyses were performed using Statistica and SPSS software with significance set at $\alpha = 0.05$ for all comparisons. Coefficients of variation were calculated to compare within-subject to between-subject variability of the post-incline lean across repeated trials. Repeated Measures ANOVA with Sheffé post-hoc analyses were used to compare how the decay time constants and the maximum lean amplitudes were affected by direction, duration, and amplitude of surface inclination. The effects of incline amplitude on trunk and head maximum lean amplitudes were evaluated using MANOVA to bypass problems of compound symmetry and sphericity. Head and trunk maximum lean variables were log-transformed prior to MANOVA analyses to equalize variance, which increased as incline amplitude increased. Linear regression was performed to determine the slope of the relationship between incline amplitude and maximum lean for body segment angles. Whenever group means are reported to compare differences across condition, we also report the standard error.

Results

Postural after-effect of stance on an inclined surface: long lasting lean

Stance on a toes-up inclined surface with eyes closed led to a long-lasting postural after-effect of forward whole body lean, involving the head, trunk, and legs. Figure 2A shows results from a 5°-toes-up incline trial for a representative subject. The subject stayed aligned near baseline, upright, posture while standing on the incline. However, when the surface returned to horizontal alignment, the subject leaned with a direction and amplitude that maintained trunk-to-surface relative alignment as if still standing on the incline. Figure 2B shows that after standing on a 5°-inclined surface, the average amplitude of the trunk lean in the post-incline period was near 5° (group mean trunk maximum lean of 6.1 ± 0.9°). The head leaned slightly more than the trunk (group mean head maximum lean of 7.2 ± 1.6°) and was more variable across subjects, with some subjects showing less and some showing more head than trunk lean. Since the head was leaned in the post-incline period, subjects had otolith information about head tilt with respect to gravity that could have indicated leaning. The large whole body lean resulted in a large forward displacement of the whole body CoM, and thus of the CoP, as can be seen in Figure 2B. Thus, subjects also had pressure information from their feet that could have indicated leaning.

In the group of 7 subjects who participated in Experiment 3 (Amplitude), the post-incline CoP decay time constant lasted 59.9 ± 7.4 s for the 5°-condition and decayed exponentially to baseline (pre-incline) alignment. Thus, the average duration of the lean lasted for 3 minutes (3 times the decay time constant). Figure 2C shows that the decay of the lean was similar for several different postural variables (trunk, CoM, CoP), indicating

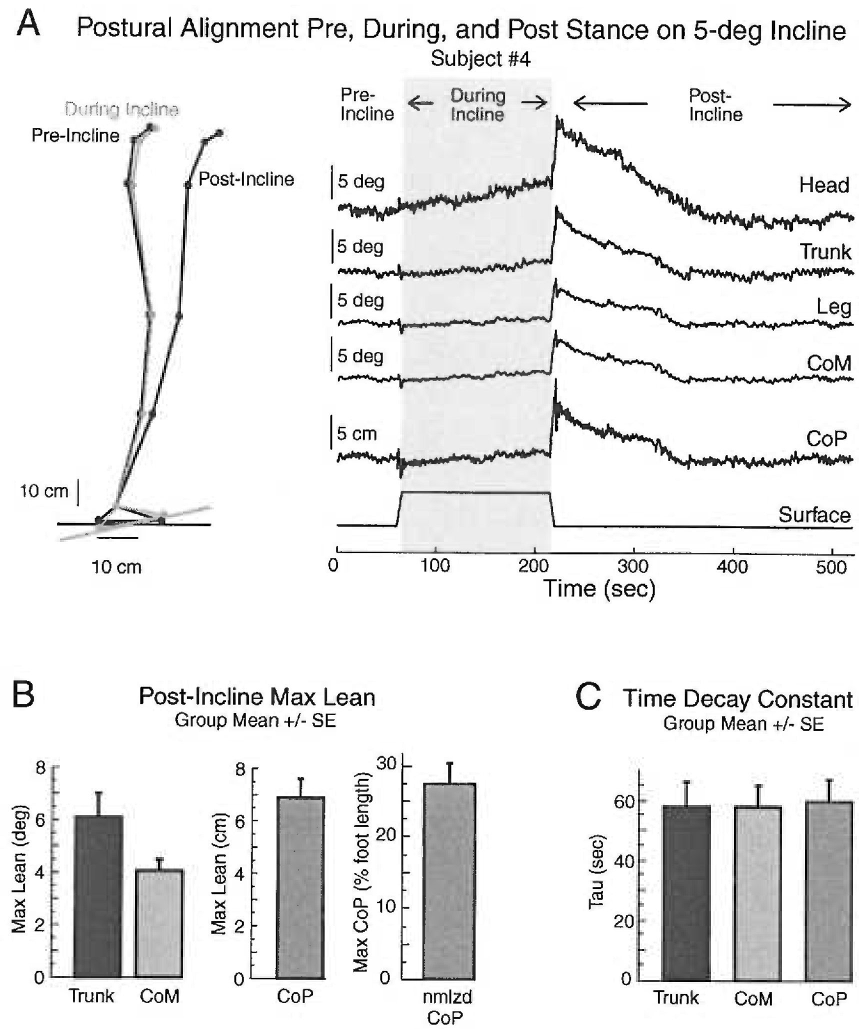

FIG. 2. The large amplitude, long lasting whole body lean after 2.5 min. of stance on a 5°-toes-up inclined surface is shown in a reconstructed stick figure and in segment angle, CoM and CoP data for a representative subject in FIG 2A. Leaning did not occur when the surface orientation changed from horizontal to inclined. The post-incline lean involved large amplitude trunk and CoM lean and large CoP displacement. FIG. 2B shows the group mean amplitudes of trunk, CoM, and CoP maximum lean that followed stance on the 5°-toes-up incline condition of Exp. 3 (Amplitudes). The group mean decay time constant for the same data set is shown in FIG 2C. The lean lasted for 3 minutes on average (3 X decay time constant) for the 5°-incline condition. The decay time constant was similar for different postural variables (C).

that the lean involved the whole body and that the decay of any one of these postural variables provides a representative measure of persistence of the leaning after-effect.

Figure 3 shows that individual subjects were highly consistent in their post-incline behavior across trials. Figure 3A shows CoP data from 6 trials for 2 representative subjects. The 6 trials were collected as parts of separate experiments (Experiments 1, 2, and 3), but the adapting condition was identical for all trials: 2.5-minute period of stance on a 5°-toe-up inclined surface. The trials shown in Figure 3A were separated by up to a year apart, yet the amplitude and the decay of the post-incline lean remained highly consistent. Figures 3B (decay time constant) and 3C (maximum lean amplitude) show that within-subject consistency of the post-incline lean was high for all subjects. Further, variability in characteristics of the post-incline lean was higher between-subjects than within-subject, as can be seen by comparing the respective coefficients of variation. Figure 3C shows that one subject's relative change in alignment from the during- to post-incline periods was much smaller than other subjects, with an average CoP maximum lean of 11.3 % of foot length as compared to the group mean of 30.5 ± 1.2 % of foot length for the remaining 6 subjects. When the initial position during baseline was taken into account, and the CoP maximum lean was determined as a location along the foot length rather than as a relative change in alignment from the during- to post-incline periods, this subject's lean amplitude was similar to other subjects, with a post-incline CoP location of 72.3 % of the foot with respect to the heel as compared to a mean post-incline CoP location of 70.2 ± 1.2 % for the remaining 6 subjects.

When subjects leaned in the post-incline period, the lean maintained the trunk-to-surface relative alignment as if subjects still stood on the inclined surface. Comparison

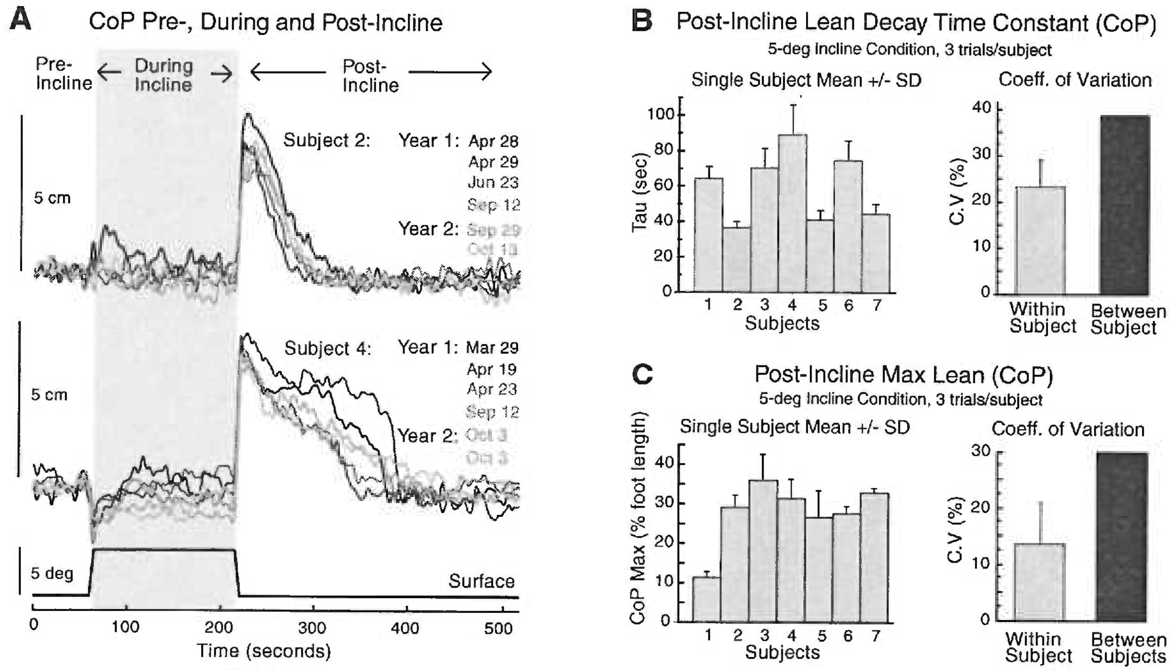

FIG 3. Within-subject consistency and between-subject variability of the post-incline lean. The decay and the amplitude of the post-incline lean were highly consistent within individual subjects, but varied among subjects. FIG. 3A shows CoP data from 6 different trials of 2 representative subjects for the 5°-toes-up, 2.5 min, incline condition. Trial dates are shown, with over a year elapsing between the 1st and last trials. Gray shading indicates the period during which the surface was inclined. FIG. 3 also shows the within-subject variability (mean ± SD for 3 trials) of the post-incline lean decay time constant (B) and maximum lean amplitude (C) for CoP data under the 5°-toes-up condition for all 7 subjects who participated in Exp. 3 (Amplitudes). The CoP maximum lean was normalized as a percentage of foot length. The variability of the post-incline lean was greater between than within-subjects as can be seen in the comparison of the between-subject and the within-subject Coefficients of Variation for the CoP decay time constant (B) and the CoP maximum lean (C).

of how different postural variables changed from the during-incline to the post-incline periods shows that the trunk-to-surface relationship remained the same (Fig. 4A), but not the trunk-to-space relationship (Fig. 4B). Plots of joint angle alignment show that the ankle angle was only partially maintained from the during- to the post-incline period (Fig. 4C). While all subjects leaned forward after stance on a toes-up inclined surface, subjects varied from one another with respect to the local joint kinematics adopted to achieve the leaned posture. Two subjects leaned with the whole body with most local joint change occurring at the ankle joint, two subjects leaned with the trunk more than the leg through a combination of ankle dorsiflexion and hip flexion, and the remaining three subjects leaned mainly with the trunk through hip flexion, the leg segment staying near upright.

Long lasting and large amplitude lean occurs only in the post-incline period

The long lasting and large amplitude lean occurred only when the surface changed from an inclined to a horizontal position and did not occur when the surface changed from a horizontal to an inclined surface, as can be seen in individual subject data in Figures 2 and 3 and in grouped subject data in Figure 4. When comparing the alignment of the trunk and the leg relative to space during the first 15-s of surface inclination to the last 15-s of surface inclination, there were no significant differences, with an average difference of $0.1 \pm 0.4°$ for the trunk and $0.3 \pm 0.3°$ for the leg under the 5°-incline condition. Thus, subjects adopted a new, steady state postural alignment within the first 15-s of the during-incline period. In contrast, under the same 5°-incline condition, the difference between the first and last 15-s of the post-incline period averaged $5.1 \pm 0.8°$ for trunk orientation and $3.7 \pm 0.5°$ for leg orientation.

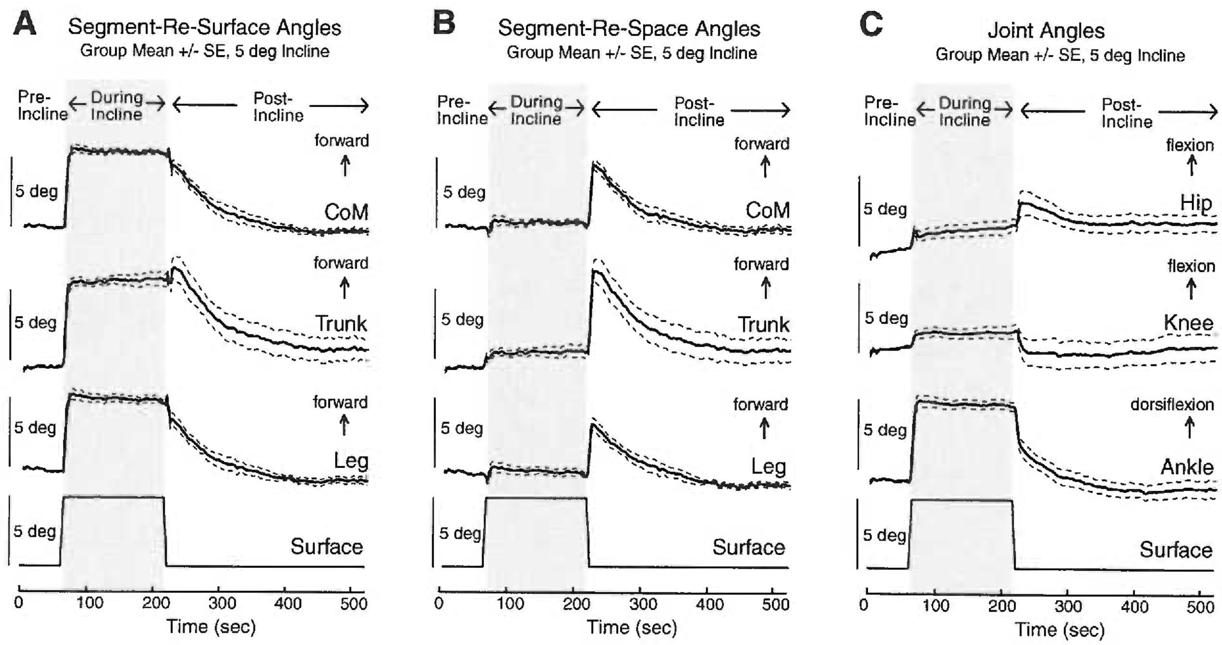

FIG 4. Segment-re-surface angle, segment-re-space angle, and joint angle data for the 5°-toes-up inclined condition from Experiment 3. Solid traces show the grand averaged data across all 7 subjects, 3 trials each, and dotted traces show the SE. Gray shading indicates the period during which the surface was inclined. Post-incline leaning maintained the immediately prior body-to-surface relative alignment (A), but did not maintain the body-to-space (gravity) relative alignment (B) or hip or knee angle configurations (C) from the during-incline to post-incline periods. Ankle angle was only partially maintained from the during to post-incline periods (C).

Ankle joint angles, but not body segment angles with respect to gravity, were altered as compared to baseline when subjects stood on the inclined surface. For all subjects, when standing on the incline, ankle joint dorsiflexion nearly matched the angle of surface inclination (Figure 4A). The dorsiflexed ankle posture allowed the body segments to maintain a similar orientation with respect to gravity as during the baseline period when the surface was horizontal. The knee and hip joints also flexed a small amount, always less than 3°, when subjects stood on the incline. Subjects varied from one another in how their trunk and leg alignment changed when standing on the inclined as compared to the horizontal surface. Six subjects leaned their trunks slightly forward while on the incline and one subject leaned slightly backward, with a group average change in trunk position of 1.1 ± 0.5° forward lean under the 5°-incline condition. Although small in amplitude, this forward lean was significantly different from trunk alignment during the pre-incline period ($p < 0.05$). Alignment of the leg in space was leaned forward slightly for 5 subjects and backward slightly for 2 subjects, with a group average change in leg alignment of 0.6 ± 0.4°.

Long lasting after-effects on low, but not high, frequency components of the CoP

Figure 5 shows that the low and high frequency components of the CoP were affected differently by exposure to stance on an incline. The high frequency CoP, which we used to quantify stability around the postural set point, showed transient changes in RMS (Fig. 5B) and in mean velocity (Fig. 5C) after the surface changed orientation. The RMS and mean velocity of the high frequency CoP returned to baseline values within 15 seconds. In contrast, the low frequency CoP, which we used to estimate changes in the

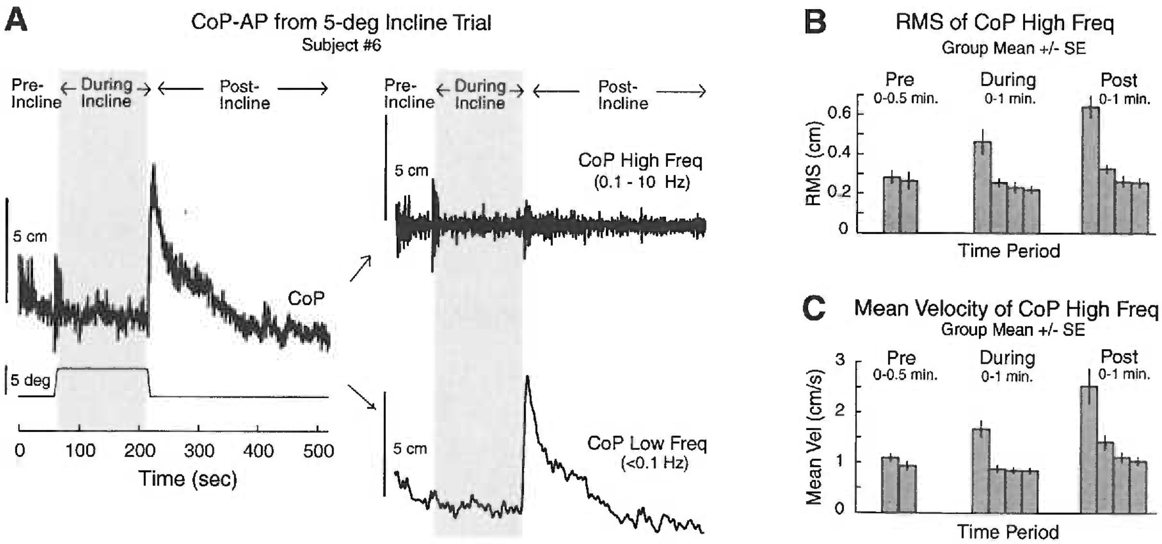

FIG 5. The after-effects of stance on an inclined surface on variability around the postural set point. The duration of after-effects was different for the high (0.1-10 Hz) and low (< 0.1 Hz) frequency components of the CoP data. FIG 5A shows decomposition of a representative subject's CoP data into high and low frequency components. This representative CoP data was collected under the 5°-toes-up, 2.5-min incline condition. In the post-incline period, the postural set point, or the low frequency CoP data, took minutes to decay back to baseline values. In contrast, stabilizing activity around the set point was affected only transiently by the preceding incline condition. The high frequency CoP data were back to baseline values within 15 seconds. Gray shading indicates the period during which the surface was inclined. FIG. 5B and 5C show the fast decay of the RMS and mean velocity of the high frequency CoP to baseline for all 7 subjects who participated in Experiment 3. For each of the 3 time periods, pre-, during- and post-incline, the first bar shown is the mean CoP location during the initial 15 seconds of the period. Remaining bars represent the mean CoP location for consecutive 15-second epochs.

postural set point, took 1 to 4 minutes to return to baseline in the post-incline period. Thus, although stance on an incline led to a long-lasting after-effect on postural orientation, the more dynamic, corrective activity around the set point was only briefly affected.

Effect of incline duration on the post-incline lean

Figure 6 shows how duration of stance on the inclined surface affected the persistence and the magnitude of the leaning after-effect. All 7 subjects showed a large, long-lasting post-incline lean after as few as 30 seconds of stance on an incline. The effects of increasing the duration of surface inclination varied across subjects. As duration of stance on an incline increased, 5 subjects showed an increase in the decay time constant, while 2 subjects showed no change. The increase in the decay time constant is shown in representative subject data in Figure 6A and in the group mean data in Figure 6B and Table 1. The group mean decay time constant increased significantly for the 5-minute incline-duration condition compared to other conditions ($p < 0.05$). Of the 5 subjects who showed longer time constants when incline duration increased, 3 showed the increase in the decay time constant from the 2.5- to the 5-minute condition, like the group mean data, while 2 showed more gradual increases across the four duration conditions.

The post-incline leaning of 5 out of 7 subjects showed plateau periods, in which the maximally leaned position was held for a variable length of time (4 to 145 s) before the onset of decay toward baseline. Data from a subject who leaned with a long lasting plateau period is shown in the bottom of Figure 6A. Of the 5 subjects who demonstrated

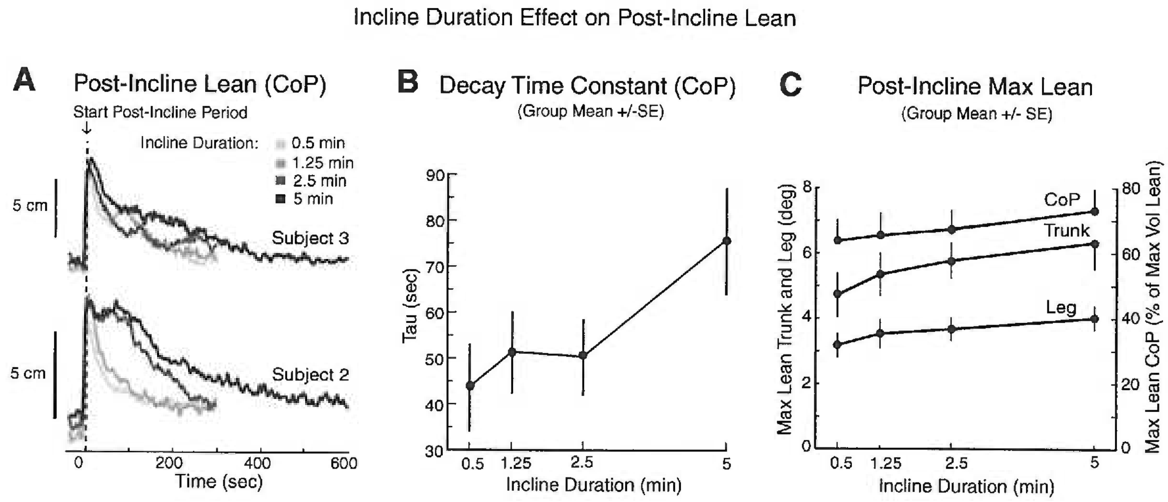

FIG 6. Effects of duration of stance on an incline upon the post-incline lean's decay time constant and maximum lean. FIG. 6A shows how increases in incline duration affected the post-incline CoP data for two individual subjects. Each data trace represents an average of 3 trials for the last 30 seconds of the during-incline period and the entire post-incline period. The dotted line indicates the beginning of the post-incline period. Subject 2's post-incline data (6A, bottom) shows plateau periods under the two longest duration conditions. During the plateau period, the subject maintained the maximally leaned position for a period of time prior to the onset of the lean's decay toward upright. FIG. 6B shows that the group mean CoP decay time constant increased significantly when incline duration increased from 2.5 to 5 minutes. FIG. 6C shows how increases in incline duration affected the amplitude of the maximum lean for the CoP, trunk, and leg segment data. The maximum lean was similar across duration conditions. The trunk leaned near 5° after as few as 30 seconds of stance on a 5°-inclined surface. The group mean CoP maximum lean values were normalized as a percentage of maximum voluntary lean.

TABLE 1 *Post-incline Lean Decay and Maximum Amplitude for Exp. 1 (Durations)*

Incline Duration	Decay Time Constant *(CoP)*	CoP Max Lean *(% voluntary lean)*	Trunk Max Lean
0.5 min	43.7 ± 9.3	63.7 ± 3.9 %	4.7 ± 0.4 deg
1.25 min	51.2 ± 8.6	65.4 ± 4.2 %	5.4 ± 0.7 deg
2.5 min	50.2 ± 8.0	67.3 ± 3.6 %	5.8 ± 0.6 deg
5 min	75.6 ± 11.4	73.1 ± 3.9 %	6.3 ± 0.8 deg

Values are means ± SE

a plateau period, 4 subjects showed an increase in the incidence and 2 subjects showed an increase in the duration of the plateau periods when incline duration increased from 1.25 to 2.5 and from 2.5 to 5 minutes.

Figure 6C and Table 1 show that, on average, when incline duration increased, the amplitude of the post-incline lean increased by small increments. This increase in the amplitude of leaning with increased incline-duration was observed in 5 subjects, whereas 2 subjects showed no change. The difference in the maximum lean of the trunk, averaged across subjects, between the shortest, 30-second condition to the longest, 5-minute condition, approached significance ($p = 0.065$), increasing from $4.7 \pm 0.7°$ to $6.3 \pm 0.8°$. The difference in maximum lean of the leg segment was small, but significant ($p < 0.05$), increasing from $3.2 \pm 0.4°$ to $4.0 \pm 0.4°$. The difference in the CoP maximum lean also approached significance when comparing the shortest to the longest incline-duration condition ($p = 0.10$).

Effect of incline direction on the post-incline lean

Figure 7A compares the post-incline CoP data of a representative subject when tested under each of the 3 directions of surface inclination. The direction of the post-incline lean was always in a direction that maintained the immediately prior body-to-surface relative relationship. All 7 subjects leaned forward after standing on a toes-up surface-incline and rightward after a right-side-up surface-incline. Five out of seven subjects leaned backward and two subjects did not lean after standing on a toes-down surface-incline. Figures 7B and 7C show that the group mean decay and amplitude of the post-incline lean were similar for the toes-up and lateral directions, but smaller for the

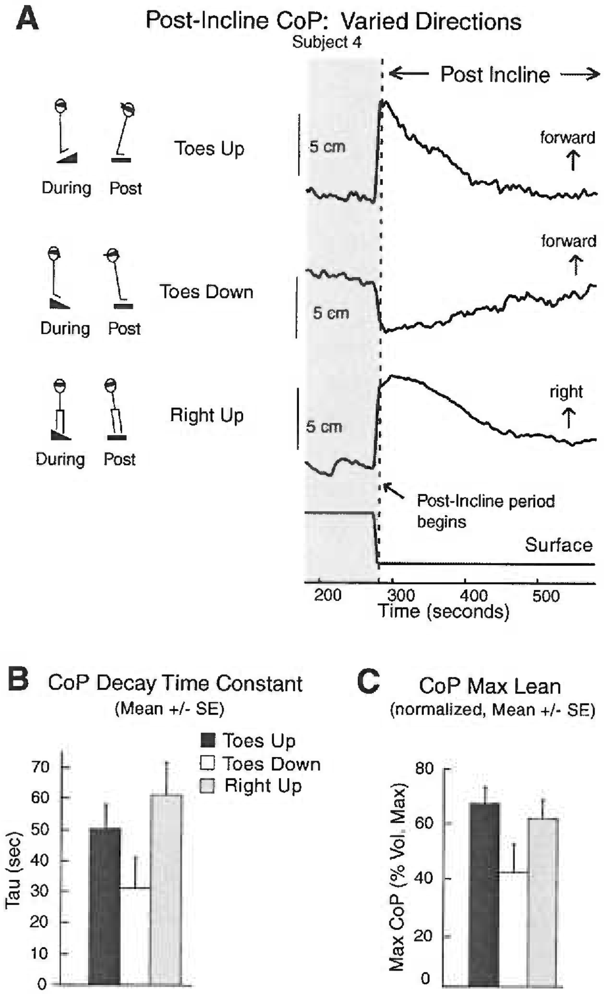

FIG. 7. Incline direction determined the direction of the post-incline lean. Leaning always occurred in a direction that maintained similar body-to-surface relative alignment as when subjects stood on the incline. Post-incline CoP data from a representative subject (A) shows that forward lean followed stance on a toes-up incline, backward lean followed a toes-down incline, and rightward lean followed a right-up incline. The shaded area indicates the end of the during-incline period and the vertical dotted line indicates the start of the post-incline period. The post-incline lean lasted for minutes for all three incline directions. The group mean decay time constant (B) and the group mean maximum lean (C) calculated from the CoP data were similar for the toes-up and right-side-up conditions, but the lean decayed faster and was smaller for the toes-down condition. The CoP maximum lean data are normalized as a percentage of maximum voluntary lean.

toes-down direction. Although post-hoc comparisons for the CoP decay time constant showed no differences between conditions, the difference between the toes-down and the lateral conditions approached significance ($p = 0.09$). The group mean CoP decay time constants for the toes-up, the lateral, and the toes-down directions were 50.2 ± 8.0, 61.3 ± 10.5, and 31.2 ± 9.8 seconds, respectively. Post-hoc comparisons for the CoP maximum lean showed a significant difference only between the toes-up and toes-down conditions ($p < 0.05$). The group mean CoP maximum leans for the toes-up, the lateral, and the toes-down directions were 67.3 ± 6.1%, 61.9 ± 6.7%, and 42.1 ± 10.1% of maximum voluntary lean, respectively.

Effect of incline amplitude on the post-incline lean

Figure 8A shows how varying the amplitude of surface inclination affected the amplitude of post-incline leaning for a representative subject. As the amplitude of surface inclination increased, the upper body, but not the lower body, leaned with increasing amplitude in the post-incline period. Figures 8C and 8D show that the group mean trunk and head maximum lean, but not the leg, the CoM, or the CoP maximum lean, increased systematically and significantly as the amplitude of surface inclination increased (trunk maximum lean: Wilks' Lambda = 0.085, $p < 0.05$; head maximum lean: Wilks' Lambda = 0.170, $p < 0.05$). On average, the amplitudes of the trunk and head post-incline lean were slightly greater than the amplitude of the preceding surface inclination (Table 2). Comparing the slope of how the post-incline maximum lean changed as a function of incline amplitude provides a gain estimate, and when averaged across all 7 subjects, this value was near 1 for both the trunk (0.9 ± 0.4) and the head (0.9

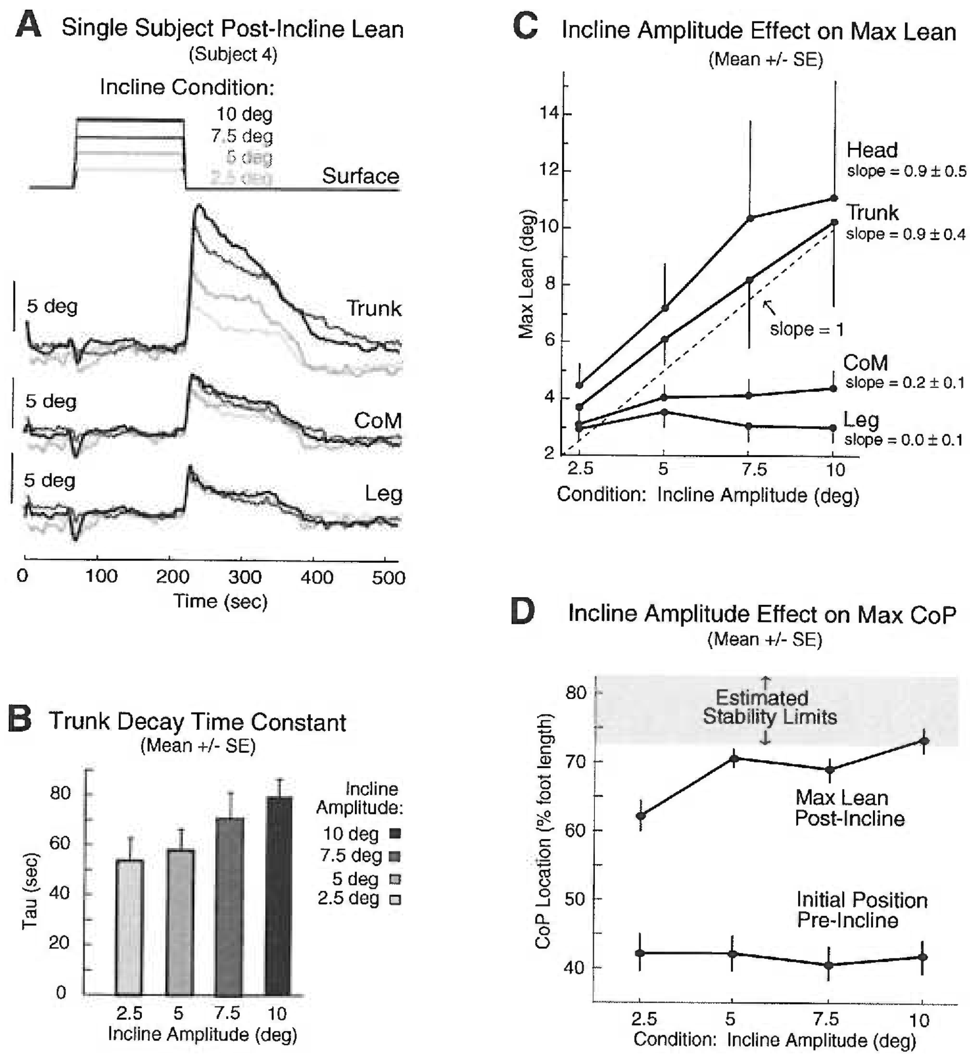

FIG 8: Effects of the amplitude of surface inclination on the post-incline lean's decay time constant and maximum lean. As the amplitude of surface inclination increased, the amplitude of lean in the upper body, but not the lower body, increased, as shown in data from trials of a representative subject (A) and in group mean maximum lean data (C, D). The maximum lean of the head and trunk increased linearly with a slope near 1 as the amplitude of surface inclination increased, while the maximum lean of the lower body saturated at the 5°-incline condition (C). After subjects stood on the larger amplitude surface inclinations of 5°, 7.5°, and 10°, they leaned with their CoP location approaching estimated postural stability limits, indicated by the gray shaded area (D). The post-incline lean decay lengthened as the amplitude of surface inclination increased (B).

TABLE 2 *Post-incline Lean Maximum Amplitude and Decay for Exp. 3 (Amplitudes)*

Incline Amplitude	Head Max (deg)	Trunk Max (deg)	Leg Max (deg)	CoM Max (deg)	Trunk Tau (s)
2.5 deg	4.5 ± 0.8	3.7 ± 0.4	2.9 ± 0.4	3.1 ± 0.3	53.7 ± 9.0
5.0 deg	7.2 ± 1.6	6.1 ± 0.9	3.5 ± 0.6	4.1 ± 0.4	57.7 ± 8.4
7.5 deg	10.4 ± 3.4	8.2 ± 2.4	3.1 ± 0.6	4.1 ± 0.6	70.7 ± 10.3
10.0 deg	11.1 ± 4.1	10.3 ± 3.0	3.0 ± 0.6	4.4 ± 0.6	79.2 ± 7.2

Values are means ± SE

± 0. 5) segments. Individual subjects varied widely from one another in the slope of the relationship between incline angle and maximum lean (Table 3).

In contrast to the increasing amplitude of upper body lean, the amplitude of lower body post-incline lean saturated under larger incline amplitude conditions, as shown in Figure 8C and Table 2. The group mean slope for the relationship between the leg's maximum lean and the amplitude of surface inclination was – 0.01 ± 0. 05. This relationship was non-linear for most subjects as shown by the low R^2 values of the linear regressions that are reported in Table 3. The post-incline maximum lean for the CoP and the whole body CoM also saturated at large incline-amplitude conditions. Figure 8D shows that the post-incline maximum lean of CoP displacement saturated at values near estimated stability limits for healthy subjects. The gray area in Figure 8D shows the range of reported stability limits for healthy young subjects who were asked to perform a maximal voluntary lean (Murray et al. 1975; Blaszczyk et al. 1994; Schieppati et al. 1994).

Figure 8B shows that the decay time constant increased as the amplitude of surface inclination increased. However, in post-hoc analyses, the increase in the decay time constant was significant only when comparing the 2.5° and 10° conditions ($p < 0.05$). Mean decay time constants for each amplitude condition are reported in Table 2. A plateau period, ranging from 7 to 48 seconds, occurred in the post-incline period for 5 out of 7 subjects and in 18% of all trials. Half of the trials with a plateau occurred at the largest, 10°-incline amplitude condition.

Subjects showed the large amplitude, long lasting leaning effect only in the post-incline period and not when first adapting to any amplitude of surface inclination.

TABLE 3 *Relationship Between Amplitudes of Surface Inclination and Maximum Lean*

	Head			Trunk			Leg		
	Slope	Offset	R^2	Slope	Offset	R^2	Slope	Offset	R^2
Subj 1	0.40	6.23	0.27	0.35	3.89	0.58	- 0.06	0.78	0.28
Subj 2	0.43	2.49	0.76	0.65	1.78	0.84	0.04	3.20	0.21
Subj 3	3.72	-2.03	0.97	2.98	- 2.67	0.98	- 0.28	4.56	0.72
Subj 4	1.31	2.97	0.94	1.04	2.39	0.91	- 0.02	4.5	0.50
Subj 5	0.44	2.80	0.74	0.29	2.61	0.78	0.16	2.65	0.80
Subj 6	0.01	3.03	0.01	0.03	2.24	0.07	0.06	3.47	0.12
Subj 7	0.16	2.02	0.34	0.79	1.03	0.72	0.06	3.10	0.09
Mean (± SE)	0.93 (0.49)			0.88 (0.37)			- 0.01 (0.05)		

Linear Regression: $y = mx+b$

y = *maximum lean;* m = *slope;* x = *incline condition;* b = *offset*

The changes in alignment of the trunk-in-space from the pre-incline to the during-incline periods were similar across incline amplitudes. When standing on the incline, subjects leaned their trunks forward an average of 1.0 ± 0.3°, 1.1 ± 0.3°, 1.2 ± 0.6°, and 0.8 ± 0.6° under the 2.5°-, 5°-, 7.5°-, and 10°-incline conditions, respectively. This result contrasts with the large effect of the incline-amplitude condition on the amplitude of the post-incline trunk lean shown in Figures 8C and 9C.

Leaning maintains the immediately prior trunk-to-surface relative alignment

Figure 9 shows that the post-incline lean maintained the same trunk-to-surface relative alignment that subjects had adopted while standing on the incline, but did not maintain the trunk-to-space relative alignment or the ankle angle. Head-to-surface relative alignment was also maintained from the during-incline to the post-incline periods. Like the ankle angle, the alignment of the whole leg segment and the location of the CoP and the CoM were not maintained from the during- to the post-incline periods when the adapting surface inclination was larger than 5° (Fig. 9 D-F). Thus, trunk and head relative alignment with respect to the surface showed the greatest adaptive after-effect of stance on an inclined surface.

Effects of surface inclination on EMG activity

Figure 10A shows how EMG activity changed across the pre-, during-, and post-incline periods for a representative subject when tested under the 5°-incline condition. The tibialis muscle was inactive throughout the trial, including when the subject stood on the inclined surface, except for a short-lasting period of increased activity when the

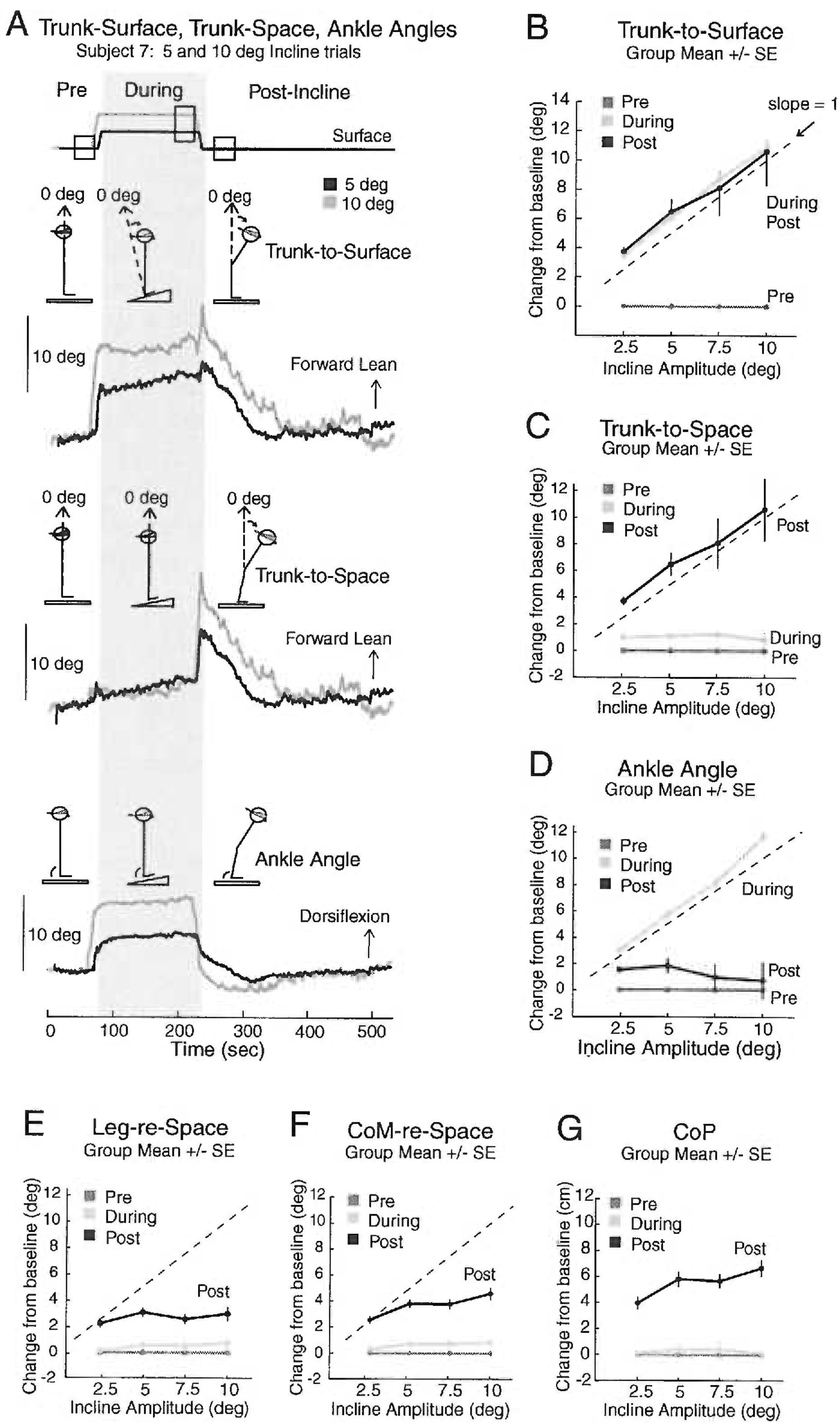
A Trunk-Surface, Trunk-Space, Ankle Angles
Subject 7: 5 and 10 deg Incline trials
Pre
During
Post-Incline
Surface
5 deg
10 deg
0 deg
Trunk-to-Surface
10 deg
Forward Lean
Trunk-to-Space
Ankle Angle
Dorsiflexion
Time (sec)
B
Trunk-to-Surface
Group Mean +/- SE
slope = 1
Change from baseline (deg)
Incline Amplitude (deg)
C
Trunk-to-Space
D
Ankle Angle
E
Leg-re-Space
F
CoM-re-Space
G
CoP
Change from baseline (cm)

FIG 9. Post-incline leaning maintained the same trunk-to-surface relative alignment, but not trunk-to-space, ankle angle, leg-in-space alignment or CoM or CoP location, adopted while standing on the inclined surface. Data from a representative subject for a 5°-incline (dark traces) and a 10°-incline (light traces) trial are shown in (A). Records are aligned at the onset of the post-incline period. Note that ankle angle is partially maintained from the during-incline to the post-incline periods for the 5°-, but not the 10°-incline condition. The plots in B-G compare how the mean value of different postural variables changed between the pre- and during incline periods and between the pre- and post-incline periods for all four incline amplitude conditions. The mean positions were calculated for 15-sec epochs at the end of the during-incline period and at the beginning of the post-incline period. The mean of the first 15-sec of the pre-incline period was then subtracted. Dashed lines indicate a slope of 1, indicating a 1:1 relationship between the adapting incline angle and change in alignment as compared to the pre-incline period. Each data point represents the group mean data for 7 subjects, 3 trials each.

surface initially rotated to a toes-up inclined position. Tonic postural extensor activity showed little change from the pre-incline to the during-incline period, but showed a large increase in activity in the post-incline period when the trunk was leaned forward. Figure 10B shows tibialis activity and Figure 10C shows gastrocnemius activity for each of the 7 subjects when tested under the 5°-incline condition. When comparing how EMG activity changed across the pre-, during-, and post-incline periods, six out of seven subjects showed patterns of change that were similar to the representative subject data shown in Figure 10A. The remaining subject showed a large increase in tonic tibialis activity when standing on the incline. At larger incline amplitudes of 7.5° and 10°, 4 out of 7 subjects showed an increase in tonic tibialis activity while standing on the incline. Although subjects differed in how their EMG activity changed when adapting to stance on the inclined surface, all subjects showed similar increases in tonic extensor muscle activity while leaning in the post-incline period. Further, EMG activity patterns adopted while standing on the inclined surface did not persist into the post-incline period for any of the 7 subjects.

Perceptual effects

Although perceptual effects were not systematically studied, subjects provided spontaneous comments when trials ended. Subjects reported that they were aware of their leaning at the beginning of the post-incline period, but that the leaned posture felt like the right place to be. Subjects did not appear to be able to judge when they had returned to their pre-incline postural alignment. Several subjects reported that they thought they were upright at times during the post-incline period, but then were surprised

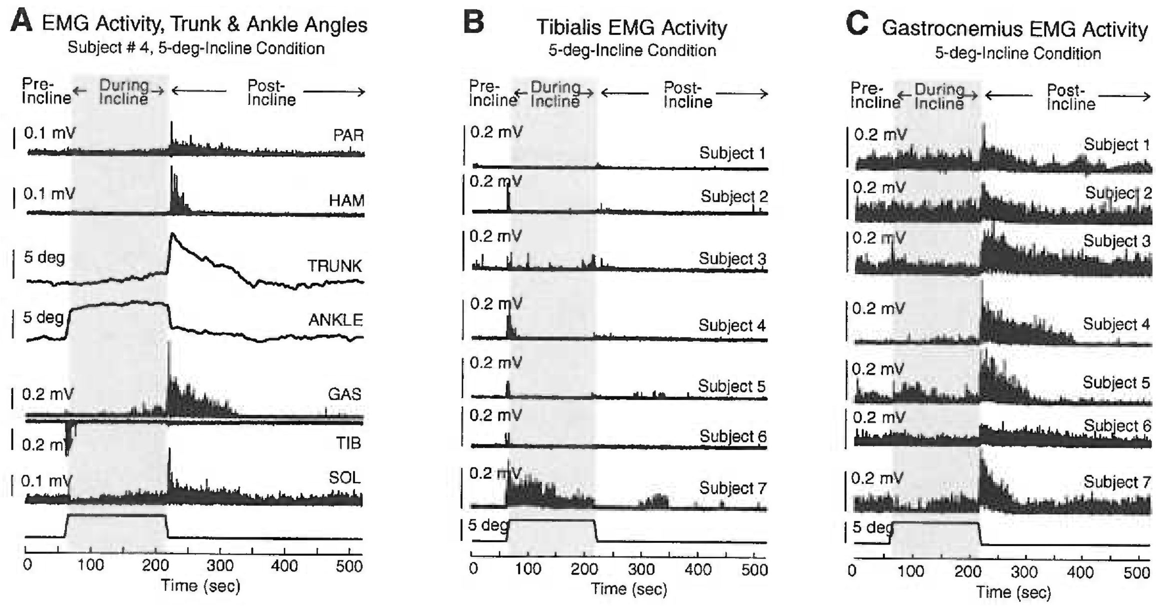

FIG 10. Comparison of EMG activity across the pre-, during-, and post-incline periods. FIG 10A shows EMG, trunk orientation, and ankle angle data for a representative subject, tested under the 5°-incline condition. EMG activity and trunk orientation were similar when comparing the pre-incline to the during-incline periods. During the post-incline period, postural extensors increased activity, counter-acting the sustained leaned posture. The effects of stance on an inclined surface on ankle EMG activity for all 7 subjects are shown in FIG 10B (tibialis) and FIG 10C (gastrocnemius). Each subject's EMG data is the average of 3 trials under the 5°-incline condition. FIG 10B shows that the tibialis was quiet throughout most of the trial for 6 out of 7 subjects, but increased during the period of surface inclination in 1 subject. Thus, the post-incline lean was not caused by an after-contraction effect in tibialis that pulled the subject forward. FIG 10C shows that subjects varied in how their gastrocnemius activity changed from the pre- to during-incline periods, but that all 7 subjects showed increased gastrocnemius activity in the post-incline period. Gray shading indicates the period during which the surface was inclined.

by the feeling of additional 'pulls' or 'corrections'. After standing on a toes-up inclined surface, when the surface first returned to horizontal alignment, 3 out of 10 subjects reported that they thought the support surface had moved to a toes-down-inclined position.

Discussion

This study shows a novel postural after-effect of stance on an inclined surface. Subjects, with eyes closed, maintained a large amplitude, long lasting lean after standing on an inclined surface. Subjects leaned despite awareness of their leaning, increased muscular effort to hold the leaned posture, and sensory cues that could signal postural deviation from gravity-vertical such as from otoliths, foot pressure receptors, trunk graviceptors and Golgi Tendon Organs. Although the post-incline lean altered the relationship of the body to gravity, it maintained the relationship of the body to the support surface, suggesting that the experience of standing on the inclined surface adaptively modified, or recalibrated, the set point for preferred postural orientation with respect to the support surface. We found that stance on an incline led to more systematic effects on the orientation of the upper body than on the position of joint angles or on the level of EMG activity, suggesting that the mechanism for the lean involves regulation of global, whole body postural variables and is not limited to changes regulating local postural variables such as the position of the ankle joint. The set point for preferred postural orientation may undergo adaptive modification because the change in surface inclination alters the relationship between the geometry of the support surface and the direction of gravity.

The set point for preferred postural orientation is modified

One hypothesis that could explain why subjects leaned, is that the experience of standing on an inclined surface led to an adaptive recalibration of the central nervous system's 'set point', or the reference value, for preferred postural orientation. In other words, the postural control system adapted to the altered geometry of the support surface by modifying the equilibrium position that it was attempting to maintain. We hypothesize that when subjects returned to standing on a horizontal surface, their modified postural set point persisted, and they leaned in order to maintain the new, preferred postural orientation with respect to the surface. Although the lean involved a large change in the location of the CoM and in the displacement of the CoP with respect to the foot, oscillations around the leaned position, as measured by the amplitude of the high-frequency component of the CoP, showed only a transient increase in amplitude when the surface changed orientation. Thus, subjects held the leaned posture with near the same level of control as they held the more upright postural orientation. Similarly, Gurfinkel and colleagues (1995a) showed that when subjects stood on a slowly tilting support surface, the low-frequency CoP underwent large amplitude displacements, while fast, corrective high-frequency CoP oscillations were unaffected. Thus, subjects appeared to organize fast-acting equilibrium postural activity around a set point that was changing continuously in response to the change in orientation of the support surface.

The presence of a long-lasting postural after-effect of leaning when the spatial coordinates of the support surface were changed from the novel state of inclination back to the original state of horizontal, suggests a central, adaptive sensorimotor recalibration (Lackner and DiZio 2000; Rieser et al. 1995; Thach et al. 1992; Earhart et al. 2001, 2002a). The direction and the amplitude of the post-incline lean depended on the direction and the amplitude of surface inclination. The leaned posture maintained the alignment between the upper body and the surface as if the subject still stood on the incline, suggesting that subjects relied on the support surface as a reference frame for their postural orientation and that the exposure to an altered surface inclination caused an adaptive recalibration of the postural set point for foot-up postural orientation.

The post-incline lean is similar to the after-effect of PKAR, an effect of a circular walking trajectory that follows a period of walking on a rotating circular treadmill (Gordon et al. 1995; Earhart et al. 2001; Weber et al. 1998). Both the post-incline lean and PKAR follow a period of maintained change in support surface conditions. Both after-effects maintain the same kinematic trunk-to-foot-to-surface relationship from the period of novel surface condition to the post-period when the surface returns to baseline condition. Both after-effects demonstrate slow, exponential decay toward the pre-adapted state. The post-incline lean and PKAR demonstrate that the surface provides strong cues for controlling body orientation in space and that the foot-up reference for postural orientation can be remodeled through experience.

Postural after-effects like the post-incline lean also occur after subjects are exposed to an altered visual reference frame. When subjects were exposed to linear visual surround motion, they leaned into the direction of visual surround motion and when visual surround motion ceased, they leaned in the opposite direction (Lestienne et al. 1977; Reason et al. 1981). The after-effect of leaning that followed exposure to linear visual surround motion decayed over a similar time course as the post-incline lean, with an average decay time constant of 50 ± 30 seconds for the post-visual flow lean

(Lestienne et al. 1977) and 50.2 ± 8.0 seconds for the post-incline lean, suggesting similar central organization for visual flow and support surface evoked after-effects on postural orientation. Studies of maintained galvanic stimulation (Magnusson et al. 1995) and of maintained ankle tendon vibration (Fransson et al. 2000) also report gradual adaptive change in postural lean responses with time constants similar to post-incline and post-visual-flow after-effects, suggesting that adaptation of the postural orientation reference might occur in a similar way regardless of the reference frame involved.

Instead of leaning because of an altered postural set point, subjects may have leaned because of adaptive changes at a peripheral or a segmental level, affecting the level of muscle contraction and/or segmental reflex activity. For example, after-contraction effects, which consist of involuntary muscle activity and an unintentional change in resting posture, have been shown to follow a period of sustained, isometric muscle activity with the muscle at a shortened length (Hagbarth and Nordin 1998; Proske et al. 1993). Subjects may have leaned because of after-contraction effects in their ankle muscles. However, the EMG data from our subjects is not compatible with a muscle after-contraction effect. When subjects stood on the incline, we found no evidence of a sustained period of elevated, isometric muscle activity, which is thought to be the basis for after-contraction effects (Hagbarth and Nordin 1998; Proske et al. 1993). Further, EMG activity in the post-incline period did not maintain the immediately prior level of EMG activity of the during-incline period, as would be expected for an after-contraction effect (Hagbarth and Nordin 1998).

The amplitude and the decay of the post-incline lean were highly consistent within individual subjects, both across repeated trials separated by days to months and across trials in which the surface was inclined in different directions. Thus, the incline after-effect was robust and little influenced by factors that fluctuate throughout the day, such as attention and fatigue. The repeatability of the form of the post-incline lean within individual subjects suggests involvement of a well-established, automatic postural mechanism. While all subjects showed many similar features of the post-incline lean, including a time scale of a few minutes and a dependence of the lean's direction and amplitude on the preceding direction and amplitude of surface inclination, subjects differed from one another in the form and duration of their lean's decay and in how strongly changes in amplitude of surface inclination affected the amplitude of the lean.

The reasons for the variability in the post-incline lean between subjects are unclear. The variability could be related to individual differences in how multisensory information is integrated and/or weighted for establishing the postural reference, to individual differences in the degree of dependence on the support surface as a reference frame for postural orientation, or to individual differences in the time characteristics of the adaptive process. Similar variability across subjects has been reported for other sensorimotor after-effect phenomenon, such as PKAR (Weber et al. 1998), post-visual flow postural after-effects (Lestienne et al. 1977), and postural after-effects of walking on a treadmill (Hashiba 1998).

The duration of the time period during which subjects stood on the inclined surface had only modest effects on lean duration and amplitude. Other adaptive after-effects such as PKAR (Weber et al. 1998) and VOR after-effects of wearing prisms that displace the visual field (Melvill Jones et al. 1988) have shown larger and longer lasting after-effects when duration of exposure to the novel condition was increased, but in these studies, subjects were adapted to the novel condition for hours. We may not have seen large effects of incline-duration on the post-incline lean in our subjects, because fatigue and discomfort limited the longest duration of surface inclination to 5 minutes.

Global postural variables are modified

An important question in understanding how the nervous system controls postural orientation is concerned with the nature of the control variables used to establish and maintain a preferred postural orientation. What is the nervous system regulating when it maintains the body in a particular configuration? When the surface changed orientation from inclined to horizontal, the leaned posture consistently maintained two global postural variables, the trunk-to-surface and the head-to-surface spatial relationships. Changes in the amplitude of surface inclination had more systematic after-effects upon the spatial orientation of the upper body than on the orientation of the lower body, the configuration of joint angles or the level of EMG activity. These results suggests that the nervous system regulates postural orientation with respect to the support surface based on global postural variables, such as the trunk-to-surface relationship, rather than local variables, such as the position of the ankle joint angle or the level of ankle muscle activity. For example, if the set point for postural orientation involved regulation of specific joint angle configurations, then the ankle angle should have been held constant when the support surface orientation changed. Instead, we found that ankle dorsiflexion was only partially maintained across the during-incline to post-incline periods, with smaller percentages maintained at larger surface incline angles. The finding that the leaned posture conserved global, but not local, postural variable suggests that a central mechanism underlies the post-incline lean. Local sensory information, alone, cannot determine trunk configuration (or head or whole body or CoM) with respect to the surface. Integration of multi-segmental sensory information is necessary.

Our findings suggests that the trunk is an important control variable for surface-referenced postural orientation, since, when the support surface changed from an inclined to a horizontal position, the post-incline lean maintained the trunk-to-surface relative alignment more than it maintained other postural variables. The amplitude and the direction of the trunk's lean were affected linearly by changes in the amplitude of surface inclination. The amplitude of the trunk's lean was, on average across subjects, close to the adapting stimulus of surface inclination. On average, subjects leaned their trunks approximately 5° after standing on a 5°-incline and 10° after standing on a 10°-incline. Constraining the trunk-to-surface geometry might enable the central nervous system to simplify regulation of the body's CoM, since the trunk is near 50% of body mass and controlling trunk alignment would have a large effect on whole body CoM location and stability (Horak and Macpherson 1996; Massion 1994). Previous studies of humans (Gurfinkel et al. 1981, 1995a) and cats (Fung and Macpherson 1995; Lacquaniti et al. 1984, 1990) under altered surface conditions also support the hypothesis that trunk orientation with respect to the surface may be an important control variable for postural orientation. For example, when subjects stand on very slowly tilting surfaces, they keep their trunks aligned to the surface rather than to gravity and the EMG activity in ankle muscles correlates more highly with trunk orientation than with ankle angle (Gurfinkel et al. 1981, 1995a).

In our studies, the upper body tended to behave as a head-trunk unit and, therefore, our results cannot distinguish between the relative importance of the trunk or the head as a control variable for surface-referenced postural orientation. The head showed similar post-incline postural effects as the trunk, though was more variable, implying that it was less tightly regulated. Vestibular and visual sensors are located within the head and the importance of head orientation and stabilization for postural and locomotor tasks is well known (Pozzo et al. 1995).

Although the average amplitude of the upper body's lean was near to the amplitude of the prior amplitude of surface inclination, this amplitude varied across subjects. The relationship, or the gain, between the amplitude of support surface inclination and the amplitude of leaning also varied. One explanation for this variability is that individual subjects may vary in the gain of the adaptive mechanism responsible for the lean, similar to the way subjects vary in the magnitude of other sensorimotor after-effects, such as podokinetic after-rotation (Weber et al. 1998). The variability in amplitude-effects across subjects could also be explained by individual variation in the relative weighting between the support surface and the gravity as reference frames for determining the preferred postural orientation.

We have suggested that subjects lean because of an adaptive change in the regulation of the orientation of body segments to the surface. An alternative explanation for upper body lean in the post-incline period could involve adaptive changes in the regulation of more global postural variables that that have an impact on the orientation of the trunk and the head. For example, standing on an inclined surface may have modified the set point for regulating the position of the CoM (Massion et al. 1994, 1995) or the set point for the level of postural tonus distributed throughout the deep postural muscles of the body (Mori et al. 1982). When the amplitude of surface inclination was large, 5° or more, our subjects leaned near their limits of stability. Linear changes in the CoM location appeared to be constrained by a postural stability requirement. The trunk may have been leaning in an effort to bring the CoM further forward, but subjects never exceeded their limits of stability by bringing their CoM projections beyond the limits of their foot support.

Alternatively, subjects may have leaned their upper bodies in order to produce an overall state of postural tonus or postural effort that was near to state of postural tonus while subjects stood on the incline. Brainstem areas that can set postural tonus to achieve a particular body orientation have been identified (Mori et al. 1982). Further, after-effects upon resting posture have been shown to follow a sustained period of holding of a particular postural configuration with an isometric muscular contraction, an effect called the Kohnstamm effect (Ghafouri et al. 1998; Gurfinkel et al. 1989, 1991). However, our EMG data show that tonic EMG activity levels while subjects stood on the incline were similar to EMG levels during the baseline, horizontal surface condition. Thus, subjects did not demonstrate elevated, sustained muscle activity while standing on the incline, a prerequisite condition for producing a Kohnstamm-like effect. The EMG data also showed that subjects did not lean to reproduce the immediately prior level of activity. A mechanism involving adaptive re-setting of postural tonus cannot fully be ruled out, however. First, interpretation of our EMG data is complicated by the length changes that occurred in muscles while subjects stood on the incline. Second, it is possible that adaptive re-setting of postural tonus occurred in deep postural muscles, from which we did not record.

At the beginning of the post-incline period, some subjects reported a misperception that the horizontal surface was inclined in the toes-down direction. A similar effect on perception of support surface orientation has been reported after jogging (Anstis 1995) or walking (Hutton 1966) on a toes-up inclined treadmill. The finding of both perceptual and postural after-effects after subjects stand on an inclined surface suggests that an adaptive change may occur at the level of a common internal representation of the state of the body that provides a basis for organizing both perception and control of postural orientation (Gurfinkel and Levik 1991; Mergner 2002a).

Reference frames for postural orientation

We have proposed that subjects lean because of an adaptive change in their set point for preferred postural orientation. Two questions arise from this hypothesis. First, what drives the change in set point during the period of adaptation to the inclined surface and during the post-incline period? Second, why does a long-lasting lean occur only when the surface changes from inclined to horizontal and not when the surface changes from baseline horizontal to inclined?

Standing on an inclined surface might result in an adaptive change in the postural set point because the condition of surface-inclination alters the relationship between two reference frames for postural orientation: the geometry of the support surface and the direction of gravity. When the support surface is stationary, both the support surface and the direction of gravity provide stable, constant references for postural orientation. This constancy results in an invariant, predictable pattern of multi-sensory feedback for each particular configuration that the body might adopt (Gibson 1952; Mergner et al. 1998, 2002a; Riccio and Stoffregen 1998). The nervous system could use this invariant pattern of sensory feedback to establish an internal representation, or an internal model, about the sensorimotor dynamics between the body and the environment and, from this internal model, establish a postural reference, or set point (Gurfinkel and Levik 1991; Horak and Macpherson 1996; Maioli and Poppele 1991; Mergner et al. 1998, 2002a, 2003; van der Kooij et al. 1999).

When the support surface initially changed from a horizontal to an inclined position, a conflict was created in postural orientation based on the gravity-reference frame and the surface-reference-frame. Postural alignment that was near to 'upright' with respect to gravity was leaned with respect to the surface. When graviceptive information, such as vestibular information indicated that the body was aligned at the preferred postural orientation, other sensory information, such as information about joint angles, muscle lengths, and pressure and shear forces under the feet would suggest a leaned postural orientation. This incongruence in postural orientation based on two different reference frames could create a condition of or ambiguity or conflict in determining how the body is aligned (Gibson 1952; van der Kooij et al. 1999).

The nervous system could resolve the sensory conflict created by the surface inclination by adaptively recalibrating the internal model and the postural set point (Lestienne and Gurfinkel 1988; Merfeld et al. 1993; van der Kooij et al. 1999; Zupan et al. 2002) and/or by altering the relative weighting given to different sources of sensory information in determining postural orientation (Black et al. 1983; Fitzpatrick et al.

1994a; Nashner et al. 1982; Oie et al. 2002; Peterka 2002). The finding that subjects stood with their body segments aligned to near gravity-vertical when they initially stood on the incline, just as in the pre-incline period, suggests that the conflict was quickly resolved by increasing dependence, or weighting, on gravity-related sensory information for postural orientation. The leaned posture in the post-incline period, which initially maintained the relationship of the upper body to the surface, suggests that prolonged standing on the inclined surface led to a modification of the surface-referenced postural set point that persisted when the subjects returned to standing on the horizontal surface. The slow decay of the postural lean to the habitual, more upright alignment could be explained by a gradual resetting of the internal model's surface-referenced postural set point to achieve congruence with the gravity-referenced postural set point.

The leaning after-effect was strong enough to over-ride feedback information and conscious perception about postural alignment with respect to gravity. The CoP was displaced far forward on the foot, providing somatosensory information that the body was leaned with respect to gravity. The head was tilted with respect to gravity, providing otolith information that the head was leaned with respect to gravity. This suggests that preferred postural orientation was organized with respect to the previous support surface orientation as the dominant reference frame as compared to gravity.

Why wasn't a long lasting lean observed each time the surface changed orientation? Why would subjects orient their bodies to gravity when the surface moved to an inclined from a horizontal position, before they had adapted to the incline, but keep their bodies aligned more to the surface than to gravity after they had adapted to the incline, when the surface returned to a horizontal from an inclined position? One explanation could be that the more novel condition of surface inclination triggered a fast sensory reweighting toward increased utilization of gravity-referenced cues (Black et al. 1983; Fitzpatrick et al. 1994a; Nashner et al. 1982; Oie et al. 2002; Peterka 2002). Pilot testing showed that it is unlikely a simple order effect, since, when subjects stood on an incline, followed by a horizontal surface, and then again on an incline, their behavior was not altered; subjects consistently leaned only when standing on an horizontal surface following stance on an incline and not vice versa.

An alternative explanation for lack of leaning when subjects initially stood an incline might be that, when the surface is in an inclined position, leaning is prevented by a reduction in the boundaries of postural stability limits. If subjects were to stay aligned to the surface when it moved from a horizontal to an inclined position, they would lean away from gravity toward the downhill side of the incline. A leaned posture while standing on an incline might bring the CoM to some critical point relative to stability boundaries that would elicit a fast acting postural stabilizing mechanism, over-riding any drive to keep body aligned with respect to the surface. However, this explanation for the absence of leaning is not compatible with the finding that in the post-incline period, subjects were able to lean with their CoM near to stability boundaries by adjusting the alignment of their lower bodies to allow their upper bodies to lean. Similar changes in body configuration might have enabled subjects to lean their upper bodies while they stood on the inclined surface.

Conclusions

The after-effect of leaning that follows a period of stance on an inclined surface shows that the body-to-surface relationship is important in the control of postural orientation. We suggest that the lean is a result of a central adaptive mechanism that adjusts the surface-referenced ‘set point’ for postural orientation when a change occurs in the spatial orientation of the surface with respect to gravity. After-effects in global kinematic postural variables, such as the relative alignment between the trunk and the surface, are more systematically affected by changes in surface inclination than are after-effects in local postural variables, such as the position of the ankle joint or the level of ankle position or ankle muscle activity. The kinematic orientation of the trunk with respect to the surface may be an important control variable for postural orientation.

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Chapter 3

A central mechanism underlies the

postural after-effects of stance on an inclined surface

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Abstract

After standing on an inclined surface with eyes closed, many healthy subjects lean for minutes when the surface returns to horizontal. The underlying mechanism for the post-incline lean could be a muscle contraction after-effect or a central adaptive mechanism controlling more global postural variables such as alignment of the trunk with respect to the surface. We conducted 2 experiments to investigate whether maintaining a constant ankle position or level of ankle muscle activity is a critical component of the mechanism underlying the post-incline lean. In Experiment 1, a restraint prevented the legs from leaning during the post-incline period. When the legs were prevented from leaning, the upper body still leaned, showing that subjects do not lean to maintain a constant ankle angle or level of ankle muscle activity. In Experiment 2, subjects stepped-in-place while on the incline and leaned for several minutes afterward, just as they had leaned after standing on the incline. This result shows that leaning was not caused by prolonged maintenance of a constant ankle angle or level of tonic muscle activity while subjects adapted to the incline. The transfer of a postural effect built-up during a locomotor task to a postural after-effect during a standing task is consistent with a central adaptive mechanism that adjusts the set point for whole body postural orientation with respect to the support surface.

Introduction

An important, but still not completely understood, problem that the nervous system must solve to control upright posture is to determine the direction of vertical and to establish a reference for postural orientation (Berthoz 1991; Mittelstaedt 1998). Several studies suggest that any one of several reference frames can be used by the nervous system for controlling postural orientation. Postural orientation can be aligned with respect to gravity (Dietz et al. 1992; Mittelstaedt 1998), to the support surface (Gurfinkel et al. 1992, 1995a; Ivanenko et al. 1997; Kavounoudias et al. 1998; Mergner and Rosenmeier 1998), or to the visual surround (Dichgans et al. 1972; Lee and Lishman 1975; Lestienne et al. 1977). The reference frame adopted by the central nervous system for postural orientation has been shown to depend on environmental conditions (Fitzpatrick et al. 1994a; Hlavacka et al. 1995; Ivanenko et al. 1999; Mergner et al. 2002b; Oie et al. 2002; Peterka 2002), on task contexts (Mergner et al. 1990, 2002a; Quoniam et al. 1990), and on individual preferences (Cremieux and Mesure 1994; Isableau et al. 1997; Lacour et al. 1997). The availability of more than one reference frame allows flexibility for adapting to changing task goals and environmental conditions. It is not well understood how the nervous system adaptively updates the central postural orientation reference when the configuration or state of a relied-upon reference frame changes, such as when the orientation of the support surface changes from horizontal to inclined.

We previously showed a postural after-effect of stance on an inclined surface that appears to be related to an adaptive process for updating the nervous system's set point for preferred postural orientation (Kluzik et al. 1999). During subject recruitment, we found that 11 out of 25 subjects leaned for 1 to 4 minutes after they stood on an inclined surface. The lean maintained the relative alignment between the upper body and the surface as if the subject still stood on the incline. Subjects leaned even though multiple sensory inputs, such as otolith, foot mechanoreceptor, and Golgi Tendon Organs, could have indicated leaning with respect to gravity and even though maintaining the leaned posture required increased extensor-muscle activity. The mechanism that underlies the post-incline lean behavior is unknown, but we interpreted the post-incline lean as evidence that subjects heavily depended on the support surface as a reference frame for postural orientation and that the central estimate of upright with respect to the surface had been adaptively modified through the experience of standing on an incline. Post-incline alignment of the trunk and the head, but not of the leg or of the ankle joint, were systematically affected when incline amplitude was increased, suggesting that the post-incline lean mechanism occurs at a central level at which whole-body sensory information is integrated and whole-body posture is regulated rather than at a local level at which activity of ankles muscles is regulated. While our previous studies provide strong support for a central adaptive mechanism that affected global, whole body postural orientation variables, an alternative explanation for the lean could be a muscle or muscle spindle after-effect that occurred because of prolonged holding of the ankle in a dorsiflexed posture while subjects stood on the inclined surface. The present study was designed to determine whether the post-incline lean could be explained by a peripheral or a segmental adaptive effect on ankle muscle activity.

When subjects stand on a toes-up inclined surface, they adopt a new body-to-surface postural configuration that keeps the body aligned near upright with respect to gravity, as shown in Chapter 2 and as shown by Leroux and colleagues (2002). Subjects accomplish an alignment of the body that is near to upright with respect to gravity mainly through a large increase in ankle dorsiflexion. The altered postural configuration while on the incline affects ankle muscle length and alters the biomechanical conditions for controlling ankle torque and for maintaining whole-body center of mass (CoM) stability. When a muscle is actively maintained in either a lengthened or a shortened period for a period of time, sensorimotor after-effects occur, including altered sensitivity of muscle spindle reflexes (Enoka et al. 1980; Gregory et al. 1990), perceptual errors of limb position (Gregory et al. 1988; Wise et al. 1996), errors in force production (Hutton et al. 1984, 1987), and, most relevant to our study, an altered resting posture (Ghafouri et al. 1998; Gilhodes et al. 1992; Gurfinkel et al. 1989; Hagbarth and Nordin 1998). These muscle contraction after-effects might contribute to the post-incline lean.

Sustained, isometric contraction of a muscle in a shortened position produces after-contraction effects, including involuntary muscle contraction and movement of the limb or trunk back toward the immediately prior posture (Ghafouri et al. 1998; Gilhodes et al. 1992; Gurfinkel et al. 1989; Hagbarth and Nordin 1998; Kohnstamm 1915). Examples of after-contraction postural effects include involuntary deltoid contraction and arm rise after a period of pushing the arm against a door frame (Hagbarth and Nordin 1998), involuntary quadriceps activity and knee extension after tonic contraction of ankle dorsiflexors while supporting a weight hung from an unsupported foot (Gurfinkel et al. 1989), and involuntary upper back muscle activity with upper trunk-shoulder rotation after tonic contraction of the trapezius muscle while supporting a weighted bag hung from the shoulder (Ghafouri et al. 1998). Both peripheral muscle spindle mechanisms

(Hagbarth and Nordin 1998) and central mechanisms (Gilhodes et al. 1992; Gurfinkel et al. 1989; Ghafouri et al. 1998) have been proposed to explain after-contraction effects. Regardless of the mechanism, the prerequisite condition for producing an after-contraction effect is sustained muscular effort during an isometric muscle contraction (Gilhodes et al. 1992; Gurfinkel et al. 1989; Hagbarth and Nordin 1998). In the present study, we aim to show that the post-incline lean is not due to after-contraction effects of ankle muscles.

We designed 2 experiments to test the hypothesis that the underlying mechanism for the post-incline lean is not limited to local adaptive changes at the level of the ankle muscles, but rather involves central adaptive changes that affect regulation of whole body posture. In the first experiment, we prevented the legs from leaning during the post-incline period. If the post-incline lean occurs because of the persistence of ankle muscle or ankle muscle spindle activity, we expected that preventing the ankle from maintaining a constant angle during the surface transition from an inclined to horizontal alignment would abolish the lean.

In the second experiment, we tested whether subjects would lean after stepping, rather than standing, on an inclined surface. When a person steps in place, continuous changes occur in ankle, knee, and hip joint angles and in corresponding muscle lengths and contractile states. Thus, leaning after stepping on an incline would be incompatible with a local adaptive mechanism that occurs because of a maintained isometric muscle contraction, but would be compatible with a central adaptive mechanism that affects postural orientation globally. The stepping-in-place experiment was also designed to test whether a postural adaptive-effect can be built up while stepping on an incline that then transfers, or generalizes, to quiet stance during the post-incline period. If the post-incline lean is due to a local, peripheral effect that depends on the prior state of activity in the ankle muscles, then generalization to post-incline leaning during stance should not occur after stepping on an incline. A finding that subjects lean after stepping on an incline would be compatible with an adaptive mechanism that affects the centrally determined reference for postural orientation with respect to the surface.

Preliminary results of this work have been reported as an abstract (Kluzik et al. 2000).

Methods

Subjects

Seven healthy subjects (5F, range 22-49 yrs, mean 36.1 ± 10.7) participated in two experiments. Subjects were screened with a short health history to ensure that they were free of musculoskeletal, neurological, or other health impairments that could affect posture or balance. Subjects were selected because they leaned for at least 1-minute after standing for 2.5-minutes on a 5°-toes-up inclined surface. Out of 25 subjects screened with the stance-on-incline pre-test, 11 showed such a long lasting lean. A comparison between the subjects who leaned and participated in these experiments and the subjects who did not lean and were excluded from participating in these experiments is addressed in a separate paper. The Institutional Review Board at Oregon Health & Science University approved the Experimental Protocol and all subjects gave their informed consent prior to participating in these experiments.

Protocol for Experiment 1: Blocked hip movement

Experiment 1 tested whether a subject standing on an inclined surface exhibits an after-effect of upper-body lean when the legs are prevented from leaning by blocking hip movement with a rigid restraint. The conditions for Experiment 1 are illustrated in Figure 1A. We measured postural activity before, during, and after stance on a toes-up-inclined surface under 2 post-incline conditions: 'hips blocked' and 'hips free'. We varied the amplitude of surface inclination at 3 positions, 2.5°, 5°, and 10°, to test whether a systematic increase in the amplitude of surface inclination would result in a similar, systematic increase in the amplitude of the post-incline lean for the hips blocked condition compared to the hips free condition. Each subject was tested on 6 separate days, one day for each of 6 trial conditions (2 Hips X 3 Amplitudes). For each experimental condition, we conducted 3 trials, which were spaced at least 2 hours apart to avoid carry-over effects. Trials for the 'hips free' condition were collected first, followed by the 'hips blocked' trials. Amplitude conditions were randomized within both sets of trials. For each subject, trials were performed across a time course of 4 to 6 weeks.

Each trial for the hips blocked and hips free conditions lasted for 8.5 minutes and consisted of a 1-minute pre-incline period when the support surface was horizontal, a 2.5-minute during-incline period when the surface was inclined, and a 5-minute post-incline period when the surface was again horizontal. The support surface rotated between the horizontal and inclined positions at a constant velocity of 1°/s, with the axis of rotation at approximately ankle height. The slow, 1°/s, rate of surface rotation was chosen to avoid sharp accelerations that could trigger fast proprioceptive-triggered balance responses.

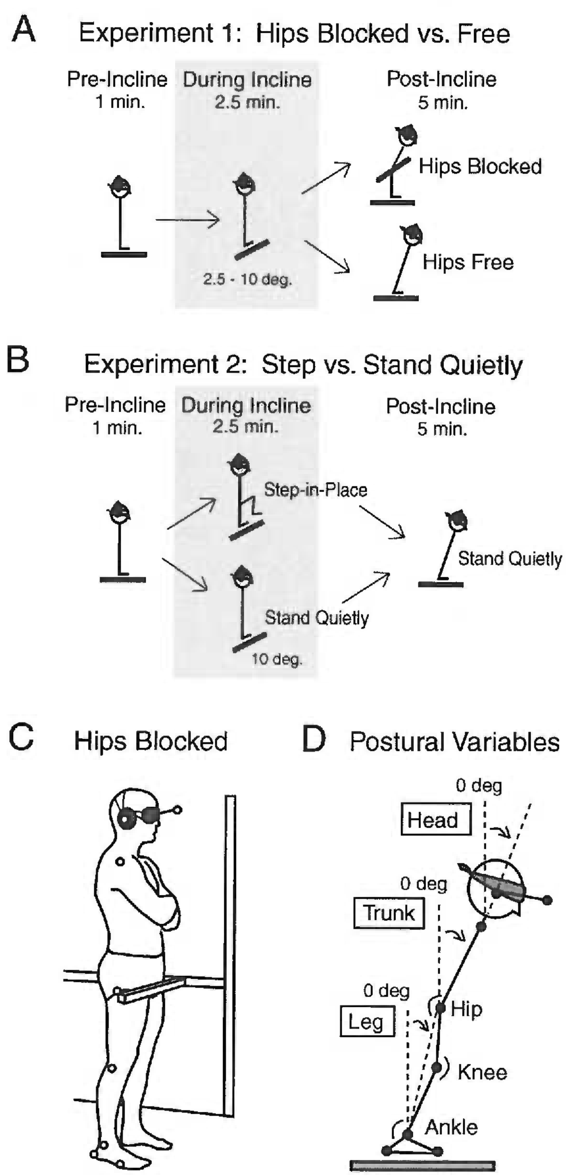


FIG. 1. Methods. FIG 1A and 1B show the experimental designs for Exp. 1 (Hips Blocked) and Exp. 2 (Step-in-Place). All trials included a 2.5-min period of either standing or stepping-in-place on a toes-up-inclined support surface. All trials also included a 1-min pre-incline and a 5-min post-incline period of stance on a horizontal surface. The gray area indicates the time period when the surface was inclined. FIG 1C depicts the restraint device used to block forward movement during the post-incline period. The horizontal bar in front of the subject was placed well forward of the subject during the pre- and the during-incline periods so that the subject could move freely without contacting the bar. When the post-incline period began, the horizontal bar was moved to and locked at a position that kept the subject's hips from leaning forward of baseline posture. FIG 1D shows the marker placements used for 3-D position acquisition and shows the derived segment and joint angles that were used to analyze postural effects.

For all trials, subjects were blindfolded to eliminate visual information and wore headphones to remove auditory information that could influence postural orientation. In addition, a short story audiotape was played through the headphones to distract each subject's attention away from postural alignment. Subjects were instructed to listen to the story and not pay attention to their posture. Subjects were also instructed to stand in a relaxed way and not to resist any pull or tendency to lean. Subjects stood with their heads facing forward, their arms crossed in front of the chest, and their feet spaced a comfortable, self-selected distance apart, approximately hip width. Foot placement for each subject was marked during the initial trial and then kept constant across all remaining trials. Subjects wore a safety harness that was tethered to an overhead beam to ensure safety during trials. The safety harness was adjusted so that it gave no directional/spatial cues for postural alignment. A research assistant stood nearby to ensure the subject's safety during the trials.

For the 'hips blocked' trials, a rigid, horizontal bar was placed in front of the hips at the height of the greater trochanter as shown in Figure 1C. The bar was used to prevent forward hip movement, and thus prevent leaning of the whole leg segment, during the post-incline period. During the pre-incline and the during-incline periods, the bar was removed and the hips were completely free to move. Thus, while subjects stood upon and were adapting to the inclined surface, stance was unrestricted and conditions were identical between 'hips blocked' and 'hips free' trials. The restraint bar was attached at one end to a stable, perpendicular bar by means of a low-friction device that allowed the bar to glide in a forward-backward direction relative to the subject. Prior to the start of each trial, we marked the location of the bar necessary to hold the subject at his or her baseline postural alignment and to prevent forward leaning. After marking this location, we moved the restraint bar out of the way for the pre- and during-incline periods. When the surface began to rotate from the inclined to horizontal positions at the beginning of the post-incline period, the bar was moved to the marked baseline location and locked into place where it stayed for the remainder of the trial.

Protocol for Experiment 2: Stepping-in-place

Experiment 2 investigated whether and how subjects would lean after they stepped-in-place on an inclined, stationary surface. The protocol for Experiment 2 is illustrated in Figure 1B. Subjects were tested under two experimental conditions, one trial each of stepping-in-place on an incline and of standing-in-place on an incline. Trials were conducted on separate days. The surface was inclined at 10°-toes-up for both the stepping-in-place and standing trials. Protocols for the stepping-in-place trials and standing trials were identical to the protocols for the hips-free trials described for Experiment 1, except that in the stepping-in-place trials of Experiment 2, subjects stepped while the surface was inclined

For the stepping-in-place trials, subjects stepped at a self-selected pace (group mean step frequency of 0.81 ± 0.09 Hz) for the entire during-incline period. Because subjects were blindfolded, they tended to unintentionally step forward or backward while stepping-in-place. To keep subjects stepping within the confines of the force plate, the volume of the short story was turned down while subjects stepped so that they could receive instructions. Subjects were verbally cued to step forward or backward when approaching the edges of the force plate. If subjects began rotating, they were cued to turn in order to maintain forward orientation.

Data collection and analysis

We quantified changes in postural orientation using two types of kinematic postural variables: 1) local, single-joint kinematic variables that consisted of ankle, knee, and hip joint angles; 2) global kinematic variables that can only be determined through integration of multi-segmental sensory information and that consisted of head, trunk, leg, and shank segment orientation relative to space as well as the location of whole-body center of mass (CoM). Kinematic data were recorded on the left side of the body using a 4-camera Motion Analysis system (Santa Rosa, CA) and were analyzed in the sagittal plane. Figure 1D illustrates the conventions used for calculating and reporting kinematic data and shows the marker placement used to define the orientation of the body segments and of the joint angles. The shank segment is not illustrated. The shank segment was defined as the link between markers placed at the ankle and the knee joints. The location of the body's CoM in the sagittal plane was calculated as a weighted sum of the location of the CoM of individual body segments, using a 5-segment model (head, trunk-arms, thighs, shanks, feet) of a subject standing with arms crossed in front of the chest. The mass of individual body segments was estimated using anthropometric measures and methods proposed by Vaughn and colleagues (1991) and Chandler and colleagues (1975). Ratios for calculating the location of CoM as percentage of the segment length are from Dempster (Winter 1990). Symmetry was assumed for the alignment of the left and right lower extremities. The CoM data are reported as angular changes with respect to the ankle joint. Kinematic data were recorded at 10 Hz and low-pass filtered at 0.1 Hz to characterize slow changes in postural orientation. We also analyzed kinematic variables with a 4-Hz low-pass filter to calculate the frequency of step cycles and the amplitude of joint motion during stepping.

For each measure of postural orientation, we quantified the duration of the post-incline lean by calculating the dominant decay time constant of return from the leaned to the more upright, final, steady state of postural orientation. We also quantified the amplitude of the post-incline lean by calculating the maximum lean away from upright alignment. For Experiment 1 (hips blocked), we defined the maximum lean as the difference between the maximally leaned position in the post-incline period and the mean position during the last 30 seconds of stance on the incline. During the stepping-in-place trials of Experiment 2, subjects leaned forward while they stepped. Therefore, we did not use the mean position while subjects stepped on the incline as the offset for calculating the maximum lean. Instead, for Experiment 2, we defined the maximum lean as the difference between the maximally leaned position in the post-incline period and the mean position during the last 30 seconds of the post-incline period.

In addition to quantifying the decay and amplitude of the post-incline lean, we also compared how postural alignment changed across the pre-, during-, and post-incline periods by calculating the mean position during the last 15 seconds of the pre-incline period and calculating the mean position during 15-second epochs at the beginnings and ends of the during- and post-incline periods.

Surface EMG activity of the soleus, medial gastrocnemius, anterior tibialis, medial hamstrings, quadriceps (rectus femoris), paraspinals (iliac crest level), and rectus abdominis were recorded to determine whether the post-incline lean was due to an attempt to maintain the immediately prior level of muscle activity and to determine whether EMG changes were similar to after-contraction effects. We compared how EMG activity in the gastrocnemius and the soleus muscles changed across the pre-, during-, and post-incline periods by calculating the mean normalized EMG activity during 15-second epochs at the beginnings and ends of the during- and post-incline periods. Prior to averaging the mean EMG activity for each time epoch across subjects, EMG data were normalized to the mean EMG activity across the last 50 seconds of the pre-incline period.

Additional details regarding dependent variables and methods for calculating the duration and amplitude of leaning are reported in Chapter 2.

Statistical analysis

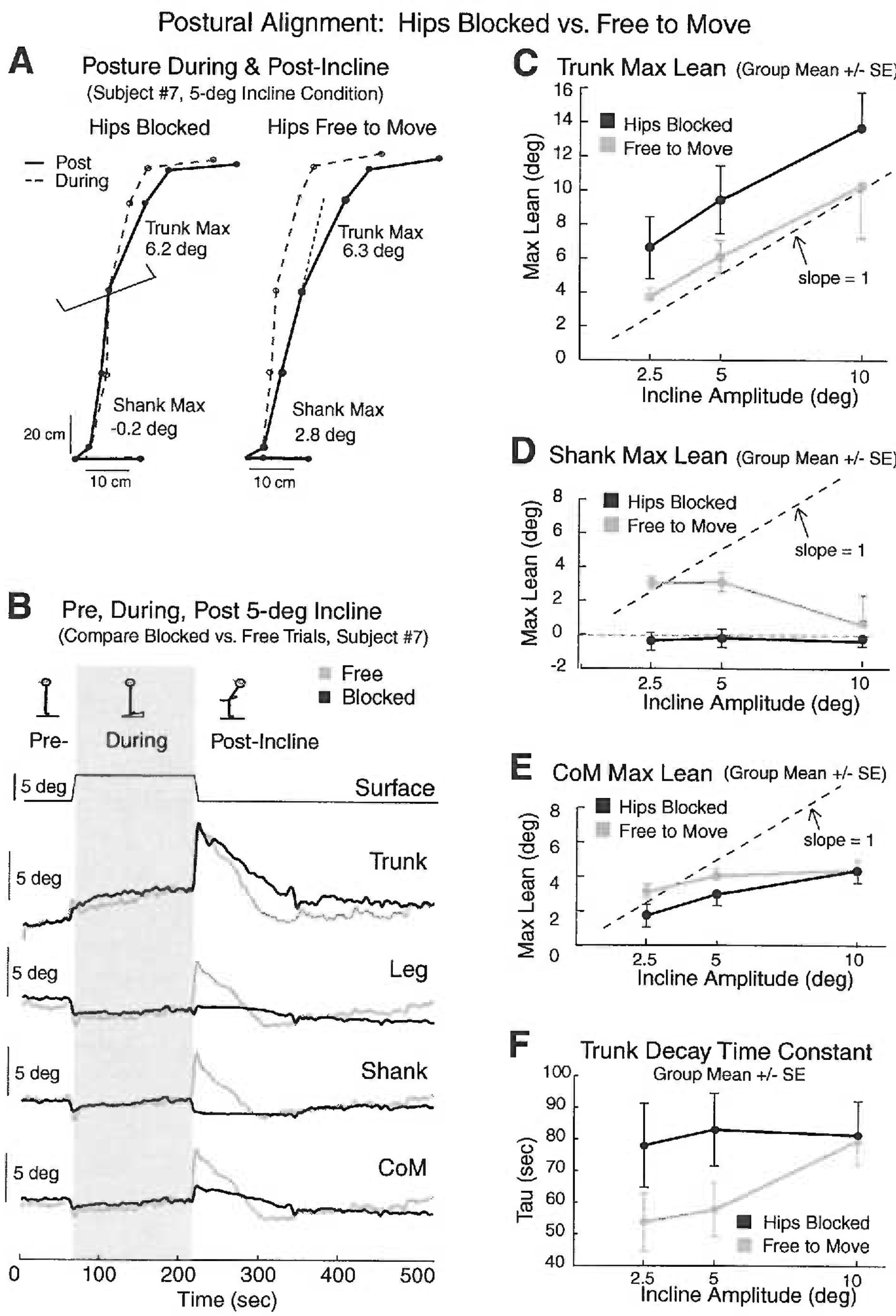
We used Statistica and SPSS software with significance set at $\alpha = 0.05$ for all statistical comparisons. To determine whether blocking forward hip movement in the post-incline period altered the post-incline lean duration or amplitude, we analyzed the decay time constant and the maximum lean using repeated measures ANOVA (2 Hips Blocked vs. Hips Free X 3 Incline Amplitude). The trunk maximum lean data were log transformed prior to statistical analysis to normalize the variance. Scheffé post-hoc comparisons were applied to estimate whether differences existed between the hips blocked condition and the hips free condition for each incline-amplitude condition. We also compared the two hip conditions, blocked versus free, in terms of the slope of the relationship between the amplitudes of surface inclination and the amplitudes of the post-incline lean.

To determine whether stepping on an inclined surface resulted in different postural after-effects than standing on an inclined surface, we used paired t-tests to compare the post-incline lean's maximum amplitude of leaning and the time constant of the decay of the lean toward upright alignment. We also tested whether subjects' postural orientation while stepping on the inclined surface differed from while standing on the incline, again using paired t-tests. Whenever group means are reported to compare differences across conditions, we also report the standard error.

Results

Leaning of the trunk and head persist when the legs are prevented from leaning

Figure 2 shows that blocking movement at the hips and preventing the legs from leaning forward during the post-incline period did not abolish leaning of the upper body. Figures 2A and 2B show data from a representative subject and each figure compares data from a trial when the hips were blocked to data from a trial when the hips were free to lean forward. The surface was inclined at 5°-toes-up for both trials. Figure 2A shows reconstructed stick figures of the representative subject's postural alignment at two different points in time, the end of the during-incline period and the beginning of the post-incline period. Figure 2B shows the representative subject's trunk, leg, shank, and CoM alignment throughout the entire trial. Both Figures 2A and 2B show that neither the whole leg segment nor the shank segment leaned forward when the hips were blocked



Postural Alignment: Hips Blocked vs. Free to Move
A
Posture During & Post-Incline
(Subject #7, 5-deg Incline Condition)
Hips Blocked
Hips Free to Move
Post
During
Trunk Max
6.2 deg
Shank Max
-0.2 deg
Trunk Max
6.3 deg
Shank Max
2.8 deg
20 cm
10 cm
10 cm
B
Pre, During, Post 5-deg Incline
(Compare Blocked vs. Free Trials, Subject #7)
Free
Blocked
Pre-
During
Post-Incline
5 deg
Surface
Trunk
Leg
Shank
CoM
Time (sec)
C
Trunk Max Lean (Group Mean +/- SE)
Hips Blocked
Free to Move
slope = 1
Max Lean (deg)
Incline Amplitude (deg)
D
Shank Max Lean (Group Mean +/- SE)
Hips Blocked
Free to Move
slope = 1
Max Lean (deg)
Incline Amplitude (deg)
E
CoM Max Lean (Group Mean +/- SE)
Hips Blocked
Free to Move
slope = 1
Max Lean (deg)
Incline Amplitude (deg)
F
Trunk Decay Time Constant
Group Mean +/- SE
Tau (sec)
Hips Blocked
Free to Move
Incline Amplitude (deg)

FIG. 2. Effects of preventing forward hip movement during the post-incline period on postural alignment. FIG 2A and FIG 2B compare data from a trial when the hips were blocked to a trial when the hips were free to lean for a representative subject who was tested under the 5°-incline condition. FIG 2A shows stick figures that were reconstructed from kinematic data at two points in time. The dashed line shows how the body segments were aligned when the during-incline period ended, immediately prior to the surface's return to horizontal. The solid line shows the position of the body segments at the beginning of the post-incline period, when subjects showed the maximum amplitude of leaning. The stick figure on the left is from a trial conducted with the hips blocked. FIG 2B compares the alignment of the trunk, leg, shank, and whole-body CoM between the hips blocked (black traces) and hips free (gray traces) conditions. When the hips were blocked, the legs were effectively prevented from leaning, yet the trunk leaned in a similar way as when the hips were free to lean. The maximum amplitude of the post-incline lean of the trunk, shank, and CoM are shown in FIG 2C-E, respectively. For each kinematic variable, the maximum lean is compared between the hips blocked (black lines) and the hips free conditions (gray lines) at each incline-amplitude condition. The dotted diagonal line shows the predicted amplitude of the maximum lean for a 1:1 relationship between the amplitude of surface inclination and the amplitude of the post-incline lean. FIG 2C shows that the amplitude of trunk lean increased systematically as the amplitude of surface-inclination increased, regardless of whether the hips were blocked or free to lean. FIG 2D shows that blocking hip movement abolished leaning of the shank segment. FIG 2F compares the decay time constant (group mean ± SE) of the trunk's lean when the hips were blocked (dark lines) to when the hips were free to move (light lines) at each incline-amplitude.

and that the trunk leaned forward with a similar amplitude when the hips were blocked as when the hips were free to lean.

Figure 2C shows that the amplitude of the post-incline trunk lean increased linearly as the amplitude of surface inclination increased with a slope that was close to 1 for both the hips blocked (group mean slope of 0.93 ± 0.13) and hips free (group mean slope of 0.87 ± 0.36) conditions. The maximum lean of the trunk was significantly larger for the hips blocked than the hips free condition, as can be seen in Figure 2C and in the group mean values reported in Table 1 ($F_{(1,6)} = 6.35$, $p < 0.05$). Five out of seven subjects showed the pattern of larger amplitude trunk lean under the hips blocked condition, while two subjects leaned with a maximum amplitude that was within 1° of the amplitude of the maximum lean when the hips were free to move. When the amplitude of surface inclination was systematically increased, the maximum lean of the head segment was affected in a similar way as the trunk segment. The slope of the relationship between the amplitude of surface inclination and the amplitude of the head's maximum lean was close to 1 for the both the hips blocked (group mean slope, 0.95 ± 0.20) and the hips free (group mean slope, 0.87 ± 0.47) conditions. The group mean for the maximum lean of the head was larger when the hips were blocked than when the hips were free to move (Table 1).

Unlike the linear relationship, with a slope near 1, that was found between the amplitude of surface inclination and the amplitude of the maximum lean of the head and trunk, the relationship between the amplitude of surface inclination and the maximum lean of the CoM was nonlinear and the slope was small (group mean slopes of 0.34 ± 0.4 and 0.18 ± 0.06 for the hips blocked and the hips free conditions, respectively). The

TABLE 1. *Upper Body Maximum Leans and Decay Time Constants*

	Incline Amplitude	Hips Blocked	Hips Free
Head Max	2.5 °	8.1 ± 2.6 °	4.5 ± 0.8 °
	5 °	10.5 ± 3.5 °	7.2 ± 1.6 °
	10 °	15.2 ± 4.1 °	11.1 ± 4.1 °
Trunk Max	2.5 °	6.6 ± 1.7 °	3.7 ± 0.4 °
	5 °	9.4 ± 1.9 °	6.1 ± 0.9 °
	10 °	13.7 ± 2.1 °	10.3 ± 3.0 °
Trunk Tau	2.5 °	78.0 ± 13.3 s	53.7 ± 9.0 s
	5 °	83.0 ± 11.4 s	57.7 ± 8.4 s
	10 °	81.4 ± 10.1 s	79.2 ± 7.2 s

Values are means ± SE.

maximum lean of the CoM showed only a small increase in maximum lean from the 5°- to the 10°-incline-amplitude condition as compared to the increase from the 2.5°- to the 5°-incline-amplitude condition (Fig. 2E). Under the 2.5°-incline-amplitude condition, and when averaged across all subjects, the maximum lean of the body CoM was larger when the hips were blocked than when the hips were free to lean, with the difference approaching a significant level ($p = 0.068$). In contrast, for the 5°- and 10°-incline-amplitude conditions, the average maximum leans of the CoM when the hips were blocked were not significantly different from when the hips were free to lean.

Leaning of the upper body during the post-incline period lasted for minutes, regardless of whether the hips were blocked or free to lean forward and regardless of the amplitude of surface inclination. Figure 2E shows how blocking hip movement affected the time constant for the decay of the trunk lean under the 2.5°-, 5°-, and 10° incline-amplitude conditions. Under the 10°-incline condition, there was no significant difference between the decay time constants of the trunk lean when comparing the hips blocked condition (81.4 ± 10.1 s) to the hips free condition (79.2 ± 7.2 s). The average duration of the post-incline lean for both conditions was approximately 4 minutes (3 X decay time constant). For the 2.5°- and 5°-incline conditions, the decay time constants were significantly longer for the hips blocked condition than for the hips free condition ($p < 0.01$). Table 1 reports the time constants for the decay of the trunk's lean, averaged across all subjects, for each incline-amplitude condition. Under all hip and amplitude conditions, the decay time constant for the CoM lean was not significantly different than the decay time constant for the trunk lean.

Effect of blocking hip movement on joint configuration and EMG activity

The main reason for using a rigid bar at the hips to block forward leg movement during the post-incline period was to determine whether subjects leaned because of a mechanism that maintained a constant ankle angle as the surface changed orientation from inclined to horizontal. The knees were free to bend when the hips were prevented from leaning forward, which would have allowed the shank to lean forward and the ankle angle to be maintained at a constant ankle angle when the surface transitioned from an inclined to a horizontal position. Instead, when the surface transitioned from the inclined to horizontal position, the knees extended, the shank segment did not lean forward, and the ankle angle was not maintained at a constant value. Figure 2C shows that, when the hips were blocked from leaning, the maximum lean of the shank segment was near 0 for all 3 incline-amplitude conditions (group mean maximum lean of - 0.4 ± 0.5°, - 0.2 ± 0.5°, and - 0.4 ± 0.4 for the 2.5°, 5°, and 10° conditions, respectively). Table 2 shows that when the surface was inclined, the ankle joint was dorsiflexed to an amplitude that was close to the amplitude of surface inclination as compared to the ankle angle during the pre-incline period. When the surface returned to horizontal and the post-incline period began, the ankle angle returned near to the pre-incline, values. Thus, the position of the ankle joint was not maintained from the during- to the post-incline periods.

Figure 3A shows data from a representative subject and compares joint angle configuration and trunk alignment during a trial when the hips were prevented from leaning to a trial when the hips were free. When the hips were blocked from leaning, the angle of the ankle joint returned to its pre-incline position immediately at the beginning of the post-incline period, yet the trunk leaned forward with an amplitude that was similar

TABLE 2: *Comparison of the ankle angle across the pre-, during-, and post-incline periods when the hips were blocked from leaning forward*

Incline Amplitude	Pre-incline period (mean of last 15 s)	During-incline period (mean of last 15 s)	Post-incline period (mean of first 15 s)
2.5°	0	2.3 ± 0.4°	- 0.5 ± 0.6°
5°	0	5.2 ± 0.3°	0.3 ± 0.4°
10°	0	11.4 ± 0.3°	1.4 ± 0.5°

Mean ankle angles were calculated with respect to the mean ankle angle across the last 15 seconds of the pre-incline period. Values are means ± SE.

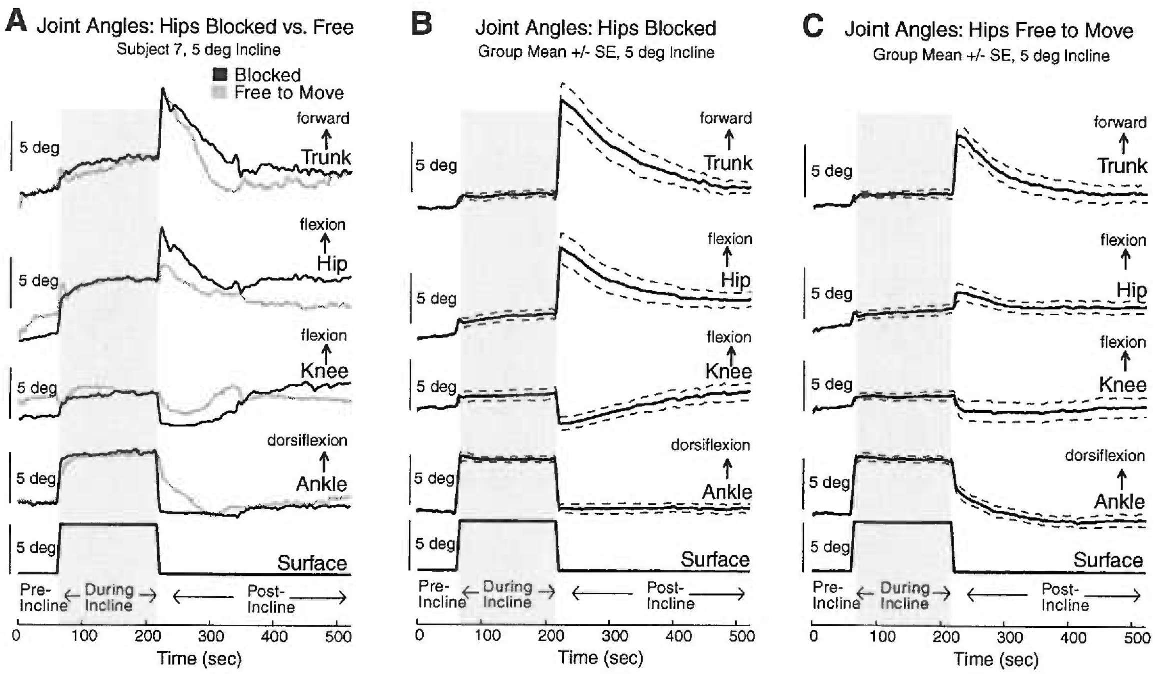


FIG 3. Effect of blocking hip movement in the post-incline period on the positions of the ankle, knee, and hip angles and on the orientation of the trunk. FIG 3A compares trials conducted under the hips blocked condition (dark trace) and the hips free condition (light trace) for a representative subject. For both trials, the surface was inclined at 5°-toes-up. When the subject's hips were blocked, ankle dorsiflexion was not maintained into the post-incline period. Further, the subject's hips flexed with a larger amplitude and the subject's trunk leaned with a similar amplitude as compared to the control condition of unrestricted leaning. Similar results were found for the group averaged data shown in FIG 3B (hips blocked condition) and FIG 3C (hips free condition). Dotted lines indicate the SE.

to when the hips were free to lean. A similar result can be seen in the group-averaged data in Figure 3B (hips blocked condition) and Figure 3C (hips free condition). When the hips were blocked from leaning, subjects accomplished forward trunk lean by flexing a greater amount at the hips. Although the configuration of the joint angles in the post-incline differed when comparing the hips blocked to the hips free conditions, the configuration of the joint angles did not differ for the period of time that subjects stood on and adapted to the inclined surface.

Figure 4 compares EMG activity between the hips blocked and the hips free conditions for a representative subject (Fig. 4A and Fig. 4B) and for the group as a whole (Fig. 4C). The alignment of the trunk in space and the position of the ankle angle are also shown. The group-averaged data in Figure 4C shows how the activity in ankle extensor muscles changed across 5 time periods, the end of the pre-incline period and the beginnings and ends of the during-incline and post-incline periods. To average the EMG activity of ankle extensor muscles across all subjects (Fig. 4C), we first normalized each subject's EMG data to their mean level of EMG activity in the pre-incline period. Because subjects showed very little tibialis, hamstring, and paraspinal EMG activity during the pre-incline period (Fig. 4A and 4B), we could not normalize EMG activity to the pre-incline level of activity for these muscle groups and thus, we could not compare the group-averaged data between the different hip conditions.

The tibialis muscle showed only transient and brief periods of activity under both the hips-free and the hips-blocked conditions, as can be seen in the representative subject data in Figures 4A and 4B. The transient increase in tibialis activity occurred only while the surface moved, both from the horizontal to the inclined position and from the inclined

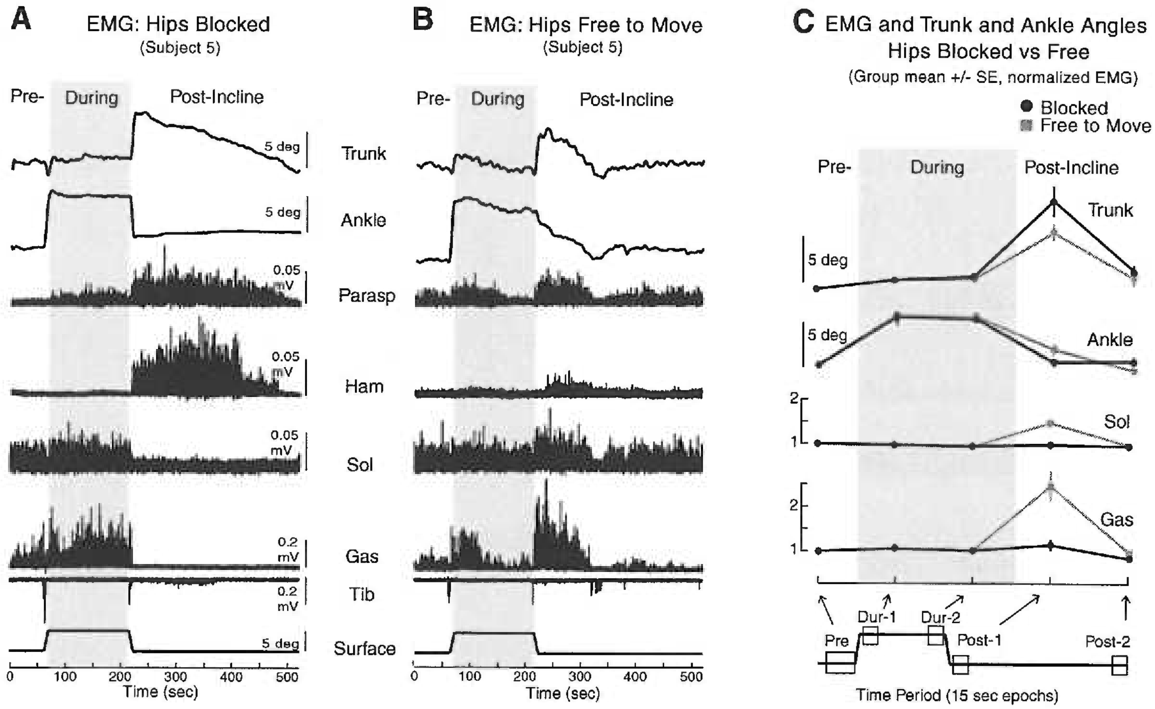


FIG 4. Comparison of EMG activity between trials when the hips were blocked and trials when the hips were free to lean. Data are shown for the 5°-incline-amplitude condition. The shaded areas indicate the time during which the surface was inclined. Figures 4A and 4B show data from a representative subject who showed reduced ankle extensor EMG in the post-incline period when the hips were blocked (4A) as compared to when the hips were free to lean (4B). The subject's trunk leaned forward during the post-incline period under both the hips-blocked and hips-free conditions. FIG 4C shows data that has been averaged across all 7 subjects, 3 trials per subject. The group-averaged data is compared between the hips blocked (black) and the hips free (gray) conditions. Each data point represents the group-average of the mean values across a 15-sec time period at one of five different time points within the inclined stance trial: the pre-incline period and the beginning and end of the during- and the post-incline periods. EMG data were normalized to the mean level of EMG activity in the pre-incline period.

to the horizontal positions. This pattern of a brief increase in tibialis activity during the surface rotations was observed in 6 of the 7 subjects. The remaining subject showed sustained, elevated tibialis activity throughout the entire period of standing on the incline, however, as soon as the surface returned to horizontal in the post-incline period, the tibialis muscle was quiet. Thus, for all subjects, persistent ankle dorsiflexor activity did not pull the body forward in the post-incline period.

Blocking hip movement in the post-incline period altered the level of EMG activity in ankle extensor muscles. At the beginning of the post-incline period, EMG activity in the gastrocnemius and the soleus was less when the hips were blocked than when the hips were free to move, as shown for both the representative subject's data (Fig. 4A and 4B) and for the group-averaged data (Fig. 4C). Despite this difference in the level of ankle extensor EMG activity between the hips blocked and hips free conditions, the trunk leaned with a similar amplitude under both conditions.

Under the hips free condition, when the representative subject returned from standing on the inclined to the horizontal support surface, the level of activity in ankle extensor muscles was not maintained, but instead, increased (Fig. 4B). A similar pattern of increased ankle extensor activity in the post-incline period was observed for all 7 subjects (Fig. 4C). This difference in EMG activity between the during-incline and the post-incline periods was significant for both the gastrocnemius and the soleus muscles ($p < 0.005$). Thus, leaning did not reproduce the immediately prior level of ankle extensor muscle activity.

EMG activity in the hamstring and paraspinal muscles increased in the post-incline period as compared to the during-incline period for both the hips blocked and the hips free conditions, as can be seen in the representative subject's data in Figures 4A and 4B. EMG activity in the hamstring and paraspinal muscles decayed with a similar time course as the trunk forward lean. The quadriceps and abdominal muscles showed little activity throughout the entire trial under both the hips blocked and hips free conditions.

Stepping-in-place on an incline results in a post-incline lean

Subjects leaned after stepping-in-place on a surface that was inclined at 10° in the toes-up-direction. Figures 5A and 5B show data from a representative subject whose trunk, leg, and CoM leaned forward after stepping on an incline (Fig. 5A) with an amplitude and a decay that were similar to the lean that followed standing on an incline (Fig. 5B). The similarity of the post-incline lean between the stepping-in-place and standing conditions occurred for 5 out of 7 subjects (Table 3). Of the remaining two subjects, one subject leaned the trunk with nearly twice the amplitude after stepping as after standing on the inclined surface and the other subject leaned only briefly after stepping on the inclined surface. Figure 5C compares the maximum lean, averaged across all 7 subjects, between the stepping and standing conditions. There were no significant differences between the stepping and standing conditions when comparing the maximum lean of the trunk (12.1 ± 4.7° for stepping, 10.4 ± 2.0° for standing), the leg (3.5 ± 0.8° for stepping, 4.1 ± 0.6° for standing), or the CoM (4.7 ± 0.7° for stepping, 5.3 ± 0.5° for standing). The group mean maximum lean was even more similar between the stepping and standing conditions when excluding the subject who leaned only briefly and the subject who leaned with a larger amplitude lean after stepping as compared to standing, with an average trunk maximum lean of 8.6 ± 1.5° versus 8.9 ± 1.9°, leg

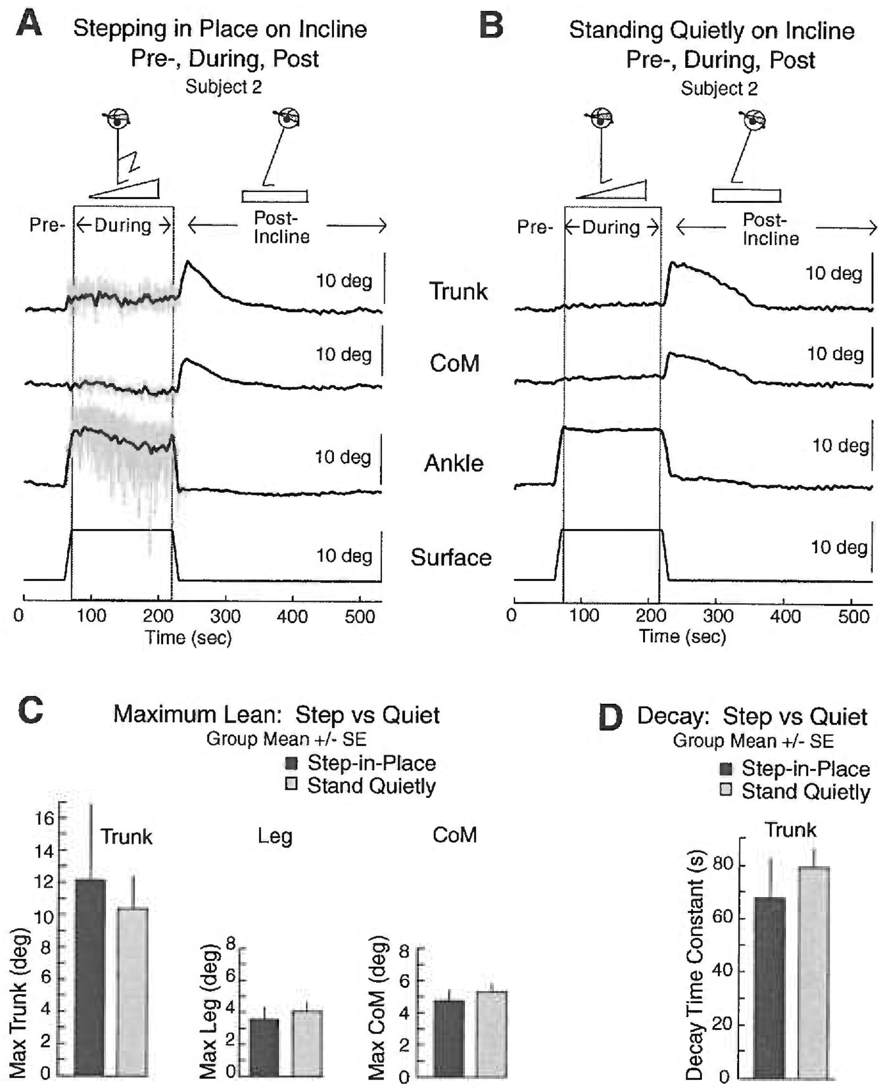


FIG 5. Comparison between the postural after-effects of stepping-in-place and standing-in-place on an inclined surface. FIG 5A and 5B show a representative subject's postural alignment during a step-on-incline trial (FIG 5A) and a stand-on-incline trial (FIG 5B). The data represented by dark traces were low pass filtered at 0.1 Hz to show the slow changes in the postural set point. The data represented by the gray traces were filtered at 4 Hz and show the amplitude of cyclical change in the position of the ankle joint and the orientation of the trunk and the CoM during stepping motion. FIG 5C and 5D show that, when data were averaged across all 7 subjects, the post-incline lean was similar for the stepping and standing conditions. The bar plots in FIG 5C show group means for the maximum lean of the trunk, the leg, and the CoM. The bar plots in FIG 5D show group means for the decay time constant of the trunk's post-incline lean. For both FIG 5C and 5D, the black bars show data from the stepping-in-place condition and the gray bars show data from the standing-in-place condition.

TABLE 3. *Comparison of Maximum Lean and Decay Time Constant of Trunk Lean Step-in-place vs. Stand on Inclined Surface*

	Decay Time Constant (s)		Maximum Lean (deg)	
	Step-in-place	Stand	Step-in-place	Stand
Subject: 1	11.1	75.1	2.5 °	8.8 °
2	43.4	79.1	9.6 °	9.7 °
3	138.2	108.2	39.5 °	19.5 °
4	78.0	95.2	12.6 °	12.5 °
5	80.9	49.8	6.3 °	5.5 °
6	72.9	81.1	4.3 °	3.6 °
7	51.4	66.1	10.1 °	13.02 °
Mean ± SE	68.0 ± 14.9	79.2 ± 7.1	12.1 ± 4.7 °	10.4 ± 2.0 °

Values are means ± SE.

0.4° versus 4.8 ± 0.4°, and CoM maximum lean of 5.3 ± 0.3° versus 5.7 ± 0.4° for the stepping and the standing conditions, respectively.

Figure 5D and Table 3 compare the decay time constant of the post-incline lean between the stepping-in-place and standing conditions. The group mean decay time constant of the trunk lean for the stepping condition (68.0 ± 14.9 s) was shorter than, but not significantly different from, the decay time constant of the trunk lean for the standing condition (79.2 ± 7,1 s). When excluding the one subject who did not lean after stepping on the incline, the group mean decay time constant for the trunk was nearly the same for the stepping (77.4 ± 13.6 s) and standing (79.9 ± 8.4 s) conditions.

We used the condition of stepping-in-place on the inclined surface to test whether continuous ankle motion would abolish the post-incline lean. In other words, we asked whether a constant ankle position is required for the adaptive mechanism that underlies post-incline leaning. When subjects stepped-in-place while on the incline, the ankle joint showed large, cyclical excursions that, across the group, averaged 15.9 ± 1.6° and ranged from 11.7° to 23.4° for the peak-to-peak excursion within a step cycle. Subjects stepped with a step cycle frequency that ranged across the group from 0.69 to 0.97 Hz. The amplitude of ankle joint motion can be seen in the light gray time series traces depicted for representative subjects in Figures 5A and 6A. The light gray traces represent data that were low-pass filtered at 4 Hz and show the peak-to-peak range of joint motion while stepping-in-place. The dark traces represent data filtered at 0.1 Hz, reflecting the mean position during stepping. Figures 5A and 6A show that subjects did not maintain their ankles in a constant position while they stepped, yet the post-incline lean still occurred.

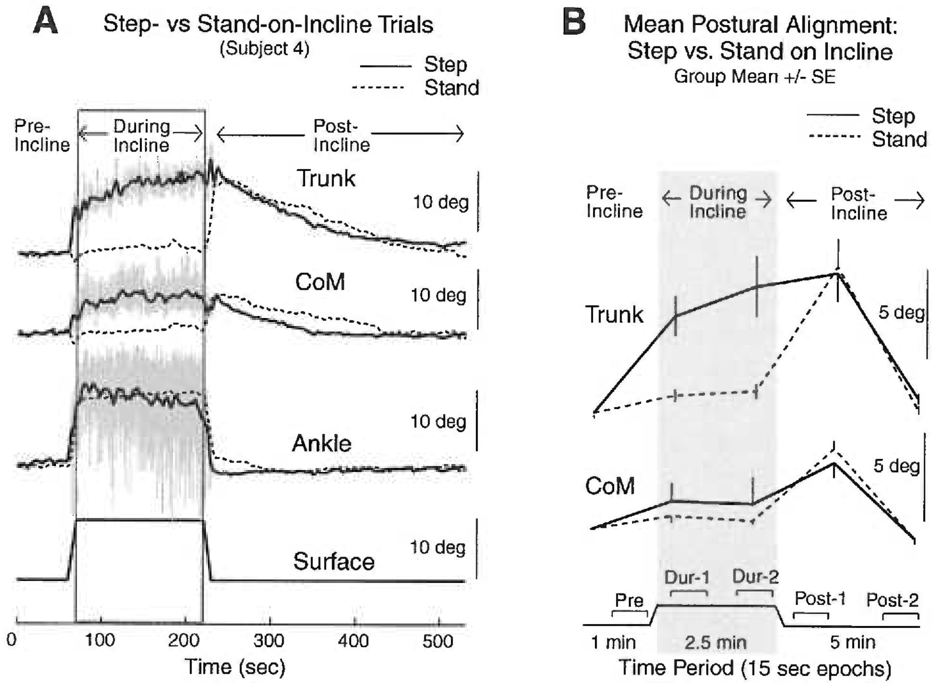


FIG. 6. Postural alignment while stepping on an incline differs from standing on an incline for most subjects, yet postural alignment during the post-incline period is the same for the two conditions. FIG 6A compares a step-on-incline trial (dark traces filtered at 0.1Hz, light traces at 4 Hz) to a stand-on-incline trial (dashed line) for a representative subject under a 10-deg incline condition. FIG 6B compares the group's trunk and CoM alignment for the step (solid line) vs. stand (dashed line) conditions. Each data point represents the group average (± SE) of the mean position during a 15-sec time period. Five time periods are represented: the pre-incline, the beginning and end of the during-incline, and the beginning and end of the post-incline periods. The shaded area indicates the time during which the surface was inclined.

Most subjects (5/7) leaned their trunks forward while stepping on the incline. Figure 6A presents data from a step-on-incline trial and a stance-on-incline trial for a representative subject who leaned the trunk and CoM forward while stepping, but not while standing, on the incline. This forward lean while stepping on the incline is also shown in group-averaged data in Figure 6B, which compares alignment of the trunk and CoM across the pre-, during-, and post-incline periods. The change in trunk alignment from the pre-incline to the during-incline periods was significantly different between the step (4.1 ± 1.5^{o}) and stance (0.8 ± 0.6^{o}) conditions ($p < 0.05$). Figures 6A and 6B show that despite the difference in trunk alignment during stepping and standing on the incline, trunk alignment in the post-incline period was similar.

Discussion

We previously showed that after subjects stood on an inclined surface, they leaned in a way that maintained their body-to-surface relative alignment as if they still stood on the incline (Kluzik et al. 1999, 2000). A possible mechanism for the after-effect of leaning could be a central, adaptive process that adjusts the set point for postural orientation with respect to the support surface when the condition of the surface changes. An alternative explanation for the lean is a mechanism that acts more locally at the level of the ankle joint, resisting change in position (muscle length) or in sensorimotor state. The present results show that a mechanism acting only at the ankle cannot explain the post-incline leaning effect because: 1) the upper body leaned even when the lower body was prevented from leaning and the ankle joint was not allowed to participate in the lean and 2) a post-incline lean occurred after subjects stepped-in-place on the incline, when the ankle, knee, and hip joints underwent large amplitude, cyclical movements instead of maintaining a constant position.

The post-incline lean is not due to a muscle after-contraction effect

One possible explanation for why subjects leaned after they stood on an inclined surface could be an after-contraction effect in ankle muscles. After- contraction effects follow a period of sustained, isometric muscle contraction with the muscle in a shortened position, and, similar to the post-incline lean, result in an unintentional movement toward the previously adopted posture (Ghafouri et al. 1998, Gilhodes et al. 1992; Gurfinkel et al. 1989; Hagbarth and Nordin 1998). The time course of the post-incline lean and after-contraction effects differ from one another, with the post-incline lean decaying across minutes and after-contraction effects decaying across tens of seconds (Gurfinkel et al. 1989; Hagbarth and Nordin 1998). Although after-contraction effects decay more quickly, they could account for part of the post-incline lean effect. Our results, however, are not consistent with the proposed mechanisms for after-contraction effects.

A peripheral mechanism of muscle spindle thixotropy, which is a history-dependent effect of stiffness in intrafusal muscle fibers, has been proposed to explain the after-contraction effects of unintentional muscle contraction and movement (Hagbarth and Nordin 1998, Proske et al. 1993) and the after-contraction effects of persistent sensory discharge and increased sensitivity of muscle spindle receptors (Enoka et al. 1980; Hagbarth 1985; Hutton et al. 1987). When a muscle is lengthened after it has maintained a period of isometric contraction at a short length, the actin and myosin cross-bridge linkages that were formed at the short muscle length persist, causing stiffness in the intrafusal fibers and greater sensitivity to stretch of the compliant receptor portion of the muscle spindle. Ankle dorsiflexor muscles were maintained in a shortened position while subjects stood on the inclined surface. When the surface upon which subjects stood returned from an inclined to a horizontal position, muscle spindle thixotropic resistance to lengthening of the tibialis muscle could have maintained a constant position of the ankle joint and thus maintained the relative alignment between the body and the surface. However, our results are not consistent with a hypothesis of a thixotropic effect in ankle dorsiflexor muscle spindles.

If the mechanism were a thixotropic effect on ankle dorsiflexors, then preventing the legs from leaning forward (Exp. 2, hips blocked condition) should have abolished the post-incline lean because elevated ankle dorsiflexor activity could not have pulled the subjects' upper bodies forward. Instead, all subjects leaned with their upper bodies when their hips were blocked. Even with the hip restraint, subjects could have bent their knees and dorsiflexed their ankles if an after-contraction effect occurred in the tibialis muscle. Instead, however, subjects extended their knees and the ankle angle returned to its pre-incline posture when the post-incline period began.

If the mechanism were a thixotropic effect on ankle dorsiflexors, then the shortened tibialis muscle should have shown sustained EMG activity while subjects stood on the incline, since the conditioning prerequisite for a thixotropic after-contraction effect is an isometric contraction in the shortened position (Hagbarth and Nordin 1998, Proske et al. 1993). Further, increased tibialis activity should have persisted into the post-incline period, pulling the subject forward. Instead, the tibialis muscle was quiet for 6 out of 7 subjects in the during-incline period and was quiet for all subjects in the post-incline period under both the hips blocked and the hips free conditions of Experiment 1. Our finding that the tibialis muscle was quiet while subjects stood on the inclined surface contradicts the findings of Aniss and colleagues (1990), who reported elevated dorsiflexor activity under similar surface conditions. The difference in our results and those of Aniss et al. could be explained by different task goals. The purpose of using the stance-on-incline task in the Aniss et al. experiments was to increase tonic activity in the ankle dorsiflexors and, therefore, their subjects could have leaned slightly backwards in comparison to our subjects, who were asked to stand in a relaxed way.

Instead of a peripheral mechanism of muscle spindle thixotropy, an alternative explanation for after-contraction effects on resting posture is a change in the central interpretation of proprioceptive information and a slow change in the set point for the state of whole body postural tonus (Gilhodes et al. 1992; Gurfinkel et al. 1989; Ghafouri et al. 1998). The post-incline lean could have resulted from a redistribution of tonic postural activity after a prolonged period of altered proprioceptive input. However, prior studies of centrally based after-contraction effects on whole body postural tonus have used a conditioning stimulus of sustained isometric muscle contraction (Ghafouri et al. 1998; Gilhodes et al. 1992; Gurfinkel et al. 1989). When our subjects stepped instead of stood on the inclined surface, their ankle, knee and hip muscles were not maintained at either a constant length or a constant level of activity (Experiment 2). Yet, subjects leaned after they stepped-in-place on the inclined surface, with similar amplitude and decay as after they stood on the incline. Thus, it is unlikely that the post-incline lean can be explained by sustained, constant muscular effort during the period of surface inclination. It is possible that both the post-incline lean and after-contraction effects act through common central pathways and that both after-effects involve a central recalibration of how proprioceptive information is interpreted for postural alignment, since both after-effects consist of an unintentional change in resting posture that gradually decays toward baseline resting posture. Post-vibratory postural effects have also been suggested to act through a similar mechanism (Gilhodes et al. 1992; Wierzbicka et al. 1998).

The post-incline lean is not due to a mechanism that acts at the ankle

In addition to ruling out an after-contraction effect in ankle muscles as an explanation for the post-incline lean, our results suggest that the post-incline lean cannot be explained by a recalibration of the postural set point for the position of the ankle (or the knee or the hip) joint. If subjects leaned to maintain a constant ankle angle from the during- to the post-incline periods, then the conditions of blocking hip movement in the post-incline period and of stepping during the incline period should have abolished the lean. However, subjects leaned. If subjects leaned to maintain a constant level of ankle muscle activity, then EMG activity in the post-incline period should have been observed in muscles that were active while subjects stood on the incline. Instead, EMG activity patterns differed between the during-incline and the post-incline periods. EMG activity patterns also differed between the lean that occurred when hips were prevented from leaning and the lean that occurred when the hips were free to move, even though the orientation of the trunk with respect to space was similar. Thus, the organization of ankle muscle activity depended on the context of available stabilizing supports (Cordo and

Nashner 1982; Nardone and Schieppati 1988) rather than on the prior level of muscle activation that occurred while subjects stood on the incline.

A central mechanism underlies the post-incline lean

We have shown that when subjects stood on the inclined surface, the postural variables that underwent adaptive change and showed a postural after-effect were not related to the position of the ankle joint or the level of activity in ankle muscles. Instead, adapting to the inclined surface affected global postural variables related to orientation of the whole body, such as the spatial relationship between the alignment of the trunk and the support surface. The trunk, the head, and the CoM of the body leaned in the same direction and with a similar time course whether or not 1) the legs were allowed to lean forward and 2) subjects stepped, instead of stood, on the inclined surface.

The finding that, for both the hips blocked and the hips free conditions, the amplitude of leaning of the trunk and head in the post-incline period increased linearly with a slope near 1 when the amplitude of surface inclination was increased, suggests that the mechanism for the post-incline lean involves regulation of the spatial relationship between the alignment of the trunk and/or the head and the alignment of the support surface. The forward leaned posture with respect to space maintained the relationship of the trunk to the support surface when the surface changed orientation from inclined to horizontal, even when the legs could not lean. On average, subjects leaned 5° farther forward after standing on a 10°-inclined surface than they had leaned after standing on a 5°-inclined surface. These results suggests that subjects leaned because of an adaptation or a recalibration of the postural set point for maintaining alignment of the upper body with respect to the support surface. These results also suggest that the trunk-to-surface relationship may be an important postural control variable, an idea that has also been proposed based on studies of humans standing on a slowly rotating surfaces (Gurfinkel et al. 1981, 1995a), of cats standing as inter-paw distance was varied (Fung and Macpherson 1995), and of astronauts standing under microgravity conditions (Baroni et al. 1999).

Although subjects leaned their upper bodies in the same direction and with a similar time course of decay when the hips were blocked as when the hips were free to move, 5 out of 7 subjects leaned their trunks further forward when the hips were blocked. One explanation for this larger amplitude lean could be that the amplitude of upper body lean is determined by an interaction between the drive to lean forward and mechanisms aimed at maintaining postural stability. When their hips were free to move, subjects may have been driven to lean further than they were able, but they could not achieve a more forward leaned upper body without loss of stability. When subjects could lean against a rigid support at their hip level, the range of forward stability limits for upper body lean may have increased.

An alternative explanation for the more forward upper body lean under the hips-blocked condition could be that subjects leaned to bring the CoM of the whole body forward, as opposed to leaning to bring the upper body forward. Subjects may have leaned their upper bodies further forward when the hips were blocked to compensate for the inability to bring the legs forward and to bring the CoM forward a similar amount as when the legs were free to lean. In support of this hypothesis, the maximum lean of the CoM was not significantly different between the hips blocked and free conditions at the larger amplitude-conditions of surface inclination. However, inconsistent with the CoM-hypothesis is that the amplitudes of CoM leans were small and increased nonlinearly as the amplitude of surface inclination increased, under both the hips blocked and the hips free conditions. Further, unlike for the relationship between the upper body and the support surface, leaning did not maintain the relationship between the CoM and the support surface when the surface moved from an inclined to a horizontal position.

Kinetic postural variables, which provide force-related sensory information, such as torque or load on ankle muscles, do not appear to undergo adaptive changes that cause leaning. The leaned posture of the upper body in the post-incline period altered the relationship of the body to gravity and thus altered the postural dynamics, as reflected in altered patterns of EMG activity in the post-incline period. In contrast, subjects maintained the kinematic relationship between the upper body and the support surface when the surface transitioned from an inclined to a horizontal position. The post-incline lean appears to be a kinematic, rather than a kinetic, after-effect. Parallel, separate, control of postural kinematic and kinetic variables have been previously proposed based on studies of cat postural activity on inclined and tilting surfaces (Lacquaniti and Maioli 1994). While it is unclear how sensory information is integrated to determine the spatial orientation of the body with respect to the surface, coding of proprioceptive information in global kinematic coordinates, as opposed to muscle parameters or to local joint angles, has been shown to occur even early in sensory processing, at the level of dorsospinocerebellar tract neurons (Bosco et al. 2000).

The post-incline lean is similar to other central after-effects that follow adaptive changes during a postural or locomotor task. For example, the post-incline lean resembles the direction-specificity and the duration of lean after-effects that follow exposure to linear optical flow. After being exposed to a moving visual field, subjects leaned for a few minutes in the opposite to the direction of the lean that occurred during the period of exposure to the moving visual field (Lestienne et al. 1977; Reason et al. 1981). The similarity between the post-incline and the post-visual flow lean suggests that similar central mechanisms may be involved in the spatial recalibration of the set point for postural orientation regardless of sensory context.

The post-incline lean is also similar to an unintentional circular locomotor trajectory that follows stepping-in-place on a rotating circular treadmill (Gordon et al. 1995; Weber et al. 1998). Just as the post-incline lean maintains the same trunk-to-surface relationship as when standing on the inclined surface, the curved walking trajectory maintains the same trunk-to-foot-to-surface relationship as when walking in place on a turning treadmill (Earhart et al. 2001; Gordon et al. 1995; Weber et al. 1998). The finding of direction-specific after-effects on trunk orientation in space after standing or stepping on an incline and after stepping on a rotating treadmill suggests that the surface provides strong cues for postural orientation. The after-effect of walking on a circular treadmill generalizes to other forms of locomotion with very different muscular and kinematic patterns, such as hopping (Earhart et al. 2002b) or walking backwards (Earhart et al. 2001), just as the post-incline lean generalizes from stepping to standing still. The generalization of the spatial after-effects from one task condition to another suggests involvement of central mechanisms related to postural orientation as opposed to a local muscle or receptor adaptation or habituation. A central mechanism for the locomotor after-effect of PKAR has also shown by the absence of adaptation in subjects with cerebellar lesions (Earhart et al. 2002a).

Generalization of adapted postural reference across tasks

Subjects leaned with a similar time course and amplitude after stepping on an incline as after standing on an inclined surface, suggesting that a common mechanism underlies the post-incline lean for both a locomotor and a solely postural task. Similar postural after-effects after subjects stepped or stood on an incline is not surprising, given that stance and locomotion share the common goal of upright head and trunk orientation in space. Effective locomotion requires appropriate alignment of the trunk and head segments over the moving base of support (Winter et al. 1990). Although the control of posture and locomotion is organized in separate and parallel neural pathways, the pathways are highly integrated (Jankowska and Edgely 1993; Matsuyama and Drew 2000; Mori 1987; Nashner et al. 1980, 1986). An internal representation, or body scheme, of posture relative to the environment has been suggested to provide the basis for perception and performance of posture and movement (Gurfinkel and Levik 1991; Lestienne and Gurfinkel 1988; Ivanenko et al. 2000). We suggest that the post-incline lean occurs because of an adaptive modification of this centrally organized internal model of body orientation, which can explain the generalization of the adaptive after-effect from a stepping to a standing task.

Subjects leaned their trunks more forward while they stepped-in-place on the inclined surface than when they stood on the inclined surface. Forward leaning of the trunk during stepping on an inclined treadmill has been reported by other investigators and has been suggested to be a task-specific postural adaptation that is related to the dynamics involved in generating propulsive forces while controlling the body CoM (Leroux et al. 2002). Because our subjects leaned forward when they stepped on the incline, they experienced a different relative trunk-to-surface alignment while they stepped on the incline as compared to when they stood on the incline. Although trunk alignment differed between the stepping and the standing adaptation-conditions, the after-effects on the amplitude of trunk lean were similar. A possible explanation for the similarity of the postural after-effects is that postural orientation is organized not only on the basis of an internal representation of the support surface in space and of the body to the support surface, but also on the task constraints that optimize postural alignment for the different tasks of stepping or standing still. Ivanenko and colleagues (2000) proposed a similar interpretation, involving an interaction between task constraints and a modified internal representation of body posture, to explain their results that the vibration of the same neck muscles caused forward trunk lean when subjects stood still, caused forward trunk lean and forward stepping when subjects attempted to step-in-place, and caused increased gait velocity when subjects stepped on a treadmill.

Conclusions

We have shown that the postural after-effect of leaning after subjects stand on an inclined surface cannot be due to local mechanisms acting at the ankle because subjects leaned their upper bodies even when their legs were prevented from leaning during the post-incline period and because subjects leaned after they stepped-in-place on an incline. We suggest that the post-incline lean involves an adaptive mechanism that affects the central representation of the body-to-support-surface relationship. When the surface changes orientation with respect to gravity, this adaptive mechanism adjusts the postural set point, or postural reference, for body alignment with respect to the surface. Control of postural orientation during standing in place and during locomotion appear to share a common internal representation of posture with respect to the surface, because subjects lean in a similar way after standing or stepping on an inclined surface.

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Chapter 4

Differences in preferred reference frames for postural orientation shown by after-effects of stance on an inclined surface

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Abstract

In previous studies, we identified a postural after-effect of leaning that follows a period of stance on an inclined surface with eyes closed. This leaning after-effect, which maintained the body-to-surface relationship as if subjects still stood on the incline, occurred in many, but not all, subjects. In the present study, we examined the incidence and robustness of the lean after-effect in 51 healthy subjects. The location of the center of pressure (CoP) under the feet and the alignment of the trunk and leg were measured before, during and after blindfolded subjects stood on a 5°-toes-up inclined surface for 2.5 minutes. When the surface was inclined, all subjects stood with their trunk and legs aligned near to gravity-vertical, similar to the alignment adopted in the pre-incline period. When the surface returned to horizontal in the post-incline period, there was a continuum of postural alignment strategies across subjects. At one extreme, subjects leaned forward, with an average trunk lean near 5°. The leaned posture decayed exponentially toward baseline postural alignment across several minutes. At the other extreme, subjects did not lean in the post-incline period, but instead, stayed aligned near upright with respect to gravity. Subjects were highly consistent in their post-incline postural behaviors upon repeated testing over days to months and across different directions of surface inclination. Our results suggest that individuals have well-established, preferred, sensory strategies for controlling postural orientation when vision is not available. Subjects who leaned in the post-incline period appear to depend more on the geometry of the support surface as a reference frame and rely more on somatosensory information to extract kinematic relationships, whereas subjects who did not lean depend more on gravity as a reference frame and rely more on sensory information related to forces and load.

Introduction

Humans typically stand with postural orientation that is near to upright with respect to the direction of gravity, but it is unclear how the nervous system combines different types of sensory information to establish a reference, or a set point, for this preferred postural orientation (Gurfinkel et al. 1995a). The nervous system has access to multiple sources of sensory information about the relative alignment of the body segments to each other and to the environment, including visual (Dichgans et al. 1972; Lee and Lishman 1975; Lestienne et al. 1977), somatosensory (Gurfinkel 1995a; Eklund 1972; Roll et al. 1989b), vestibular (Day, 1997; Hlavacka et al. 1995, 1996; Lund and Broberg 1983), and truncal graviceptor (Mittelstaedt 1996, 1998) information. However, to establish and maintain a set point for postural orientation, this multimodal sensory information must be integrated and interpreted with respect to a stable frame of reference that is relevant to the postural task (Berthoz 1991; Gibson 1952; Mergner and Rosenmeier 1998; Mittelstaedt 1998; Stoffregen and Riccio 1988).

When a subject stands on a stable, horizontal surface, it is difficult to determine the particular reference frame upon which the subject relies for postural orientation, because the task of standing is well learned and the sensory information related to the support surface, gravity, and vision are readily available and congruent. However, when the support surface is inclined, the typically perpendicular relationship between the support surface and gravitational vertical is altered, allowing investigation of the relative contributions of the support surface and gravity as reference frames for postural orientation. In the present study, we investigated how blindfolded subjects adapt their postural orientation to statically maintained changes in surface inclination to determine the relative contributions of the support surface and gravity in establishing postural orientation.

We recently identified a postural after-effect of standing on a statically inclined surface that suggests a preferential reliance on the support surface, as opposed to gravity, as a reference frame for establishing postural orientation (Chapter 2). When our blind-folded subjects returned to stance on a horizontal surface after a period of stance on an inclined surface, they leaned away from their typical orientation with respect to gravity, with a direction and amplitude that maintained the relative alignment of their trunks to the surface as if they still stood on an incline. The lean persisted for minutes. We concluded that during the period of exposure to the incline, the central nervous system adaptively recalibrated the set point for postural orientation to take into account the new orientation of the support surface, and that subjects leaned in order to maintain their postural orientation around this adapted, body-to-surface set point. We eliminated an after-contraction effect in ankle muscles as an explanation for the post-incline lean (Chapter 3). In addition to the post-incline lean effect, the power of the support surface as a reference frame for postural orientation has been shown by the finding that subjects maintain consistent postural alignment with respect to a slowly changing inclination of the support surface (Creath et al. 2002; Gurfinkel et al. 1981, 1995a; Walsh 1973).

Not all subjects leaned after they stood on an inclined surface. In our prior studies, which focused on characterizing the postural after-effects of stance on an incline, we excluded from further study 14 out of 25 screened subjects because these subjects did not lean for at least 1 minute after they stood on a- 5°-inclined surface for 2.5-minutes (Chapter 2). These excluded subjects may have preferentially relied on the direction of gravity, as opposed to the geometry of the support surface, as a reference for establishing postural orientation. Similar individual variation has been shown for the degree to which subjects depend on visual information as a reference for their postural stability and orientation (Chiari et al. 2000; Collins and Deluca 1995; Cremieux and Mesure 1994; Golomer et al. 1999; Isableau et al. 1997; Lacour et al. 1997). Healthy subjects also vary from one another in how strongly they respond to tendon vibration (Eklund and Hagbarth 1966; Gurfinkel et al. 1995b; Gurfinkel et al. 1998; Ivanenko et al. 2000) and to galvanic vestibular stimulation (Horak and Hlavacka, 2001), supporting the hypothesis that individuals differ in the degree to which they weight proprioceptive and vestibular information for controlling the orientation of their bodies. This variation across healthy subjects in their postural sensitivity to sensory manipulations is often ignored and subjects who are unresponsive are usually excluded from studies. However, this variation in sensory sensitivity among healthy subjects may reflect important differences in a-priori sensory weighting that is related to each subject's unique prior experiences or genetic makeup (Chiari et al. 2000; Lacour et al. 1997).

The present study was designed to identify and understand the differences among healthy subjects in the postural after-effects of standing on an inclined surface. We investigated two main questions. First, we asked whether there are two, distinct groups of subjects among healthy subjects, one group who leans with a large amplitude that decays slowly across minutes and one group who does not lean, or, instead, whether there is a continuum among healthy subjects in the amplitude and duration of post-incline leaning. If there are 2 groups, leaners and non-leaners, this suggests that the nervous system selects between 2 discrete possible adaptive orientation strategies, whereas if there is a continuum of strength of the leaning after-effect, this suggests a common adaptive mechanism with varying rates of adaptation and/or varying degrees of relative weighting of the support surface versus gravity as a reference frame for postural orientation. Second, we asked whether individual subjects show consistent post-incline responses when tested repeatedly across different days. If the presence or absence of leaning is related to a difference among subjects in their preferred reference frame for determining postural orientation, then, when tested days or weeks apart, subjects would be expected to show similar amplitudes and decay time constants of leaning.

Methods

We conducted 3 experiments to investigate the frequency and consistency of the post-incline lean in healthy subjects. In Experiment 1, we tested a large number of subjects before, during, and after stance on an inclined surface to determine the frequency and amplitude of post-incline leaning in healthy adults. In Experiments 2 and 3, we tested two groups of subjects who showed either a strong or an absent post-incline lean effect in order to determine the consistency of the post-incline lean across days to weeks (Experiment 2) and across different directions of surface inclination (Experiment 3).

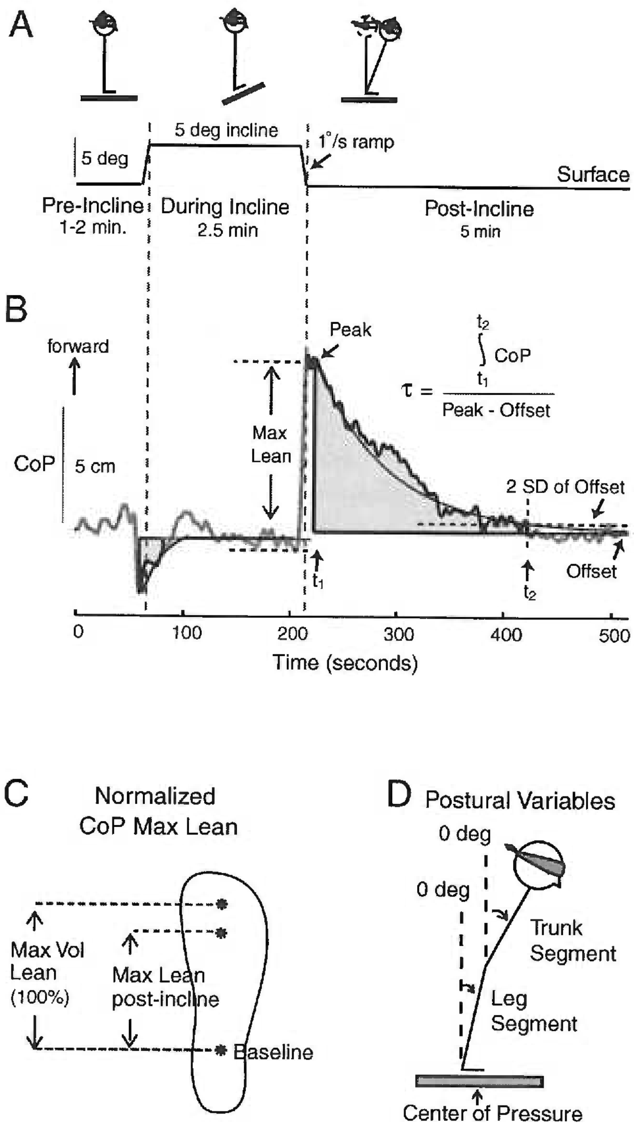
Subjects

We tested 51 healthy subjects, ranging in age from 20 to 49 years (29 F, 31.4 ± 8.6 yrs; 22 M, 29.6 ± 8.2 yrs). Inclusion criteria for participation in the study consisted of: 1) free of neurological and musculoskeletal impairments that could affect balance and posture, ruled out by a health history; 2) normal balance and vestibulospinal function based on the ability to stand for 60 seconds with eyes closed on 4-inch, medium-density temper-foam and for 30 seconds with eyes closed in a tandem Romberg stance (Shumway-Cook et al. 1996); and 3) normal cutaneous and proprioceptive sensation in the feet and ankles based on Semmes-Weinstein monofilament and joint position testing (Dickstein et al. 2001; Mueller 1996). The Institutional Review Board at Oregon Health & Science University approved the experimental protocol, and all subjects gave their informed consent prior to participating in experiments.

Protocol for Experiment 1

Experiment 1 was designed to determine the frequency with which the post-incline lean after-effect occurs in a group of 51 healthy adults. Each subject participated in a single trial, in which their postural alignment was measured before, during, and after they stood on a 5° toes-up inclined surface. Each subject also participated in a set of trials designed to measure the amplitude of voluntary, or intentional, leaning as far as possible without losing balance. The amplitude of voluntary leaning was used to normalize the amplitude of the unintentional post-incline lean. Data for Experiment 1 were collected in two laboratories (Laboratory 1, 39 subjects; Laboratory 2, 12 subjects). While there were minor differences in the methods for data collection that will be explained below, there were no important differences in the trial protocol or among the experimental results from the two laboratories.

Figure 1A shows the surface conditions for the stance-on-incline trial. Subjects stood, head facing forward and arms crossed, on a force platform that could rotate. Each trial consisted of a 1- to –2-minute pre-incline period when the surface was horizontal, a



$$\tau = \frac{\int_{t_1}^{t_2} CoP}{Peak - Offset}$$

FIG. 1. Experimental conditions and dependent variables. FIG. 1A shows the pre-, during-, and post-incline time periods within each stance-on-incline trial. Dotted vertical lines show the onsets of the during- and the post-incline periods. FIG. 1B shows the method used to quantify the maximum lean and the decay time constant for the return from a leaned to an upright posture for a representative subject's CoP data. The post-incline maximum lean was defined as the peak displacement from the mean CoP location during the last 30 seconds of the during-incline period. The decay time constant was defined as the area under the CoP trajectory divided by the amplitude of the peak displacement relative to the offset. The offset is the mean position of the CoP during the last 30-s of the trial. The area, shaded in gray, was calculated by integration from the time of peak lean (t1) to the time when the CoP decayed to and stayed within 2 standard deviations of the offset for 10 consecutive seconds (t2). FIG. 1C illustrates how the maximum lean of the CoP was normalized to each subject's voluntary maximum lean. FIG. 1D shows how orientation of the trunk and leg segments were defined.

2.5-minute during-incline period when the surface was inclined at 5° toes-up, and a 5-minute post-incline period when the surface was again horizontal. The surface rotated between the horizontal and inclined positions at a constant velocity of 1°/s, with the axis of rotation at approximately ankle height. In Laboratory 1, subjects stood with the center of their heels spaced 17 cm apart, a distance reported to be the average when healthy subjects were asked to stand comfortably (McIlroy and Maki, 1997). In Laboratory 2, subjects selected a comfortable foot position, and the distance between the heel-centers averaged 15.9 ± 2.4 cm.

Subjects were blindfolded to eliminate visual information and wore headphones to remove auditory information that could influence postural orientation. In addition, a short story audiotape was played through the headphones in order to distract each subject's attention away from postural alignment. Subjects were instructed to: 'stand in a relaxed way; listen to the story and try not to pay attention to your posture'. Subjects wore a safety harness that was tethered to an overhead beam to ensure safety during trials. The safety harness was adjusted so that it gave no directional/spatial cues for postural alignment. A research assistant stood near the subjects to ensure their safety during the trials.

To normalize the amplitude of the post-incline lean, we measured the amplitude of each subject's maximum voluntary lean, illustrated in Figure 1C. When performing maximum voluntary leans, each subject was blind-folded and then instructed to lean as far forward or backward as possible while still maintaining balance. Subjects were instructed to lean by rotating mainly at the ankle joint, while maintaining contact between the entire foot and the surface. In Laboratory 1, the amplitudes of forward and backward maximum voluntary leans were determined from two 1-minute trials, one trial for each direction. Each maximum voluntary lean trial consisted of 3 alternating cycles of 10 seconds of baseline stance and 10 seconds of holding the maximally leaned posture. In Laboratory 2, forward and backward maximal voluntary leans were determined from a single 2-minute trial that consisted of 3-4 cycles of slow movement between baseline, maximum forward, and maximum backward leaned positions. Subjects were instructed to hold each position for 4 to 6 seconds.

Protocol for Experiment 2

In Experiment 2, we tested whether subjects who leaned with a large amplitude and long duration would consistently show such a strong post-incline effect when tested with trials that were days or longer apart. We also asked whether subjects who did not lean would consistently show an absence of leaning. From the group of subjects who participated in Experiment 1, we identified two smaller groups of subjects whose responses represented the two extremes of post-incline postural effects: leaners (n = 8, 36.3 ± 9.5 yrs, 5F) and non-leaners (n = 8, 35.3 ± 7.6 yrs, 6F). Each leaner and non-leaner participated in 3 stance-on-incline trials. Trials were separated by at least one day, with the time span ranging between one day and 7 months. The experimental protocol was identical to Experiment 1. Subjects stood with their feet a comfortable distance apart, approximately hip width. For each subject, foot placement was kept constant across all trials. All trials for Experiment 2 were conducted in Laboratory 2.

Protocol for Experiment 3

In Experiment 3, we tested the within-subject consistency of post-incline postural after-effects across different directions of surface inclination in the 8 leaners and 7 out of 8 of the non-leaners who participated in Experiment 2. Three directions of surface inclination were tested: 5°-toes-up, 5°-toes-down, and 5°-right-side up. Except for the direction of surface inclination, trial conditions were identical to Experiment 2. Subjects were tested with one trial for each direction-condition. The 3 trials for each subject were conducted at least one day and up to 3 months apart. All trials for Experiment 3 were conducted in Laboratory 2.

Influence of instruction

To determine whether instructions given to the subject could influence the strength of the post-incline lean, 3 leaners were instructed to 'stand vertically' rather than to 'stand in a relaxed way; listen to the story and try not to pay attention to your posture'. Except for this different instruction, conditions were identical to Experiment 2.

Data collection and analysis

The location of the CoP was used to quantify the amplitude and the duration of post-incline effects. The CoP was calculated from vertical force data collected at 50 Hz and filtered with a 0.1 Hz low-pass, recursive, 2nd order Butterworth filter. The 0.1 Hz filter cut-off frequency was selected in order to quantify slow changes in postural alignment and to eliminate the fast fluctuations of stabilizing postural corrections (Fransson et al. 2000; Gurfinkel et al. 1995a). See Chapter 2 for additional details.

For Experiment 2, we also quantified trunk and leg postural alignment in the sagittal plane. Figure 1D shows the conventions used to define the alignment of the trunk and leg segments. The trunk segment was defined as a line between the hip and the shoulder joints, and the leg segment was defined as a line between the ankle and hip joints. Positive values indicate forward angular rotation. Changes in the alignment of the trunk and the legs were compared with respect to their alignment during the pre-incline period. The trunk and leg segment angles were calculated using shoulder, hip, and ankle position data and trigonometric relationships. Horizontal displacements of the shoulder and of the hip in the anterior-posterior direction were recorded using lightweight metal rods that were attached to the subject at shoulder or hip height on one end and attached to a potentiometer on the other end. Position data were recorded at 50 Hz and then filtered at 0.1 Hz, like the CoP data, to characterize the slow changes in postural orientation.

Figure 1B illustrates the two variables that we used to quantify the strength of the post-incline after-effect: the maximum lean and the decay time constant. We also calculated the maximum lean and the decay time constant of the lean that occurred when the surface transitioned from a horizontal to an inclined position. Both the maximum lean and the decay time constant were calculated from CoP data. For Experiment 2, we also calculated the amplitude of the maximum lean for the trunk and leg segment data.

The maximum lean was defined as the difference between the peak displacement in the post-incline period and the mean value during the last 30 seconds of the incline-period. The peak displacement was measured 5 seconds *after* the surface rotated to a new position in order to avoid transient body movements made to compensate for instability imposed by the surface rotation. When measured using CoP data, the maximum lean was normalized as a percentage of the maximum voluntary lean for each subject (Figure 1B).

The post-incline lean decayed exponentially. We determined the time constant of the lean's decay from a leaned to an upright posture to quantify the persistence of the post-incline after-effect. We calculated the dominant decay time constant by dividing the integrated area under the data trajectory by the peak lean as illustrated in Figure 1B (Cohen et al. 1977). This method was chosen over an optimization method for estimating the time constant because the decay of the lean, while exponential in nature, varied in form across subjects. Prior to integration of the data to determine the area, we removed the offset, defined as the mean CoP location during the last 30 seconds of the trial. If subjects showed a sudden, large, sustained displacement (shift) or a gradual drifting of the CoP towards the end of the trial, after they had maintained a steady position for at least 30 seconds, we defined offset as the mean CoP during the 30 seconds immediately prior to the shift or drift (Duarte and Zatsiorsky, 1999).

For Experiment 2, we quantified the degree to which leaners and non-leaners oriented their posture to the moving surface *during* the surface ramps by calculating a velocity ratio for the trunk segment and the leg segment. The velocity ratio was defined as the angular velocity of rotation of the body segment divided by the angular velocity of rotation of the support surface. A velocity ratio of '1' indicates that the subject stayed aligned with respect to the surface as it rotated, with body segment velocity matching surface velocity. A velocity ratio of '0' indicates that the subject stayed aligned to vertical with respect to gravity. Trunk and leg velocity during the surface rotation were calculated using linear regression from 500 msec after the surface began to rotate to 500 msec after the surface reached the new position. We added the 500-msec delay because of the delay in movement of the body segments in response to surface rotation.

Statistical Analysis

Statistical analyses were performed using Statistica and SPSS software, with the significance set at $\alpha = 0.05$ for all comparisons. For Experiment 1, we examined the relationship between the leans that followed the two surface transitions, horizontal to inclined and inclined to horizontal. We used paired t-tests to determine whether the leans that followed the two surface transitions were different from one another in terms of their decay time constants and in terms of their amplitudes of maximum leans. We calculated correlation coefficients to quantify the strength of the relationship between the decay time constants and between the maximum leans of each surface transition. We asked whether the orientation of the trunk while subjects stood on the incline was related to the amplitude and the persistence of the post-incline lean by calculating the correlation coefficient between trunk orientation and the maximum lean and between trunk orientation and the lean's decay time constant.

For Experiment 2, we used unpaired t-tests with Bonferroni corrections to analyze whether leaners and non-leaners were different from one another in terms of their base of support length and width, height, and age. We also used paired t-tests to analyze how the two groups differed in terms of postural changes that followed the two surface transitions, horizontal-to-inclined, and inclined-to-horizontal.

For Experiment 3, we used repeated measures ANOVA to analyze the effect of incline direction on the maximum lean and decay time constant of the post-incline lean.

We used Sheffe´ post-hoc comparisons to determine whether, for each group of subjects, the maximum lean and the decay time constant of the post-incline lean differed across the toes-up, toes-down, and lateral directions of inclination. We also used the post-hoc analyses to determine whether the leaners differed from non-leaners in the maximum lean and the decay of their leaning for each direction of surface inclination.

Results

Post-incline postural effects

Figure 2 compares the postural alignment of a representative subject who leaned (Fig. 2A) to the postural alignment of a representative subject who did not lean (Fig. 2B) before, during, and after the subjects stood on 5°-toes-up-inclined surface for 2.5 minutes. For the subject who leaned, the amplitude of the lean was large and the lean persisted for minutes, decaying exponentially toward baseline postural alignment. The lean involved both trunk and leg forward rotation and an accompanying forward shift of the CoP. The initial forward lean of the body maintained the relative alignment between the body and the surface similar to when the subject stood on the inclined surface. In contrast to the leaner, the non-leaner showed only a transient perturbation in postural alignment when the surface rotated from an inclined to a horizontal position. The non-leaner maintained a postural orientation that was near to upright with respect to gravity, with the orientation of the trunk and legs and the location of the CoP held near constant values throughout the pre-, during-, and post-incline periods.

The presence and strength of leaning after-effects varied widely and along a continuum across the 51 subjects that we tested, as illustrated in Figure 3, which shows

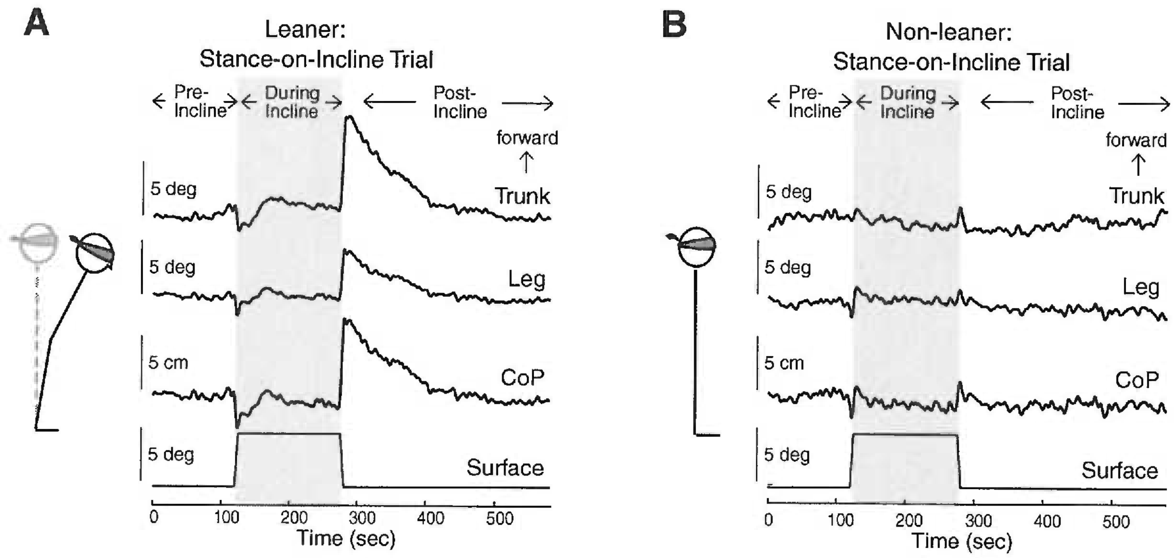


FIG. 2. Post-incline postural effects for a leaner and a non-leaner. Each set of data is from a representative stance-on-incline trial. The shaded area indicates the time period during which the surface was inclined at 5°-toes-up. FIG. 2A shows the long lasting forward lean of the whole body after stance on a toes-up inclined surface in a representative subject who leaned. FIG. 2B shows the upright postural alignment adopted throughout the stance-on-incline trial for a representative subjects who did not lean.

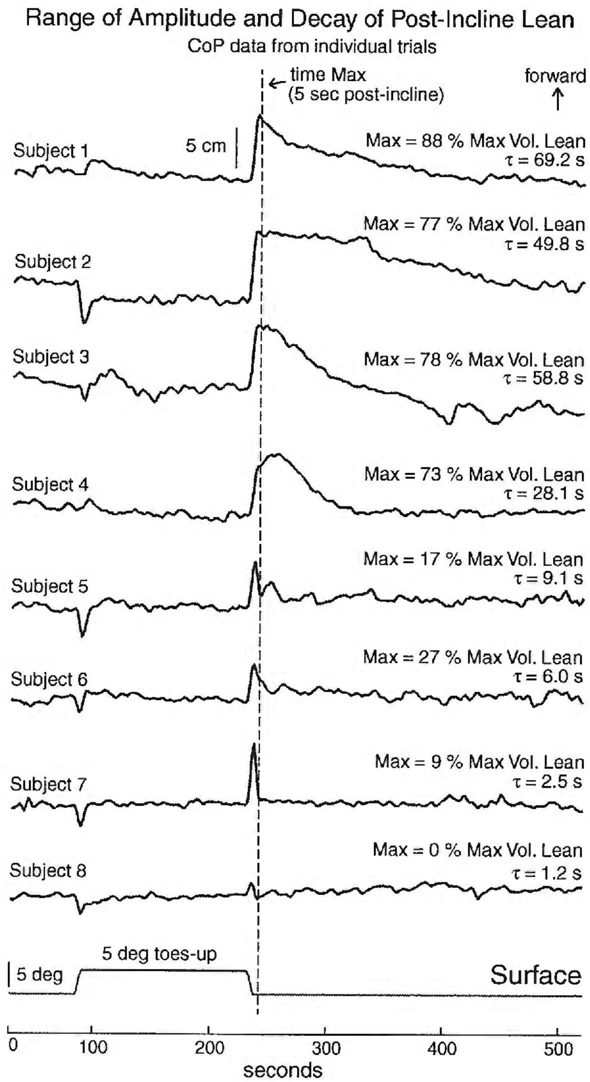


FIG. 3. The between-subject variability of post-incline postural effects is illustrated by the CoP time series traces from the stance-on-incline trials of 8 representative subjects. The dashed line indicates the beginning of the post-incline period. The values for each subject's maximum lean amplitude (Max) and decay time constant (τ) are shown.

data from 8 representative subjects. For each subject, the location of the CoP is shown before, during, and after the subject stood on a 5°-toes-up-inclined surface. The duration of the leaning after-effect ranged from 0 to 4 minutes, and the lean decayed toward baseline postural alignment with a time constant that ranged from 0 to 69.2 seconds (mean 20.5 ± 20.2 s). Half (53%) of the subjects leaned with a decay time constant that was greater than 10 seconds in the post-incline period, thus, these subject took at least 30 seconds to return to their baseline posture. Like the decay time constant, the amplitude of the maximum lean also varied widely across the 51 subjects, with a mean of 38.3 ± 28.8% of maximum voluntary lean (range: 0 - 109.7%).

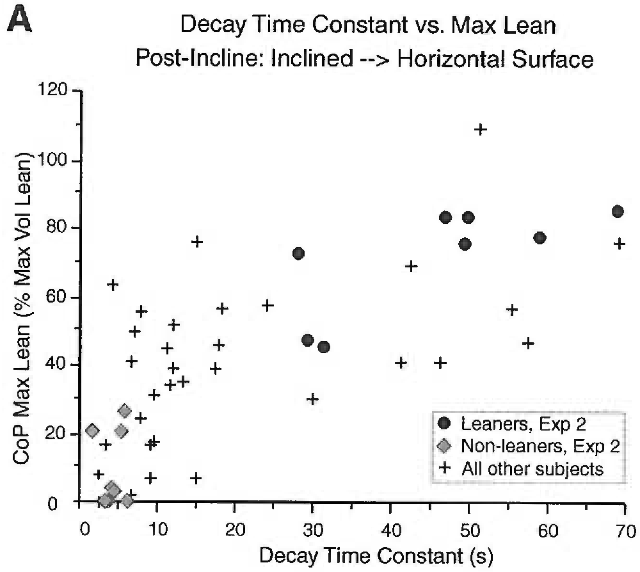
Two additional features of the post-incline lean's decay toward upright were observed for some subjects: a plateau period and an overshoot period. Seven of the 51 subjects demonstrated a plateau period, in which they maintained a nearly constant maximum lean before their leaned posture began to decay towards baseline postural alignment. The duration of the plateau period ranged from 8-21 seconds for 6 subjects and 99 seconds for 1 subject. The plateau period is illustrated in the data of Subjects 2, 3, and 4 in Figure 3. Only subjects who had large, long lasting leans demonstrated plateau periods (mean decay time constant: 50.4 ± 13.6 s; mean maximum lean: 74.5 ± 21.7% maximum voluntary lean). The second feature, observed in 6 subjects, was an overshoot past baseline position, illustrated in the data of Subject 3 in Figure 3. When these subjects slowly moved their bodies from the forward leaned posture toward their pre-incline, baseline posture, they did not stop and hold their baseline posture, but instead, over-corrected and leaned backwards before returning to baseline.

For most subjects (39/51), by the time the post-incline period ended, the location of the CoP had returned to within 1 cm of the pre-incline location. This suggests that the 5-minute post-incline period was sufficiently long to characterize the postural after-effects of stance on an incline for the majority of subjects. In the remaining 12 subjects, the location of the CoP at the end of the post-incline period was shifted more than 1 cm forward in 7 subjects, and more than 1 cm backward in 5 subjects, with respect to the pre-incline location.

Figure 4A shows how the amplitude and the decay of the post-incline lean varied across all subjects. Subjects who leaned for at least 1-minute in the post-incline period had relatively large amplitudes of lean (nearly 80% of maximum voluntary lean). The relationship between the decay time constant and maximum lean was moderately correlated (linear regression $R^2 = 0.57$), but nonlinear. The maximum lean saturated as subjects approached 80 to 90% of their voluntary maximum lean.

Figure 4B shows that subjects did not vary from one another in the duration of backward leaning that followed the first surface transition, from a horizontal to an inclined position. When the surface moved to a toes-up, inclined position, all subjects leaned backward with only small amplitudes, followed by a rapid return of the leaned posture toward upright alignment with respect to gravity. Note the contrast between the large between-subject variability in features of the post-incline lean that followed the inclined-to-horizontal surface transition in Figure 4A, and the small between-subject variability for the lean that followed the horizontal-to-incline surface transition in Figure 4B. The leans that followed the two surface transitions were significantly different from one another, both in terms of the decay time constant (mean of 4.1 ± 3.3 s versus $20.5 \pm$

A



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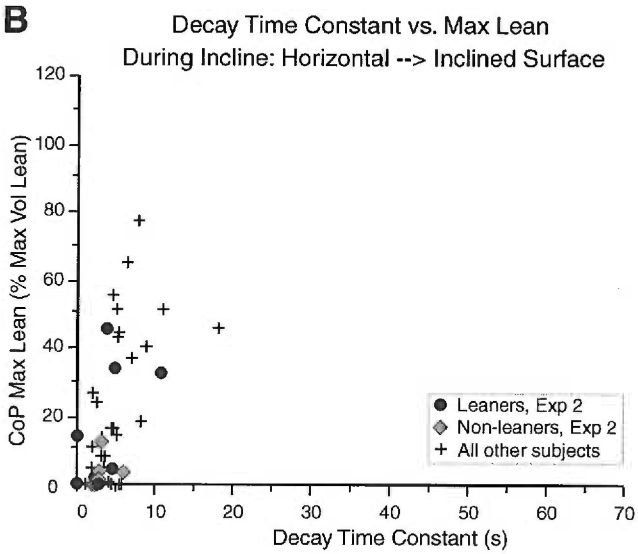

FIG. 4. Plot of the CoP decay time constants and CoP maximum leans for all 51 subjects. FIG. 4A shows data that characterizes the forward lean that occured in the post-incline period, when the surface changed conditions from inclined to horizontal. FIG. 4B shows data that characterizes the backward lean that occurred in the during-incline period, when the surface changed conditions from horizontal to inclined. The black circles identify the 8 leaners and the gray diamonds identify the 8 non-leaners who participated in Experiment 2 and 3. Crosses indicate the subjects who only participated in Experiment 1.

20.2 s for the first and second surface transitions, respectively, $p < 0.0001$) and in terms of the maximum lean (mean of 17.6 ± 21.0% and 28.3 ± 28.8% of maximum voluntary lean for the first and second surface transitions, respectively, $p < 0.0001$). There was no significant correlation of the decay time constants ($r = 0.216$), nor the maximum leans ($r = 0.081$) among the leans that followed the two surface transitions.

While subjects stood on the inclined surface, they maintained similar orientation of their trunks with respect to gravity as when they stood on the horizontal surface in the pre-incline period, with an average change in trunk alignment of 0.28 ± 1.2°. The change in trunk alignment from the pre-incline to the during-incline periods was not correlated with the strength of the post-incline, both in terms of the amplitude of maximum lean ($r = 0.035$) and the decay time constant ($r = 0.13$).

Repeatability of the after-effects of standing on an inclined surface

Leaners and non-leaners were highly consistent, across days to months, in how their postural alignment was affected by a period of stance on an inclined surface. Figure 4 identifies the 8 leaners (black circles) and the 8 non-leaners (grey diamonds) who participated in the additional stance-on-incline trials of Experiments 2 and 3. Figure 5A shows the postural alignment of each leaner and non-leaner, as measured by the location of the CoP, during the 3 trials in which the subjects stood on a toes-up-incline surface. The leaners showed little variation over time in the amplitude of their leans and in the form and the rate of the decay of their leaned posture toward baseline postural alignment. For leaners, the amplitude of leaning was close to the adapting stimulus of the 5°-surface inclination (mean trunk maximum lean: 5.6 ± 1.5°; mean leg maximum lean: 3.6 ± 0.9°).

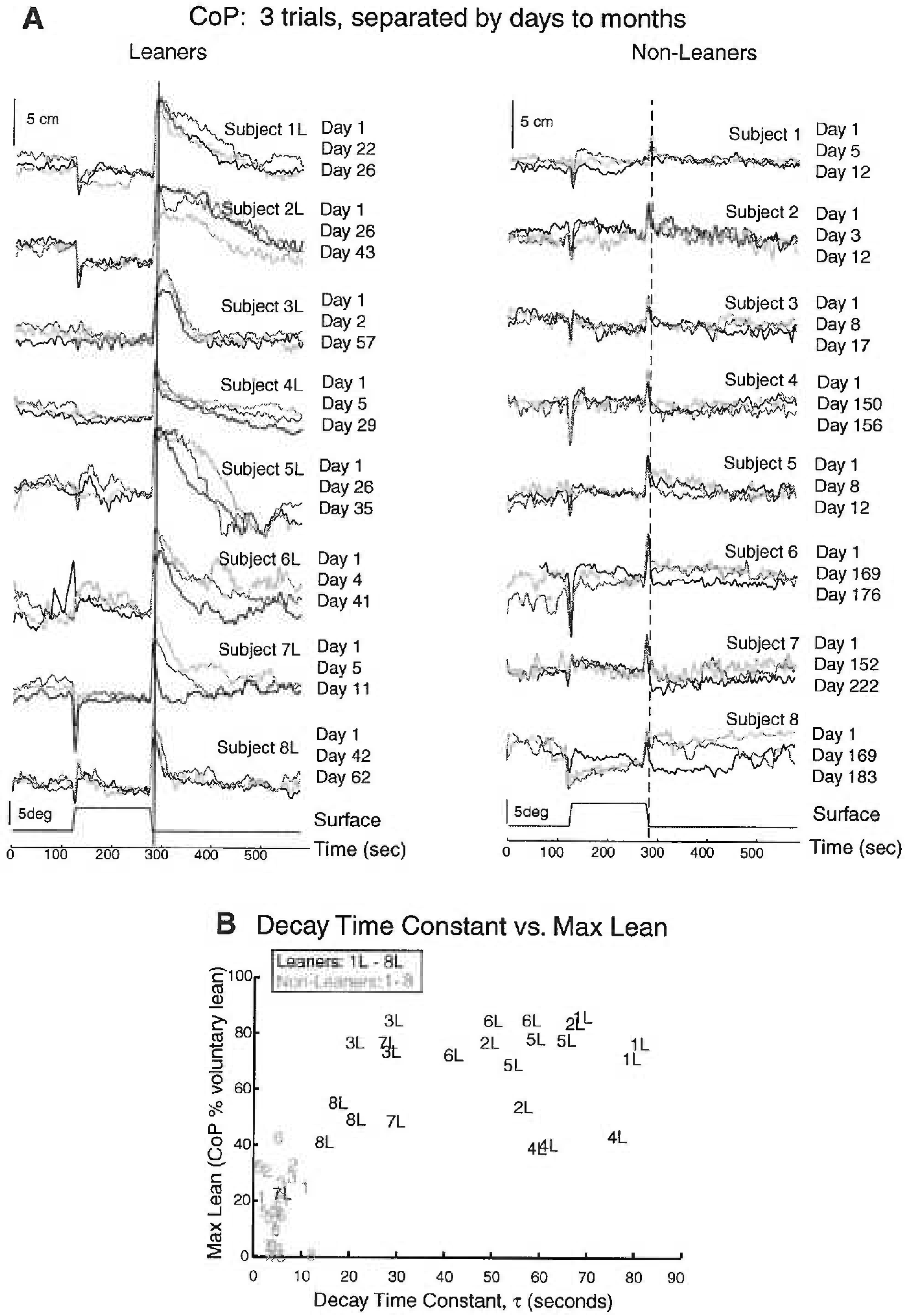

FIG. 5. Within-subject consistency of the postural after-effects of stance on an inclined surface. FIG 5A shows the CoP data from each of the 3 trials when the leaners (left) and non-leaners (right) stood on a toes-up inclined surface. The 1st trial is the darkest and the 3rd trial is the lightest trace. The 3 trials, collected days to months apart, show the high degree of within-subject consistency of incline after-effects. FIG. 5B further shows this within-subject consistency by plotting the maximum lean and the decay time constant for each trial of each subject.

The average decay time constant of the lean was 46.5 ± 22.3 seconds. In contrast, the non-leaners consistently showed only transient changes in the orientation of their trunks (mean maximum lean: 0.4 ± 0.1°) and their legs (mean maximum lean: 0.5 ± 0.3°), and the transient lean decayed with an average time constant of 5.5 ± 1.5 seconds. Figure 5B further illustrates the high degree of within-subject consistency in the after-effects of standing on incline, by plotting the post-incline maximum lean against the decay time constant for each trial.

Additional differences between leaners and non-leaners

Figure 6A and 6B show that leaners had a large and long-lasting lean in the post-incline period but a quick re-alignment to upright when standing on the incline. In contrast, non-leaners behaved symmetrically for the two surface transitions, with small maximum leans and short time constants.

The leaners and the non-leaners differed from one another in the time that they reached their peak forward lean in the post-incline period $p < 0.005$). Leaners did not reach their peak lean until *after* the surface had stopped rotating, with a mean time of peak lean of 3.2 ± 3.2 seconds *after* the surface was stationary. The leaners showed no signs of postural correction toward gravity-vertical while the surface moved. In contrast, non-leaners reached their peak lean and began to re-orient toward gravity-vertical *during* the surface rotation, with a mean time of peak lean of 0.6 ± 0.4 seconds *prior* to the surface becoming stationary. When the surface rotated from a horizontal to an inclined position, there was no difference in the time of peak lean between the leaners (2.3 ± 0.7 s

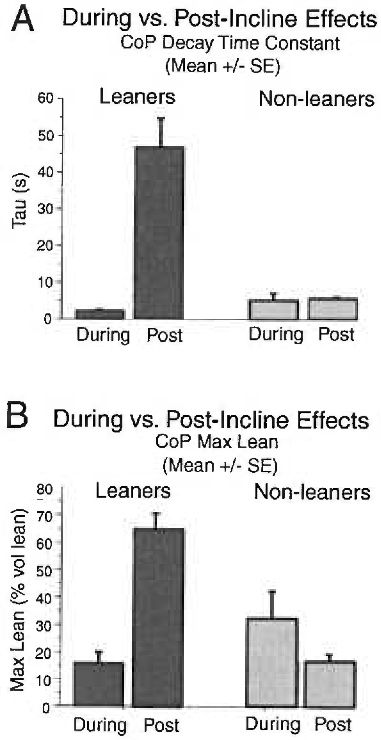

FIG. 6. Comparison of the decay time constant and the maximum lean for the two time periods that followed a change in surface orientation, showing the more asymmetrical pattern of behavior for the leaners than the non-leaners. The bar plots labeled 'During' quantify the lean that occurred after the surface moved from the horizontal to the inclined position. The bar plots labeled 'Post' quantify the lean that occurred after the surface moved from the inclined back to the horizontal position. FIG. 6A shows the group mean decay time constant and FIG. 6B shows the group mean maximum lean for each surface transition period for the leaners (black bars) and non-leaners (gray bars).

before the surface was stationary) and the non-leaners (1.3 ± 0.5 s before the surface was stationary).

Leaners and non-leaners differed in their postural orientation *during* the surface rotation from the inclined position back to the horizontal position. Figure 7 shows that leaners kept their trunks aligned to the surface as it rotated from a toes-up-inclined to a horizontal position, nearly matching trunk velocity to surface velocity. In contrast, non-leaners maintained a near constant alignment of their trunks during the surface rotation, so that the body remained aligned near to upright with gravity rather leaning. The difference in relative alignment to the moving surface between leaners and non-leaners was quantified with a ratio of the velocity of body segment rotation to the velocity of surface rotation. The mean trunk-to-surface velocity ratio for leaners was close to 1 (1.08 ± 0.12), indicating tight coupling between surface orientation and trunk alignment. The leg velocity ratio for leaners averaged 0.71 ± 0.06. Figure 7C shows that while all leaners aligned their trunks and legs to the surface as it rotated, the velocity ratio varied from subject to subject. Non-leaners demonstrated a strikingly different behavior than leaners, as shown in Figure 7D. Both trunk-to-surface (0.19 ± 0.18) and leg-to surface (0.16 ± 0.08) velocity ratios were near 0, indicating upright postural orientation. Velocity ratios were significantly different between leaners and non-leaners (trunk velocity ratio, $p < 0.0001$; leg velocity ratio, $p < 0.0001$). When the surface rotated from the horizontal to the inclined position, both groups demonstrated trunk velocity ratios (leaners 0.2 ± 0.1; non-leaners 0.3 ± 0.1) and leg velocity ratios (leaners 0.1 ± 0.1; non-leaners 0.1 ± 0.1) near zero.

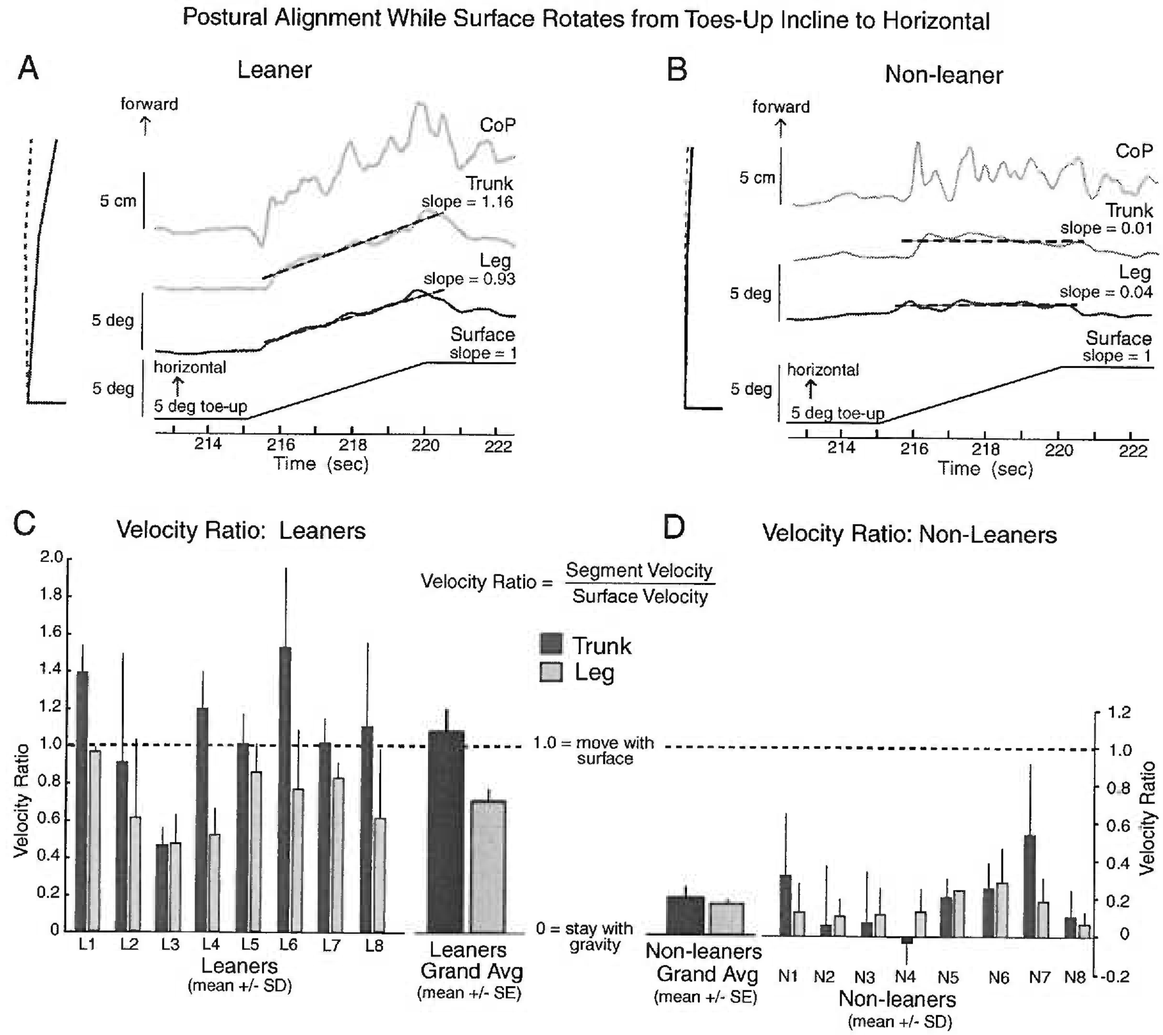

FIG. 7. While the surface rotated from the inclined to the horizontal position, leaners stayed aligned to the surface and non-leaners maintained their trunks and legs near upright with respect to gravity. FIG. 7A and 7B show the position of the CoP and the orientation of the trunk and the leg while the surface rotated from a toes-up inclined to a horizontal position for a representative leaner (7A) and non-leaner (7B). The slopes (velocities) of the trunk and leg segments during the surface rotation were calculated using linear regression from 500 msec after the surface began to rotate to 500 msec after the surface reached horizontal. Because the surface rotated at 1 °/s, the slopes of the trunk and leg segments are also body-segment-to-surface velocity ratios. The bar plots in FIG. 7C (leaners) and FIG. 7D (non-leaners) show the trunk-to-surface (black bars) and leg-to-surface (gray bars) velocity ratios for each subject, with each bar representing the average velocity ratio for the 3 trials conducted under the toes-up-incline condition. The bar plots on the far right show the group mean velocity ratios for the leaners (FIG 7C) and the non-leaners (FIG 7D). The horizontal dotted line represents a velocity ratio of 1, indicating tight coupling between rotation of the trunk or leg and rotation of the surface, with the body maintaining constant relative alignment to the surface.

Several factors were compared between leaners and non-leaners to determine why one group leaned and one did not. Leaners and non-leaners did not differ in their initial position during baseline stance on the horizontal surface (mean distance of CoP from ankle joint: leaners 19.7 ± 3.7% versus non-leaners 22.2 ± 3.6% of foot length, $p = 0.195$). Leaners and non-leaners did not differ significantly in their base of support length (24.9 ± 1.6 versus 25.1 ± 1.8 cm, $p = 0.817$) or base of support width (widest point 32.6 ± 4.0 versus 33.6 ± 5.0 cm, $p = 0.679$). Further, no differences in height (168.3 ± 6.0 versus 173.1 ± 12.7 cm, $p = 0.353$) or in age (36.3 ± 9.5 versus 35.3 ± 7.6 yrs, $p = 0.820$) were found between these two groups.

Experiment 3: Effects of incline direction

Figure 8A shows how varying the direction of surface inclination affected the post-incline behavior for a representative leaner and a representative non-leaner. Leaners and non-leaners were highly consistent in the degree to which they leaned after they stood on an incline, regardless of the direction of surface inclination. Leaners leaned forward after they stood on a toes-up inclined surface, rightward after they stood on a right side-up inclined surface, and backward after they stood on a toes-down-inclined surface (2/8 did not lean after toes-down inclination). In contrast, non-leaners did not lean after any of the 3 incline-directions. Figure 8B shows that the rate of decay of the lean did not differ significantly when the direction of surface inclination was varied, both for the leaners (toes-up 43.8 ± 22.6 s, lateral 46.7 ± 23.9 s, down 33.6 ± 23.1 s), and for the non-leaners (toes-up 5.2 ± 1.5 s, lateral 8.7 ± 5.7 s, down 2.4 ± 2.9 s). An exception to this was one leaner, whose decay time constants were excluded from statistical

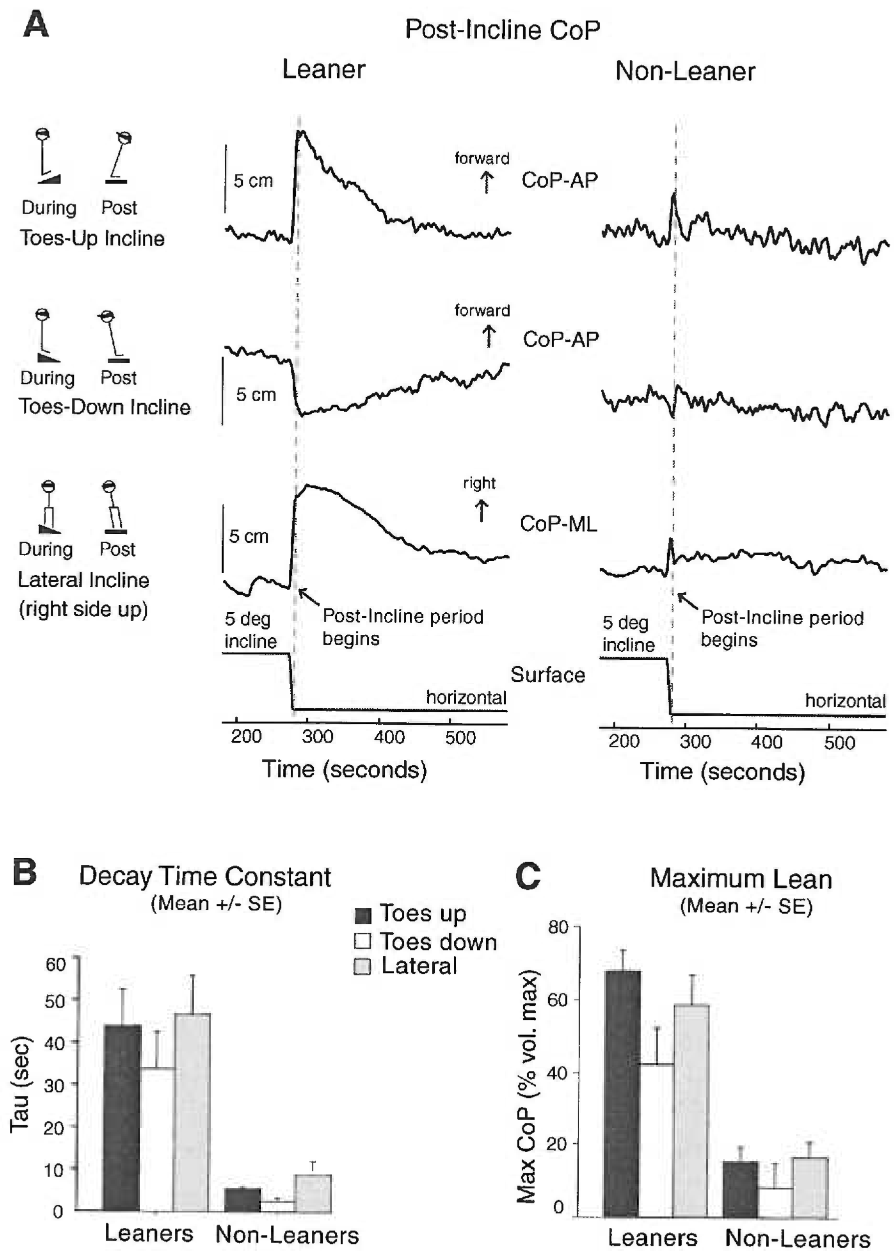

FIG. 8. Leaners and non-leaners were consistent in their post-incline behavior across direction of inclination. FIG. 8A shows CoP data from a toes-up (top), toes-down (middle), and right-side-up (bottom) trial for a representative leaner (left traces) and non-leaner (right traces). FIG. 8B compares the CoP decay time constant (group mean ± SE) and FIG. 8C compares the CoP maximum lean (group mean ± SE) across direction for the leaners (left) and non-leaners (right). Black bars indicate the toes-up condition, white bars indicate the toes-down condition, and gray bars indicate the right-side-up condition.

analyses because of very large variations (toes-up 65.6 s; lateral 111.2 s; toes-down 0 s) unlike the more consistent within-subject values observed in other subjects.

Figure 8C shows how the direction of surface inclination affected the amplitude of post-incline leaning. Under each direction of surface inclination, the amplitude of leaning for the leaners was significantly larger than for the non-leaners ($p < 0.05$). Thus, although subjects were selected based on whether or not they leaned after standing on a toes-up inclined surface, when the direction of surface inclination was altered, subjects stayed consistent in whether or not, and how much, they leaned. For both leaners and non-leaners, the amplitude of backward leaning after they stood on a toes-down-inclined surface was smaller as compared to the amplitude of forward leaning after they stood on a toes-up-inclined surface or the amplitude of rightward leaning after they stood on a right-side-up-inclined surface. The average amplitudes of the maximum lean, computed as a CoP displacement and as a percentage of the voluntary maximum lean, for the toes-up, lateral, and toes-down directions were 67.3 ± 6.1%, 61.9 ± 6.7%, and 42.1 ± 10.1% for the leaners and 17.4 ± 3.6%, 16.6 ± 4.6%, and 8.5 ± 6.4% for the non-leaners.

Effects of attention on postural verticality

Figure 9 shows that leaning in the post-incline period was greatly reduced when leaners were instructed to 'stand vertical' rather than to 'stand in a relaxed way'. When asked how they accomplished 'standing vertical', all three subjects reported that they paid attention to the pressure underneath their feet.

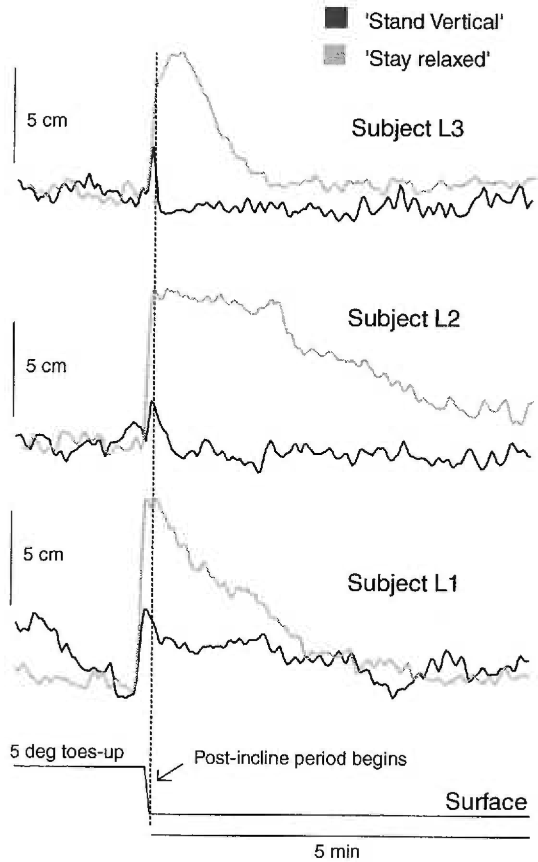

FIG. 9. The post-incline lean is diminished when subjects pay attention to 'standing vertical'. CoP data from trials when subjects were instructed to stay relaxed (light traces) are compared to trials when subjects were told to pay attention to standing vertical (dark traces). Plots show the last part of during-incline period and the entire post-incline period.

Discussion

This study demonstrated that the after-effects of standing on an inclined surface varied widely across a large group of healthy subjects. Many subjects showed a postural after-effect of leaning that lasted for minutes, while other subjects stayed upright. When subjects leaned, they leaned in a direction and with an amplitude that kept the trunk-to-surface relative alignment constant when the surface changed from an inclined to a horizontal position. This finding suggests that leaners depended more heavily than non-leaners on the geometry of the support surface for their postural orientation and that leaning occurred because the set point established by the central nervous system for postural orientation with respect to the surface was modified by the experience of standing on the incline. In contrast to the leaners, the non-leaners kept a near constant orientation of their bodies throughout the inclined stance trial, with only transient postural changes when the surface rotated, suggesting that non-leaners relied on graviceptive force and vestibular sensory information more strongly than the geometry of the support surface for their postural orientation. The finding that subjects were highly consistent in their post-incline postural alignment, yet varied from one another along a continuum, suggests that each individual has a preferred strategy for how the support surface and gravity are used as reference frames for postural orientation and for determining the set point for postural upright.

Differences in reliance on the geometry of the support surface for postural orientation

When subjects leaned after they stood on an inclined surface, they maintained a constant orientation of the body with respect to the support surface. This finding suggests that the experience of standing an incline adaptively modified the set point for postural orientation, and that leaners preferentially relied on the geometry of the support surface as a frame of reference for establishing their postural orientation. The direction of leaning always maintained the immediately prior body-to-surface relative alignment, regardless of whether the surface was inclined toes-up, toes-down, or laterally. The average amplitude of the leaners' post-incline trunk lean was 5.6° ± 1.5°, which is close to the adapting stimulus of a 5°-surface inclination. During the dynamic surface rotation from an inclined to a horizontal position, leaners' trunks moved at the same velocity as the surface, maintaining a constant trunk-to-surface relative alignment during the dynamic surface rotation from inclined to horizontal. Leg orientation did not follow surface rotation as closely as the trunk, a finding that is in accordance with our previous findings that the trunk-to-surface relationship may be the main postural variable to undergo adaptation when surface inclination changes (Chapter 2). Alternatively, leaners might have been attempting to maintain their body's center of mass (CoM) oriented with respect to the changing orientation of the support surface, achieving this goal with varied combinations of trunk and leg alignment. Leaners kept their bodies oriented to the surface in the post-incline period despite the availability of multiple sources of sensory information that the body was leaned with respect to gravity. When subjects leaned, the location of the CoP was displaced forward, which could have been sensed by pressure receptors under the feet (Kavounoudias et al 1998, 1999; Maurer et al. 2001). The head and trunk were leaned with respect to gravity and the body's CoM was displaced forward, which could have been sensed by otolith receptors (Young 1984), trunk graviceptors (Mittelstaedt 1996, 1998), or by load receptors in the postural muscles

(Dietz et al. 1992). The persistence of postural alignment that was leaned away from gravity, but that maintained the body-to-surface relationship, suggests that leaners preferentially relied on a surface-based as opposed to a gravity-based or a dynamics-based frame of reference for their postural orientation.

In about 25% of all subjects, there was no observable after-effect on postural orientation following stance on an inclined surface. In these non-leaning subjects, postural alignment during the post-incline period was not significantly different from alignment during the pre-incline period. The non-leaners were highly consistent in their absence of post-incline leaning when trials were conducted days to months apart and when the direction of surface inclination was varied, a finding that is consistent with non-leaners having a robust, preferred postural orientation strategy that does not rely on surface orientation. In comparison to leaners, non-leaners appeared to give more weight to sensory information about gravity and/or forces exerted against the support surface force rather than to the geometry of the support surface geometry for establishing the set point for their postural orientation. Alternatively, when the surface was horizontal and was stationary, non-leaners may have relied on the geometry of the support surface as a reference frame for their postural orientation as much as leaners, increasing their reliance on gravity-related information only when the surface-conditions changed (Black et al. 1983; Maurer et al. 2000; Mergner and Rosenmeier 1998; Nashner and Wolfson 1974; Peterka 2002). Although some non-leaners showed a small amplitude of trunk lean when the surface first began to rotate from an inclined to a horizontal position, all of the non-leaners began to re-align their trunks and legs toward upright postural alignment well before the surface stopped rotating, suggesting a possible switching mechanism or rapid sensory reweighting mechanism triggered by surface tilt.

The leaning and non-leaning strategies were not all or none, but rather there was a continuum of behaviors across healthy subjects in terms of the decay time constant of the return from a leaned to an upright posture and in terms of the amplitude of leaning. The wide variability in post-incline postural effects across subjects could be explained by differences in how individual subjects distribute the relative weighting between the support surface geometry and gravity when establishing a reference for postural orientation. Similar wide variation among healthy subjects has been reported for the degree to which tendon vibration induces a change in postural alignment (Fransson et al. 2000; Gurfinkel and Levik 1991; Wierzbicka et al. 1998), a finding that supports the idea that individuals vary in the degree to which they weight proprioceptive, kinematic information for their postural orientation. Alternatively, the variation across subjects could be explained by differences in their rate of adaptation to altered postural conditions. While it is possible that the difference in the post-incline lean between subjects could be explained by a biomechanical variable, it is unlikely, as we ruled out simple morphological differences.

Different adaptation rates

When subjects leaned, the post-incline lean decayed toward baseline postural alignment exponentially, over a time course of minutes, suggesting a central adaptive mechanism that slowly recalibrated the surface-referenced postural orientation set point to align with the gravitational vertical set point. Similar persistent after-effects in the spatial tasks of body orientation and navigation have been shown to occur when other features of the environment are altered (Anstis 1995; Gordon et al. 1995; Lackner and DiZio 2000; Rieser et al. 1995). For example, following a period of walking-in-place on a circular treadmill, when subjects were asked to walk straight ahead with their eyes closed, they unintentionally walked with a curved trajectory, an effect called Podokinetic After-rotation or PKAR (Gordon et al. 1995; Weber et al. 1998). Like the post-incline lean, the PKAR curved walking trajectory maintained the immediately prior trunk-to-surface relationship and the effect decayed slowly and exponentially, suggesting that both PKAR and the post-incline lean may involve an adaptive modification of the central estimate of the trunk-to-surface relationship (Earhart et al. 2001, Weber et al. 1998).

Individuals have been shown to differ from one another in the rate of decay of sensorimotor after-effects that follow a changed environmental condition, such as PKAR (Weber et al. 1998) and optokinetic after-nystagmus (Brandt et al. 1974; Zasorin et al. 1983). Thus, instead of, or in addition to, inter-subject differences in the preferred reference frame or the preferred combination of sensory weighting for postural orientation, an alternative explanation for the wide variation of post-incline lean effects could be that subjects vary from one another in the rate at which the postural set point is adaptively updated when conditions change (Fransson et al. 2002). However, such an explanation does not account for the finding that leaners showed as fast as an adaptation to altered surface conditions as non-leaners when the surface changed from a horizontal to an inclined position. The persistent leaning effect occurred only after standing on an incline, when the surface returned to horizontal.

A possible explanation for why leaners quickly aligned to upright when the surface changed from a horizontal to an inclined position, but slowly aligned to upright when the surface changed from an inclined to a horizontal position, could be that, regardless of the preferred reference frame for postural orientation, the relatively novel and more atypical condition of surface inclination triggered a compensatory balance mechanism for maintaining stability, with a rapid sensory reweighting from surface to gravity related information (Black et al. 1983; Fitzpatrick et al. 1994a; Nashner and Wolfson 1974). Rather than the novelty of the incline condition, rapid sensory reweighting could instead be triggered by the biomechanical constraints of maintaining stability on an inclined surface. Leaning while standing on an inclined surface might bring the CoM too close to a critical distance with respect to stability limits, triggering a switch to a different postural orientation strategy and/or a rapid sensory reorganization. In comparison to maintaining a leaned posture when standing on an inclined surface, maintaining a forward leaned posture on a horizontal surface may be less threatening to postural stability, thus stability constraints would not override the postural strategy of reliance on a postural set point that is undergoing a slowly recalibration.

Preferred reference frames for postural orientation

We have proposed that the striking and consistent differences in post-incline postural alignment between leaners and non-leaners can be explained by individual differences in the degree of reliance on different frames of reference for establishing postural orientation. Leaners appear to strongly weight kinematic sensory information related to body-to-surface spatial orientation because of their consistency in keeping the body aligned with respect to the surface rather than to gravity in the post-incline period. In contrast, non-leaners appear to strongly weight kinetic sensory information that is related to the direction of gravitational and other forces. The idea that posture can be oriented to either a surface-kinematic or a gravity-kinetic postural reference frame fits with other proposed models of postural control (Massion, 1998; Mergner et al. 2002a, 2002b) and with other reported data (Ivanenko et al. 1999; Lacquaniti and Maoili 1994). For example, two different strategies for controlling posture have been reported for subjects standing on a rocker-board that could tip in the pitch direction (Ivanenko et al. 1999). When subjects stood on the rocker board, with the center of their feet placed either forward or backward of the rocker-board's center, some subjects kept the rocker-board near horizontal, thus minimizing changes in the position of their ankles. Other subjects allowed greater tilt of the rocker-board, thus minimizing changes in ankle torque. In studies of cats, separate control of limb kinematic orientation and of contact forces under the paws has been demonstrated on inclined surfaces (Lacquaniti and Maoili 1994). In a study of dynamic control of head posture in subjects who were seated in an accelerating sled in the dark, Vibert and colleagues (2001) found that in one group of subjects, the head tilted with respect to the trunk and depended on the direction of acceleration forces, while in another group of subjects, the head stayed aligned with the trunk. If subjects in the first group focused on an imaginary visual target, their heads stayed more aligned with the trunk then when they did not focus on a target, suggesting that the second strategy of keeping the head aligned with the trunk may have depended on a frame of reference frame based on the spatial or kinematic relationship of the body to the surrounding environment.

The hypothesis that non-leaners preferentially rely on kinetic sensory information and that leaners rely on kinematic sensory information for postural orientation is supported by the finding that the post-incline lean was diminished in leaners who were instructed to 'stand vertical'. These leaners reported that they increased their attention to foot pressure in order to stay vertical. This result suggests that information about foot pressure is important for the non-leaning strategy and fits with the body of evidence showing that 'graviceptor' somatosensory information from pressure underneath the feet influences postural orientation (Kavounoudias et al. 1998, 1999, 2001; Maurer et al. 2000). The finding that leaning was diminished when subjects paid attention to 'standing vertical' also shows that the context of a task influences how the central nervous system preferentially weights different reference frames for postural orientation. Similarly, the task goal upon which subjects focus their attention has been shown to affect the postural orientation effects of tendon vibration (Quoniam et al. 1990).

Similar to our finding of individual differences in the extent to which subjects rely on the geometry of the support surface as a reference frame for postural orientation, healthy subjects have been shown to vary in the extent to which they depend on the visual background as a reference frame for postural control (Chiari et al, 2000; Cremieux and Mesure 1994; Harm et al. 1998; Isableau et al. 1997, 2003; Lacour et al. 1997) and for estimating the direction of vertical (Asch and Witkin1948; Witkin et al. 1948, 1949). For example, healthy subjects differ from one another in the degree to which they are susceptible to swaying or leaning in response to a moving visual surround (Dichgans et al. 1972; Lestienne et al. 1977). Healthy subjects also differ from one another in terms of how their postural orientation is affected by eye closure (Chiari et al. 2000; Collins and

Deluca 1995; Lacour et al. 1997) or by the availability of dynamic visual information (Cremieux and Mesure 1994. A classic test to measure how much subjects depend on the visual background for their perception of the direction of vertical is the Rod and Frame Test, in which subjects are asked to align a luminous rod to vertical in the presence of a tilted luminous frame (Witkin and Asch 1948). Recent studies show that individuals who differ from one another in their degree of dependence on the visual field for determining the direction of vertical also differ from one another in their postural stability under varied visual conditions (Isableau et al. 1997, 2003), suggesting that dependence on a particular reference frame may act at a global level within the central nervous system that affects multiple spatial orientation tasks.

The factors that contribute to building a preferred reference frame for postural control are unknown, but evidence comparing gymnasts (Bringoux et al. 2000), dancers (Golomer et al. 1999; Mouchnino et al. 1992), and judo experts (Perrin et al. 2002) to novices suggests that past sensorimotor experience is one important factor. For example, gymnasts showed less dependence on somatosensory information than non-gymnasts when asked to bring their bodies to vertical while wearing a body cast that minimized somatosensory information about postural orientation (Bringoux et al. 2000). We did not learn about our subjects' preferred physical activities. However, our findings that the post-incline postural orientation strategy differs across healthy subjects and that the strategy can be altered by task direction, coupled with the findings that sport-specific training can influence how subjects organize sensory information for postural control, predict that prior sensorimotor experience or practice would influence the degree to which subjects depend on the support surface as a postural reference frame and would affect the strength of the postural after-effects of standing on in inclined surface.

Conclusions

Postural after-effects of stance on an inclined surface varied widely in our group of 51 healthy subjects, with some subjects leaning for minutes, other subjects aligning immediately to their baseline postural orientation, and the remaining subjects forming a continuum between leaners and non-leaners. Individual subjects were highly consistent in whether and how much they leaned in the post-incline period, even when trials were months apart, suggesting that postural alignment after standing on an incline is related to a well-established and preferred sensory strategy for postural orientation. We interpret the difference between leaners and non-leaners in postural after-effects of standing on an inclined surface as a difference in preferential weighting of different reference frames for postural orientation when the surface conditions change. Leaners rely more strongly on a support surface or kinematic-based reference frame, while non-leaners rely more strongly on a gravity or kinetic-based reference frame.

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Chapter 5: Conclusions and future directions

This collection of studies shows, for the first time, that a period of stance or stepping on an inclined surface with eyes closed leads to a postural after-effect of leaning that decays exponentially across minutes. When subjects leaned, the lean maintained the relative alignment between the upper body and the surface as if the subjects still stood on the incline. This result suggests that the experience of standing on an inclined surface adaptively modified the centrally-determined set point for postural orientation with respect to the support surface. Not all subjects leaned, which suggests that healthy individuals differ from one another in how much they preferentially rely on the geometry of the support surface, as opposed to the direction of gravity, as a reference frame for their postural orientation. The leaning after-effect provides a tool for investigating how the nervous system adapts the postural set point in response to a maintained change in environmental conditions, how the nervous system integrates information from more than one sensory system, and how the nervous system alters the relative weighting between support-surface-related and gravity-related sensory information for determining the direction of postural orientation.

Adaptive modification of the postural set point for upright

The large amplitude, slowly decaying lean that occurred in the post-incline period suggests that the experience of standing on an inclined surface adaptively modified the set point for preferred postural orientation. In contrast to the long-lasting after-effect on postural orientation, variability around the leaned postural increased only transiently in the post-incline period, returning to baseline values in under 15 seconds. This suggests that adaptation affected the postural set point, but did not affect the faster-acting postural mechanisms that act to maintain and stabilize the set point. This separation in roles of the postural control system between the setting, or the establishment of the postural set point and the maintenance of equilibrium around the set point have been previously proposed based on studies of postural adaptation in astronauts adjusting to microgravity conditions (Clement et al. 1984; Lestienne and Gurfinkel 1988). The slow return of the lean to upright posture with respect to gravity can be interpreted as a gradual recalibration of the set point for postural upright with respect to the surface until it is congruent with gravity upright. The slow decay of the lean toward the habitual, upright-to-gravity posture fits with the previously proposed concept of a 'conservative' system that is concerned with specifying and modifying the postural set point and is resistant to transient changes in condition (Clement et al. 1984; Gurfinkel et al. 1995; Lestienne and Gurfinkel 1988).

Future experiments should be designed to show, more definitively, that the postural set point for upright was modified by the experience of stance on the incline. For example, in the post-incline period, subjects could be exposed to a transient surface translation to determine if subjects would make a postural response that returned the body to the new, leaned posture or whether the body would return to an upright posture. Additional experiments could also explore whether the after-effects of stance on an incline are restricted to changes in the postural set point. Might the perceived orientation of the support surface in space also undergo adaptive change? A postural control model proposed by Mergner and colleagues (1998, 2002a) suggests that the nervous system first determines orientation of the support surface in space and then determines orientation of the body on the support surface. Some of our subjects reported an initial perception of downward floor inclination when the surface returned from inclined to horizontal, suggesting that the after-effects are not limited to automatic postural activity. An experiment could be conducted in which subjects set the alignment of the support surface at an estimated horizontal in the post-incline period to investigate how perception of surface orientation correlates with postural alignment.

The direction and magnitude of the lean was determined by the direction and magnitude of surface inclination such that leaning maintained the trunk-to-surface and head-to-surface relative relationships adopted while on the incline. For example, after standing on a 5°-toes-up incline, subjects leaned the upper body approximately 5° forward. Although leaning maintained a constant trunk-to-surface kinematic relative relationship, leaning did not maintain a constant trunk-to-gravity relationship. This suggests that when subjects leaned, they preferentially used sensory information related to the support surface geometry, rather than to gravity or other forces for postural orientation. Trunk alignment, in particular, was systematically affected by maintained changes in surface geometry, a finding that is compatible with other studies suggesting that the trunk may be a main controlled variable in postural orientation tasks (Fung and Macpherson 1995; Gurfinkel et al. 1981, 1995a). Both the head and the trunk showed similar post-incline effects across all of the experimental conditions tested, thus, the relative importance of the head or the trunk for postural orientation with respect to the surface cannot be distinguished. It might be interesting to restrain the trunk from leaning in the post-incline period to determine whether the head still shows a post-incline lean after-effect.

Chapter 3 showed that a peripheral or a segmental adaptive mechanism, such as an after-contraction effect in ankle muscles, cannot explain the post-incline lean effect. Blocking the hips to prevent lower body lean did not abolish upper body lean. Further, leaning during quiet stance in the post-incline period occurred following a period of stepping on an incline, showing transfer of adaptive effects on the postural set point from a locomotor task to a strictly postural task. Similar generalization has been shown for other sensorimotor after-effects (Earhart et al. 2001, 2002b; Rieser et al. 1995). Determining whether or not adaptive after-effects transfer between tasks provides insight into the nature of the variables that have undergone an adaptive change as well as insight into which levels of the nervous system might be involved in the adaptive mechanism. We showed transfer of the post-incline lean from a stepping to a standing task, both of which involve postural control of upright stance. Future studies could investigate whether post-incline effects are effector-specific. For example, does adaptation in standing transfer to an effect on kneeling, or does adaptation during stance with a narrow base of support transfer to stance with a wide base of support?

Chapters 2 and 4 showed that leaners were highly consistent in the amplitude and the form of their post-incline lean decay, even when trials were conducted months apart and even when direction of inclination was varied. Furthermore, although leaners varied from one another in the form and the rate at which their post-incline lean decayed, the basic pattern of lean decay was similar among subjects. The within-subject consistency and the between-subject similarity of the post-incline lean suggest a specific, robust mechanism used by the nervous system for adapting to changes in surface geometry. The finding that subjects lean similarly whether standing quietly on the incline or stepping in place and that the upper body leans even when the lower body is blocked from leaning suggests this adaptive mechanism must be located at sites within the nervous system that can explain effects on global postural orientation variables.

Preferred strategies for postural orientation

The finding of a continuum of post-incline behaviors among subjects together with the finding that leaners and non-leaners were highly consistent in their post-incline postural behaviors suggests that the nervous system can vary the relative weighting given to either a surface-based or gravity-based reference frame for determining the direction of postural upright. Furthermore, this consistency of the post-incline behavior over time and directions suggests that individuals have preferred postural orientation strategies. Leaners appear to rely more heavily on sensory information related to support surface geometry and kinematic orientation in space, whereas non-leaners appear to rely more heavily on gravity, force, and load information for their orientation. Leaners were able to suppress leaning when instructed to 'stand vertical', showing that the nervous system has flexibility in which reference frame, support surface or gravity, is more heavily weighted, depending on task context. The idea of two possible reference frames, a kinematic reference that utilizes a reference frame based on support surface geometry and a kinetic reference that utilizes a reference frame based on the direction of gravity and balance of forces, is similar to conclusions reached in studies of other postural tasks (Ivanenko et al. 1999; Lacquaniti and Maoili 1994; Mergner et al. 2002a, 2002b).

What sensory systems do leaners rely upon when they keep their bodies aligned with respect to the support surface, instead of to gravity, in the post-incline period? One possibility is that leaners increase weighting of all sources of somatosensory information related to the support surface. However, kinematic, but not force- or load-related, postural variables showed evidence of systematic post-incline effects based on characteristics of the surface incline. Leaning maintained a constant trunk-to-surface relative alignment when the surface changed from an inclined to a horizontal condition. In contrast, leaning did not maintain a constant foot-CoP, whole body CoM, EMG activity, or ankle angle. During forward leaning after standing on a toes-up-inclined surface, the location of the CoP was displaced far forward, changing mechanoreceptor input from the foot soles. Extensor EMG activity increased in the post-incline period, signaling changes in load. Thus, leaners did not rely on gravity-related somatosensory information. Static otolith and truncal graviceptor information would also signal tilt away from gravity vertical during the post-incline leaned posture. The persistence of the lean for minutes despite multiple sources of gravity-related sensory information that could have indicated leaning suggests that the nervous system preferentially weighted kinematic, support surface-related sensory information over gravity-related information for selecting a preferred postural orientation or postural set point.

Future studies could further investigate the hypothesis that leaners are more surface- and kinematic-dependent and that non-leaners are more gravity- and kinetic-dependent for organizing their postural orientation. For example, leaners might be more responsive to the postural effects of tendon vibration than non-leaners if they are more dependent on muscle spindle, proprioceptive sensory information for orientation. Non-leaners might, in contrast, be more susceptible to the postural effects of galvanic vestibular stimulation or to changes in distribution of body load. Flexibility in utilizing either a kinematic or a kinetic postural orientation strategy could be investigated by determining whether different sensory conditions, or concurrent cognitive tasks, or training can cause a leaner to switch to become a non-leaner and vise versa. Non-leaners could be tested with the inclined stance trial while tipping the head backward to shift reliance from vestibular toward somatosensory information and thus increasing the likelihood of a leaning after-effect (Brandt et al. 1981; Simoneau et al. 1995). We showed that the instruction to stand vertical diminished leaning in leaners. This suggests that increased attention to the postural task to maintaining postural orientation to gravity may result in increased reliance on gravity-related sensory information. Perhaps non-leaners would lean if attention were diverted with a concurrent cognitive task, such as mental arithmetic. Non-leaners could also be tested with the inclined stance trial under conditions that reduce the availability of foot-pressure graviceptor information, such as anesthesia of the foot soles through cooling (Magnusson et al. 1990), to determine the importance of foot sole pressure information for the non-leaning strategy.

Studies have shown that training and experience affect the particular sensory strategy used by an individual (Bringoux et al. 2000; Golomer et al. 1999; Mouchnino et al. 1992; Perrin et al. 2002). The importance of prior experience in determining whether an individual shows greater dependence on a support surface- or a gravity-based reference frame could be studied by testing for post-incline leaning in subjects with different types of sports-specific training. For example, subjects who are well experienced in Tai Chi might be expected to rely more on support surface geometry for a postural reference, whereas subjects who are well experienced in windsurfing might rely more on gravity.

Which sensory systems are necessary for a leaning strategy versus a non-leaning strategy? One approach to address this question is to determine the post-incline strategy of subjects with loss of a specific peripheral sensory input. It has been suggested that vestibular loss subjects increase sensory weighting of somatosensory information for postural control tasks as shown by increased sensitivity to ankle tendon vibration (Enbom et al. 1988; Pyykkö et al. 1983) and by increased instability when standing on foam or a sway-referenced support surface (Black et al. 1988; Nashner et al. 1982; Peterka 2002). Clark and Graybiel (1964) showed that vestibular loss subjects made larger errors than healthy subjects in estimating postural vertical when seated and strapped into a rotatable chair that was first held in a laterally tilted position for 2-minutes. Thus, vestibular loss subjects might be expected to be leaners, who not only lean, but who lean with larger amplitudes or for longer periods of time than healthy leaners. In contrast, a vestibular-derived estimate of gravity-upright may be necessary to differentiate between surface-rotation and self-rotation, as well as for recalibrating the estimate of upright based on the support surface (Mergner et al. 1998, 2002b). If this were true, vestibular loss subjects would be expected to be non-leaners. In fact, we tested 8 subjects with bilateral, profound loss of vestibular function. None of them leaned after exposure to a 5°-incline for 5 minutes. These preliminary results support the hypothesis that vestibular information is required for recalibrating postural orientation from the surface-dependence to gravity dependence. However, these vestibular loss subjects also showed more postural instability while standing on the inclined surface than the control subjects, and this instability may have interfered with building a new postural orientation reference based on kinematic-based sensory information from the support surface. These results will soon be prepared for publication.

Just as vestibular loss subjects are more dependent on surface information for postural orientation, subjects with diabetic peripheral neuropathy have been shown to be more sensitive to galvanic vestibular stimulation effects on posture, suggesting an increased weighting of vestibular information (Horak and Hlavacka 2001). Thus, subjects with peripheral neuropathy would be predicted to be non-leaners. However, subjects with peripheral neuropathy often have impaired sensation in their feet, which could affect foot sole graviceptive information for kinetic control with respect to gravity and foot and ankle proprioception information for kinematic control with respect to the surface. An additional complication of studying post-incline effects with subjects with neuropathy is their increased postural instability when their eyes are closed (Simoneau et al. 1995).

Visual reference frame availability

Subjects were blindfolded to limit the investigation to the relative weighting of surface-based and gravity-based reference frames for postural orientation. However, information about the visual surround is also well known to affect postural orientation (Bles et al. 1977; Dichgans et al. 1972; Lee and Lishman 1975; Lestienne et al. 1977; Peterka and Benolken 1995; van Asten et al. 1988). Furthermore, the nervous system increases weighting of visual information when the support surface conditions change, such as when the surface is compliant or unstable (Bles et al. 1977; Lee and Lishman 1975). Future studies should examine whether the availability of vision during exposure to the incline and after the incline affects the likelihood of and strength of post-incline leaning. One hypothesis is that availability of a stationary, full-field visual surround would 'dump', or eliminate, the incline after-effect of leaning (Cohen et al. 1977, 1981). Preliminary experiments have been conducted that suggest that opening the eyes for short time periods does not completely dump the post-incline lean. Upon eye opening, leaned subjects immediately returned to their initial, upright posture. However, when eyes were again closed, subjects immediately returned to their leaned posture, which proceeded to decay toward upright with a similar exponential decay rate as if they had never opened their eyes. Similar hypotheses as for vision can be raised for haptic information gained from fingertip contact with a stable object in the environment (Holden et al. 1994; Jeka et al. 1997, 1998).

Model of postural adaptation to altered reference frames

Several models of postural control have been developed to help understand how the nervous system integrates and changes the relative weighting between different sensory systems for estimating the state of the body and the state of reference frames (Mergner et al. 1998, 2002a, 2002b; Oie et al. 2002; Peterka 2002; van der Kooij et al. 1999). Can these models explain how differential sensory weighting can lead to the leaning and non-leaning behaviors our experiments have identified? Can factors be identified that make one subject lean and one subject stay upright in the post-incline period? Can the effects of changing duration of inclination be explained? Can the reason for the asymmetrical behavior of staying upright during the initial change in surface conditions from horizontal to inclined and for leaning in the post-incline period be explained? A conceptual model for explaining the postural after-effects of standing on an incline was provided in Chapter 2. This model was based on postural control models that employ an internal model of postural sensorimotor dynamics and multiple internal estimates of postural upright that are adaptively modified when two internal estimates of postural upright conflict. The literature suggests that the cerebellum is ideally suited to adaptively modify postural orientation based on prior experience (Horak and Diener 1995). Future work could develop a more detailed model, or to modify an existing model, to explain the experimental results that this dissertation reports.

Implications for rehabilitation

The results of these studies suggest that individuals enter rehabilitation with a pre-existing, well-established preferred sensory strategy for postural orientation. Differences in how individuals preferentially weight or rely on particular reference frames for their postural orientation may explain why some individuals have particular ease or difficulty with their postural control under various task and environmental conditions. The preferred postural orientation strategy may determine how well an individual successfully compensates for postural impairments. Thus, when establishing prognoses and developing intervention programs for individuals with postural control problems, rehabilitation therapists should take into account pre-existing sensory preferences. Future research efforts should explore whether and how individuals develop preferred postural orientation strategies, whether and how individuals can switch or alter their postural orientation strategies, and which postural orientation strategies are optimal for various environmental and task constraints.

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