ABSTRACT

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Recent studies have shown co-existing trunk-leg coordination patterns during quiet stance: in-phase and anti-phase for frequencies below and above 1 Hz, respectively. Two experiments investigated whether the nervous system assumes a multilinked internal model in sensory coupling? In the first experiment, we investigated the influence of the addition or removal of sensory information on these patterns. Trunk-leg coherence decreased with the addition of static vision and light touch, in the AP and ML directions, respectively, at frequencies below 1 Hz, suggesting the in-phase pattern may be more affected by neural control than the anti-phase pattern. In the second experiment, we compared translation of the visual field to a rotation relative to the ankle/hip. Gain and phase between the trunk/leg angles relative to the visual display showed only minor condition differences. The overall results suggest the nervous system adopts a simple control strategy of a single-link internal model at low frequencies.

POSTURAL COORDINATION PATTERNS: VISUAL ROTATION AND TRANSLATION

By

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Chapter 1: Introduction

VISUAL COUPLING

Vision informs body sway with respect to the environment. The role of vision in postural control has been studied for many years. Before 1970s, scientists explored this mainly by asking the question whether vision stabilizes or destabilizes the body and by comparing body sway in eyes closed or eyes open conditions. For instance, Edwards (1946) reported that adults with blindness or had their eyes closed swayed more than the normal sighted or eyes-open subjects. However, there were also some conflicts. It was found that blind adults with residual vision swayed less when have their eyes closed (Edwards, 1946). Later on, experimental results showed that when visual scene is stable, it stabilizes the body; while visual motion enhances sway. It became obvious that it is the structure of the visual scene that really affects the body sway. After the introducing of the "moving room paradigm" by Lee and Lishman (1972), many studies in visual motion were inspired. More recently, as computer techniques developed, computer-generated visual display has been used to simulate visual motion. Some of the techniques and methods that are relevant to this study will be presented in the following sessions.

Visual Components

The visual optic flow field can be decomposed into different components, such as translation, rotation and so on. By looking at these individual components, we can get an insight into the effect of vision on posture with integrated components. In a recent study done by Racaioli et al. (2005), both translation and oscillation were used simultaneously. The triangles in the visual field oscillated at a constant speed while

translating from left to right at different velocities (0, 1, 2 or 4 cm/s) across conditions. Another component that often used is rotation. Peterka (2002) rotated the visual surround with the rotation axis collinear with the ankle joint at a pseudorandom sequence of frequencies with the range from 0.0165 to 2.48 Hz.

Peterka and Benolken (1995) compared the rotation they used to the small amplitude translational (in the anterior-posterior direction) visual surround Lee and Lishman used in the 1975, and argued that this translation movement corresponded to a 0.1° visual surround rotation about the ankle joint. However, no evidence was provided for this argument.

Frequency Manipulation

Frequency manipulation has been used in order to understand the temporal relationship between postural sway and visual motion. Djikstra and colleagues (1994) drove the moving room sinusoidally in AP direction at frequencies of 0.05, 0.1, 0.2, 0.3, 0.4 and 0.5 Hz with velocity constant. Results showed that when frequencies were lower than 0.2 Hz, there was a phase lead, meaning that the postural sway is leading the visual motion. When frequencies were higher than 0.3 Hz, there was a phase lag, indicating that postural sway was lagging the visual motion. Later on, many studies showed that phase decreases constantly as frequencies increase regardless of amplitudes of the stimuli.

Amplitude Manipulation

The traditional moving room had really large amplitudes. The moving room used in Lee et al. (1974) moved 47 cm in 2.5 sec with a peak velocity of 40 cm/ sec. As a result of these large-amplitude stimuli, many subjects fell and it was hard to

study the reweighting process. Peterka et al. (1995) started to use small-amplitude rotation with peak displacement amplitudes of 0.2°, 0.5°, 1°, 2°, 5° and 10°. Gains of center-of-gravity sway with respect to the visual motion at small frequencies were found to be higher than unity. This was an unexpected finding, which the authors attributed to the small amplitudes used.

The changes of gain in response to different amplitudes of visual stimuli give insights into sensory reweighting. Within a certain stimulus amplitude range, there is a linear relationship between sensory integration and postural control. However, as amplitude changes, nonlinearity appears. When the perturbations of vision increased to large amplitudes, healthy subjects were able to down-weight vision information and keep their balance. While bilateral vestibular loss patients increased their sway linearly with the stimulus amplitude (Peterka, 2002).

MULTICOMPONENT BODY DYNAMICS

However, perception and action are mutually dependent (SchÖner, 1991): body sway affects the perception of vision too. Human body is not a rigid body, but sways in both AP and ML directions. Further complications arise considering the upright stance has been approximated as a single inverted pendulum rotating around the ankle joint or a two-segment inverted pendulum rotating around the hip joint.

Ankle and hip synergies have been studied extensively with a perturbed platform and thought to be "selected" depending upon available sensory information (Horak, et al., 1991). For example, somatosensory and vestibular information was thought to be important to elicit ankle synergy and hip synergy, respectively. A recent study in our lab (Creath, et al., 2005) showed that these two synergies co-exist during

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quiet stance. Which one of these synergies predominates depends on the sensory information and task constraints.

In a recent study I just finished, we asked how addition or removal of sensory information affects these two synergies. The subjects were instructed to either open eyes or close eyes with or without light touching (< 100g) a touch bar. The resulted four conditions were identified as: Neither = eyes closed no touch; Touch = eyes closed touch; Vision = eyes open no touch; Both = eyes open touch. The relationship between upper and lower body was mainly demonstrated by calculating complex coherence between ankle and trunk vertical angles. The resulted complex coherence was then decomposed into real and imaginary part. The results are demonstrated in Figure 1.1. The top two figures show the complex coherence from the Neither condition in the complex plane. The circles pointed with arrows are the first points of complex coherence trajectories. Here, the complex coherence changed from in-phase to anti-phase as the real part changed from zero to 180 degrees with the imaginary part near zero in the complex plane. The in-phase and anti-phase patterns are related to the ankle and hip synergy respectively. This is consistent with the previous finding that ankle and hip synergies co-exit during quiet stance in our lab (Creath, et al., 2005). Because the imaginary part is near zero, the real part predominates in the relationship between upper and lower body. Vision effect was found in the AP direction: 1) when the real part shifts from in-phase to anti-phase: adding vision made the shift point happened in a lower frequency than in the Neither condition; 2) the real part of coherence is lower in the Vision than in the Neither condition at low frequencies. In this study, the visual scene was static with an array of lab equipment

against a wall about 280 cm away. Adding visual information affects the coordination
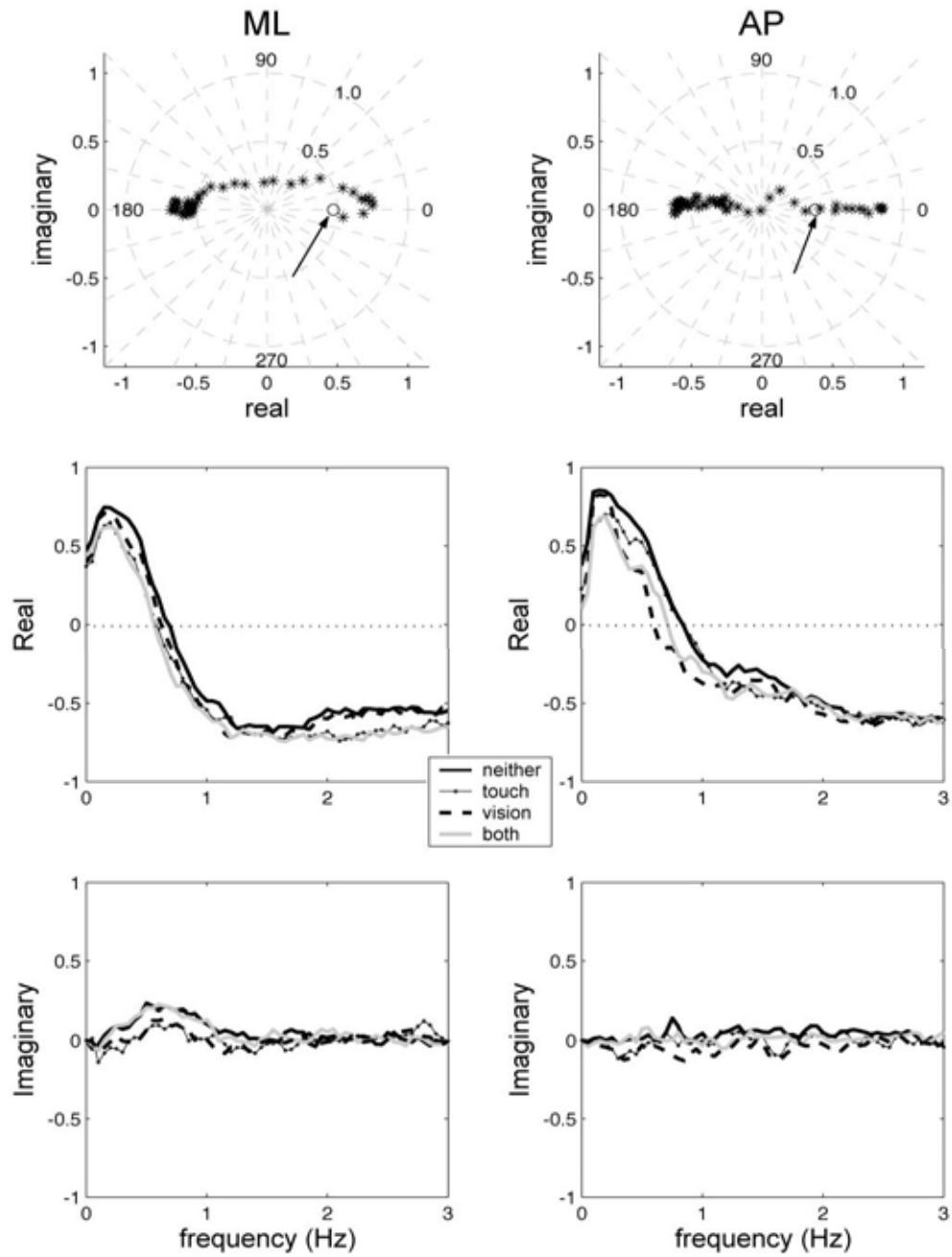
between upper and lower body.

Figure 1.1 Complex coherence between upper and lower body in the ML and AP directions. The top two figures show the complex coherence from Neither condition in the complex plane. The arrows point to the circles which are the first points of complex coherence. The middle two are real parts of complex coherence for ML and AP direction respectively. The lower two are imaginary parts of complex coherence for ML and AP direction respectively. Vision decreases the frequency where coherence shift from in-phase to anti-phase.

HYPOTHESES AND PREDICTIONS

In the current study, we are interested in whether coupling to a visual stimulus depends on visual rotation and translation. Comparison between visual rotation and translation will be provided. Also, we want to know how the nature of the optic flow influences multicomponent patterns. Two alternative hypotheses are compared.

Two alternative hypotheses

In the first hypothesis, a multi-link (trunk and legs) internal model of the body is used by the nervous system to interpret visual information. The control strategy attempts to align both the legs and the trunk with respect to the vertical. That is, these two segments respond to the visual information separately. For example, if the nervous system detects a visual motion around the ankle joint and interprets this as a self-motion around the ankle joint in the opposite direction, then both the trunk and the legs segments will actively try to return to vertical and the body behaves as a single inverted pendulum. If the nervous system detects a visual motion around the hip joint, it will interpret this movement as a self-motion around the hip joint. In this case, because the nervous system interprets the legs as in vertical so that it will only correct the movement of the trunk and the body rotates around the hip joint. In a third

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case, if the visual motion is translated in the AP direction, then the trunk is "thought" to be vertical and the legs are activated to compensate for this translation movement.

However, this is not the only possible way that the nervous system responds to these visual stimuli. In the alternative hypothesis, a single link (ankle) internal model of the body is used by the nervous system to interpret visual information. A separate control strategy, one not dependent on visual information, attempts to align the two segments with each other. As a result, no matter the visual stimulus is rotated around the ankle or hip joint, or translated in the AP direction, the nervous system interprets them as rotation around the ankle joint and the body behaves as a single inverted pendulum. Predictions are made according to these hypotheses.

Predictions

It has been reported that body sway is influenced by visual scene velocity rather than position (Kiemel, et al., 2005; Sch¨oner, 1991; Dijkstra et al., 1994; Jeka et al., 2000). However, in order to compare results in the literature, position displacements are used in calculation. Furthermore, as an inverted pendulum, the velocity of displacement precedes the position of displacement for 90 degrees. As a result, a 90-degree phase lead between the body segment with respect to the visual scene in terms of position corresponds to an in-phase relationship between these two in terms of velocity. The segment (trunk or legs) that is actively catching the visual stimulus should have a 90-degree phase lead and high gain with respect to the visual motion. For the reason of simplicity, the phase and gain between leg/ trunk and visual motion will be called phase and gain of leg/trunk respectively. Three visual

conditions will be tested in this study: 1 = rotation around ankle joint; 2 = rotation

around hip joint; 3 = translation in AP direction.

Predictions for the first hypothesis. For the first hypothesis, if the visual

motion is a rotation around ankle joint, both leg and trunk will have a 90-degree

phase lead and high gains. If the visual motion is a rotation around hip joint, trunk

will have a 90-degree phase lead and high gain for trunk.

Condition	phase	gain
1	90 degree for both leg and trunk w.r.t visual scene	High gain for both
2	90 degree for trunk w.r.t visual scene	Higher gain for trunk Lower gain for leg
3	90 degree for both leg w.r.t visual scene	Low gain for trunk High gain for leg

Table 1.1. predictions for the first hypothesis

Leg will have a low gain and hence the phase relationship is not considered. If the

visual motion is a translation in the AP direction, leg will have a 90-degree phase lead

and high gain, while the trunk will have low gain and phase is not considered in this

case. Please refer to table 1 for a summary of these predictions.

Prediction for the second hypothesis. For the second hypothesis, if the

visual motion is a rotation around ankle joint, then both trunk and leg have 90 degree

phase lead and high gain. For visual motions that are rotation around hip joint and

translation in the AP direction, both legs and trunk have low gain, therefore, the phase

relationships are not considered. As an inverted pendulum rotating around ankle joint,

the phase relationship between legs and trunk will be in-phase. Please refer to table 2

for a summary of these predictions. .

Condition	phase	gain

1	90 degree for both leg and trunk w.r.t visual scene	High gain for both
2	Legs and trunk are in-phase	Low gain for trunk Low gain for leg
3	Legs and trunk are in-phase	Low gain for trunk Low gain for leg

Table 2.2. predictions for the second hypothesis

This thesis is organized into four chapters, with this introduction chapter as the first one. The second one is a review of the literature that gives a brief overview of the classic and modern view of postural control. The third chapter is the first experiment written as a manuscript that investigated the influence of the addition or removal of sensory information on the characteristics of postural coordination patterns. The forth chapter is the second experiment written as a manuscript, which tested translation of visual field and rotation with respect to ankle and hip joint.

Chapter 2: A Review of Literature

Movement is critical in our ability to walk, run, and many other activities in daily life. The mechanism of movement, such as how the motor and nervous systems allow us to maintain balance and posture, has been an interesting question to many researchers. Although postural control may not seem so obvious when we stand or walk around the environment, it is a challenging task.

WHAT IS POSTURAL CONTROL?

A Classical View of Postural Control

In the late 1800s and early 1900s, Sherrington argued that the nervous system controls the motor system by reflexes, which are stereotyped movements elicited by peripheral receptors, such as muscles or skin (Kandel, Schwartz & Jessell, 2000). It is a simple stimulus-response reaction and the higher-level central nervous system is not necessary. Reflexes require a minimum of two neurons, a sensory neuron and a motor neuron. Spinal reflexes are typical in postural control. The afferent fibers pass information from peripheral sensors onto the spinal cord, from which the motor neurons send commands to the muscles through efferent fibers. The sensory inputs into the spinal cord either make direct connection to the motor neurons (monosynaptic reflexes, eg. Stretch reflex) or synapse on the interneurons, which connect both ipsilateral flexor muscles and contralteral extensor muscles (polysynaptic reflexes, eg. Flexion and crossed-extension reflex). Spinal reflexes, especially stretch reflexes, serve to resist the lengthening of muscles, thus providing muscle tone, which was even proposed as the single factor in posture stabilization

(Winter, Patla, Prince & Ishac, 1998). Other reflexes, such as vestibtulo-spinal and cervico-spinal reflexes are also important. The vestibule-spinal reflexes are activated when the head position is changed, while the cervico-spinal reflexes are used when the trunk is moved (Kandel, et al., 2000). They act synergistically to decide whether the head and trunk move together or independently in experiments done on cats. Cervico-spinal reflexes exist only in newborn babies in human. Despite its simplicity, people argued against this theory: it doesn't explain motor control without external perturbation and the adjustment to new environment (Shumway-Cook & Woollacott, 2000a).

Magnus (1924, 1925) suggested that postural control is a summation of different reflex pathways, which are part of a hierarchical motor control system. This reflex/hierarchical theory became predominant in the 70s. "According to the hierarchical theory, the brain generates movements in a similar way by prescribing a sequence of stereotyped patterns which are then executed by peripheral generators and fine-tuned by the somatosensory inputs to suit the particular conditions of the task." (Nashner & Woollacott, 1979, p244). In this theory, reflexes are not the only dominant factor of motor control any more (Shumway-Cook, et al., 2000) and sensory information is thought to be important. The implicit assumption is that the low-level behaviors are nonadaptive and immature, while the high-level behaviors are adaptive and mature (Shumway-Cook, et al., 2000). In other words, the basic movement patterns among the limbs, such as muscles and mechanical linkages, are reflexes and fixed; the human body adapts to the environment by prescribing different sequences of patterns (Nashner, et al., 1979). However, this sequential organization

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requires that each step in the sequence to be fast enough, which is conflict with the relative slowness of synaptic processing in the nervous system (Morasso & Sanguineti, 2003).

A Modern View of Postural Control

Reflexes are not the only process in the nervous system. In order to maintain human body's position in space, the motor system must be able to maintain a steady stance, anticipate volitional goal-directed movements, and be adaptive (Kandel, et al., 2000). More recently, postural control is viewed as the meaningful integration of many different neural systems, including those associated with cognition, to achieve two behavioral goals: postural orientation and postural equilibrium (Kandel, et a., 2000; Horak & Macpherson, 1996). Postural orientation is defined as the ability to orient the body to the environment and body parts relative to each other (Horak, et al., 1996). Postural equilibrium (or balance) is an ability to keep the body either in a desired position or in steady motion, which are referred to as static equilibrium and dynamic equilibrium respectively (Horak, et al., 1996). These two goals require complex interactions among multiple neural and musculoskeletal subsystems, which are briefly described in the following sections.

Neurophysiology

Control of posture requires continuous inflow of somatosensory, visual and vestibular information to the motor system. There are three reference frames of the posture: first, the relative position of different body parts; second, the body with respect to the environment; third, the gravitational field (Kandel, et al., 2000). Different modalities of sensory channels provide information for different reference

frame. The somatosensory system provides information about body configuration according to the environment, such as the support surface. Visual and vestibular sensors are located in the head and provide information about head movement relative to the environment and the gravitation field respectively (Horak, et al., 1996).

Peripheral Sensory Systems

      Somatosensory System. The somatosensory system, including muscle proprioception, joint and cutaneous afferents, serves two roles, it provides information about: 1) the relative position and velocity between body segments and; 2) force and surface properties of the surrounding environment. Proprioception is carried by muscle spindles and golgi tendon organs, which inform about the velocity and position of the muscle and muscle force respectively. For instance, the length of the ankle muscles will provide an estimation of the degree of body tilt and hence postural orientation (Horak, et al., 1996). The joint receptors are excited by moving the joint to its extremes and sensing flexion and extension of a joint (Matthews, 1988). The cutaneous inputs are important for the phasic information about movement (for a review, see Matthews, 1988). Sudden changes between the support surface and the feet result in stretching and deformation of skin. The rate of firing of the resulted shearing forces informs the velocity of the perturbation (Horak, et al., 1996). At the low level of the central nervous system (CNS) hierarchy, the cutaneous inputs are also responsible for reflex movements (Shumway-Cook, et al., 2000). In adults, the stimulation of the sole of the feet usually causes the toes to reflex. Because of the fact that somatosensors are distributed throughout the body, they are believed to contribute most to the configuration of the body segments (Horak et al., 1996).

Furthermore, there is evidence that the somatosensory information is the most sensitive source of small increments of posture sway (Fitzpatrick & McCloskey, 1994). It was found that light touch (<100g) of the fingertip on a stationary surface could reduce body sway (Jeka & Lackner, 1994). When bilateral vestibular loss patients were asked to stand with their eyes closed on a tilting platform, they kept their balance successfully, despite having only somatosensory information as their only resource (Maurer, Mergner, Bolha & Hlavacka, 2000).

Vestibular System. The nervous system uses the vestibular information to detect the position and motion of the head relative to gravity (for review, see Horak & Shupert, 1994). The semicircular canals and otoliths are the vestibular sensors involved in the angular and linear acceleration of the head respectively. These organs are surrounded by membranous and bony labyrinth with perilymph separating the two layers. The membranous labyrinth is filled with endolymph and lined with clusters of hair cells. The relative movement between the endolymph and perilymph caused by the acceleration of the head makes the hair cells bend, which in turn detects the motion of the head. The otoliths are activated when the head tilts with respect to the gravity. The semicircular canals sense fast head motions (Horak, et al., 1996), such as a sudden trip, which indicate that they don't play an important role in quiet stance. According to Nashner (1981), semicircular canals and otoliths are sensitive to dynamic information above and below 0.1 Hz respectively. The estimation of sway angle based on the integration of semicircular inputs is not accurate and the otoliths could not detect dynamic information above 0.1 Hz. Therefore, they are not sufficient to stabilize the human body alone and are less efficient than the somatosensory and

visual input. However, the vestibular system is important when other modalities of

information are disrupted. It was found that the vestibular loss patients change their

postural alignment (Schaefer & Meyer, 1978), indicating that vestibular information

plays an important role in maintaining the body to vertical (Horak, et al., 1994).

Vestibular system is believed to be a purely exproprioception, which informs

information about the position and movement of the head with respect to the

gravitational fields. Because vestibular information is detected with respect to the

gravitational fields, which don't change on earth, it is not subject to external

perturbation and useful to recognize other sensory errors, such as the disruption of

somatosensory or visual information and conflicts among the three inputs (Nashner,

1981).

Visual system. Vision is important to identifying the location and shape of

objects in space by detecting the relative three-dimensional motion between head and

the visual scene, thus guiding movements. It has been indicated that vision input

dominates at the low frequencies of body sway (Berthoz, Lacour, Soechting & Vidal,

1979). However, some other research showed that vision also affects the rapid

posture adjustment (Nashner & Berthoz, 1978; Nashner, 1981). Vision is very

important in the feedforward control in balance, such as to ovoid an obstacle (Gibson,

1952). Despite vision's important role, it is not absolutely needed. Because when we

close our eyes, we can still maintain balance during quiet stance. And sometimes,

vision can be misleading when the information of self-motion is not accurate

(Shumway-Cook, et al., 2000). For instance, two trains stopped next to each other and

you are in one of them. If another train moves slightly forward, you may think the

train you are on is moving backward. Self-motion and displacement from external objects can have the same impact on motion, therefore, postural control by vision relies on other sensory information, such as the vestibular information to differentiate them (Guerraz, Shallo-Hoffmann, Yarrow, Tbilo, Bronstein & Gresty, 2000). It is worthy to note that this ambiguity of sensory information also exists in other two sensory modalities.

  Central Systems. Sensory information passes from the periphery onto the central system, where the input information is processed to control posture. These hierarchically organized systems include spinal cord, brain stem and the cortex. Moreover, basil ganglia and cerebellum also contribute to the planning and execution of postural control. Each level has circuits that can organize or regulate complex motor responses. Sensory information in these systems is operated in parallel (Kandel, et al., 2000).

Spinal Cord and Brain Stem

  The spinal cord is the lowest level in the central nervous system. Spinal cord circuits alone don't produce the organized equilibrium responses in postural control, but mediate the reflexes (Kandel, et al. 2000; Horak, et al., 1996). This was supported by the fact that adult cats with a complete transection can maintain balance for a short period of time. It was suggested that this might be achieved by local segmental reflex mechanism (Pratt, Fung & Macpherson, 1994, as cited in Horak, et al., 1996).

  The next level of the hierarchy is the brain stem, which obtains inputs from the cerebral cortex and subcortical nuclei and projects to the spinal cord by two descending systems: 1) the medial descending systems, including the reticulospinal,

medial and lateral vestibulospinal and tectospinal tracts, which integrate visual, vestibular and somatosensory information to control postural orientation and equilibrium, and 2) the lateral descending systems, including the rubrospinal tract, which are important for goal directed movement (Kandel, et al. 2000). In the brain stem, there are 4 vestibular nuclei projecting to the motor neurons of eye and head movements through the vestibulospinal tract. These connections make vestibule-ocular control possible. When the head moves, the eyes move in a compensatory direction at the same speed as the motion of the head, thus stabilize the body.

The Cortex

"The primary motor cortex and several other premotor areas project directly to the spinal cord through the corticospinal tract and also regulate motor tracts that originate in the brain stem." (Kandel, et al., 2000, p663) There are two descending pathways from motor areas in the cortex: 1) the corticobulbar pathways controlling the motor nuclei in the brain stem, primarily involved in movements of the face and tongue and; 2) the corticospinal pathways control the spinal motor neurons that innervate the trunk and limb muscles (Kandel, et al., 2000). Neurons in the motor cortex are sensitive to unexpected perturbation of stance. When cats modify gait to avoid obstacles, activity of cells in motor cortex are modulated (Drew, 1993, as cited in Horak, et al., 1996).

Basal Ganglia and Cerebellum. Both basal ganglia and cerebellum are useful for smooth movement and posture. The motor cortex sends information to both of them, which in turn send feedback to the motor cortex via the thalamus. The output of cerebellum is excitatory, while the output of basal ganglia is inhibitory. The basal

ganglia don't have direct connections with the spinal cord. Therefore, most of their motor functions are mediated by motor areas in the frontal cortex (Kandel, et al., 2000). Parkinsonism is ideal for studying basil ganglia postural disorder. It is characterized by rigidity caused by increased muscle tone (Kandel, et al., 2000), which is the force muscle uses to resist lengthening. The role of muscle tone in postural control will be presented in the next session. Furthermore, Parkinsonian patients used the same pattern of muscle activation to respond to surface perturbations, suggesting that basal ganglia are important for the adaptation of motor patterns to context (Horak, Nutt & Nashner, 1992).

The cerebellar syndromes are characterized by ataxia, evidence for postural coordination function of the cerebellum. The cerebellum influences postural coordination by comparing disparities between intention and action through feedback signals, and by adjusting the operation of motor centers in the cortex and brain stem (Kandel, et al., 2000). It has been showed that the cerebellum generates corrective signals and gradually reduces errors when a movement is repeated, suggesting a role in motor learning.

BIOMECHANICS

COM & COP

The human body in quiet stance is not a rigid body, but sways spontaneously in both anterior-posterior and media-lateral directions. Center of Mass (COM), the point at which the total body mass is balanced, and the Center of Pressure (COP), the point location of vertical ground reaction forces, are often used to characterize body sway. It is a generally accepted idea that in order to keep balance, the COM must be

within stability limits (Horak, et al., 1996). Effective posture control is related to COP amplitude: small amplitudes of COP movements are regarded as good balance control (Shumway-Cook, et al., 2000). Winter (1990) suggested that COP moves with respect to COM to correct the deviation from upright stance. However, Morasso and Schieppati (1999) have argued that the COM-COP relationship is merely a physical rule and should not be used as evidence that the nervous system controls a certain variable.

Single and Double Inverted Pendulum

Based on the assumption that muscles act as springs to keep the COP within the base of support, Winter and colleagues (1998) proposed an inverted pendulum to approximate quiet stance. According to this idea, during quiet stance, the body is balanced in the anterior-posterior direction by moving around the ankles with ankle musculature under the control of nervous system (Lakie, Caplan & Loram, 2003). Body segments are aligned through passive neuromuscular properties of the muscles and joints while small deviations around the ankle are controlled through active (tonic) soleus muscle activity (Horak, et al., 1996). In addition to the ankle, hip was also thought to contribute to maintain balanced and a double inverted pendulum moving about both the ankle and hip was proposed.

Overall, this is a reductionism way to look at human body in quiet stance. It provides insights into the complex problem. For example, Loram and Lakie (2002) constrained the human body as a single inverted pendulum to look at the argument that stiffness alone is sufficient to obtain postural balance. They showed that balance is achieved by neural generation of active torque to control both body position and

sway size. Thus, they came to the conclusion that stiffness alone is insufficient to maintain balance.

Stiffness

Upright stance has been thought to be accomplished by activating the muscles to generate joint torques in order to counteract the effects of gravity (Mergner & Rosemeier, 1998). The force that muscles use to resist being lengthened is called stiffness, also known as muscle tone (Basmajian & De Luca, as cited in Shumway-Cook, et al., 2000). Muscle and joint stiffness are important to resist displacement from external forces (Horak, et al., 1996). Winter and colleagues even proposed that modulation of muscle stiffness is a simple strategy that the nervous system could use to maintain upright quiet stance (Winter, Patla, Prince, & Ishac, 1998). Lakie et al (2003) disagreed: "The problem with taking stiffness as the source of postural stability is that the muscles must operate in series with the tendon and tissues of the foot" (p357). The muscles are always stiffer than the tendon, which prevails during quiet standing. Directly measurement of the intrinsic ankle stiffness showed that ankle stiffness is not enough to provide the minimal effective stiffness. In order to maintain balance, the active changes in muscle produce extra force by stretching the tendon, which is a neural modulation.

Coordination Patterns

Support Surface Perturbation studies. With a static, horizontal platform, it is hard to differentiate how vestibular or proprioceptive information is used for control of upright stance as both modalities of information are present. Begbie (1967) introduced a moving platform triggered by foot pressure (as cited in Nashner, 1981).

By changing the somatosensory information at feet with vision disruption, the adaptation of this situation is mainly based on vestibular information.

Some techniques that are often used include sway referencing, tilting the platform or driving the platform by a specified signal. Nashner and colleagues (1976; Nashner, Black & Wall, 1982) introduced the sway referencing technique, in which the platform rotates around the ankle joint in proportion to the subject's body sway, thereby reducing or eliminating proprioception from the feet/ankles (Horak, et al., 1994). A tilted platform was inclined in either the AP or ML direction, giving incorrect proprioceptive information. The logic is that if the subjects depend on the gravitational reference from the vestibular system, then body orientation in space should be constant; likewise, if the subjects depend on somatosensory information from the platform, then body orientation should change with the changing platform. Driving a platform with specified sinusoidal signals makes calculation of gain and phase between the body sway and driving signal possible, thus providing a direct measurement of sensory coupling.

Nashner and colleagues used this moving platform paradigm to study postural coordination patterns. They (1976, 1982) explored the muscle patterns and proposed that maintenance of stance is determined by the organization of the neuromuscular system and the underlying movement strategies for balance. A movement strategy is a high-level plan that functionally couples the interrelated muscles to achieve the goal of maintaining postural stability and orientation in space, thus simplifying the control demands on the central nervous system (Shumway-Cook, et al., 2000; Horak et al., 1996). Postural strategies focus on the relationships among ankles, hips and knees.

As the knee joints remain approximately stationary in the AP sway, knee joints are always ignored in postural control patterns (Alexandrov, Frolov, & Massion, 2001). The standing human can maintain balance against the perturbations mainly using two strategies: the ankle strategy and hip strategy.

During the ankle strategy, the body is moving about the ankle joint and human upright stance is often approximated as a single segment inverted pendulum. This strategy is often used when the external perturbation is small and the support surface is firm. During the hip strategy, the body is moving about the hip joint through counter-rotation of the ankle angle and approximated as a two-segment (trunk and leg segments) inverted pendulum. The hip strategy is useful for rapid or large amplitude perturbations. The ankle and hip strategies are simplified and extreme conditions. They are usually used in combination (Horak et al., 1996; Creath, Kiemel, Horak, & Jeka, 2002). When the perturbation is very large or fast and exceeds the stability limitations, a third strategy, namely, stepping strategy is used.

The generally accepted idea is that these basic patterns are centrally selected from a set of motor programs (Horak & Nashner, 1986). Horak and colleagues (1990) compared vestibular loss patients, somatosensory loss and control subjects on a translation platform with or without changing the length of support surface. Results showed that somatosenory loss subjects didn't elicit ankle strategy and vestibular patients didn't trigger hip strategy. They argued that these subjects can produce ankle and hip strategies, but could not select them when experiencing platform perturbation.

However, recently study by Creath and colleagues (2005) suggested that this idea of "selected" postural strategies might not be true when the surface is

unperturbed. They found that the relationship between ankle and hip angles is in-phase (ankle strategy) for frequencies lower than 1 Hz and anti-phase (hip strategy) for frequencies higher than 1 Hz, thus indicating that these two strategies co-exist. The co-existing of postural strategies suggests that the predominance of these patterns depends on the characteristics of the available sensory information.

Moving Room Studies

Lee and Lishman (1975) were among those who first used the "moving room" paradigm to demonstrate visual coupling. This moving room paradigm is achieved by physically moving the walls of a room while the floor remains stationary with the subjects placed in the environment. Later on, as computer techniques develop, simulating movement with a computer-generated large screen visual display is used. Methods in these studies assume that the sensory coupling system is linear. That is, response of the motor system is driven by both spatial and temporal structures of the visual stimulus: 1) postural sway is induced in the direction of the visual motion; 2) the coordination patterns are temporally stable, in another word, the coordination patterns are reproducible and sustain inspire of perturbations (Schöner, 1991).

Many of these studies focusing on vision coupling had consistent results that static visual field reduces body sway (Brant, Dichgans & Koenig, 1979) and visual motion enhances body sway (Lee & Aronson, 1974; van Asten, Gielen & Denier van der Gon, 1988). Moreover, different amplitudes and frequencies of visual motion have been studied. The change of body sway with respect to the manipulation of visual motion amplitudes has been taken as a process of sensory reweighting. There is a saturation effect, which means that body sway doesn't increase further as a

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function of the vision stimulus as the amplitude reaches a saturation level (van Asten, et al., 1988; Peterka & Benolken, 1995). Different frequencies were used to characterize the temporal relationship between visual scene and postural sway.

The studies of different stimulus amplitudes and frequencies involve using continues stimuli, rather than the discrete movements as in the 70s or 80s, and calculation of transfer function. Transforming both postural responses and stimuli into the frequency domain makes a direct estimation of the response at each driving frequency, thus characterizing the dynamic behaviors of the system. Gain and phase indicate the sensitivity of response and timing change as a function of stimulus frequency, respectively (Peterka, 2002). A unity gain implies that the sway amplitude closely matches the stimulus amplitude. Effects of vision are observed at low frequencies of stimuli (of an order of 0.1 Hz) with phase lock regardless of stimulus amplitudes.

Recently, this moving room paradigm has been expanded to look at other sensory coupling. A moving touch bar method that allows subjects apply light touch not enough to support the body was developed by Jeka and colleagues (Jeka, et al., 1994) to look at the somatosensory coupling. In that study, the touch bar was driven at frequencies of 0.1, 0.2, 0.4 and 0.6 Hz at a constant peak velocity of 0.65 cm/s. It was found that the stability of human body decreases with the increasing of frequency of the somatosensory input and body sway is sensitive to both position and velocity of somatosensory information (Jeka, et al., 1998). Later on, by using the touch bar method, Lackner and colleagues found that the light touch of the fingertip can be as

effective or even better than the vestibular information in stabilizing the human body in quiet stance (Lackner, DiZio, Jeka, Horak, Krebs & Rabin, 1999).

ADAPTIVE PROCESSES

Adaptation is the ability to change perception or perceptual-motor coordination in order to reduce or eliminate the discrepancy between sensory modalities or correct the behavioral errors generated by the discrepancy (Welch 1986). Adaptation in postural control is more often mentioned as sensory reweighting, which was introduced by Nashner and colleagues early in the 70s (Nashner, 1976; Nashner, et al., 1982). They changed the somatosensory and visual information alternatively for both vestibular deficit and normal healthy participants to see how they adapted to the changed conditions. It was found that the weighting of sensory inputs was a function of changing environment. The vestibular deficit patients suffered from instability not because of the loss of vestibular information itself, but inability to reweight the remaining sensory information. Some important features of adaptation are discussed in the following sessions.

Multisensory Fusion

   Redundancy and Integration of Multisensory. Redundancy and integration of multisensory are two important aspects in adaptation. Redundancy means even if one or two of the sources of the sensory information are missing, the body can still stay balanced (Nashner, 1981; Horak, et al., 1996). Because not all the sensory information is always available, such as in a dark room or standing on a floating boat, the motor control system weights more the intact sensory channels; a particular channel is critical important when others are not available (Nashner, 1981).

Moreover, this property is necessary to solve the perceptual ambiguities in postural control (Horak, et al., 1996). For example, when waiting in the bus station, if the bus passes the station, there is a relative movement between the head and the bus. In this case, vision can not tell if this is a self-motion or not and vestibular information is needed to solve this ambiguity. Because of this, the vestibular loss patients may lose their balance and fall in this situation. Redundancy also explains the variability of performance in stance. Kluzik and colleagues (Kluzik, Horak & Peterka, 2005) had subjects stand on a toes-up tilted platform and measured their body movements after the platform tilted back to horizontal. Results showed that some of the subjects, who preferred proprioception, leaned forward after the platform was back to horizontal and slowly returned to vertical; while other subjects, who preferred vestiular information, kept their body vertical as soon as the platform returned to horizontal.

Different modalities of sensory information combine and contribute to postural control. The mechanism of this sensorimotor integration is only partially known. One possibilities of how this is working is that each sensory system detects the error indicating the deviation from body orientation in its own reference frame and the errors sum linearly (Peterka , 2002). However, the sensorimotor integration is not a simple summation of different sensory information, but dynamic reweighting as the environmental conditions change (Peterka, 2002). In another word, as the afferent activity changes, the sensory-perceptual and sensory-motor relationships rearrange accordingly at the high level of integration (Benson, 1982). One experiment demonstrating this issue was finished by Peterka and colleagues (Peterka & Loughlin, 2004). The experiment was consisted of two conditions: sway –referencing and

reverse sway -referencing. In the sway-referencing condition, the subjects were instructed to stand with their eyes closed on a platform that was fixed for 60 seconds, sway-referencing for 60 seconds and back to fixed for 60 seconds. In the reverse sway-referencing condition, an additional 60 seconds reverse sway-referencing was added following the sway-referencing. A negative feedback control model was used to simulate the process of reweighting when subjects stood on the platform. Two modalities of sensory information are available in this case: proprioception and gravitation (vestibular information). Simulation results showed that the as soon as the sway-referencing begins, the weight for proprioception went down and the weight for gravitation went up in order to compensate for the down-weighting proprioception. After sway-referencing, some subjects down-weighted the gravitation quickly; while others did not and showed an oscillation sway after back to fixed platform.

Manipulation of Sensory Modalities. Many studies looked at sensory reweighting manipulated only one sensory modality, such as somatosensory information coupling with light touch (Jeka, Schöner, Dijkstra, Ribeiro, & Lackner, 1997); vision using the moving room paradigm (Oie, et al. 2002). Manipulation of one sensory modality gives insights into the properties of each sensory modality in sensory reweighting. However, the study of multisensory reweighting requires looking at different modalities of sensory information simultaneously. As mentioned before, the contribution of each sensory modality is not fixed and cannot be identified separately in different experiments and summed together (Peterka et al., 2004). According to Peterka's (2002) model, because mulstisensory information integrates in

unity, downweighting in one sensory modality will cause upweighting of other sensory modalities (Ravaioli, Oie, Kiemel, Chiari & Jeka, 2005).

Some studies have done in our lab to understand the sensory reweighting process by manipulating more than one modality of sensory information at the same time. One of the experiments was designed to look at the simultaneous reweighting of vision and somatosensory (touch) (Oie, et al., 2002).   In this study, approximately sinusoidal visual and touch stimuli with peak amplitudes of the motion were manipulated as: (touch amplitude (mm): visual amplitude (mm)) 8:2, 4:2, 2:2, 2:4, 2:8. Results showed that the gain to visual motion increased as the increasing of touch amplitudes, but not the other way around. This indicates an intra-modality reweighting, which means in the sensory reweighting process, the CNS not only reweights the particular sensory channel changed, but also the unchanged ones. It is consistent with previous studies that increasing the amplitude of a particular sensory input resulted in decreasing in the gain to the input. Another finding in this study is that by fitting the model, it verified that changes in coupling coefficient can be regarded as changes in sensory reweigting rather than stability.

Moreover, these results also demonstrated that sensory reweighting process is nonlinear as gain to both vision and touch motion depended on the amplitude of the stimuli. Because linear theories and models are inadequate to explain some recent findings, investigations also start to explore the nonlinearity of the reweighting. In a study by Ravaioli et al. (2005), a visual stimulus with constant-frequency, low-amplitude medial-lateral oscillation and constant-velocity translation from left to right were used at the same time. Results suggested that gain to the oscillation component

first increased as the velocity of translation increased, but then decreased. Both sway velocity and position variability increased as the translation velocity increased with a level lower than in the eyes closed condition. This supports that when one modality of sensory information is lost, it can not be fully compensated as the sway variability levels are not constant.

In summary, although some progress has made to understand the process of sensor adaptation, this field is still in its infancy, and more studies are needed.

Internal Models

It has been suggested that the nervous system integrates all the sensory information according to an internal model (Lackner & Levine, 1979). Following Oman's theory (1980), Nashner (1982) argued that rapid reorganization of sensory inputs to the motor system is a fixed "non-adaptive" process, while the process that involves modifying the internal model is "adaptive". The internal model is a bridge not only between perception (the translation of sensory information into organized experience) and action, but also between the outside world and the body (Morasso & Sanguineti 2003). Some scientists also refer internal model as internal representation (eg. Horak et al. 1996), which connects the loop between sensory and motor systems.

There are two types of internal model: forward models and inverse models (Wolpert, Ghahramani, & Jordan, 1995). A forward model, which performs the motor-to-sensory transformation, serves as a fast internal loop that uses the motor command to control the motor system and predicts the next state (e.g. velocity and position). A state includes the dynamics of both the system and sensor (Carver, et al., 2002). Transformation from sensory variables to motor variables is known as internal

inverse model, which estimates the motor commands that induce a certain state transition (Wolpert, et al., 1995). An example of the inverse model is the vestibulo-ocular reflex, which generates the desired motor command according to a particular eye velocity. Correcting and updating the discrepancy between the input and output of the internal model form the process of adaptation. (Miall & Wolpert, 1996).

Although the idea of an internal model has been widely accepted, issues such as the location and coding of the internal model are yet to be resolved. Miall et al. (1996) proposed some locations of internal models according to their functions. For example, an internal model of ocularmotor control could be located in brain stem; the forward models used in internal feedback control of movement are likely to be found in the cerebellum. To support their argument of a forward model for motor systems coordination, they cited the experiment by Vercher and Gauthier (1998): the monkeys' ability to make eye movements follow movement of a cursor controlled by their hands was damaged when the cerebellum was inactivated. However, such evidences for the existence of an internal model are indirect.

So far, model is a useful tool to approach internal model. The argument of the role of environment sensory information in motor control is an example. According to Miall and Wolpert (1996), the sensory information has two sources: the environment (external) and sensory consequences of movement (internal). Van der Kooij et al. (2001) were among those who first proposed that there is a dynamic environment component in postural control. They used visual motion as a simulation of the environment and implemented a Kalman filter model to reproduce the behavior of postural control. Even though their model succeeded in capturing the postural control

behavior, Caver et al. (2005) used a simplified version of van der Kooij model and found that including the environment component didn't reproduce the famous experiment results that the phases of postural sway in response to sinusoidal stimuli decrease constantly as frequencies increase regardless of amplitudes. Therefore, the visual environment is not involved in the internal model in response to visual stimuli.

COGNITIVE PROCESSES

The perception of postural control depends not only on sensory information, but also cognition, which is the mental functions, such as attention and central set. Attention is the capacity that an individual processes information. The assumption is that the capacity for each individual is limited and the performance of any task requires a given portion of capacity (Woollacott & Shumway-Cook, 2002). In the studies of attention, subjects are usually asked to perform a secondary task, such as memory task, besides postural control. It was found that in both young and older adults, the effects of attention on postural control depend on the complexity and type of secondary task (for a review, see Woollacott, et al., 2002). Shumway-Cook and Woollacott (2000b) had young and older adults respond to an auditory tone when the proprioception at feet and vision were changed alternatively. They found that with aging, the need of attention for postural control increased with the decreases of sensory information.

Central set involves the modification of automatic motor responses based on expectation of stimulus and task characteristics, that is, the subjects' prediction and knowledge about the environment and experiences in the past will affect their postural control (Horak, et al., 1996). For instance, after subjects were exposed to 6-

11 trials of small amplitude platform perturbation, they underresponded with smaller initial ankle torques when presented to randomly inserted (unexpected) large amplitude platform perturbation, and vice versa (Horak, Diener & Nashner, 1989).

THEORIES

In addition to theories mentioned above, there are many theories concerning postural control these years, some of them are presented as following.

Motor program theories have expanded our understanding of motor control. These theories argue that different sensory modalities are mediated and integrated by the nervous system according to an internal representation of the body's motor and sensory dynamics (Horak et al., 1996). The internal representation of the world is created to serve as a framework. Motor systems plan, coordinate and execute the motor programs with respect to this framework (Kandel, et al., 2000). Nashner and Wollacott (1979) noted that the "intersegmental" somatosensory inputs are used by the peripheral motor programs to form a pattern of movement, while the combination of all sensory modalities are executed by the central programs to suit the external conditions. However, some scientists (eg. Morasso, et al., 2003) have argued that this theory implies a sequential organization, which is effective when the individual steps are sufficiently fast. Furthermore, this is not consistent with the parallel, distributed processing because of the slowly synaptic processing.

There are many theories, such as the stabilogram –diffusion theory, the negative control theory or the optimal control theory, derived from the concept of feedback and feedforward control. Feedback control, also called the closed-loop, uses output of the information that sent out earlier to regulate actions. While feedforward

control, also called the open-loop, uses sensory inputs and is not affected by the previous action. Stabilogram is a variable generated by standing on a force plate and measuring the COP (Nashner, 1981; Peterka, 2000). It is a combination of gravitational, inertial, and muscle forces (Nashner, 1981). Collins and De Luca (1993) introduced a method for analyzing COP known as stabilogram diffusion analysis (SDA), which summarizes the mean square COP displacement as a function of the time interval. They proposed that a short-term open-loop and a long-term closed-loop are involved in controlling the undisturbed, upright stance. Furthermore, the open-loop is a basic resource in postural control, while the closed-loop is an implement. Following this model, Peterka (2000) came to a different conclusion and suggested that a simple closed-loop control model can control body dynamics. Sensory information is dynamically weighted according to the changing environment to provide feedback, which is used to maintain stability (Peterka & Loughlin, 2004). Later on, he went further to propose that a negative feedback control can capture the main features of postural control in the sensorimotor control perspective. The feedback control has two sides: positive and negative. The positive feedback control increases the input, while the negative feedback control decreases the input. The negative feedback control theory argued that change in a condition triggers the counteract effect to prevent further change. Mergner and Rosemeier (1998) also argued that postural control is built around an ankle proprioceptive negative feedback control.

According to the optimal control theory, motor control is an input-output system, which has a state representation (estimation) and a control selection center

(control) as mentioned before. The estimation provides a mechanical state of the human body and control selects the type and amount of response necessary to counteract the perturbation (Kuo, 1995). The selection includes choosing appropriate either a feedforward trajectory or feedback gains, or both. A high-gain system is efficient in minimizing deviations from the optimal target state, but unstable with large phase lag (Kandel, et al., 2000).

Although there are different arguments about how the feedback and feedforward control affect postural control among these theories, one thing is in common: sensory information is important. The stiffness control theory has been proposed to argue against this. Winter and colleagues (1998) suggested that the different sensory modalities either dosen't contribute to or is below threshold in quiet stance. They proposed that muscle stiffness itself can stabilize the human body.

The theories mentioned here are not exhaustive, but rather give different aspects of postural control.

Chapter 3: The Influence of Sensory Information on Two-Component Coordination during Quiet Stance

ABSTRACT

When standing quietly, human upright stance is typically approximated as a single segment inverted pendulum. In contrast, investigations which perturb upright stance with support surface translations or visual driving stimuli have shown that the body behaves like a two-segment pendulum, displaying both in-phase and anti-phase patterns between the upper and lower body. We have recently shown that these patterns co-exist during quiet stance; in-phase for frequencies below 1 Hz and anti-phase for frequencies above 1 Hz. Here we investigated whether the characteristics of these basic patterns were influenced by the addition or removal of sensory information.

Ten healthy young subjects stood upright on a rigid platform with different combinations of sensory information: eyes were open or closed with or without light touch contact (< 100 g) of the right index fingertip with a 5 cm diameter rigid force plate. Coordination between the trunk and leg segments showed that the in-phase and anti-phase pattern co-exist in both the AP and ML directions of sway. Trunk-leg coherence decreased with the addition of vision and light touch, in the AP and ML directions, respectively, but only at frequencies below 1 Hz where the in-phase pattern predominates. Additional sensory information had no effect on coherence at sway frequencies above 1 Hz, where the anti-phase pattern predominates. These results suggest that the in-phase pattern may be more influenced by neural control

than the anti-phase pattern, which may be primarily the result of two-link biomechanics.

INTRODUCTION

Human upright stance is often approximated as a single-joint inverted pendulum, pivoting around the ankle during quiet stance (Jeka, et al., 2005; Peterka, 2002). When perturbed, additional patterns associated with a double-linked pendulum are then observed, such as the anti-phase hip strategy (Horak, et al., 1986). The generally accepted idea is that these basic patterns are centrally selected from a set of motor programs, arising from high-level neural strategies and implemented by complex sensorimotor control processes to most effectively counteract the physical characteristics of the perturbation (Horak, et al., 1996). However, recent work has questioned this distinction between quiet and perturbed stance (Creath, et al., 2005). The same in-phase (i.e., ankle strategy) and anti-phase (i.e., hip strategy) patterns between upper and lower body segments observed in response to perturbed stance co-exist at different frequency ranges during quiet unperturbed stance. At frequencies below approximately 1 Hz, coordination between the trunk and legs assumes an in-phase pattern, while above 1 Hz, an anti-phase pattern predominates.

The coexistence of in-phase and anti-phase body sway during quiet, unperturbed stance raises a number of issues regarding how these patterns arise. Are both patterns specified by neurally defined motor programs or are the mechanical characteristics of a multilink inverted pendulum playing a significant role? Are these patterns "selected" by the central nervous system to compensate for a particular

perturbation or are they merely "excited" by a perturbation, negating any need for selection? In the present study, we investigated how the addition or removal of sensory information influences the co-existing in-phase and anti-phase patterns observed during quiet stance. The logic is that if a particular pattern is actively controlled by neural processes, then the characteristics of that pattern will be influenced by the manipulation of available sensory information. If a pattern is more of a function of the biomechanics of the multi-joint body, then sensory manipulations should have little effect. We also studied the relationship between upper and lower body segments in both the anterior-posterior (AP) and medial-lateral (ML) directions to determine whether the in-phase and anti-phase patterns coexist in both directions of sway.

METHODS

Subjects

Ten individuals participated, three women and seven men, ranging in age from 18 to 31 years (mean age = 23.9, SD = 4.4). All subjects were right-handed, healthy and physically active, with no known musculoskeletal injuries or neurological disorders that might affect their ability to maintain balance. The procedures used in the experiment were approved by the Institutional Review Board at the University of Maryland. Informed written consent was obtained from all participants in the study.

Apparatus

The subjects stood on a rigid platform with their right index finger touching a static touch plate placed in front of the subject's right shoulder. The touch device

consisted of a smooth horizontal metal plate (5 cm in diameter) supported by a tripod. The plate was adjusted in height and position to allow subjects to assume a comfortable arm position, typically with ≈10-15 degrees of elbow flexion. When the subjects applied forces of more than 1N, an auditory alarm sounded. The visual environment consisted of an array of lab equipment against a wall approximately 280 cm away, with normal ambient light levels. Kinematics of the shoulder (the scapula), hip (the greater trochanter), knee (the lateral femoral condyle) and ankle (the lateral malleolus) were measured by attaching four LED markers on the left side of the subject and were sampled at 100 Hz using an Optotrak (Northern Digital, Inc.) system. Three LED markers were put on the force platform aligned with the corner facing the cameras as a reference, so that the data could be rotated from the cameras' own coordinate system into the subject's global coordinate system later in the data analysis. A bank of three cameras was placed to the left front of the subjects to measure the movements of the markers.

Procedures

The subjects stood upright with heels 1 cm apart pointed outward at an angle of 15 degrees between each foot and the midline. The floor was marked with tape so that the same foot position could be repeated on each trial and subject. The experimental trials included two visual conditions, eyes closed or eyes open and two fingertip contact conditions, no contact, or light touch contact, in which the vertical touch force applied on the touch plate by the right index fingertip was limited to 1 N. The four conditions were identified as follows: Neither = eyes closed and no touch

contact, Touch = eyes closed and touch contact, Vision = eyes open and no touch contact, Both = eyes open and touch contact.

Subjects began each trial by looking straight ahead at fixation target against a wall approximately 3 m away. In the Touch conditions, subjects were instructed to take as much time as possible to find a comfortable position and keep the fingertip on the same spot on the touch plate throughout the trial. If the alarm sounded, the subjects were told to keep their fingertip in contact with the touch plate while reducing the force at the fingertip. During the no touch trials, the subjects were asked to keep both arms crossed behind their back so that their hands were touching at approximately waist level. This prevented the arms from blocking the markers as subjects faced the camera. Once the subjects felt ready, they said "yes" and the experimenter initiated data acquisition 5 seconds later.

Each condition was run three times for a total of 12 trials for each subject. All trials were 240 seconds, the order of the trials across conditions were randomized for each subject. The subject was asked to sit and rest for two minutes after completing a trial. One trial was discarded due to technical difficulties.

Analysis

Kinematics. The trunk and leg segment were assumed to lie on the line connecting the two adjacent joints with the knee being ignored, which was based on the fact that knee joints remain approximately stationary during AP sway motions (Alexandrov, et al., 2005). AP trunk and leg angles with respect to vertical were calculated using the AP and vertical positions of the ankle, hip and shoulder markers.

ML trunk and leg angles with respect to vertical were calculated using the ML and vertical positions of the same three markers. All subsequent analysis was applied separately for the AP and ML directions.

Sway Variability. For each segment angle trajectory, a velocity trajectory was calculated using finite differences with a time step of 0.1 s. *Position variability* and *velocity variability* was computed as the standard deviations of the angle trajectory and its velocity trajectory, respectively, and averaged across trials.

Spectral Analysis. For each trial means were subtracted from the leg and trunk angle trajectories and the power spectral densities (PSDs) of the legs and trunk and cross spectral density (CSD) between the legs and trunk were computed in Matlab using Welch's method with a 20 second Hanning window and 50% overlap. PSDs and CSDs were averaged across the three trials (one subject had only 2 Touch trials).

For each subject and condition, complex coherence was computed as the CSD divided by the square root of the product of the trunk and leg PSDs. 3.1a shows the trunk-leg complex coherence in the complex plane from a single trial. Each symbol indicates a different frequency in steps of 0.05 Hz. There are two common ways to decompose complex coherence. Figure 3.1b-c shows a decomposition into real and imaginary parts. Figure 3.1d-e shows a decomposition into (mean-squared) coherence r^2 and cophase θ, where the distance r and angle θ are defined in Figure 3.1a. A positive cophase indicates that the leg segment led the trunk segment.
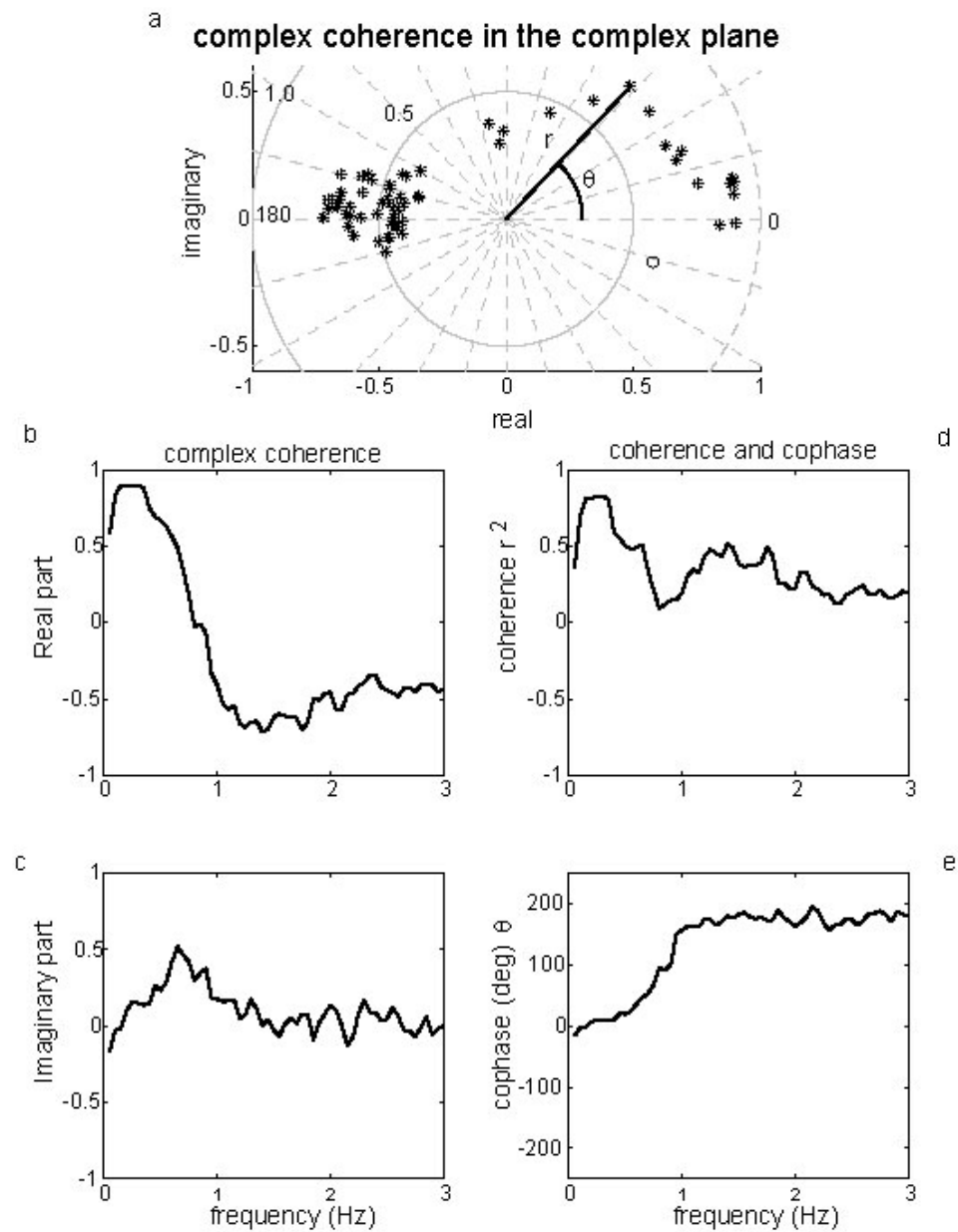
Figure 3.1. Complex coherence describing the linear relationship between the leg and trunk angles for a single trial in the ML direction. (a) Complex coherence plotted in the complex plane. Each symbol indicates a different frequency in steps of 0.05 Hz. (b-c) Complex coherence decomposed into its real and imaginary parts. (d-e) Complex coherence decomposed into (mean-squared) coherence r^2 and cophase θ.

In this paper we use the real-imaginary decomposition of complex coherence for two reasons. First, the imaginary part of complex coherence was generally small so that changes in complex coherence were primarily due to changes in its real part. Second, complex coherence was often near the origin at some frequencies, which complicates the statistical analysis of cophase. When interpreting our results it will be useful to understand how the real-imaginary and coherence-cophase decompositions of complex coherence are related, since the latter decomposition is often used in the literature (Creath, et al., 2005). For example, if the imaginary part of complex coherence remains small while the real part goes from positive to negative with increasing frequency (Fig. 3.1b-c), then cophase shows a sudden transition from nearly in-phase (0 deg) to nearly anti-phase (180 deg) accompanied by a drop in coherence at the transition (Fig. 3.1d-e).

Statistics. The log of the position and velocity variability in the AP and ML directions was analyzed using Condition x Segment repeated-measure ANOVAs with Greenhouse-Geisser adjusted p values. Use of the log transform tends to reduce skewness and deviations from sphericity. Pairwise comparisons were performed using paired t-tests with the Tukey-Kramer adjustment for multiple comparisons and the Kenward-Roger adjustment for reducing small sample bias. For plotting variability we used the geometric mean of the subjects' variabilities to be consistent with our use of the log transform in our statistical analysis: the log of the geometric mean equals the arithmetic mean of the logs.

Separate statistical analyses were performed on power spectral density (PSD) of the trunk and legs, as well as the coherence between the trunk and the legs. PSDs

were analyzed between 0.05 and 3 Hz in steps of 0.05 Hz. In order to reduce the chance of Type 1 error, power was binned into frequency steps of 0.2 Hz (4 x 0.05 Hz/bin). A Condition x Segment x Bin (4 x 2 x 15) repeated measures ANOVA was performed on trunk and leg PSDs in the AP and ML directions, with Greenhouse-Geisser adjusted p values. All possible pairwise comparisons between conditions were performed using paired t-tests with the Tukey-Kramer adjustment for multiple comparisons and the Kenward-Roger adjustment for reducing small sample bias. Follow-up paired t-tests at each of the 15 frequency bins were used to determine the frequency range of the differences, using the method of Benjamini and Hochberg (Benjamini, et al., 1995) to control the false discovery rate (FDR). Because p values at different frequencies are dependent, control of the FDR is approximate. For plotting variability and PSDs we used geometric means to be consistent with our use of the log transform in our statistical analyses: the log of the geometric mean equals the arithmetic mean of the logs.

RESULTS

Sway Variability. Figure 3.2 shows the mean position and velocity sway variability in the AP and ML directions. The variability of the trunk segment was higher than the leg segment, supported by significant main Segment effects (ps < 0.004). There were highly significant main Condition effects for both AP and ML velocity variability (ps < 0.001). For position variability, the main Condition effect was significant in the AP direction ($p = 0.035$) but not in the ML direction ($p = 0.76$).

The only significant Condition x Segment interaction was found for AP velocity variability ($p = 0.0032$); adding sensory information decreased variability more for the leg segment than for the trunk segment, that is, the percentage decrease in variability was greater for the leg segment.
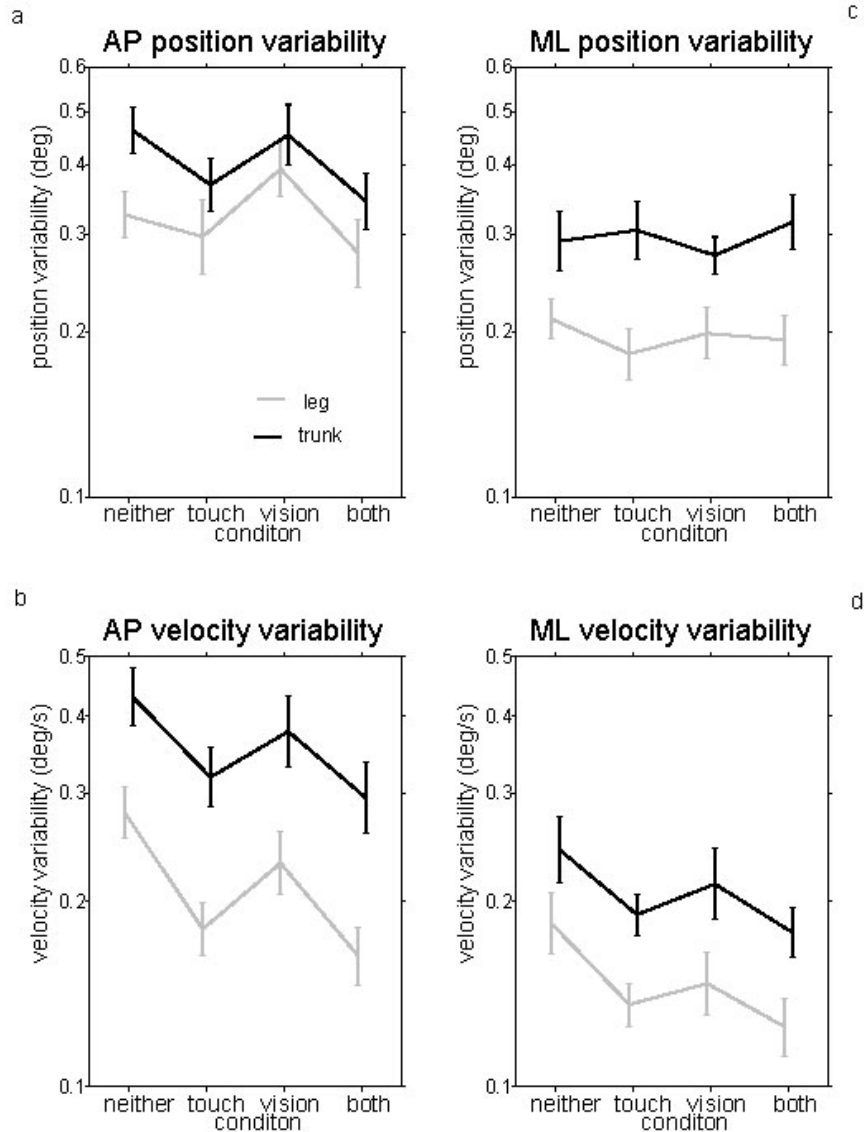

Figure 3.2. Position viability in the AP (a) and ML (c) directions for each condition. Velocity variability in the AP (b) and ML (d) directions for each condition.

Trunk and Legs Segment PSDs. Figure 3.3a-h shows the mean PSDs for the leg and trunk segments in the AP and ML directions. Repeated-measure ANOVAs revealed significant Condition x Frequency interactions ($ps < 0.005$) and Segment x Frequency interactions ($ps < 0.0001$) for both the AP and ML directions. All main effects were also significant ($ps < 0.02$); the Condition x Segment and Condition x Segment x Frequency interactions were not significant ($ps > 0.05$).
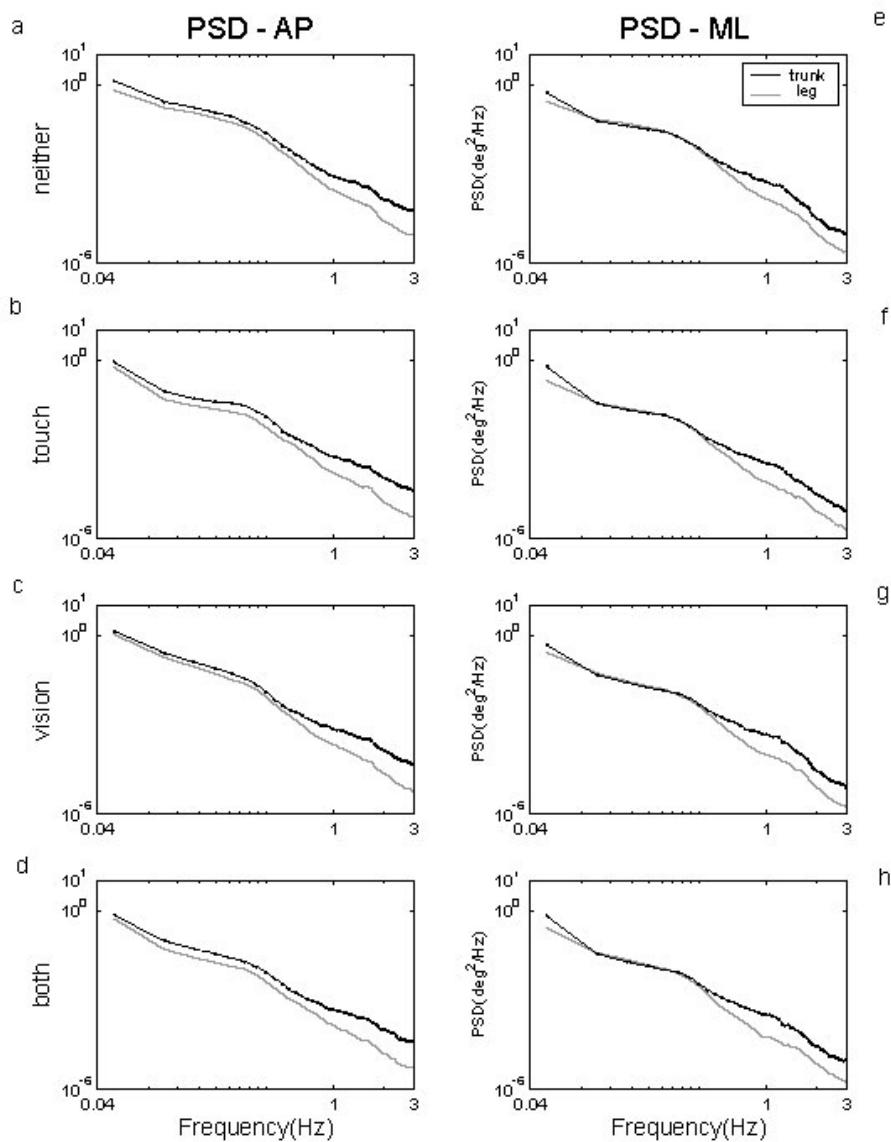
Figure 3.3. Power spectral density of the trunk and leg angle in the (a-d) AP and (e-h) ML directions for each condition.

The presence of a Segment x Frequency interaction for the log-PSD indicates that the difference between segments was not uniform across frequency. Equivalently, the percentage difference between the geometric-mean PSDs was not uniform across frequency. The trunk PSD tended to be greater than the leg PSD, with the largest percentage differences occurring at the higher frequencies (Fig. 3.3). To further test for segment effects, we averaged the log-PSD across condition and tested for a segment effect at each frequency bin. For the AP direction, the log-PSD was greater for the trunk than the legs for all frequency bins (FDR < 0.05; see Methods). For the ML direction, this was true for all frequency bins except for 0.25-0.40 Hz, where we found no significant difference.

Trunk-Leg Coordination. Consistent with a previous study (Creath, et al., 2005), trunk-leg coordination showed co-existence of in-phase and anti-phase patterns during quiet stance in both the AP and ML directions. The co-existence of these patterns is illustrated in the complex plane in Figure 3.4.

Figure 3.4a-d show trunk-leg coherence separated into its real and imaginary parts for each condition. Both the ML and AP directions show a similar trajectory in the real part of complex coherence. The real part of coherence begins close to 0.5 at the lowest frequency, rises slightly, decreases, crosses the x-axis to signify a shift from the right side to left side of the complex plane, and then finally increases again to approximately 0.5. Negative values of the real part of coherence represents the same magnitude as positive values, with the sign merely reflecting its position on the

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left or right side of the complex plane, respectively. Plots of the imaginary part of coherence in Figures 3.4b and 4d show that it was approximately zero across all frequencies in both the ML and AP directions, except for a small increase at frequencies below 1 Hz in the ML direction. Values of the imaginary part of coherence close to zero means that it is contributing very little to the calculation of complex coherence, making the real part the primary determinant of complex coherence.
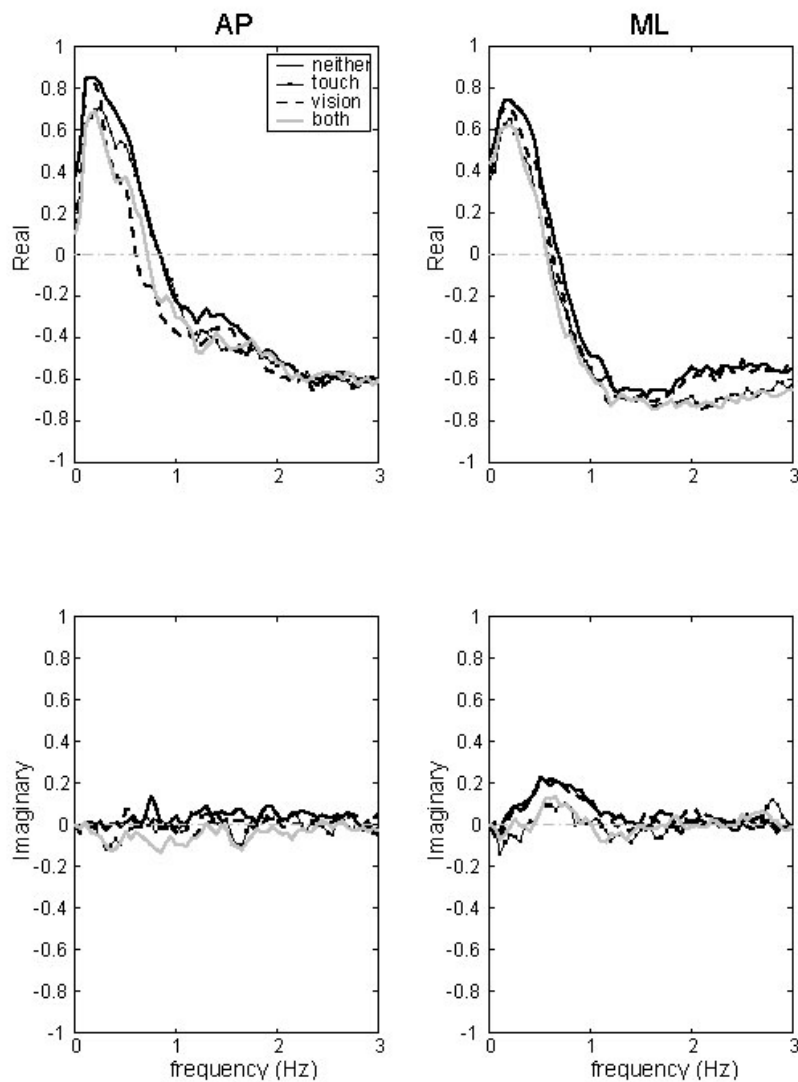
Figure 3.4. The real and imaginary parts of complex coherence plotted separately in the (a-b) ML and (c-d) AP directions.

Statistical analysis of coherence showed strong effects of Condition, supported by significant Condition x Bin effects in both the ML ($p < .0001$) and AP ($p < .003$) directions. In both the AP and ML directions, the vast majority of Condition differences were found below 1 Hz. For the AP direction, the most consistent difference in coherence was found between the Neither and the Vision condition, at all bins in the frequency band between 0.4-0.80 Hz ($ps < .002$). No other comparison between conditions had multiple successive bins that were significantly different, with only individual bins showing marginal significance. In the ML direction, coherence differed between the Neither and Touch conditions, as well as the Neither and Both conditions in the range of frequencies between 0.2-0.8 Hz ($ps < .001$).

DISCUSSION

The coordination between trunk and leg segment angles during quiet stance was studied to determine how the addition or removal of sensory information influenced their coordinative relationship at different frequencies. We found three main results. First, additional touch or visual information led to a decrease in variability of both the trunk and leg segments. The trunk segment displayed higher variability than the leg segment in all conditions, with the difference in segment variability larger at higher frequencies. Minor differences were observed between the

segments due to condition, indicating that additional sensory information led to a similar decrease in segment variability.

Second, co-existing patterns of coordination were found in the ML direction of sway, similar to that found previously in the AP direction of sway (Creath, et al., 2005). At sway frequencies below 1 Hz, the trunk and legs were primarily in-phase in the AP direction. In the ML direction, an increase in imaginary coherence above the horizontal axis (see Figure 3.4d) indicated a trunk-leg pattern that was continually shifting with frequency, traveling above the horizontal axis as illustrated in Figure 3.1a. Presently, the mechanism underlying the difference in phase between the ML and AP directions below 1 Hz is unknown. Above 1 Hz, the AP and ML directions both assume an anti-phase pattern.

It has been argued that control of sway in the AP and ML directions are independent, based upon recordings of separate center of pressure profiles under each foot. AP balance is primarily under ankle (plantar/dorsiflexor) control, whereas ML balance is under hip (abductor/adductor) control (Winter, et al., 1996). Despite different muscular synergies involved in each direction of sway, the present results showing similar patterns of coordination between the trunk and legs question whether different control strategies are involved. Instead, the same control strategy may be realized through different muscular components.

Third, additional touch or visual information lowered coherence, suggesting that the linear dependence between the trunk and legs was weaker with additional sensory information. The decrease in coherence was highly dependent upon frequency. Differences in coherence between conditions were found primarily below

1 Hz, the frequency range in which the trunk and legs maintain an approximately in-phase relationship. These condition effects for coherence were observed for successive frequency bins, resulting in a relatively wide frequency band of significant differences. In contrast, only intermittent condition differences for coherence were observed above 1 Hz, with nothing resembling a band of successive frequencies. Above 1 Hz, the phase relationship between the trunk and legs is predominantly anti-phase, suggesting that the anti-phase pattern is less influenced by sensory information than the in-phase pattern observed below 1 Hz.

We also observed an effect of sensory information on sway direction, depending upon whether touch or vision was available. The presence of light touch led to a decrease in coherence in the ML direction of sway while vision led to a decrease in coherence in the AP direction of sway. These effects are related to how the sensory environment is structured. Placement of the touch plate lateral to the body on the right side allowed the hand/arm to be oriented comfortably to the right and emphasized touch information in the ML direction. Previous experiments have shown that if the touch plate is placed in front of the body with the hand/arm oriented along the midline of the body, light touch effects sway primarily in the AP direction (Jeka, et al., 1998). Similar effects on sway are observed depending on whether the visual display moves in the medial-lateral or anterior-posterior direction (Jeka, et al., 2002; Stoffregen, 1985). Even though the touch and visual information in the present experiment was static, the structure of the touch and visual inputs were such that they influenced sway in a particular direction.

Mechanical vs Neural Control

These results replicate and add to the recent finding of (Creath, et al., 2005), who showed that the in-phase and anti-phase patterns, corresponding to the ankle and hip strategies, respectively, co-exist during quiet stance. This finding questions the current thinking that these two fundamental patterns of coordination are centrally selected from a set of motor programs (Horak, et al., 1996). Instead, these patterns can be viewed as fundamental modes, either of which may become more prevalent if a perturbation or task excites it preferentially (Alexandrov, et al., 2005). The present results add to this view, showing that the in-phase pattern is more sensitive to sensory information than the anti-phase pattern. This suggests that the in-phase pattern may be more under the influence of neural processes than the anti-phase pattern, whose underlying basis may be primarily due to the biomechanics of the human body approximated as a double pendulum (McCollum, et al., 1989). Recent experiments also provide support for this view. Biomechanical manipulations such as adding weights to the body have proven to influence coherence at frequencies above 1 Hz, where the anti-phase pattern predominates while having little effect on coherence where the in-phase pattern predominates (Elahi, et al., 2005). Moreover, EMG recordings during quiet stance have shown a consistent phase relationship between muscles as well as between muscle activity and limb kinematics at lower frequencies below 1 Hz, but no consistent phase at frequencies above 1 Hz (Saffer, et al., 2005). The lack of coherent EMG activity above 1 Hz suggests a diminished role for active neural control of the anti-phase pattern. Clearly both neural and mechanical processes are important in the control of the in-phase and anti-phase coordination modes

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observed during quiet stance. However, the degree to which such modes of control play a role in each pattern may differ substantially.

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Chapter 4: Postural Coordination Patterns: Visual Rotation and Translation

ABSTRACT

Flow of the visual field is an important component of upright stance control, enabling compensatory corrections to small deviations from vertical. Movement of the visual flow field is typically imposed experimentally as a translation, with the underlying assumption that body sway consists primarily of rotation around the ankle (i.e., inverted pendulum). However, recent evidence has shown that in-phase and anti-phase patterns of trunk-leg coordination co-exist during quiet stance. The co-existence of these coordinative patterns raises the issue of how they interact with the interpretation of visual flow. Thus, we tested whether a single-link or multi-link internal model is used by the nervous system to interpret translatory versus rotary stimuli relative to the ankle and to the hip.

Fifteen healthy adults were exposed to sum-of-sines visual movement, which was either translated in the AP direction or rotated around ankle or hip joint. Results showed that gain and phase between the trunk and leg angles relative to the visual display showed only minor differences between conditions. Phase between trunk and leg angle showed an in-phase relationship at low frequencies and an anti-phase pattern at higher frequencies. The shift in trunk-leg phase was accompanied by a steady decrease in gain in all conditions. These results suggest that coupling of body sway to a visual stimulus is dependent not only on the structure of the optic flow field, but also by coordinative patterns. The coupling between sensory information

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and body sway is highest at low frequencies when the trunk and legs are primarily in-phase. The minor condition effects observed for gain and phase indicate that the nervous system uses an internal model close to a single-link inverted pendulum to interpret visual information. The control strategy tries to align the trunk and leg segment together when making compensatory responses to deviations from vertical.

INTRODUCTION

Human perception and action are mutually dependent (Schöner, 1991), more specifically in the context of visual coupling in postural control: the structure of visual scene affects body sway, which in turn may influence visual perception. In this study, we examined the effect of neural interpretation of visual translation and rotation provided that human body is approximated as a single-link or double inverted pendulum.

Vision can either destabilize or stabilize postural sway depending on the structure of visual scene: a static visual scene reduces body sway, while visual motion enhances it. The "moving room" paradigm, introduced by Lee and Lishman (1975), has been very useful to study visual motion. It is achieved by either physically moving the walls of visual environment or by computer simulating visual motion. The visual optic flow field can be decomposed into different components, such as translation and rotation. By looking at these individual components, we can get an insight into the effect of vision on posture with integrated components.

Previous studies have shown that translatory movement can induce the illusion of self-motion (Lee, et al., 1975), similar to walking by a slowly moving

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train. Peterka and Benolken (1995) compared the rotation (around ankle joint) they used to the small amplitude translational visual surround in the anterior-posterior direction Lee and Lishman used in the 1975, and argued that this translation movement corresponded to a 0.1° visual surround rotation about the ankle joint. However, no evidence was provided for this argument.

Amplitude manipulation is involved in sensory reweighting. Within a certain stimulus amplitude range, there is a linear relationship between visual motion and postural control. As amplitude exceeds saturation, nonlinearity takes place. When the perturbations of vision increased to large amplitudes, healthy subjects were able to down-weight visual information and keep their balance; while bilateral vestibular loss patients increased their sway linearly with the stimulus amplitude (Peterka, 2002).

Frequency manipulation has been used to understand the temporal relationship between postural sway and visual motion (Dijkstra, SchÖner, Giese, & Gielen, 1994). It has become a famous result that phase between body sway and visual motion decreases as the frequencies increase regardless the amplitudes.

The human body is not rigid, but sways in both AP and ML directions. Complications arise considering that upright stance has been approximated as a single inverted pendulum rotating around the ankle joint or a two-segment inverted pendulum rotating around the hip joint. A recent study (Creath, et al, 2005) showed that the ankle and hip synergies co-exist during quiet stance. Which one of these synergies predominates depends on the sensory information and task constraints (Creath, et al., 2005). More recently (Zhang et al., 2005), we asked how addition or removal of sensory information affects these two synergies. The subjects were

instructed to either open eyes looking at a static visual scene or close eyes with or without light touching (< 100g) a touch bar. The relationship between upper and lower body was mainly demonstrated by calculating coherence between leg and trunk vertical angles. Addition of vision decreased the trunk-leg coherence at low frequencies.

In the current study, we investigated whether coupling to a visual stimulus depends on the structure of the visual flow field. Comparison between visual rotation and translation will be provided. Rotation is compatible when we consider the body as a single inverted pendulum. Furthermore, the co-existing coordination pattern makes a rotary visual signal inadequate, a rotation around the hip is needed. Also, we want to know how the nature of the optic flow influences postural coordination patterns. Two alternative hypotheses are promoted.

Two alternative hypotheses

In the first hypothesis, a multi-link (trunk and legs) internal model of the body is used by the nervous system to interpret visual information. A control strategy attempts to align both the legs and the trunk with respect to the vertical. That is, these two segments respond to the visual information separately. For example, if the nervous system interprets a visual motion around the ankle joint as a self-motion in the opposite direction, then both the trunk and the legs segments will actively try to return to vertical and the body behaves as a single inverted pendulum. If the nervous system represents a visual motion as self-motion around the hip joint, in this case, because the legs are defined as in vertical, the nervous system will only correct the movement of the trunk and the body rotates around the hip joint. In a third case, if the

visual motion is translated in the anterior-posterior (AP) direction, then the trunk is "thought" to be vertical and translating with the legs moving to compensate for this translation. As a result, the legs are activated to adjust for this translation movement.

However, this is not the only possible way that the nervous system responds to these visual stimuli. In the alternative hypothesis, a single link (ankle) internal model of the body is used by the nervous system to interpret visual information. A separate control strategy, one not dependent on visual information, attempts to align the two segments with each other. As a result, no matter the visual stimulus is rotated around the ankle or hip joint, or translated in the AP direction, the nervous system interprets it as rotation around the ankle joint and the body behaves as a single inverted pendulum. Predictions are made according to these hypotheses.

Predictions

It has been reported that body sway is influenced by visual scene velocity rather than position (Kiemel, Oie, & Jeka, 2006; Sch¨oner, 1991; Dijkstra et al., 1994; Jeka, Oie, & Kiemel, 2000). However, in order to compare results in the literature, position displacements are used in calculation. Furthermore, as an inverted pendulum, the velocity of displacement precedes the position of displacement for 90 degrees. As a result, a 90-degree phase lead between the body segment with respect to the visual scene in terms of position corresponds to an in-phase relationship in terms of velocity. The segment (trunk or legs) that is actively catching the visual stimulus should have a 90-degree phase lead and high gain with respect to the visual motion. For the reason of simplicity, the phase and gain between leg/ trunk segment and visual motion will be called phase and gain of leg/trunk respectively. Three visual conditions will be

tested in this study: 1 = rotation around ankle joint; 2 = rotation around hip joint; 3 = translation in AP direction. All the predictions focus on behaviors at low frequencies.

Predictions for the First Hypothesis. For the first hypothesis, if the visual motion is interpreted as a rotation around the ankle joint, both leg and trunk are predicted to have a 90-degree phase lead and high gains. If the visual motion is interpreted as a rotation around the hip joint, the trunk is predicted to have a 90-degree phase lead and high gain for trunk.

Condition	phase	gain
1	90 degree for both leg and trunk w.r.t visual scene	High gain for both
2	90 degree for trunk w.r.t visual scene	Higher gain for trunk Lower gain for leg
3	90 degree for leg w.r.t visual scene	Low gain for trunk High gain for leg

Table 4.1. predictions for the first hypothesis

Leg gain will be low and hence the phase relationship is not considered. If the visual motion is interpreted as a translation in the AP direction, leg angle will have a 90-degree phase lead and high gain, while the trunk angle will have low gain and phase cannot be reliably estimated. Please refer to table 1 for a summary of these predictions.

Prediction for the Second Hypothesis. For the second hypothesis, if the visual motion is interpreted as a rotation around the ankle joint, then both trunk and leg are predicted to have 90-degree phase lead and high gain. For visual motions that are interpreted as rotation around the hip joint and for translation in the AP direction, both legs and trunk will have low gain, therefore, phase relationships cannot be reliably estimated. As an inverted pendulum rotating around ankle joint, the phase

relationship between leg and trunk angles will be in-phase. Please refer to table 2 for

a summary of these predictions. .

Condition	phase	gain
1	90 degree for both leg and trunk w.r.t visual scene	High gain for both
2	Legs and trunk are in-phase	Low gain for trunk Low gain for leg
3	Legs and trunk are in-phase	Low gain for trunk Low gain for leg

Table 4.2. predictions for the second hypothesis

METHODS

Subjects

15 subjects (9 males, 6 females) at the University of Maryland, aged 19 – 30

(mean age 21±3), participated in this study. The procedures used in the experiment

were approved by the Institutional Review Board at the University of Maryland. All

subjects received instructions for the test procedures. Informed written consents were

obtained from all participants in the study. All the subjects were physically active,

with no known musculoskeletal injuries or neurological disorders that might affect

their ability to maintain balance.

Procedures

Apparatus. A visual cave consists of three screens (Fakespace, Inc,

Marshalltown, Iowa, USA): one in the middle, two on either side with seamless

corner technique was used in this experiment. Subjects were placed in the middle of

the visual cave facing the font screen at a distance of 3.5 feet and equivalent distance

to both sides. The visual display was projected by JVC projectors (Model: DLA-

M15U, Victor Company of Japan, Japan) to three mirrors, which reflected and rear-projected to the screens. Each screen consisted of 500 white small triangles on a black background. The triangles were randomly rotated with 3.4x3.4x3 cm on each side. No triangles were displayed within about a horizontal band of ±5 degree in height about the vertical horizontal of the subject's eye height. This procedure can reduce aliasing effects in the fovea region. The visual display was written by using CaveLib software (Fakespace, Inc). The frame rate of the visual display is 60 Hz.

Kinematics information of the subjects was captured by Optotrak (Northern Digital, Inc., Waterloo, Ontario, Canada), an active infrared position tracking system. The Optotrak uses a bank of three cameras, which were placed behind subjects to measure movements of the markers. The shoulder (the scapula), hip (the greater trochanter), knee (the lateral femoral condyle) and ankle (the lateral malleolus) were measured by attaching four LED markers on the right side of the subject. The markers were sampled at 60 Hz. Three markers were placed on a 6x6x6 cm triangle board with one marker on each corner. The triangle board was then attached on the subject's head with the center pointed to the inion. Another three markers were put on the fixed platform, which the subjects stood on, aligned the corner facing the cameras and used as a reference to check the data.

Design. An assumption of the experimental design is that the amplitude of visual flow at eye height determines the postural response. This assumption means that amplitude of visual flow at eye level was scaled in the translation and hip joint conditions to be equal to the ankle joint condition. Without this assumption, calculation of gain across conditions is problematic. First, the signal in the translation

condition is in units of cm, leading to a dimensional gain, while gains in the other two conditions would be dimensionless. Second, because the distance from hip to eye is shorter than ankle to eye, rotation angle at eye level in the hip joint condition would be smaller for a given rotation. This would artificially inflate gain in the hip joint condition.

Subjects were exposed to a sum-of-sines signal: U(t), which was either translated in the AP direction or rotated around the ankle or hip joint. Rotation around ankle was used as the reference condition and the other two conditions were scaled accordingly to maintain an equivalent amplitude of visual flow at eye height in each condition. The sum-of-sines signal consisted of 10 sinusoids, with a vector of frequencies (in Hz) defined as:

$$f = (3; 7; 13; 23; 43; 73; 113; 179; 263; 367)/125$$

The numbers in the bracket are cycles that repeat in 125 seconds. Prime numbers insured no common low-order harmonics. The resulted frequencies ranged from 0.024 to 2.936 Hz as prime multiples of a basic frequency of 0.008 Hz. To maintain the same peak velocity across frequency, the amplitudes (A) of the sinusoids were defined as the inverse of frequencies: A divided by f. In a previous experiment (Kiemel, et al., 2006), A was equal to 0.05 cm for the low amplitude condition. Based on the average eye height and ankle height of the subjects and approximating the amplitude as the rotation arc, rotation amplitudes were converted to degrees with A = 0.02. For the last 2 sinusoids, the amplitude of the eighth sinusoid was used due to previous results which showed gains that were not significantly different from 0 at the same two frequencies (Oie et al., in prep). The sum-of-sines signal had five (even)

zero-phase and five (odd) 180 degrees phase-lead sinusoids, so that the summation of

the sinusoids started at zero-phase without a large change in phase at the beginning of

the trial. For the rotation around the hip condition, the rotation origin was the hip joint

and the signal was: U(t) x ((eye height – ankle height) / (eye height – hip

height)).The translation signal was scaled as: U(t) x ((eye height – ankle height) x 2π
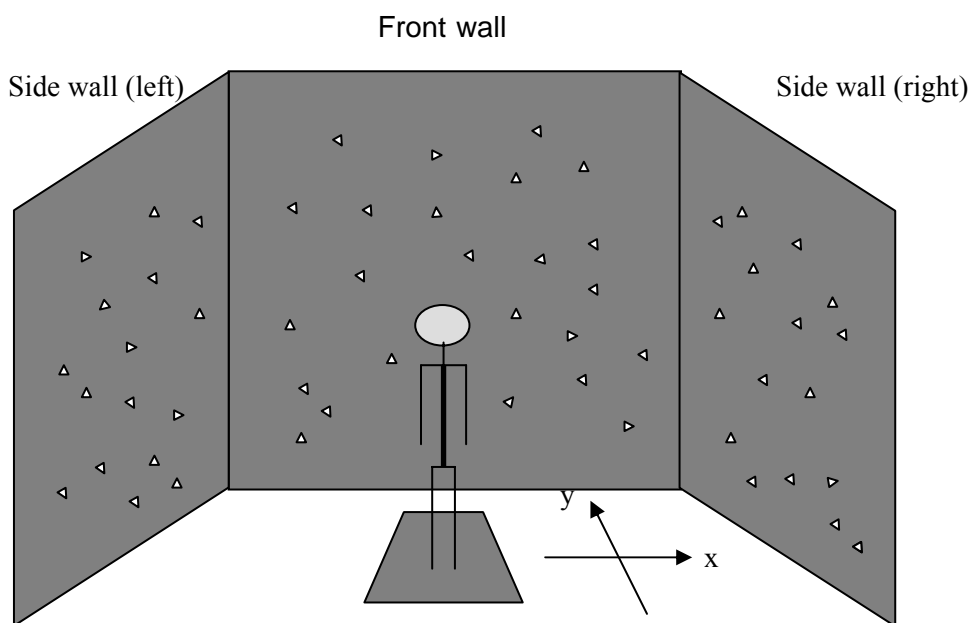
/ 360).

a

Figure 4.1. Visual stimuli. a) Experimental setup: the subject was placed in a visual cave consisting of three walls. The subject stood on a fixed platform with his/her ankle joint 1.16 m and 1.07 m from the front (y) and side (x) screens, respectively. b – e) Visual stimuli viewed from the left side wall. The triangles on the wall were moving as a whole around an axis (white dash lines) collinear with the subject's ankle joint. Three triangles are shown at the subject's eye height, hip height and ankle height to illustrate the movements of all triangles. b) The initial positions of the triangles. c) Translation; d) Rotation around ankle e) Rotation around hip. Note that the rotation angles are exaggerated to show differences between conditions.

All 12 trials were randomized in blocks for individual subjects with each of these conditions appearing once in each block, four trials per condition. Each trial was 260 seconds including two cycles of the sum-of-sines movements and 5 seconds of quiet stance at the beginning and end. Body sway was analyzed only during visual movement.

Subject stood with feet apart at a distance of 11% of her/his height between the toes and an angle of 14 degrees between the mid line and each foot on a fixed platform (McIlroy, et al., 1997). Ankle height was measured as the vertical distance between the sole of subject's foot and ankle (the lateral malleolus); hip height was measured as the distance between the sole of the subject's foot and hip (the greater trochanter); eye height was measured as the distance between the sole of the subject's foot and eyes (paropia). The subjects began each trial by looking straight ahead at the visual display with their arms crossed at their chest. Between trials, the subjects were required to sit down for at least 2 minutes to reduce fatigue. All the subjects finished the experiment; one trial and one cycle of the rotation around the ankle condition were discarded due to technical difficulty.

Analysis. The trunk and leg segment were assumed to lie on the line connecting the shoulder and hip and the hip and ankle markers, respectively. The knee marker was ignored based on the previous study showed that knees are static during quiet stance (Alexandrov, Frolov, & Massion, 2001). Trunk and leg angle with respect to vertical were determined by the AP and vertical displacement of the shoulder, hip and ankle marker. We used the average of the three head markers to represent the head displacement. The shoulder and hip marker were used directly for shoulder and hip displacement respectively.

The frequency-response function (FRF) at the stimulus frequency was computed as the Fourier spectra of the time series of output signal divided by the Fourier spectra of the stimulus: U(t), the signal used in the rotation around ankle condition. The output signals used included trunk/leg angle and displacements of head, shoulder and hip. Gain and phase was calculated as the absolute value and the argument of the FRF. A unity gain means the magnitude of body sway at the driving frequency exactly matches the magnitude of the visual motion. A positive phase means that the body segment is leading the visual motion.

Because a large range of stimulus frequencies was probed simultaneously, responses at extremely low or high frequencies tended to have low power. The result is low gains that are centered close to the origin in the complex plane, which can lead to large differences in phase from trial-to-trial because of measurement error. Consequently, two mean values of gain and phase are relevant. Group gain/phase refers to extracting the gain/phase from the average FRF calculated across subjects in a given condition. Mean gain/phase is calculated by averaging gain and phase

extracted from single trial FRFs across subjects. Based on the assumption that the real and imaginary parts of the FRFs have a bivariate normal distribution, we used F statistics to see if the FRFs are significantly different from zero. A significant difference means that the responses are detectable. FRFs of each driving frequency and condition from all the subjects were plotted in the complex plane to determine if all values were roughly in a 90-degree range. If so, then group gain-phase and mean gain-phase are approximately equivalent. If not, then only frequencies that encompass the 90-degree range were used.

Cophase between trunk-leg at the driving frequencies was computed as leg phase minus trunk phase. A positive phase means the leg segment leads the trunk segment. Power spectrum density (PSD) of the trunk/leg segment and cross spectrum density (CSD) between trunk and leg segment were calculated using Welch's method. Complex coherence was computed as CSD divided by the square root of the product of trunk and leg PSDs for each trial. Coherence (also called magnitude squared coherence) was extracted as the absolute value of mean complex coherence averaged across subject at each driving frequencies. Non-driving-frequency cophase is the argument of complex coherence averaged across trials and subjects. Coherence and cophase between hip-shoulder and head-shoulder were calculated in the same manner.

Statistics. Phase and the log of gain was analyzed with a Segment x Condition x Frequency repeated-measure ANOVA analysis with Greenhouse-Geisser adjust P value for both trunk/leg angle and displacement of head, shoulder and hip. The use of log transformation for gain reduced the skewness. Follow-up paired t-test was applied

to perform the paired comparison. A frequency x condition repeated-measure ANOVA with Greenhouse-Geisser adjust P value was used to analyze coherence at the driving frequencies.

For the non-driving-frequency gain and phase, because the frequencies adjacent to the driving frequency (i) may be contaminated, an average of the complex coherence of the i-2th and i+2th frequency is used to compare with the ith driving frequency. The same method applied for FRF is used here.
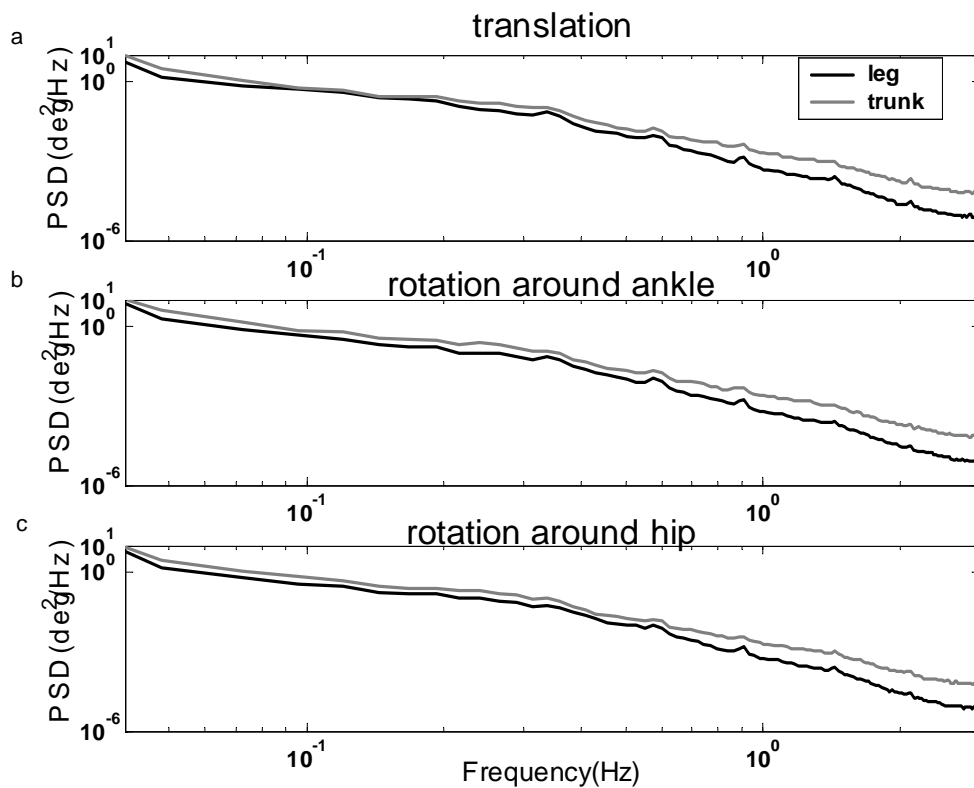
RESULTS

Figure 4.2. PSDs average across subjects.

PSDs. Figure 4.2 shows the power spectrum density (PSD) of trunk and leg segment average across subjects. PSDs for both segments decrease from

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approximately10 to 10^{-5} (degree^2/Hz) across frequencies. Furthermore, although

responses to the visual stimulus are detectable across frequencies, FRFs plotted in the

complex plane showed that phases for subjects at the $2^{nd} - 7^{th}$ frequencies were in an

approximate 90 degrees range, suggesting consistent responses, while phases at the

1st and highest three frequencies were in a range greater than 180 degrees, indicating

unreliable responses. Thus, the analysis focused on the $2^{nd} - 7^{th}$ stimulus frequencies.

Gain of Trunk/leg angle. Figure 4.3 shows mean gain and phase for both leg

and trunk segment relative to the visual movement. Gains are small at low

frequencies, rise gradually to a much higher level, typically reaching a peak at the

fifth frequency (0.344 Hz), then decrease more abruptly and arrive at values that are

lower than the first frequency. All the gains are significantly different from zero ($P <$

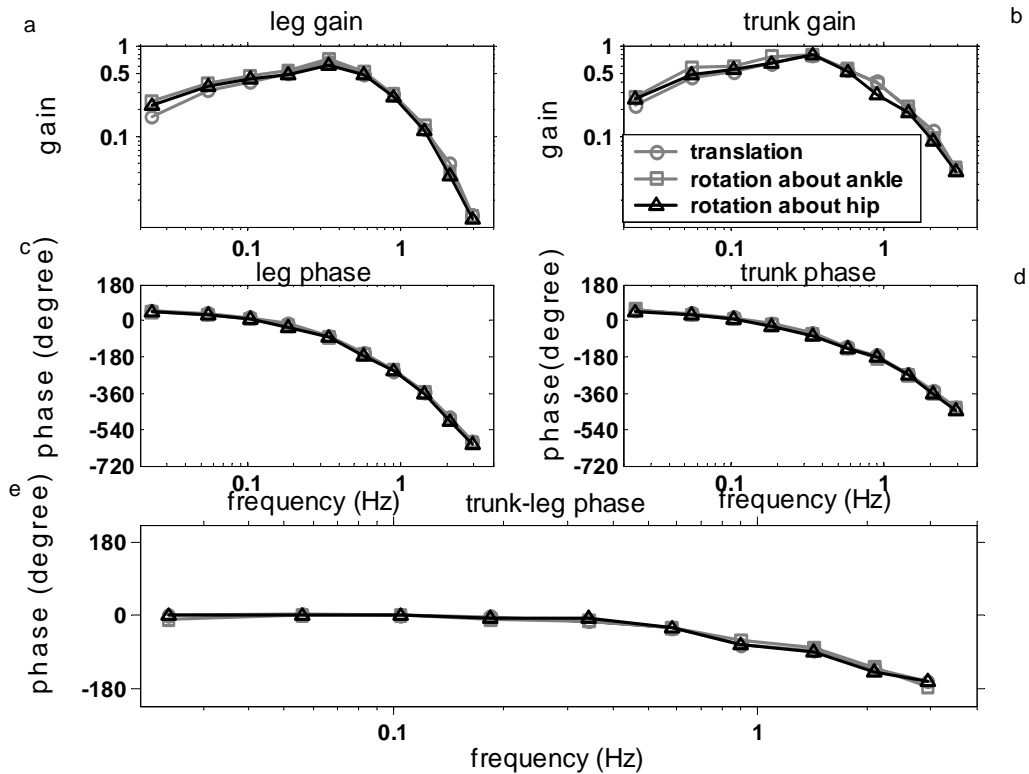0.05). For most of the subjects, the peak gain is greater than 0.5.

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Figure 4.3. group average of gain, phase and trunk-leg phase. a) and c) are gain and phase for the leg segment; b) and d) are gain and phase for the trunk segment. e) is the trunk-leg cophase.

There was significant segment x condition effect on gain ($P = 0.0325$, MANOVA). Follow-up paired t-test revealed that trunk gain was significantly different between translation and rotation around ankle at the 2nd, 4th and 5th frequency. No effects for gain were observed for the leg segment.
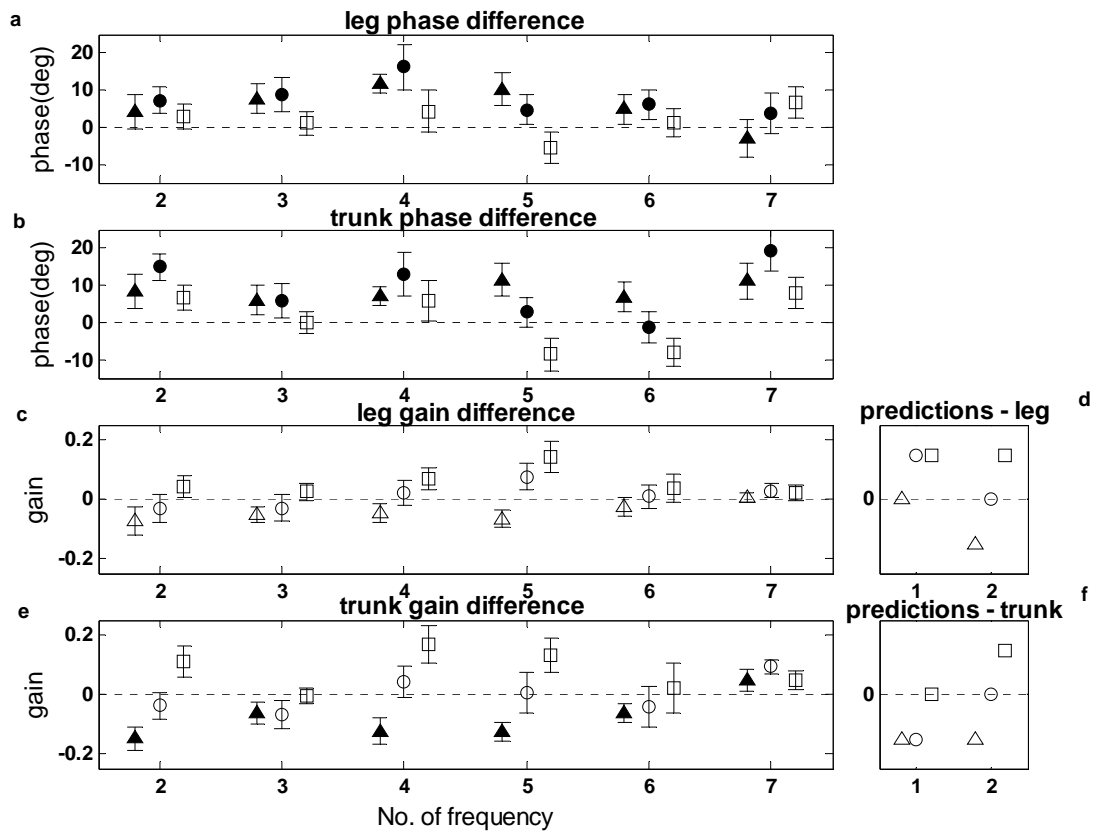

Figure 4.4. Phase and gain differences between conditions. The triangles (Δ) represent the differences between translation and rotation around ankle; the circles (O) are the differences between translation and rotation around hip; the squares ($\square$) show the differences between rotation around ankle and rotation around hip. The pairs with filled markers were significantly different from each other. For both a) and b), translation has higher phase than the two rotation conditions. For e), rotation around ankle has higher gain than translation. d) and f) are predictions for the first

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and second hypothesis (y axis). If the pairs are not different from each other, then the value is on the zero line; a value above or below the zero line represents the first condition of the pair has a higher or lower gain than the second condition.

Phase of trunk/leg angle. Consistent with previous studies, the phase of both leg and trunk segments with respect to the visual scene decreased as frequency increased for all the conditions. In general, an approximate 90-degree phase lead is seen at the first one or two frequencies. The phases then decreased below 0 degrees at higher frequencies, indicating a phase lag between the body segments and the visual scene. A segment x frequency interaction effect ($P = 0.0052$, MANOVA) and main condition effect ($P = 0.0066$) were found. Follow-up paired t-tests showed that differences existed for pairs: translation and rotation around ankle, translation and rotation around hip for both segments. Figure 4.4 shows the phase and gain differences for condition comparisons. The pattern of gain difference is consistent with predictions for the second hypothesis – a single-link internal model for both trunk and leg segment: rotation around ankle has higher gain than both translation and rotation around hip condition, with the difference between translation and rotation around hip small.

Gain of Displacement. Gain for displacement of head, shoulder and hip reflect their geometric positions with hip gain the lowest and head gain the highest at the low frequencies (Figure 4.5). This was confirmed by a main Condition effect ($P = 0.0022$). However, gain at the high frequencies merge close to each other, supported by a Segment x Frequency effect ($P = 0.0020$).

Phase of Displacement. A Segment x Frequency ($P = 0.0142$) and main

Condition effect was found for phase ($P = 0.0004$). These results are further explored
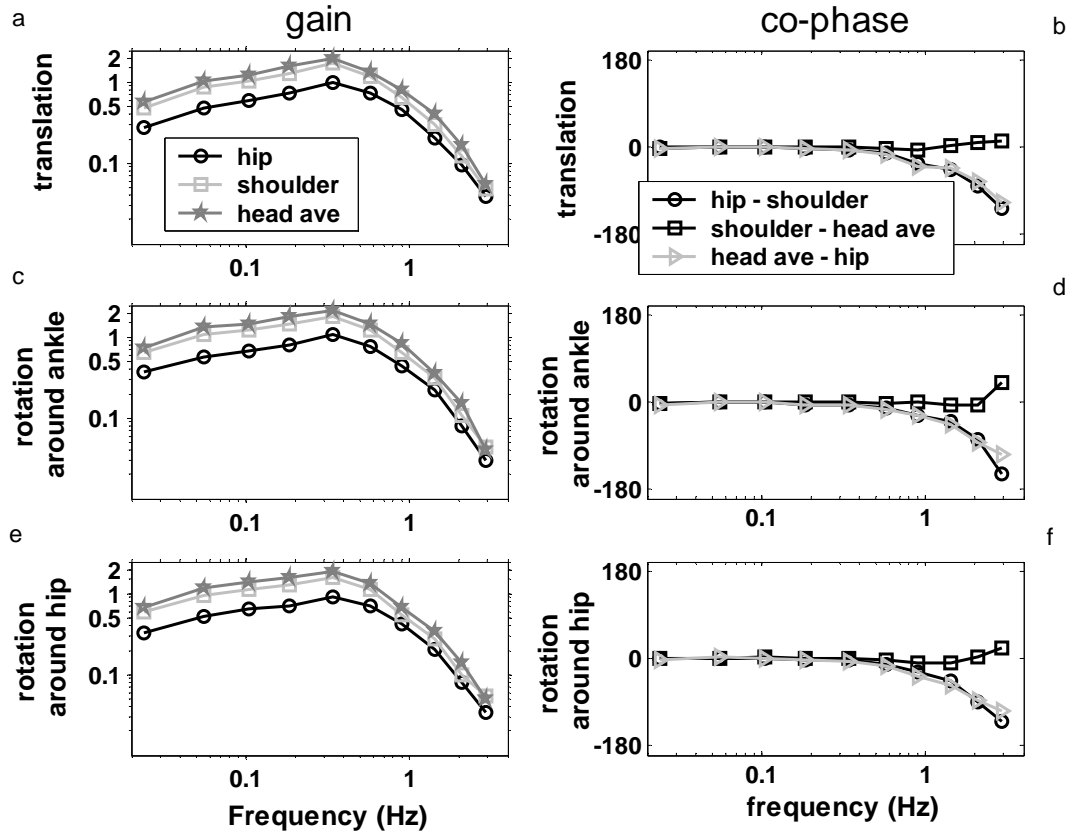
in terms of cophase below.

Figure 4.5. (a, c, e) Gain and (b, d, f) cophase for head, shoulder and hip displacement. At low frequencies, head, shoulder and hip are in-phase. At higher frequencies, head and shoulder were in-phase, while the hip lagged both the head and shoulder.

Trunk-leg Coordination. Trunk-leg cophase, shown in Figure 4.6, for all

three conditions was approximately 0 degrees at low frequencies up until the fifth

frequency (0.344 Hz) and then gradually decreased at the high frequencies towards

180 degrees, with the trunk leading the leg segment. Non-driving-frequency trunk-leg

cophase was in-phase at low frequencies and anti-phase at high frequencies. No

Condition effect was found for coherence.

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Displacement cophase, shown in Figure 4.5, indicated that head and shoulder were in-phase across frequencies. Hip was in-phase with both head and shoulder at low frequencies, but lagged behind them at high frequencies.
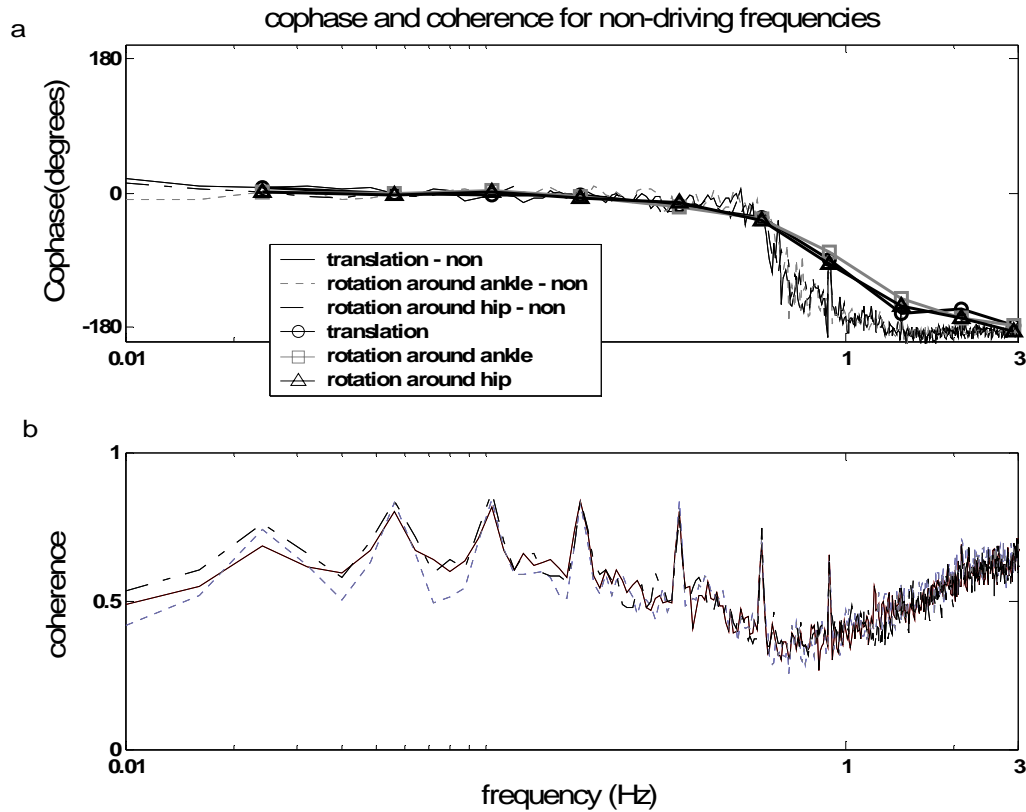

Figure 4.6. Cophase and coherence at the non-driving frequencies. The lines without markers are for non-driving frequencies (a&b).

Cophase at the driving frequencies and non-driving frequencies were different at the 7th, 8th and 9th frequency ($P < 0.05$). Coherence was different at the first 7 frequencies ($P < 0.05$).

DISCUSSION

We tested whether a single-joint or multi-joint internal model of upright stance is used to interpret different types of visual flow. The visual signal was either translated in the AP direction or rotated around subject's ankle or hip joint in three separate conditions. Systematic gain and phase changes were found for both the trunk and leg segments relative to visual movement. However, only minor differences were observed as a function of the visual display structure. Such results support the second hypothesis: a single-link internal model is used by the nervous system to interpret visual motion with the trunk and leg segment aligned to each other.

A Single-link Internal Model

The key of our second hypothesis is that the nervous system uses a single-link internal model interpretation in all the conditions. Our prediction was based on extreme situations. Therefore, if only small deviations from the prediction were found, our hypothesis is still supported. The first support comes from the results that the pattern of gain difference for both segments is coherent with predictions of the second hypothesis (Figure 4.4). With a single-link internal model, one would expect gains in the rotation around ankle higher than translation and rotation around hip condition for both trunk and leg segment. Because both translation and rotation around hip condition have low gains, the differences between these two conditions would be small. Moreover, phases for all conditions at the first one or two frequencies have a 90-degree phase lead between body segment position and visual motion. This is consistent with our prediction for the second hypothesis that body segment leads the visual scene for 90 degrees at low frequencies. Further and more direct evidence

comes from trunk-leg phase: the trunk and leg were in phase at low frequencies. That is, the body uses a single-link inverted pendulum.

The common view of motor control is that the nervous system tends to use simple interpretations to control the motor system, especially when ankle and hip synergies are used to explain sensory coupling. For example, somatosensory and vestibular information is important for ankle and hip synergy, respectively. Somatosensory loss subjects showed only hip synergy, while bilateral vestibular loss patients showed only ankle synergy when the subjects were exposed to perturbed surface (Horak, Nashner, & Diener, 1990). The argument was that this behavior is related to the sensor locations. The implicit assumption is that the nervous system controls the trunk and leg segment separately when responding to perturbation. That is, sensors of vestibular information are located in the head; the loss of vestibular information makes control of the trunk segment impossible so that only the leg segment is controlled. Likewise, proprioception comes from feet and is related to the ankle synergy. However, our results suggest that the subjects always tried to align these two segments together when responding to either visual rotation or translation. Although this is far from conclusive that vestibular and somatosenosry information would have the same impact, it indicates that the nervous system may try to control human body as a whole when responds to visual perturbation.

A single-link model has an advantage for feedback control: it reduces time delay, which is usually considered as a constraint for feedback control. A long time delay might destabilize the system. The more degree of freedom the nervous system needs to control, the more time delay. A single-link model simplifies the segments

needed to be controlled. The control strategy may try to align both segments together when respond to the visual motion. For example, tonic muscle activity might be used to create stiffness and damping at the hip. This adds to the view that although an ankle synergy is more energy efficient, trunk vertically may have precedence (Horak, et al., 1996).

Coexisting Postural Coordination Patterns

Coexisting postural coordination patterns were found: phase between the trunk and leg segment was around 0 degree at low frequencies and gradually increased towards 180 degrees at high frequencies, consistent with previous study (Creath et al., 2005). This coexisting pattern argues against the generally accepted view that the ankle and hip synergies are centrally selected before the perturbations based on current sensory information and prior experience (Horak et al., 1990). Different sensory information manipulations and patient population showed consistent co-existing coordination pattern from studies in our lab: platform sway-referencing, foam surface (Creath, et al., 2005), light touch and bilateral vestibular loss patients (Zhang, et al., 2005). Furthermore, mechanical manipulation by adding weights to the subjects didn't change the pattern either (Elahi, et al., 2005). These results replicate the view that the ankle and hip synergies are basic coordination patterns, the predominance of which depends on the sensory information available (Alexandrov et al., 2001).

Non-driving-frequency cophase and cophase are different at high frequencies. Non-driving-frequency cophase changed abruptly from in-phase; while cophase decreased gradually and did not reach 180 degrees at the highest frequency. Some

studies in our lab have shown this different transition from in-phase to anti-phase between conditions (i.e., Creath, et al., 2005) or direction (i.e., Zhang et al., 2005). The mechanism is not yet clear and a model is needed.

Associated with the shift in trunk-leg phase above approximately 0.6 Hz was a steady decrease in gain for all the subjects in all the conditions. Gains increased gradually at the low frequencies and usually reached a peak at the fifth frequency, where the trunk-leg phase started to shift from in-phase and gradually changed to anti-phase. These results suggest that coupling of body sway to a visual stimulus is dependent not only on the structure of the optic flow field, but interacts with the coordinative patterns that may reflect biomechanical constraints (Creath et al., 2005; Zhang et al., 2005).

The cophase of head, shoulder and hip displacement confirmed that trunk and head moved in the same direction and in opposite direction to the hip at the high frequencies. The anti-phase relationship of head and hip at the high frequencies emphasized the view that head actively tracking visual information, thus leading the whole trunk segment counter-rotating with the hip in a hip synergy (Horack, et al., 1996).

Visual Rotation and Translation

As mentioned before, Peterka et al. (1995) stated that visual translation and rotation have the same influence on postural sway without providing evidence. The logic was that the arc of rotation could be approximated to the translation amplitude mathematically. In order to test this, we kept the amount of stimuli the same at eye level. As part of the experiment, we asked subjects if they detected how the visual

display was moving and the difference between conditions after they finished the trials. None of our participants was able to tell how many conditions were in the experiment, not to mention the difference between conditions. The only main Condition effect for gain was found between translation and rotation around ankle in the trunk segment. Phase differences between these two conditions were found for both the leg and trunk segment. As a result, although these two conditions are mathematically the same, one needs to be cautious when it comes to neural representation of these two visual motions.

There is the possibility that lack of differences between conditions were due to lack of power to detect significant differences. However, this possibility seems unlikely. First, pilot data showed that 15 subjects have enough power to detect differences. Second, gains were significantly different from zero across all the frequencies with peak average gain close to 1. Results showed main condition effects for gain in the leg segment and phase in both segments. Phase differences of approximately 20 degrees were found to be significant, indicating enough sensitivity to detect even small differences.

CONCLUSION

The current study emphasized the human body as an inverted pendulum in response to visual motion. Our results support the hypothesis that a simple strategy of single-link inverted pendulum is used to interpret visual motion at low frequencies. This was supported by: 1) the pattern of gain difference between conditions is consistent with predictions of the single-link model hypothesis; 2) an in-phase

relationship between trunk and leg angle at low frequencies. The control strategy

aligns the trunk and leg segment together while the nervous system tries to

compensate deviation of the body vertical. The co-existing coordination patterns

argue against the view that ankle and hip synergies are centrally selected. Small gain

difference showed between translation and rotation around ankle brings caution to the

argument that translation and rotation are equal.

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