ABSTRACT

Title of Dissertation: CHARACTERIZING SENSORY RE-WEIGHTING FOR
                           HUMAN POSTURAL CONTROL

                           Kelvin Shigeyuki Oie, Doctor of Philosophy, 2006

Dissertation directed by: Professor John J. Jeka, Program for Neuroscience and
                           Cognitive Sciences and the Department of Kinesiology

In order to survive in the wide range of sensory contexts that comprise our physical world, the nervous system employs adaptive mechanisms that optimize functional behaviors within a given sensory environment. Human bipedal stance control requires that the nervous system obtain relevant information about the environment and the body's relationship with it from multiple sensory systems. How does the nervous system accomplish this when the sensory environment compromises the information available from a given sensory system?

In previous theoretical and empirical work, we have provided evidence of nonlinearities that are consistent with an hypothesis of sensory re-weighting: The nervous system adapts to changing sensory contexts by decreasing its dependence, or weighting, on the compromised system and increases its weighting of other inputs. This thesis presents empirical findings that further support the sensory re-weighting hypothesis and further efforts towards characterizing sensory re-weighting by providing empirical results that provide important constraints on any proposed sensory re-weighting scheme.

First, postural responses to complex visual motion consisting of the sum of 10 different sinusoidal components, were measured at two different amplitudes. Changes in the gain of body sway to visual motion were consistent with the nonlinearities previously interpreted as evidence for sensory re-weighting. Further, the observed changes in gain did not vary significantly as a function of stimulus frequency. Second, we found evidence indicating a temporal asymmetry in the sensory re-weighting process dependent upon the direction of the change in stimulus motion amplitude: the change in postural response is faster to a rapid increase versus decrease in stimulus amplitude. This temporal asymmetry was interpreted functionally: an increase in visual environmental motion may threaten balance, requiring a rapid down-weighting of vision if a strong dependence upon visual information would increase postural response beyond the stability boundaries of stance. Conversely, if stance is already stable in the face of large visual motion amplitude, a decrease in motion amplitude does not threaten balance and adapting rapidly to the new sensory conditions is not critical to avoid falling.

CHARACTERIZING SENSORY RE-WEIGHTING FOR

HUMAN POSTURAL CONTROL

by

Kelvin S Oie

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Advisory Committee:

Professor John J Jeka, Chair
Professor Jane E Clark
Professor Timothy Horiuchi
Professor Norbert Hornstein
Doctor Tim Kiemel

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TABLE OF CONTENTS

LIST OF FIGURES

Chapter 1: A Review of the Literature

It is common for authors, in justifying their investigations examining human postural control, to refer to statistics that reflect the costs to the health care system due to injuries resulting from falls. Indeed, the costs are high. Loughlin and Redfern (2003) state that costs due to injuries from falls are second only to injuries resulting from automobile accidents, while Maki et al., (2003) report that falls result in approximately 300,000 hip fractures per year in the United States alone, with associated costs of $10 billion. Therefore, improving our understanding of ability to maintain postural stability, as well as what factors and disorders affect this ability and may put individuals at heightened risks for falls has both pragmatic, economic value, and obvious clinical relevance.

However, the study of postural control and, in particular, our ability to maintain an upright standing position is important in its own right as a platform for understanding sensorimotor integration and multisensory processing in the human nervous system. As we will detail, the maintenance of upright stance control is considered as a complex, feedback control process that involves the integration of sensory inputs from multiple systems, in particular, the visual, somatosensory and vestibular systems. We are

interested in understanding and elucidating the mechanism(s) by which the human nervous system is able to utilize information about the body's configuration and its relationship to the environment obtained by these different sensory systems to produce a functional behavior such as upright standing.

As Gagey (2003) points out, scientific interest in the control of upright stance stretches back to as early as Sir Charles Bell in 1837. Further, the first published recordings of the behavior we now call postural sway were likely to have been made by von Vierordt (c. 1860). Since that time, a vast literature encompassing both experimental and conceptual investigations of how we maintain stance has been developed that has shown the remarkable complexity underlying this quite fundamental sensorimotor behavior.

Over the past several years, we have contributed to this dialogue in a series of studies aimed at identifying 1) the properties of sensory input that are relevant for postural control, 2) the non-linear nature of postural sway under different sensory conditions, and 3) a potential mechanism for multisensory integration in postural control, sensory re-weighting (cf., Jeka et al., 2000; Kiemel et al., 2002; Oie et al., 2001, 2002; Ravaioli et al., 2005). Sensory re-weighting is the idea that the nervous system is able to adaptively change its reliance upon a given sensory input depending upon current sensory conditions. For example, in a dark room, information about our visual environment, which is known to be used in controlling stance, is no longer available. Under such conditions, it is thought that the dependence upon vestibular and somatosensory information can be increased, and the dependence on visual information decreased, in order to maintain upright standing. However, that sensory re-weighting occurs has only

recently been more rigorously demonstrated (cf. Oie et al., 2002) and the mechanisms by which re-weighting may occur remain to be elucidated.

The goals of this thesis, then, are 1) to obtain empirical results that identify how human postural responses reflect the re-weighting of sensory information for the control of upright stance 2) to discover constraints upon any potential re-weighting mechanism 3) with the aim of providing an initial characterization of sensory re-weighting that will inform future models of the human postural control system. One of the important current objectives in the field of postural control is to provide a model of the human postural control system that identifies and implements the underlying mechanisms involved in this complex sensorimotor behavior. Sensory re-weighting is one such mechanism, and characterizing how sensory re-weighting affects postural sway behavior, and how fast it does so, will be an important step in achieving the aim of a complete mechanistic model of human postural control.

In the following literature review, we will examine a number of studies that demonstrate the various influences that the multisensory inputs to the postural control system – namely, visual, vestibular, somatosensory and proprioceptive – have upon experimentally observed postural sway behavior, and we will frame the various lines of argument that have suggested the need to include a sensory re-weighting mechanism in potential models of posture.

What is postural sway?

To begin, let us first consider what we mean by 'postural sway.' As we have mentioned above, perhaps the earliest measurements of what we call postural sway were made in the mid 19th century by Karl von Vierordt (1860/1877). His equipment was

crude: A paintbrush was affixed to the peak of a helmet and was used to scratch out a figure on a glass plate covered in lampblack that was situated above the subjects' heads. They were asked to maintain several different body configurations including different upright bipedal stances, standing on one leg and sitting in a chair. While we might consider these methods and his subsequent analyses rudimentary by today's standards, the irregular patterns of bodily motions (see Figure 1.1 for a more modern example) recorded in these studies already identified: 1) a crude approximation of a measure still used in some forms today, sway area (e.g., Chiari et al., 2002; Prieto et al., 1996), which quantifies the two-dimensional area over which the subject's body moves in space, 2) that closing one's eyes can lead to an increase in sway area, and 3) that different stance configurations can induce increases (e.g., standing on one leg) or decreases (e.g., sitting) in sway area.

In Figure 1.1(A-C), we see an example of a typical postural sway trajectory of the estimated total body center of mass of a healthy, young adult subject standing quietly with feet parallel and eyes closed. It is well established, and one can plainly see, that the sway associated with upright stance is characterized by continuous deviations within a limited spatial range rather than the maintenance of a fixed or static position. Such motions would be similar to what von Vierordt observed almost one and one-half centuries ago. Of course, the methods that we use in measuring postural sway behavior and the variables that are used to describe it are at least somewhat more refined, and certainly more numerous, today.
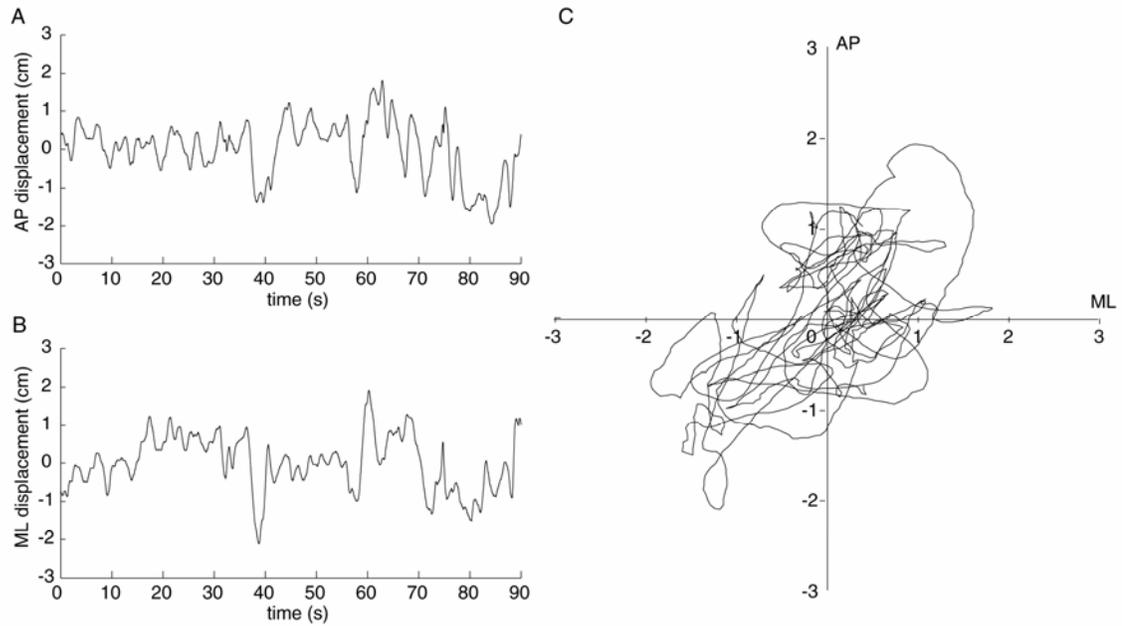
Figure 1.1. Examples of estimated center-of-mass postural sway trajectories. Data were collected using an OptoTrak motion capture system and the position of the total body center of mass was estimated from a three-segment model (Winter, 1991) at each time sample for A) anterior-posterior and B) medial-lateral directions, with the mean subtracted from each trajectory. The resultant planar trajectory is presented in C). [Unpublished data.]

The most common method of measuring the sway associated with upright standing has been by recording the horizontal and vertical ground reaction forces applied by a subject's feet upon an instrumented force platform and computing the position of the center of pressure (CoP) applied at the feet upon the support surface as the resultant of all ground reaction forces at a given time (e.g., Bronstein et al., 1990; Winter et al., 1996, 2003). Alternatively, other authors have used numerous other measures to capture sway, for example: total body center of mass (CoM) either estimated as a single point (e.g., Jeka et al., 1998a,b; Black et al., 1988) or from a multi-segment model (e.g., Gu et al., 1996; Winter et al., 2003; Ravaioli et al., 2005)(see also, Figure 1.1, above), changes in the angle at the ankle (e.g., Fitzpatrick et al., 1996; Kavounoudias et al., 2001; Rogers et al., 2001), spatial positions of the head or other body landmark (e.g., Black et al., 1988;

Dijkstra et al., 1994a; Keshner et al., 1987) to name a few. These measurements are recorded using a variety of devices including camera systems (e.g., Bardy et al., 1996; Guerrez et al., 2001; Horak and Nashner, 1986; Ravaioli et al., 2005) and accelerometers or potentiometers (e.g., Black et al., 1988; Horak et al., 1994; Peterka and Benolken, 1995; Soechting and Berthoz, 1979).

Eventually, of course, the mechanistic model that we hope for will also include mechanisms for the control of the effectors of the postural system. As a point of interest, according to Gagey (2003), the first force platform was constructed in France by Scherrer around 1950. At about that same time, a number of investigations were undertaken using a different but also then quite new technology, electromyography (EMG). These studies examined not postural sway itself, but the potential role of the leg and trunk musculature that underlies the control of upright, quiet standing (e.g., Basmajian and Bentzon, 1954; Joseph, 1953, 1955, 1962, 1964; Joseph et al., 1952, 1954, 1955; Kelton and Wright, 1949).

Activity during quiet standing above baseline resting levels was observed in numerous muscle groups: trapezius (Carlsöö, 1961), erector spinae (Carlsöö, 1961, Clemmesen, 1951), quadriceps and hamstrings (Lewko, 1996) and gluteus maximus, minimus or medius (Carlsöö, 1961; Jonsson and Synnerstad, 1966), though results varied across studies (cf., Joseph, 1964). The majority of these studies, though, examined muscles of the lower leg that control ankle angle. The most consistent result found continuous activity in the calf muscles collectively (Jacobson, 1943; de Vries, 1965) or more specifically in soleus (e.g., Carlsöö, 1961; Joseph, 1953, 1955, 1962, 1964; Joseph et al., 1952, 1954, 1955; Naponiello, 1957). Intermittent or phasic activity of

gastrocnemius (Carlsöö, 1961; Joseph, 1962, 1964; Joseph and Nightingale, 1952) and in tibialis anterior (Basmajian and Bentzon, 1954; Hoefer, 1941; Kelton and Wright, 1949) was also commonly observed, though others reported no activity in tibialis (Joseph, 1953; Joseph et al., 1952, 1954; Smith 1954).

The use of surface EMG in examining quiet stance behavior, however, seemed to fall out of style after this period, with the field coming to favor various ways of manipulating sensory inputs to subjects or the use of sensory or physical perturbations and their effects on CoP or CoM responses. Though EMG techniques have often been employed when examining responses to physical or sensory perturbations (e.g., Fitzpatrick et al., 1996; Henry et al., 1998), very few studies in the interim have used EMG to study quiet stance behavior (e.g., Lewko, 1996; Soames and Atha, 1981). Moreover, the analyses employed in most of these studies did not move beyond subjective, visual inspection of strip chart recordings to indicate increased activity relative to a baseline resting condition as the only variable to characterize muscular activity during quiet, upright standing. In the past few years, the role of muscular activity and the use of EMG during quiet stance has begun to spark some interest (e.g., Gatev et al., 1999; Masani et al., 2003), and more quantitative analysis. For example, Gatev et al (1999) showed positive correlations (~0.2-0.4) between changes in muscle activation of the lateral gastrocnemius and both center-of-gravity (CoG) and CoP displacements, with body sway lagging EMG activity by ~250-300 ms. The strength of these observed correlations was found to depend upon both stance width (normal v close (Romberg)) and eye closure. Still, examination of EMG of postural muscles during quiet stance certainly remains underrepresented in the literature. It would be worthwhile to provide a more

quantitative and comprehensive analysis of the relationship between body sway and activity in different muscle groups (cf. Masani et al., 2003) in one or both legs. An understanding of how the nervous system controls muscular activations in maintaining quiet stance behavior will be crucial for implementing effector mechanisms in future models.

The more extensive study of postural sway behavior itself, on the other hand, is reflected in the quite large number of variables computed to capture the characteristics of postural sway. Prieto et al., (1996) identified 14 variables that could be computed from the components of center-of-pressure (CoP) postural sway trajectories. These range from commonly used time-domain variables such as sway path length (e.g, Bronstein 1986; Bronstein et al., 1990; Wade et al., 1995) sway area (e.g., Lacour et al., 1997; Rocchi et al., 2002), root-mean square distance (e.g., Kunkel et al., 1998; Rocchi et al., 2002) and sway range (e.g., Blaszczyk JW et al., 1993; Gu et al., 1996) to frequency-domain variables such as mean, 50% or 90% power frequency or total spectral power (e.g., Carpenter et al., 2001; Duarte and Zatsiorsky, 2002; Jeka and Lackner, 1994; Jeka et al., 1998a,b; Krafczyk et al., 1999) to other, more esoteric variables such as fractal dimension (Stambolieva et al., 2001), which has had more limited usage in the field.

As Chiari et al. (2002) point out, many of these so-called 'summary statistic scores' are attractive for clinical use as they are 'easy to use and computationally undemanding.' In the literature, they are often used to characterize differences in quiet stance sway behavior under different sensory conditions (e.g., Clapp and Wing, 1999; Fitzgerald et al., 1994; Jeka and Lackner, 1994) or among different population cohorts or patient groups (e.g., Bronstein et al., 1990; Hay et al., 1996; Panzer et al., 1995). But as

Prieto et al. (1996) demonstrated, the between- and within-subject variability often associated with such measures limits their sensitivity to discriminate sway responses in different experimental manipulations and among different subject populations. In Prieto (1996), the authors simply compared CoP sway trajectories in healthy young and elderly subjects with eyes either open or closed. Analysis of the correlations between visual condition and subject group among 37 identified variable showed that only measures of sway velocity identified age-related changes in both visual conditions, as well as differences between visual conditions in both age groups. The sensitivity of the postural system to velocity is a point that we will return to later.

For now, it suffices to say that the variety of variables used to characterize sway behavior - and the above list is certainly not exhaustive – and their lack of sensitivity to experimental conditions is suggestive both of the difficulty that exists in trying to quantify upright stance behavior and the necessity for different techniques to understand how we maintain upright stance. Indeed, as some have pointed out (e.g., Chiari et al., 2002; Collins and DeLuca, 1993), summary statistic scores only characterize mean behavior and are unable to take into account the intrinsic, dynamic properties of postural sway (Chiari et al., 2002; Collins and DeLuca, 1993, 1995a, b; Newell et al., 1997). So, how do we examine these dynamic properties of sway behavior to gain a more complete understanding of how we maintain upright stance?

The Nature Of Human Postural Sway

In the previous section, I have suggested that, while summary statistics have been employed both successfully and extensively, they do not fully characterize the dynamic properties of postural sway behavior. The question is how does one view postural sway

trajectories to examine the nature of postural sway and the underlying system that produces it? Here, I will discuss three prominent ways in which postural sway trajectories have been characterized: 1) as non-stationary (e.g., Carroll and Freedman, 1993; Cao et al., 1998), 2) as a linear, stochastic process (e.g., Johansson, 1988, 1995; Kiemel et al., 2002), and 3) as a stochastic process comprised of coupled random walks (e.g., Collins and DeLuca, 1993, 1995a,b).

In one of the earliest and most often cited examples of the non-stationarity of postural sway (e.g., Cao et al., 1998; Chiari et al., 2000; Duarte and Zatsiorsky, 1999; Loughlin et al., 2003a, b), Carroll and Freedman (1995), observed a transient decay of the position and variance of sway at the beginning of trials. This decay was present during quiet standing with eyes open or closed, or when standing on one foot. If postural sway under such conditions is stationary (i.e., its statistical properties are invariant over time), ensemble averages (n = 51) of the sway trajectories at each time step should not have been statistically different from zero. However, for three subjects, the initial position of anterior-posterior (AP) CoP trajectories was found to be statistically different from zero, while points from approximately 20 s until the end of the 60 s trial duration were, generally, not statistically different from zero. These results were taken to indicate a transient non-stationarity in postural sway trajectories at the beginning of trials, in agreement with previously reported observations (e.g., Maki et al., 1987; Werness and Anderson, 1984). The presence of such transients could obviously bias the values of summary statistic scores computed over the entire trial, which rely in one way or another on the result of time averaging. As a potential, but rather course, solution, the authors suggest that one could simply not include the first 20-30 s of data in the computation of

time-invariant variables, which some authors have put into practice (e.g., Stoffregen et al., 1999, 2000).

However, the non-stationarity identified by Carroll and Freedman (1995), though potentially important in the practice of examining postural sway, is rather limited in characterizing the statistical properties of sway behavior, in general. Indeed, the authors attributed the observed transient to a peculiarity of their experimental protocol; that subjects always assumed the required standing posture by stepping onto a force platform from the rear, which may have simply biased the initial position at the start of trials. A more general commentary on non-stationarity in CoP sway trajectories comes from Cao et al. (1998) who showed that removing a 10th-order polynomial trend, artificially making the data 'more stationary,' improved fits using three different prediction methods for identifying the underlying dynamics of the postural system. The authors thus suggested that the (assumed) intrinsic non-stationarity of postural sway can affect analyses that assume statistical properties that are time-invariant.

Such a result certainly has potential implications for the summary statistics we have discussed previously, but also for commonly-used spectral (Fourier) analyses that also assume stationarity. Schumann et al. (1995) suggest instead that the use of time-varying spectral methods may be more appropriate. Evolutionary spectral methods (cf. El-Jaroudi et al., 1996) allow for the resolution of changes in the frequency content of a signal over time. Exemplar time-frequency distributions in Schumann et al. (1995) demonstrated some fluctuations in the estimates of frequency content over time, as well as that a patient with vestibular deficit generally showed more power across frequency

than a healthy adult subject, though their analysis did not go beyond simple visual inspection.

A potentially more interesting use of time-varying frequency analyses, though, is offered by El-Jaroudi et al. (1996). Healthy adult and vestibular-impaired patients were exposed to sinusoidally moving visual scenes at 0.1 or 0.25 Hz (see also below). Inspection of the time-frequency distributions of subjects' responses indicated that a peak in the spectral distributions of healthy individuals appeared immediately following the onset of visual motion (cf., Dijkstra et al., 1994a, b; Jeka et al., 2000; Lee and Aronson, 1974; Oie et al., 2001, 2002), indicating a dependence of postural responses upon stimulus motion. El-Jaroudi et al. (1996) found that the amplitude of this peak tended to decrease over the duration of the 60 s trial, which would clearly suggest a non-stationarity, as well as a possible adaptation of postural responses to stimulus motion. On the other hand, vestibular-deficient patients' responses tended to show a delay relative to stimulus onset, and amplitude did not decay or may have increased over time. Unfortunately, as the authors point out, the use of time-varying spectral analyses are still descriptive in nature and further development of these techniques may make them more useful in the analysis of postural sway.

Duarte and Zatsiorsky (1999) identified a qualitatively different type of non-stationarity than those considered above in three descriptive motion patterns observed during prolonged (> 30 min), unrestrained standing versus the typical laboratory standard of requiring subjects to 'stand quietly'; that is, to try to maintain a single foot position and body configuration throughout a trial. Identified as 'shifting', 'fidgeting', and 'drifting', respectively, all of these patterns of CoP motion would affect the computation

of variables that assume stationarity if one examines unconstrained standing: 1) Shifting – a fast displacement of the average CoP position, 2) Fidgeting – a fast, large displacement of CoP position and a return to approximately the same position, and 3) Drifting – a slow, continuous displacement of the average CoP position. Describing these patterns of motion does point out that differences in observed behaviors exist between that typically asked of subjects in the laboratory and the more natural behaviors examined in this study and what, if any, differences might exist in future models of the postural control system that account for stance behavior in constrained versus unconstrained conditions.

As we have seen, one of the shortcomings of the above studies that propose the non-stationary nature of postural sway is that they are generally descriptive in nature. In a companion paper to the one we have just reviewed, Zatsiorsky and Duarte (1999) forward a similarly descriptive interpretation of CoP sway trajectories in constrained standing by decomposition into two distinct components, which they termed 'rambling' and 'trembling'. The rambling trajectory was found to be a relatively slow process, with most of its spectral power in the range of 0-0.25 Hz, and to account for about 80% of the variability observed in CoP sway trajectories during quiet standing. This rambling component was found by first identifying zero-points in the horizontal ground reaction force, when the body is assumed to be at rest or its center of mass moving with constant velocity. A cubic spline fit to these 'Instant Equilibrium Points' was hypothesized to represent the trajectory of a set point or reference point reflecting the central command for the postural control system. The trembling component was obtained by subtracting the rambling component from the original CoP sway trajectory. It was smaller in

amplitude and higher in frequency (mean ~0.5 Hz) than the rambling component, and was interpreted to reflect the control about the drifting reference point due to the intrinsic elastic properties of the musculoskeletal system.

As we will see in the following section, the identification of slow (low-frequency) and fast (high-frequency) components of sway has been suggested by several different authors within different theoretical contexts (e.g., Collins and DeLuca, 1995; Dijkstra, 2000; Kiemel et al., 2002). Indeed, if one looks more closely at the exemplar trajectories presented in Figure 1.1A and 1.1B, simple visual inspection can reveal these two components. Next, we will discuss work from our laboratory that more rigorously identified these slow and fast components and how these results have gone beyond description to suggest the existence of two separate underlying processes, that are interpreted differently than that forwarded by Zatsiorsky and Duarte (1999).

Cao et al. (1998) utilized three different nonlinear prediction methods to try and identify the dynamics of the postural control system. Their findings suggested 3rd-order dynamics, though they could not distinguish if the system was intrinsically linear or nonlinear. A potential shortcoming of their approach, though, was the use of quite short stretches of data (30 s), where the slow component of sway – the rambling component of Zatsiorsky and Duarte (1999) – might considerably alter the observed statistical properties from one short section of data to the next. In Kiemel et al. (2002), we instead used longer sway trajectories (240 s); data segments long enough to adequately capture the slow component of sway. In this way, this slow component, which would contribute most to findings of non-stationarities over shorter data stretches, could be considered as an inherent part of the stochastic structure of observed postural sway trajectories.

14

In Kiemel et al., (2002), models of varying order were fit directly to CoM trajectories using autoregressive moving average (ARMA) techniques in nine healthy, young subjects across four different sensory conditions: 1) eyes closed, 2) eyes closed while lightly touching a stationary surface, 3) eyes open, and 4) eyes open with light touch (see also discussion of sensory influences on postural sway, below). It was found that the observed postural sway trajectories were best described by at least a 3rd-order model in terms of its eigenvalues and the coefficients of the autocovariance functions, whose makeup suggested two distinct processes: 1) In all cases, the eigenvalue accounting for the greatest proportion of the observed variance was negative and real-valued, corresponding to a first-order decay process. 2) In 33 of the 36 cases, a pair of complex-valued eigenvalues was also found, corresponding to a damped oscillatory component. In most cases, the decay and damped-oscillatory eigenvalues were the only eigenvalues found to account for a significant proportion of the variance.

In all cases the real part of the complex-valued eigenvalues was more negative than the eigenvalue of the first-order decay, indicating that these two processes operate on different time scales in the postural system, with the first-order decay process being slower than the damped oscillatory process. Further, the slow-decay process was also found to account for almost all of the observed variance in the sway trajectories. Thus, the comparison of the slow decay and damped oscillatory processes with the 'rambling' and 'trembling' components of Zatsiorsky and Duarte (1999) is quite clear. The results are also consistent with observations of Johansson et al. (1988, 1995) who also used ARMA techniques and found 3rd-order dynamics in sway under the influence of

vibration applied to the calf muscles (Johansson et al., 1988) or 4th-order dynamics with galvanic vestibular stimulation (Johansson et al., 1995).

Dijkstra (2000) also presented a model, the dynamic set-point model, that proposes both slow and fast processes. Like similar dynamical models (cf., Schöner, 1991; Dijkstra et al., 1994a,b; Jeka et al., 1997, 1998a, 2000), the deterministic response of the postural system is captured by a 2nd-order, damped oscillatory process. The model then includes an additional dynamic variable that determines the stable point of the dynamics of the postural system. This so-called dynamic set-point variable accounts for the low-frequency components of sway, which operates on a slower time scale then the 2nd-order oscillation.

Recall that Zatsiorsky and Duarte (1999) suggest that their rambling trajectory reflected a migrating or drifting reference point of the postural control system similar to that of Dijkstra (2000). However, it is unclear why the reference point, which hypothetically reflects the central command of the nervous system to maintain an upright position, should drift at all. By comparing the results of the ARMA model descriptions of the stochastic structure of postural sway to the behavior of an optimal control theory model, Kiemel et al. (2002) suggests specific mechanisms that account for the slow and fast components of sway. Specifically, the slower, first-order decay process, which accounted for the majority of sway variance, corresponds to the model eigenvalue that reflects the time-scale of the dynamics of state estimation; that is, the fusion of multisensory information to produce estimates of postural state. The faster second-order oscillatory process corresponds to the model eigenvalues associated with the control function; the use of those state estimates to produce the muscular activations for the

control of upright stance. This view of postural control in terms of separate processes of estimation and control provides us with an important theoretical context for understanding the control of posture.

A different approach, and one of the most prominent methods used over the past decade to examine the stochastic nature of postural sway was forwarded by Collins and DeLuca (1993). This approach considers CoP displacements in upright stance behavior as the result of both deterministic and stochastic mechanisms, which can be modeled as a system of two coupled, correlated random walks. The prototypical stabilogram-diffusion analysis of postural sway – extracting parameters from plots of the mean squared displacement as a function of time step – produces a function whose slope changes over time, typically in two regions separated by a (subjectively identified) critical point. This result suggested that sway is not a simple random walk process, and the authors adopted a two-process model with short-term and long-term regions described by separate but coupled random walk components. Their model has six parameters: critical point coordinates (Δt, $<\Delta r^2>$), which separate the short- and long-term regions, and a diffusion coefficient (D) and scaling exponent (H) for each region. Fitting such a model has been shown to typically account for around 97% of the variance observed in experimentally observed stabilogram diffusion plots.

The authors interpreted the identification of short-term and long-term regions in CoP stabilogram diffusion functions to infer two linked mechanisms for the control of upright standing. One operates in open-loop over short time intervals, and the other operates over long time intervals in closed loop. Under this hypothesis, stabilogram-diffusion analysis has spawned numerous empirical investigations utilizing the method

17

showing systematic changes in stabilogram diffusion function parameters with changes in visual input (Collins and DeLuca, 1995a; Riley et al. 1998; Rougier and Farenc, 2000), age (Collins et al., 1995b) and fingertip contact with a stationary surface (Riley et al., 1997), as well as a number of theoretical attempts at characterizing the underlying dynamics of the postural system (Eurich and Milton, 1996; Lauk et al., 1998).

Several authors have pointed out shortcomings in and alternatives to this approach (Chiari et al., 2000; Newell et al., 1997; Peterka, 2000). Both Chiari et al. (2000) and Newell et al. (1997) argue that the two-process model of Collins and DeLuca (1993) can be adequately and more parsimoniously accounted for with models having fewer than six parameters. Newell et al. (1997) compared the two-process random walk model with a single, continuous linear- process, with only two parameters. Fitting of this model to CoP trajectories in eyes-open and eyes-closed conditions with subject groups in four different age groups showed that this model fit the data almost as well as the six-parameter model, accounting for about 92% (versus 96%) of the variance across all visual conditions and age groups.

Similarly, Chiari et al., (2000) used a four-parameter nonlinear random walk model. Examination of the intra-class correlations of parameters across eyes-open and eyes-closed conditions showed that, overall, the four-parameter model yielded more reliable estimates than either the six-parameter model or a group of four summary statistic scores (mean velocity, 95% confidence ellipse area, fractal dimension and centroidal frequency). Further, the four parameter model was able to improve both reliability and sensitivity to sensory conditions on diffusion function estimates based

upon fewer trials than that of Collins and DeLuca, an important aspect when proposing such analyses for clinical assessment.

Peterka (2000), on the other hand, showed that realistic stabilogram diffusion functions could be produced by a simple feedback control model. The model he employed treats the body as a single-link inverted pendulum. Sensory systems are assumed to detect angular deviations from the vertical, which are used to generate a corrective torque to compensate for these disturbances. The controller takes the form of a common PID (proportional, integral, derivative) controller with a time delay. A second input to the controller is an external disturbance torque that is used to capture the stochastic fluctuations observed in sway behavior. The model has two outputs: AP body sway angle, and, via a simple transformation, AP CoP displacement. Analyzing simulated sway trajectories showed that within certain parameter regimes of the PID controller and time delay, fairly typical stabilogram diffusion functions could be produced, with simulation diffusion function parameters in the range of those found experimentally in Collins and DeLuca (1993).

That a simple feedback control model could account for the statistical properties of sway trajectories revealed by stabilogram diffusion analyses clearly challenges the open-loop/closed loop hypothesis of Collins and DeLuca (1993). The results in Peterka (2000) indicate that there is no need to postulate a nonlinear open-loop mechanism that operates below some sensory, perceptual or temporal threshold as posited by Collins and DeLuca. Instead, the dynamics of sway behavior can be determined by a single, continuous, closed-loop control mechanism.

However, it is an important point to appreciate that the simplicity of the model presented in Peterka (2000) belies the complexity of the multisensory processing required for the control of stance. As the author points out, the model's PID controller generates its corrective torque in proportion to the angular position, angular velocity and the integral of the body's center of gravity relative to the inertial frame of reference. This suggests that to implement such control, the nervous system must be able to estimate center of gravity motion in space in order to compute appropriate motor commands. Alternatively, this sensorimotor transformation may be accomplished directly from the multiple sensory inputs available to the postural control system into motor commands. In any case, such processing requires that the nervous system make use of information from its sensory systems. We have already considered a number of ways in which changes in sensory inputs affect sway behavior in our discussion of the nature of postural sway. In the next section, we will examine in more detail what is known about how sensory information, and a number of other factors, affects how we maintain upright stance.

Sensory (and Other) Influences on Human Postural Control

It is widely accepted that the maintenance of upright stance can be conceived of as a complex, sensorimotor feedback control process (e.g., van der Kooij et al., 1999, 2001; Mergner, 2003; Morasso, 1999; Peterka, 2000). Numerous experimental results have shown that the postural control system is able to utilize sensory information from at least: somatosensation from foot contact with the support surface (e.g., Aniss et al., 1992; Kavanoudias et al., 2001), proprioception regarding the configuration of body segments (e.g., Fitzpatrick et al., 1996; Wierzbicka et al., 1998), vision (e.g., Bardy et al., 1996; Berthoz et al., 1979; Lee and Lishman, 1975) and the vestibular system (e.g., Hlavacka et

20

al., 1996; Johansson et al., 1995). Further, sensory feedback from touch contact with external surfaces (e.g., Clapp and Wing, 1999; Jeka and Lackner, 1994, 1995; Riley et al., 1997; Rogers et al., 2001) and, even audition (e.g., Easton et al., 1998) has been shown to influence postural responses.

A common way to consider the role of sensory information for postural control is in terms of the information that each sensory system can provide (for a review, see Horak and Macpherson, 1996). For example, Nashner and colleagues (e.g., Black et al., 1984; Nashner, 1982) have suggested that information from the vestibular system – the otolith organs and semicircular canals – serves as a reference frame for postural orientation (cf., Hlavacka et al., 1996), as it registers a sum of all accelerations acting on the head, including the acceleration due to gravity. Somatosensory and proprioceptive input from cutaneous and proprioceptive receptors in the skin, musculature and connective tissues provides crucial information about both the configuration of body segments relative to each other and functional information about contact with external objects and surfaces (Jeka et al., 1998b), and it has been shown to be sensitive to at least the velocity of a stimulus (e.g., Jeka et al., 1998a, 2000). Similarly, vision, which provides information about the external environment, has also been shown to be velocity-sensitive (Dijkstra et al., 1994b; Jeka et al., 2000; Schöner, 1991; Stoffregen, 1986). The ability to maintain upright stance is also associated with numerous other factors including age (e.g., Okuzumi et al., 1996; Perrin et al., 1997), task demands (e.g., Hunter and Hoffman, 2001; Stoffregen et al., 1999, 2000), and various disease states including vestibular loss (e.g., Black et al., 1988; Horak et al., 1990; Lacour et al., 1997), cerebellar dysfunction (e.g., Bronstein et al., 1990; Horak and Diener, 1994), spinal cord injury (e.g., Lewko, 1996),

peripheral neuropathy (e.g., Ingliss et al., 1994) and Parkinson's syndrome (e.g., Bronstein et al., 1990; Rocchi et al., 2002).

Many different methods have been used to manipulate sensory inputs to examine how we use sensory information to maintain upright stance. For example, one method that has been employed to examine the role of the vestibular system in postural control is galvanic stimulation: the application of small-amplitude (< 4 mA), bipolar vestibular stimulation applied to the mastoid bones, which has been repeatedly shown to modulate the firing of peripheral vestibular afferents. It has been shown to elicit reproducible, directionally-specific postural responses (e.g., Fitzpatrick et al., 1996; Hlavacka et al., 1996; Johansson et al., 1995; Pavlik et al., 1999). Hlavacka et al. (1996) observed stimulation with the anode on the right mastoid produces an illusory perception of left body lean and produces a compensatory postural response to the right. When the anode was on the left mastoid, sway was induced to the left. With pseudorandom variation of the galvanic current (~0 to ~5-10 Hz) across the mastoid bones, Johansson et al. (1995) showed coherence of ~0.6-0.7 between ML sway with subject's facing forward and galvanic stimulation between 1-5 Hz, but not with AP sway, again illustrating the directional specificity of such stimuli. Indeed, AP sway can be elicited if the subject's head is turned either to the right or left (cf., Pavlik et al., 1999; Fitzpatrick et al., 1996) Coats (1973) also showed that the amplitude of the sway response varies with increasing stimulus current, and Coats (1972) and Petersen et al. (1994) showed that sinusoidally varying the stimulus current leads to sinusoidally varying sway.

The directional specificity of postural responses to galvanic stimulation certainly suggests an important role for vestibular information in the control of posture. In a novel study, Fitzpatrick et al. (1996) utilized both galvanic stimulation and an external physical perturbation applied to the waist to examine how the postural control system uses feedback control to resist disturbances, both sensory and mechanical. The human stance control system was conceived of as a simple, closed feedback control loop between the muscle systems and load and the reflex control of the effectors. Perturbations of stance - the load - create postural sway displacements about an axis of rotation at the ankle joint. Reflex responses (short, medium or long latency) under sensory input from visual, proprioceptive or vestibular systems (cf., Nakazawa et al., 2003; Wu and Chiang, 1997), are activated by these postural movements. The reflex recruitment of motor neurons activates specific muscle systems to produce torques about the ankle that oppose sway. Each of these three components – load, reflex and muscle systems - can theoretically be described by a transfer function or input-output function that characterizes the amplification (gain) and temporal relationship (phase) between correlated components of the input and output signals at any given frequency.

The authors' method was to apply low-amplitude, external perturbations at two different points in the control loop, under the assumption that the responses generated were linearly related to the perturbations. The transfer function of the reflex pathways was measured using the random mechanical perturbation to induce body sway and evoke an EMG response to obtain a perturbation-to-EMG transfer function, which, when divided by the perturbation-to-sway transfer function, yielded an estimate of the reflex transfer function in open-loop conditions. The galvanic stimulation was used to drive a

vestibular-induced sway, and dividing stimulus-to-sway transfer functions by the stimulus-to-EMG transfer function estimated the muscle-load transfer function. The gains of the reflex and muscle-load transfer functions, then, describe the amount of EMG evoked per unit of movement and the amount of movement evoked per unit EMG, respectively, and the product of the reflex and muscle-load transfer functions describes the behavior of the entire closed loop system.

As the authors point out, in many engineering feedback systems, high loop gains are utilized such that external disturbances are strongly resisted. However, in systems with non-negligible feedback delays (e.g., the nervous system), high loop gains may cause instability. Standard techniques in engineering systems exist to deal with feedback delays (e.g., the Smith predictor), and have indeed been employed in some recent models of human posture (e.g., van der Kooij et al., 1999, 2001; Morasso et al., 1999). The authors found that loop gain estimates were not high, but rather only slightly greater than unity at low frequency and decreasing slightly with increasing frequency, suggesting that the postural control system does not operate entirely upon feedback control, with the authors proposing a feed-forward component to the human postural control system.

Earlier, we discussed the use of EMG in characterizing the way in which the nervous system produces the control necessary for stance control. While I have noted that the use of EMG during quiet standing has been underrepresented in the literature, examining how muscular activity is related to postural responses to large mechanical perturbations has been a significant paradigm in the examination of human postural control (e.g., Allum et al., 2001; Inglis et al., 1994; Horak and Nashner, 1986). In Horak

and Nashner (1986), subjects stood on support surfaces of various lengths and were exposed to short forward and backward translations of the support. On a sufficiently long support surface, subjects showed fairly stereotyped patterns of muscular activation (EMG), beginning around the ankle joint and proceeding temporally in a distal-to-proximal order with an onset latency of about 100 ms. Because this pattern of muscle activation compensated for body motions away from equilibrium primarily through motion about the ankle joint, it was termed the 'ankle strategy.' By contrast, with short support surface lengths, the pattern of activation was proximal-to-distal, generating corrective torques about the hip rather than ankle joint; thus, the pattern was termed the 'hip strategy.'

In part, the interpretation of ankle and hip strategies has affirmed the belief that quiet standing under normal support surface conditions is primarily driven by corrective torques applied about the ankle joint (e.g., Fitzpatrick et al., 1996; Lee and Lishman, 1975). Aramaki et al. (2001), however, has reported findings that showed that angular displacements, velocity and acceleration of the hip are significantly higher than those of the ankle, indicating an important role of hip-joint motion even in quiet standing. Interestingly, the authors also observed an anti-phase relationship between ankle and hip angular acceleration that was not evident in the relationship between ankle and hip displacement, suggesting that rotations about the ankle and hip may serve to minimize CoM acceleration.

In Horak and Nashner (1986), support surface translations with intermediate-length surfaces elicited more complex motions that were interpreted as being different temporal combinations of the ankle and hip strategies. The authors suggested, then, that

the ankle and hip strategies may represent a limited set of central programs that can be organized to produce more complex motions. However, using multidirectional support-surface translations, Henry et al. (1998) found a more complex organization of muscle recruitment. For example, shank and thigh muscles were activated with constant latencies regardless of translation direction, while the latencies of trunk muscles (erector spinae and rectus abdmonus) were dependent upon the direction of perturbation. Different muscle groups responded maximally in different directions, sometimes orthogonal to the predicted direction (rectus femoris and adductor longus) and some of the muscles active in synergic regions were not anatomic synergists. These results suggested that postural responses are produced by flexible combinations of muscle activations that can be modified in a task-dependent manner.

Sensory perturbations, rather than the mechanical perturbations used in the studies we have just discussed, can similarly produce muscular activations relevant for stance control. For example, Aniss et al., (1992) showed that electrical stimulation of cutaneous receptors of the foot elicited reflex patterns of activation in leg muscles in standing subjects. Kavounoudias et al. (2001) demonstrated that vibratory stimulation of the tendons of the tibialis anterior and of the sole of the foot elicited predictable postural responses. Vibration of cutaneous receptors in the forefoot produced earliest EMG responses (latencies ~120 ms) in soleus, followed by initial backwards CoP sway. Conversely, vibration of the tendons of the tibialis anterior produced earliest EMG responses in tibialis, followed by an initial forward CoP motion. The application of vibratory stimuli to the forefoot or tendon, then, produces illusory perceptions of changes in foot pressure or of muscle length, respectively. This in turn leads to illusory

perceptions of forward or backward lean, respectively, and results in compensatory postural responses. With both stimuli, the amplitude of CoP displacements was found to be dependent upon the frequency of vibration, and tactile stimulation was found to be more effective in lower frequency ranges than proprioceptive stimulation, which yields responses more strongly in higher frequency ranges. The linear summation of the CoP responses to single-modality stimulations agreed well with the CoP response during concurrent stimulation, which the authors interpreted to suggest that somatosensory and proprioceptive inputs may sub-serve complementary functions dependent upon the frequency of peripheral sensory activation.

Further, in a paradigm that combined both vibratory stimulation of tibialis and galvanic stimulation applied to the mastoids (see also, above) Hlavacka et al. (1996) demonstrated that combined stimulation elicited complex postural responses. Galvanic stimulation, as seen previously, produced postural sway in the direction of the anode, either to the left or the right. Vibration of the right tibialis anterior muscle predictably produced sway forward and to the right. When both galvanic and vibratory stimuli were applied at different intervals with respect to each other, the resultant postural responses were found to be approximated by a summation of responses to the individual vestibular and proprioceptive inputs. The authors took these results to suggest a multisensory reference frame of body vertical for the control of posture, which is obtained by the continuous integration of proprioceptive and vestibular inputs. Proprioceptive input is assumed to register an estimate of the body relative to the support surface (e.g., earth horizontal) and vestibular input is assumed to register an estimate of the head in space relative to the gravitational vector (earth vertical). These estimates are summed to

provide an estimate of body in space relative to vertical, consistent with the observation

that postural responses with multisensory information reflected the summation of the

single sensory responses. Any body lean away from vertical, then, could be corrected for

by the postural control system.

Thus far, we have considered paradigms in which external disturbances, whether

they were primarily sensory or mechanical in nature, elicited predictable postural sway

responses. As noted repeatedly above, another way of examining the sensory influences

upon sway is to change the availability or reliability of sensory inputs and then to

examine the effects upon postural sway deviations, for example, by removing visual

information via eye closure (e.g., Clapp and Wing, 1999; Jeka and Lackner, 1994;

Kiemel et al., 2002; Prieto et al., 1996). The removal of a sensory input can be considered

to lead to increases in sway due to the necessity of producing estimates of the postural

state given source of sensory information (Kiemel et al., 2002). Conversely, providing

additional sources of sensory information should lead to improved estimation and,

potentially, to decreases in postural sway. For example, Rogers et al. (1997) has shown

that passive tactile stimuli applied to the leg and shoulder can also provide somatosensory

information relevant for postural control. Subjects were exposed to light contact forces

(~0.25 N) via a small (5.0 X 2.0 cm) textured material on the back of the right leg or on

the top of right shoulder. Across all subjects in four different groups (young adult, older

adult, older adult fallers and patients with peripheral neuropathy), the passive tactile input

was found to significantly decrease sway (root-mean-square amplitude). Shoulder stimuli

decreased sway (root-mean-square amplitude of ankle angle) significantly more than leg

stimuli (29% v 22%), while combined stimuli decreased sway significantly more (42%) than either stimuli in isolation.

Earlier investigations showed that active fingertip contact with a stationary surface also stabilizes sway. Jeka and Lackner (1994) had subjects stand with one foot in front of the other (tandem Romberg), which challenged the subjects postural stability primarily in the ML direction. Results showed that somatosensory information obtained from light fingertip contact that was limited to < 1 N of vertical force attenuates ML CoP sway to the same extent as when subjects were allowed to apply as much force to the contact surface as desired, where mean vertical contact forces were observed at ~5 N. Time lags between touch contact force and ML CoP sway in the force contact conditions were < 100 ms, suggesting that fingertip contact was being used to physically counteracting sway motion. By contrast, in the light contact conditions, time lags were much higher, between 300-400 ms, suggesting that under these conditions, fingertip contact provides sensory information allowing anticipatory actions serving to reduce sway. The effectiveness of fingertip somatosensory information has been supported by subsequent studies that have shown sway attenuation with light touch in bipedal stance, primarily in the AP direction (Clapp and Wing, 1999), equivalent degrees of sway attenuation with rough or slippery surfaces with significant differences in observed EMG activity in postural muscles of the leg during between light and force contact conditions, suggesting increased sensory-evoked, reflex muscle activation rather than physical support with light touch contact (Jeka and Lackner, 1995), as well as decreased stochastic activity with light touch as characterized by stabilogram diffusion parameters (Riley et al., 1997).

Beyond the above effects of tactile contact, the results of Rogers et al., (2001) also demonstrated some other commonly observed effects: When proprioceptive information from the ankles is altered or disrupted, in this case by standing on a compliant foam pad, postural sway is increased (cf., Bronstein, 1986; Lee and Lishman, 1975; with ischemic blocking of ankle proprioception: Diener et al, 1984; Horak et al., 1990). Increased sway is associated with increased age (cf., Bronstein et al., 1990; Wade et al., 1995), with increased risk of falls (cf., Lord et al., 1994) and with various disease states, in this case, peripheral neuropathy due to diabetes (cf., Bronstein, 1986).

Finally, Rogers et al. (2001) also showed that vision, as well as tactile input, stabilizes sway; an oft-reproduced result reflecting the important role of vision in postural control (cf., Dichgans and Brandt, 1978; Collins and DeLuca, 1995a; Jeka and Lackner, 1994, 1995; Prieto et al., 1996). Thus far, we have considered the effect of various vestibular and somatosensory stimuli on sway behavior. In the final section of this chapter, I will focus how visual information affects postural control in terms of the most prominent method that we use in our laboratory, one of the classical methods for examining the influence of vision on posture; the 'moving room' paradigm (e.g., van Asten et al., 1988a,b; Berthoz et al., 1979; Dichgans and Brandt, 1978; Dijkstra et al., 1994a,b; Lee and Aronson, 1974; Lee and Lishman, 1975; Lestienne et al., 1977; Ravaioli et al., in press; Stoffregen, 1985).

The 'moving room' paradigm

Following from the early work of Lee and colleagues, the moving room paradigm normally involves placing a subject on a stationary support surface while the visual environment is moved relative to the fixed inertial frame of reference. This can be

achieved by physically moving the walls of a visual surround (e.g., Lee and Aronson, 1974; Lee and Lishman, 1975; Stoffregen, 1985; Peterka, 2000) or by projecting computer-generated visual displays that simulate this movement (e.g., Dijkstra et al., 1994a,b; Jeka et al., 2000; Oie et al., 2001, 2002; Warren et al., 1996).

Examining postural responses to motions of the visual environment reveals the compelling influence of visual information on the control of stance. Lee and Aronson (1974) showed that with discrete forward or backward motions of the visual environment, toddlers produced destabilizing postural motions in the direction of motion, often to the point of falling over. In adults, while they generally do not fall over, visual environmental motion has been found to elicit postural sway in the direction of linear motion (Bronstein et al., 1986, 1990; Lestienne et al., 1977), in the direction of a visual rotation (van Asten et al., 1988b), and sway responses are found to be sensitive to the three-dimensional structure of the visual environment (Bardy et al., 1996; Masson et al., 1995; Stoffregen, 1985), distance (virtual or real) between the eye and the visual field (Dijkstra et al., 1994b; Stoffregen, 2000), the direction of gaze (Gielen and van Asten, 1990) and spatial frequency (Kunkel et al., 1998).

Early on, Lee and Lishman (1975) showed that oscillatory motion of the visual surround elicited postural responses that clearly reflected the spatiotemporal structure of visual motion. This result has been replicated often (e.g., Dijkstra et al., 1994a,b; Masson et al., 1995; Stoffregen, 1996) and is of particular importance in the methodologies we have adopted (cf., Jeka et al., 1998a,b, 2000; Oie et al., 2002). Specifically, visual environmental motion has been presented at different frequencies to characterize a transfer function, or frequency response function, of sway response to visual motion in

31

both the AP (Dijkstra et al., 1994a; Peterka, 2002; Peterka and Benolken, 1995) and ML directions (Jeka et al., 2000).

The transfer function, as above, is generally described in terms of the variables gain and phase. Gain is a measure of the dependence between induced postural sway amplitude and stimulus motion amplitude and phase is a measure of the temporal relationship. In both AP and ML directions, gain to the position of visual motion is around unity, with a slight peak in the gain function in the range of 0.2-0.4 Hz. Phase generally starts at a slight phase lead at very low frequencies, is about in-phase (i.e., 0) around 0.2-0.4 Hz, with an increasing phase lag as frequency increases.

In our lab, we have also demonstrated that small-amplitude oscillations of a surface that subjects contact lightly with their fingertip induces sway responses in a similar fashion as whole-field visual motion (e.g., Jeka et al., 1997, 1998a,b, 2000). Further, we have utilized a paradigm that combines both visual and touch surface motion to provide a multisensory moving room (Jeka et al., 2000; Oie et al., 2002), which has allowed us to examine how multiple sensory inputs are integrated in the control of upright stance. In Chapter 2, I will detail the series of studies we have conducted over the past several years utilizing these techniques, as well as how it has led us to an examination of one of the more prevalent hypotheses regarding multisensory integration in human postural control: sensory re-weighting.

Chapter 2: The Sensory Re-weighting Hypothesis

As I have suggested, the control of upright stance is dependent upon the integration of multiple sensory inputs – visual, somatosensory, proprioceptive, vestibular. In our lab, we have conducted a number of studies over the past several years (Jeka et al., 1998a, b, 2000; Oie et al., 2001, 2002; Ravaioli et al., in submission) aimed at characterizing how visual and somatosensory information are used and integrated with each other for stance control. One of our major accomplishments is the establishment of sensory re-weighting as a candidate mechanism for multisensory integration. Sensory re-weighting as argued for in the postural control literature is the idea that the human postural control system can change its dependence upon a given sensory input adaptively to maintain upright stance dependent upon current environmental conditions (cf. Horak and Macpherson, 1996). The focus of this thesis, then, is to provide an initial characterization of sensory re-weighting in terms of 1) its effect on the transfer function of the postural system and 2) the time scale of its dynamics.

An Historical View of The Sensory Re-weighting Hypothesis

Nashner and colleagues introduced the idea of sensory re-weighting over 20 years ago (cf. Black et al., 1984; Nashner, 1982). The paradigm that was utilized allowed the experimenters to selectively diminish both visual and proprioceptive inputs by rotating either a visual surround or the platform upon which the subject stood in direct proportion to anterior-posterior (AP) body sway motions, a technique now known as sway-referencing. The effect is to keep the ankle or visual angle relatively constant, and in this way, sway-referencing disrupts the sensory cues that are normally available during stance by diminishing visual and/or ankle proprioceptive information regarding self-motion normally available with sway motions relative to a stationary visual environment or stable support surface.

Following from the work of Martin (1965), the authors suggested that the relative dependence of visual, vestibular, somatosensory and proprioceptive inputs for the control of stance is context dependent; while visual, somatosensory and proprioceptive inputs may dominate under stable support surface conditions, vestibular inputs about the gravitational reference may play a more critical role when support surface and/or visual inputs become unreliable or unpredictable for the control of upright stance. Therefore, Nashner et al. (1982) examined the postural responses of normal and vestibular deficit patients under varying conditions of visual or support surface sway referencing.

In all conditions, eye closure increased sway, similar to many other observations already identified in Chapter 1 (e.g., Collins and DeLuca, 1995a; Jeka and Lackner, 1994, 1995; Prieto et al., 1996). Visual sway referencing increased sway even further than eye closure. With a fixed support surface, the 12 vestibular patients showed only small

differences in both normalized sway and EMG activation of four leg muscle groups

compared to normal, age-matched controls in conditions with eyes open, eyes closed and

with a sway-referenced visual surround. This suggested that all subjects, including the

patients, were able to utilize somatosensory inputs from the support surface.

The vestibular patients ranged in the severity of their deficits, with the least

affected subjects showing clinical balance evaluations within normal ranges. However,

the degree of deficit was found to be associated with their ability to maintain under

sensory conditions where information relevant for stance control became progressively

unreliable. When the support surface was sway-referenced, sway was increased versus

the eyes-open conditions for all subjects. All but the most severely affected vestibular-

deficient subject able to maintain stance for the duration of the 50-s trials. With eyes

closed and the support surface sway referenced, sway was increased still further, and the

second most-affected vestibular subject was unable to maintain the required standing

posture. However, when both visual and support surfaces sway-referenced making both

visual and somatosensory inputs unreliable for stance control, 6 of the patients were

unable to maintain stance. So, as sensory information was made progressively less

reliable for stance control – from eyes open to visual sway-referenced to eyes closed to

support surface sway-referenced to both visual and support surface sway-referenced –

those with progressively severe vestibular deficits were increasingly less able to maintain

the required standing position.

Additionally, all but one subject exhibited an attenuation of EMG amplitude in

response to discrete, repeated, support surface translations or rotations. The degree of

adaptation corresponded strongly with subjects' performance in the visual and support

surface sway-referencing conditions. That is, those affected most by sway-referencing showed the least attenuation and the longest latencies of EMG response.

The authors interpreted these results to suggest two important roles for the vestibular system: First, vestibular inputs provide an orientation reference frame (cf., Hlavacka et al., 1996) against which conflicts among visual, somatosensory and proprioceptive inputs can be identified. Second, vestibular inputs, along with visual, somatosensory and proprioceptive inputs can then be re-weighted selectively to directly mediate postural control under different conditions of sensory input. Thus, the authors proposed that subjects with the most severe vestibular deficits lacked the gravitational reference provided by the vestibular system necessary for successful sensory re-weighting, and therefore could not suppress the increasingly conflicting orientation inputs derived from the sway-referenced support surface and visual surround. Subjects with less severe deficits were able to successfully re-weight the inappropriate visual and/or somatosensory and proprioceptive cues under sway-referenced conditions in order to maintain stance, though not to the extent of the normal controls.

Bronstein (1986) and Bronstein et al. (1990) forwarded a similar interpretation of sensory re-weighting in experiments with short, discrete, linear visual perturbations in the medial-lateral direction utilizing a moving room paradigm. In normals, exposure to such perturbations elicits an initial response in the direction of visual motion, with a subsequent compensatory response in the opposite direction. Repetition of the perturbations, however, showed a strong attenuation of both the initial and secondary components of these responses. When subjects were standing on a foam pad, this degree of attenuation was decreased (Bronstein, 1986), suggesting that the observed attenuation

depends upon the availability of reliable somatosensory inputs. These results were interpreted as consistent with sensory re-weighting: When visual information is known to be destabilizing for stance control, visual inputs can be suppressed or down-weighted in favor of the congruent information provided by the vestibular and somatosensory systems under stable support surface conditions, which are less reliable for stance control when subjects stood on foam.

It was also shown that both vestibular patients (Bronstein, 1986) and cerebellar patients (Bronstein et al., 1990) were able to suppress the inappropriate visual cues when on a stable support surface. However, a patient with tabes dorsalis, which precluded proprioceptive input from below the knees (Bronstein, 1986), as well as Parkinson's patients, showed no attenuation of the postural response with repetitive visual motions. The first result is consistent with the authors' interpretations of sensory re-weighting relative to the vestibular reference frame: without reliable somatosensory inputs, the destabilizing of visual information provided by the moving visual surround was not suppressed. The latter finding was taken to suggest a role for the basal ganglia in sensory re-weighting for stance control.

Following from studies such as Nashner et al. (1982) and Bronstein et al. (1986), others have interpreted other experimental results supporting sensory re-weighting in similar fashions (e.g., Horak et al., 1994; Johansson et al., 1995). We maintain, however, that such accounts of sensory re-weighting are based upon indirect evidence, which may be subject to alternative interpretations (cf., Oie et al., 2002). For example, changes in other parameters of the postural control system, for example damping, could have similarly account for the observed postural responses. The idea that the postural control

system adapts to changes in sensory conditions, whether via a sensory re-weighting mechanism or not, clearly suggests nonlinear aspects to posture. Indeed, despite the success of a number linear models of posture (e.g., Dijkstra et al., 1994a,b; Gusev and Semenov, 1992; Jeka et al., 1997, 1998a, 2000; Schöner, 1991), experimental results have suggested nonlinearities in the human postural control system when sensory conditions change (e.g., Peterka and Benolken, 1995; Oie et al., 2002; Sasaki et al., 2002), indicating the necessity of a mechanism such as sensory re-weighting in future models of postural control.

Peterka and Benolken (1995) provided a crucial empirical finding in support of sensory re-weighting. In this study, healthy young adult and bilateral vestibular loss subjects were exposed to rotations of a physical visual surround at 0.1, 0.2, 0.5 Hz at 5 amplitudes (0.2-10 deg peak amplitude) in either fixed or sway-referenced support surface conditions. Similar to results we cite above, in both groups, visual and support surface motions elicited sway responses at the stimulus frequency, with sway referencing increasing response amplitude at the drive versus fixed surface condition. Computation of a ratio of sway amplitudes in fixed and sway-referenced conditions showed no trend with frequency or amplitude and was about equal in normals and patients, suggesting that sway referencing had fairly equal effects upon postural responses across frequency and amplitude in both subject groups. Phase generally showed an increasing lag with increasing frequency, with vestibular loss subjects tending to show a phase advance compared to normals at any given frequency. Response at the stimulus frequencies was found to depend upon frequency, surface condition, and stimulus amplitude. Phase typically did not vary with stimulus amplitude, and importantly, at a given stimulus

frequency, gain was found to decrease with increasing stimulus amplitude in both surface conditions.

This result clearly emphasizes the need to develop nonlinear models that capture the dependence of gain upon stimulus amplitude. The fact that gain was found to vary with different stimulus amplitudes at the same frequency demonstrates nonlinearity. Any strictly linear model predicts constant gain at a given frequency regardless of stimulus amplitude.

Over the past several years, I have been involved in a series of studies that has lead us to just this task; developing a mechanistic model that implements sensory re-weighting in the multisensory fusion for postural control. In the following section I will review this body of work, which has lead my colleagues and I to our present views on sensory re-weighting, as well as the experiments explained later in Chapters 3 and 4.

Briefly, early efforts in our laboratory utilized simple linear dynamical systems models, extending from previous findings with vision, to identify what properties of somatosensory input were relevant for postural control. As with vision, the human postural control system was found to be sensitive to at least the velocity of somatosensory stimuli. We next extended the model to try to account for the integration of both vision and somatosensation. While the model achieved some qualitative success, quantitative analysis of model predictions with experimental data clearly showed the failure of general linear models of multisensory integration, and suggested the need for nonlinear mechanisms, such as sensory re-weighting.

Theoretical Beginnings: The Importance of Sensory Information for Human Postural Control

Schöner (1991), and later Dijkstra et al. (1994a,b) provided a conceptual/experimental approach that strongly influenced the early empirical and modeling efforts that have led us to our current understanding. Briefly, a simple model of the postural control system under the influence of visual environmental motion was formulated as a second-order, linear dynamical system (Schöner, 1991):

$$\ddot{x} + \alpha \dot{x} + \omega_0^2 x - \sqrt{Q_x}\xi_t = -c_{env}e(x,t) \qquad (2.1)$$

where $x(t)$ is the position of the eye in the inertial frame, α and ω_0 are damping and eigenfrequency parameters, respectively, ξ_t is Gaussian white noise (zero mean, unit variance) and Q_x is the noise strength. The influence of sensory information on the postural system is explicitly represented in the model as the visual expansion rate, $e(x,t)$, where:

$$e(x,t) = \frac{\dot{x} - \dot{D}(t)}{x - D(t)} \qquad (2.2)$$

$D(t)$ represents motion of the visual environment, and the visual expansion rate is related to the postural system through the coupling constant, c_{env}.

This simple model was shown in simulation (Schöner, 1991) to largely capture several of the aspects of postural behavior under conditions of visual stimulation that we have discussed previously: 1) A static visual environment decreases postural sway displacements. In the model, stabilization of posture by visual information is accomplished by increasing the effective damping, $\tilde{\alpha} = \alpha + c_{env}/D_0$, when $D(t) = D_0$, a constant when the visual environmental motion is present. 2) Linear motion of the visual

environment relative to the subject induces a transient postural response (e.g., Bronstein et al., 1986, 1990) in the direction of visual motion. 3) Slow oscillatory motions (~0.2 Hz) of the visual environment induce oscillatory sway that is phase-locked to stimulus motion, stabilizing the postural system relative to the dynamic visual environment.

Following from these efforts, Jeka et al. (1997; 1998a) extended this approach to examine the influence of dynamic somatosensory input obtained by fingertip contact with an external surface (see also above) on center-of-mass postural sway displacements. Here, the model of Schöner (1991)(Eq 2.1, above) was adapted for the case of contact surface motion with sensory information explicitly represented in model now in terms of somatosensory information regarding motion of the touch surface:

$$\ddot{x} + \alpha \dot{x} + \omega_0^2 x + \sqrt{Q_x} \xi_t = c_{s1}(\dot{d} - \dot{x}) \qquad (2.3)$$

where $x(t)$ is the position of the center of mass and $d(t)$ is the time-varying position of the contact surface (Note: In Eq 2.3, and in the following, the subscript notation specifies sensory modality (s = somatosensation or v = vision) or the order of derivative (1 = velocity, 0 = position)). Similar to vision, in Eq. 2.3, contact with a static surface leads to a decrease in sway by increasing the effective damping, $\tilde{\alpha} = \alpha + c_v$. We fit parameters of model 2.3 to transfer function estimates obtained by presenting subjects with sinusoidal motions of the contact surface at frequencies ranging from 0.1-0.8 Hz in different trials. Fitted gain and phase revealed systematic errors: 1) Phase was overestimated, particularly at very low and high frequencies. 2) Gain was underestimated at high frequencies, and overestimated at low frequencies. This led us to consider an extended model that included coupling to the position of the contact surface:

$$\ddot{x} + \alpha \dot{x} + \omega_0^2 x + \sqrt{Q_x} \xi_t = c_{s1}(\dot{d} - \dot{x}) + c_{s0}d(t) \qquad (2.4)$$

The addition of this position coupling term, c_p, resulted in much-improved fits

with gain being well-approximated up to a stimulus frequency of 0.6 Hz, while phase was

well-fit between 0.2-0.6 Hz. At high frequencies, phase remained slightly overestimated,

while at low frequencies phase was slightly underestimated. We will return to these

residual errors, as well as those observed in Dijkstra et al. (1994) and addressed in Giese

et al. (1996), later in this chapter. What is important here in considering the application of

these modeling techniques is that velocity information is derived from visual and

somatosensory stimuli for the control of posture. Similarly, velocity information at low

frequencies is thought to be provided, if indirectly, by the vestibular system through

transformation of head acceleration (Wilson and Melvill Jones, 1979).

Multisensory Integration of Vision and Somatosensation for Postural Control

Next, given that the commonalities between these models for visual and

somatosensory control of posture, we turned to the question of how these different

sensory inputs might be integrated in the control of posture. As the culmination of my

master's thesis work, later published as Jeka et al. (2000), we built directly upon the

previous empirical and modeling work examining visual (Dijkstra et al., 1994b; Giese et

al., 1996; Schöner, 1991) and somatosensory (Jeka et al., 1997, 1998a) inputs by

proposing a model that conceives of the multisensory integration for postural control as a

linear, additive process. The initial model characterizing this integration of vision and

somatosensory information was:

$$\ddot{x} + \alpha\dot{x} + \omega_0^2 x + \sqrt{Q_x}\xi_t = c_{v1}\left(\dot{d}_v - \kappa\dot{x}\right) + c_{s1}\left(\dot{d}_s - \dot{x}\right) + c_{s0}d_s(t) \tag{2.5}$$

where $x(t)$ is the position of the center of mass, $d_v(t)$ and $d_s(t)$ are the position of the visual environment and the contact surface, respectively, and κ is a correction factor ($\approx$ 2); the approximate ratio of sway amplitude of the head at eye level divided by the sway amplitude of the center of mass, as visual environmental motion is registered by the eyes and contact surface motion is registered by the finger at approximately waist level.

The model (Eq. 2.5) proposed in Jeka et al. (2000) was, in large part, chosen as the simplest extension of models 2.1 and 2.4 to the multisensory case. Still, this relatively simple additive model qualitatively supported a number of predictions in terms of the patterns of gain and phase observed in five experimental conditions: no contact/dynamic vision, dynamic vision/no contact, static contact/dynamic vision, dynamic contact/static vision, dynamic contact/dynamic vision. Indeed, a number of authors have had some success using linear models to capture the multisensory integration involved in postural control (e.g., Gusev and Semenov, 1992; Zacharias and Young, 1981) in a similarly qualitative fashion.

However, in Jeka et al. (2000), more strict quantitative comparisons revealed significant deviations from model predictions. Specifically, it was predicted that the observed transfer functions in the dynamic contact/dynamic vision condition should equal the sum of the transfer functions of the two dynamic/static conditions. Fitting of the transfer functions showed that, while phase was quite well-predicted across most subjects, gain was not, with some subjects showing differences greater than 50% at lower frequencies and all subjects showing differences between 30-70% at high stimulus frequencies. The failing of the linear additive model in Jeka et al., (2000) to account for

the sensory fusion process was interpreted to indicate nonlinearities in the multisensory integration for postural control under different sensory conditions.

It should be noted that the earlier modeling efforts of Jeka et al. (1998a) and of Dijkstra et al. (1994b) and Giese et al. (1996) both interpreted the residual errors in model predictions as evidence of nonlinearities in the sensorimotor integration for postural control. Specifically, both groups suggested parameter adaptation to account for the model errors. While Giese et al. (1996) proposed adaptation of the system's eigenfrequency, ω_0, both Jeka et al. (1998a) and Giese et al. (1996) suggested adaptation of the effective damping, $\tilde{\alpha}$, with Giese et al. (1996) showing a dependence of $\tilde{\alpha}$ on stimulus frequency. In retrospect, adaptation of $\tilde{\alpha}$ as stimulus frequency changes could also have been interpreted in terms of sensory re-weighting in these single-sensory conditions, as the coupling to sensory information in models 2.3-2.5 add to the effective damping. However, in Kiemel et al. (2002), eigenvalues of linear stochastic models fitted to postural sway trajectories in four different sensory conditions (eyes closed/no light fingertip contact, eyes closed/light contact, eyes open/no contact, eyes open/light contact), expressed as model parameters, showed that changing sensory information across conditions did not affect the damping of the postural system.

Identifying the mechanism underlying the nonlinearities observed in Dijkstra et al. (1994b) and Jeka et al. (1998a) is an important issue that needs to be addressed. At the time however, the general finding of nonlinearities in the multisensory control of posture led us towards attempts to identify nonlinear behaviors that would constrain future multisensory models.
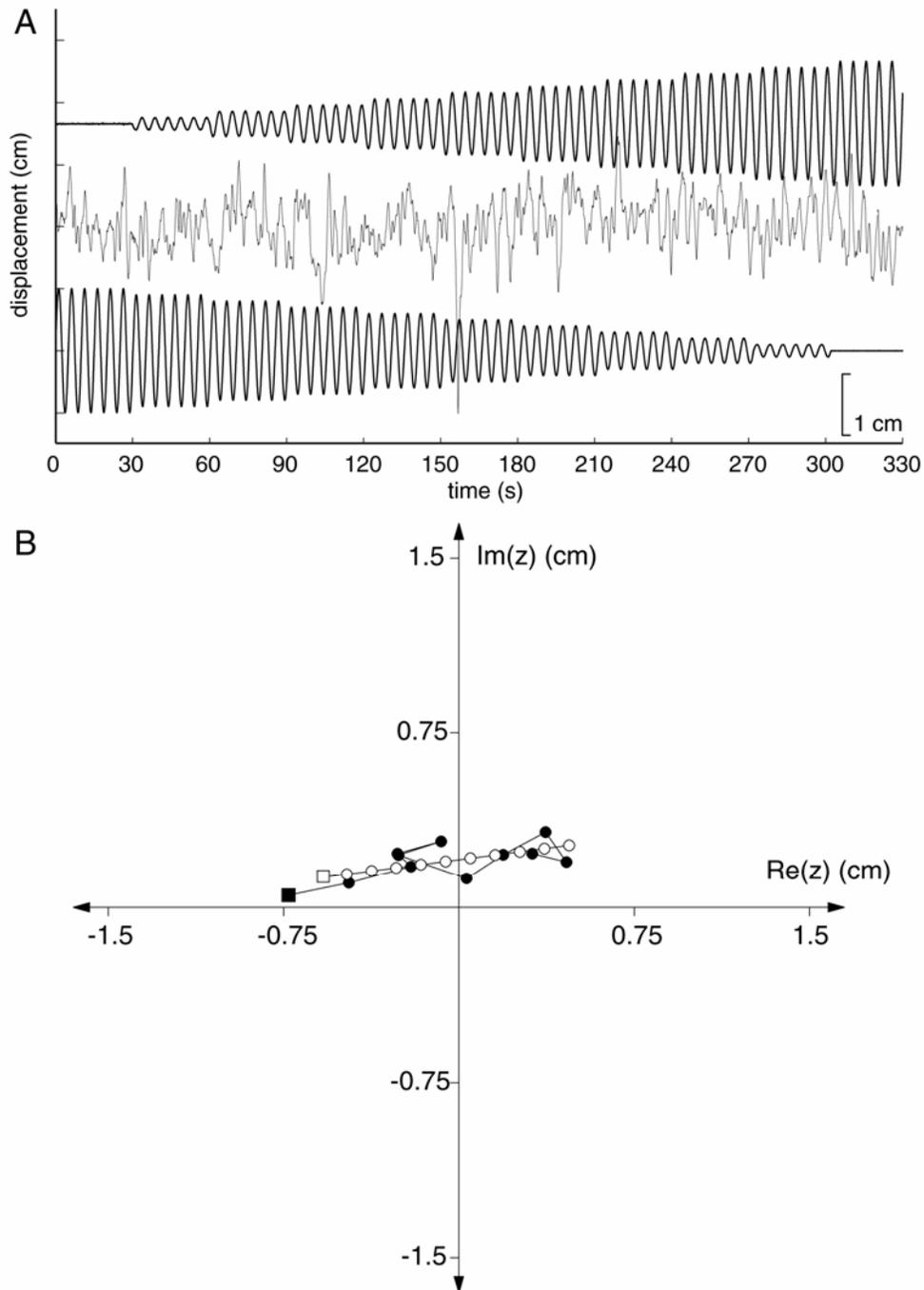
Figure 2.1. Exemplar trial indicating a linear response. (A) Time series of center-of-mass displacement (middle), visual display position (upper) and touch surface motion (lower). B. Observed (dark circles) and predicted (open circles) Fourier transforms. The Fourier transform and the predicted Fourier transform from the linear fit for the initial plateau where the visual display was stationary and touch surface oscillated with 1.0 cm amplitude are indicated by the respective square symbols. A linear model was found to be the best fit for this trial, which would be consistent with constant weighting of sensory inputs.

Nonlinear Aspects of Postural Sway Behavior – Sensory Re-weighting

In the next study (Oie et al., 2001), the amplitudes of anti-phase, 0.2 Hz visual and somatosensory inputs were co-varied within six-cycle steps during a trial and postural responses were characterized by examining how the Fourier transforms of postural sway as the stimulus motion amplitudes changed. The original intent was to examine the postural system for the potential existence of hysteresis in terms of the phase relationship between postural sway and stimulus motion (recall that at 0.2 Hz, sway response was shown to be roughly in-phase with both visual and somatosensory motion (Dijkstra et al., 1994a; Jeka et al., 1998a, 2000)).

No strong evidence of hysteresis was found. However, transfer functions computed across the six-cycles of each amplitude step within a trial often showed a dependence upon the amplitudes of stimulus motion. A typical trial is presented for a single subject in Figure 2.1, where the somatosensory input, which was applied through fingertip contact with a servo-motor controlled touch surface (cf., Jeka et al., 1998, 2000), was initially stationary and increased in 0.1 cm amplitude steps every 30 s throughout the course of the trial, while visual stimulus motion began at 1.0 cm then decreased and was anti-phase relative to touch surface motion (see Figure 2.1A). The Fourier transform was computed at the stimulus frequency (0.2 Hz) for each 30-s trial segment, and plotted in the complex plane (Figure 2.1B).

In this case, the transform in the initial segment (indicated by the black square), was observed at approximately 180 degrees, which indicated a roughly in-phase relationship with visual motion. This was consistent with previous findings at this

46
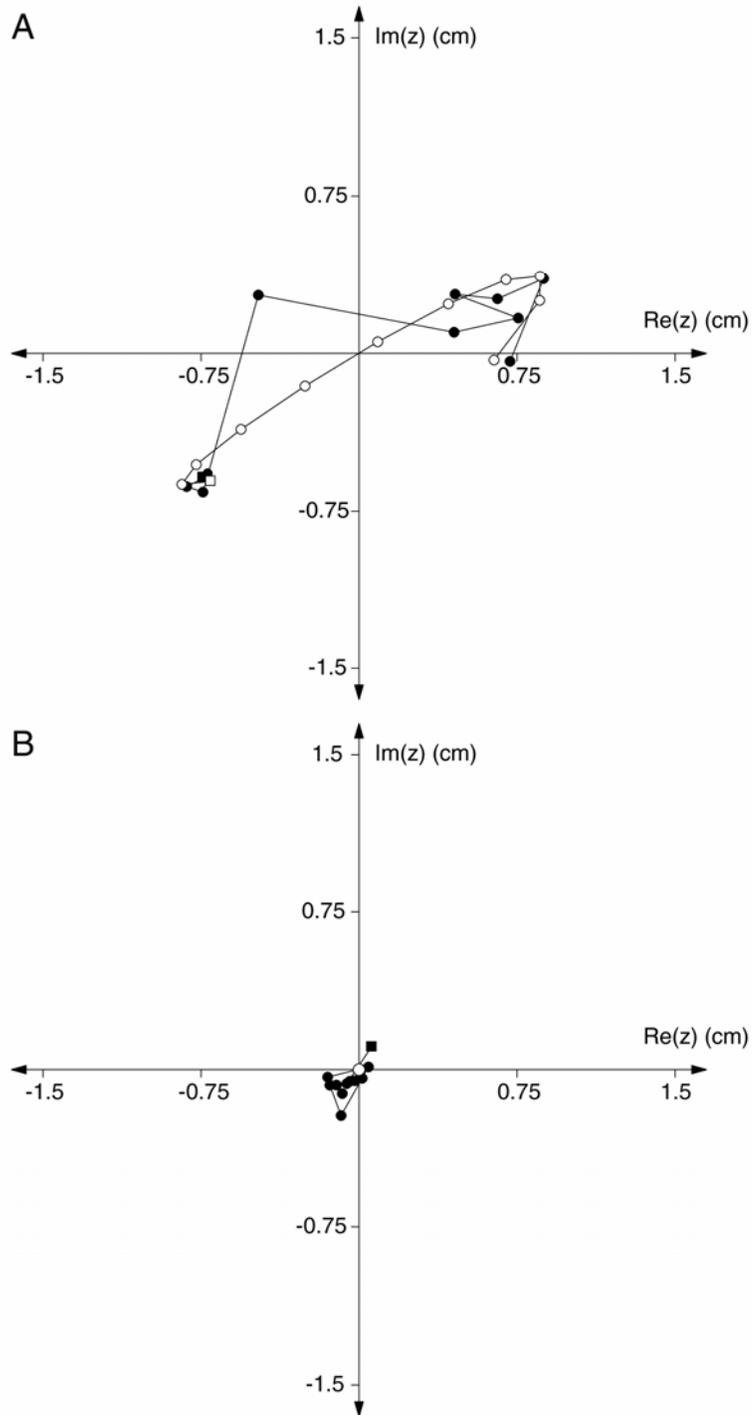
**Figure 2.2. Examples of nonlinear and constant responses to stimulus motion**. (A) Cubic model, indicating non-linearity. The cubic fit for this trial was found to be significantly better than all fits of lower order (P < 0.05). B) Constant model (zero mean). Response was not fit significantly better by any higher order models. This is consistent with a response that is uncoupled to stimulus motion.

stimulus frequency (e.g., Dijkstra et al., 1994a,b; Jeka et al., 1998, 2000; Oie et al., 2002). As the trial progressed and stimulus motion amplitudes were co-varied relative to each other, the response changed giving an indication of how the multisensory fusion process in the postural system solved the anti-phase motions of the stimuli. Thus, the observed patterns of Fourier transforms within a trial were interpretable as a reflection of the underlying process of multisensory fusion. If the fusion process was linear with constant weights (i.e., no sensory re-weighting), then the Fourier transforms would be a linear function of stimulus amplitude in the complex plane. In this case, the transforms did change in an approximately linear way in the complex plane, which is indicated by the linear fit represented by the white circles in Figure 2.1B.

However, in 28 of 58 trials, fitting of different order models to the patterns of Fourier transforms in the complex plane revealed non-linear responses, while a linear model was selected in only 15 trials. These results indicated that the nonlinearity in gain response observed in Peterka and Benolken (1995), who also varied stimulus amplitudes, but between trials and by larger steps of at least 9 mm, is observable even with very small changes (1 mm) in stimulus amplitude within a trial. We interpreted the results to be consistent with sensory re-weighting, which as we have already pointed out, had been proposed in the literature (e.g., Black et al., 1984; Bronstein, 1986; Bronstein et al., 1990; Horak and Macpherson, 1996; Nashner, 1982).

However, while the results of Oie et al. (2001) indicate nonlinearities in postural response, they can not directly support the sensory re-weighting hypothesis. It was not until a more recent empirical and modeling study that more direct evidence for the existence of sensory re-weighting was actually given (Oie et al., 2002). Oscillatory visual

and somatosensory stimuli were presented simultaneously to subjects at 0.2 and 0.28 Hz, respectively, while their amplitudes were co-varied from 2-8 mm in different conditions. We based our interpretation of the existence of sensory re-weighting upon the following: 1) Clear, systematic changes in gain to a given stimulus (vision or somatosensation) were observed when its amplitude was increased from 2 mm to 4 mm to 8 mm. 2) In the case of vision, increases in touch motion produced significant increases in the gain to the motion of a visual stimulus even when its amplitude remained constant. 3) Fitting third-order, linear, stochastic time series models to postural responses in each condition showed that different models were necessary for different conditions, and the only parameters that changed significantly with changes in stimulus amplitude were those that determined the dependence of the postural system upon visual or somatosensory input (i.e., the sensory weights). The first two points indicate the presence of nonlinearities in the gain response across stimulus amplitude conditions, as we have pointed out above. The last point, importantly, suggests that the mechanism for gain adaptation by the postural control system in response to changes in the stimulus amplitude can be thought to be primarily due to changes in sensory weights. Taken together, these findings showed that changes in gain may reflect, both within a sensory modality (i.e., intra-modality) and between modalities (i.e., inter-modality), a sensory re-weighting mechanism consistent with the view generally held in the field.

In a more recent investigation (Ravaioli et al., in submission), we have provided even further empirical evidence that can also be interpreted as consistent with sensory re-weighting. We had subjects stand within visual environment whose motion consisted of two distinct components: a constant-frequency, low-amplitude oscillation (0.2 Hz, 4 mm

amplitude) and a constant-velocity translation from left to right (0-4 cm/s in 4 separate conditions). The variability of postural sway increased systematically with translation velocity, but remained significantly lower than that observed in a control condition with eyes closed. This indicates that the postural control system is able to use visual information to stabilize sway even with visual translation velocities as high as 4 cm/s. Importantly, gain showed a significant dependence on translation velocity, with gain relatively constant at low translation velocities and decreasing as translation velocity increased. These changes in gain, again, clearly indicated nonlinearity in the postural response across conditions, which we interpreted in terms of sensory re-weighting; decreasing gain suggests that the dependence of the postural system upon visual information (i.e., the weighting of visual input) also decreases as the velocity of visual translation increases.

Having thus established sensory re-weighting as a potential mechanism in the multisensory integration for human stance control, it is now our intent to develop a model of the postural control system that implements such a mechanism. Peterka (2002) has presented a model that suggests the presence of inter-modality re-weighting, however no mechanism for how such re-weighting occurs is presented. There is a single model in the current literature that explicitly represents sensory re-weighting (van der Kooij et al., 2001). The van der Kooij (2001) model dynamically re-weights sensory error signals computed as a difference between sensory measurements and estimates based upon internal models of the sensory environment, and it has been shown to largely reproduce the intra-modality changes in gain as observed by Peterka and Benolken (1995) when fit to observed estimates of gain and phase.

However, it remains an open question whether a general adaptive scheme like that employed in van der Kooij et al. (2001) captures the sensory re-weighting observed in human stance control. We are taking a different approach by first identifying the properties of sensory re-weighting in postural control that will constrain future modeling efforts. Specifically, in this thesis, two experiments will be presented that examine the questions: 1) How does sensory re-weighting affect the transfer function of visual input to sway response? and 2) What is the time scale over which this sensory re-weighting occurs?

Chapter 3: Experiment – Sum-of-sines Visual Input

In the previous chapter, it was argued that sensory re-weighting can be considered as a potential mechanism in the multisensory integration for the maintenance of upright stance. One of the important goals of our investigations has been to implement such a sensory re-weighting mechanism into models of the human postural control system. To do so, our approach was to identify properties of postural sway behavior that can be interpreted in terms of sensory re-weighting and that provided important constraints for any proposed re-weighting mechanism.

The experiment presented in this chapter examined how sensory re-weighting affects the shape of the transfer function of the postural control system as stimulus amplitude is varied. That is, does the dependence of gain previously observed as a function of stimulus amplitude, which we have interpreted in terms of sensory re-weighting (Oie et al., 2002), change uniformly across different stimulus frequency? Stimuli consisted of a summation of ten different sinusoids at two different amplitudes. This provides a more efficient method of estimating the postural system's transfer function by examining the postural system at multiple frequencies simultaneously where

the dynamics of the postural system can be assumed to be the same across stimulus frequencies at a given amplitude. This method, then, avoids a potential limitation of previous studies that obtained transfer function estimates at a single frequency in a given trial.[1]

Introduction

As discussed in Chapter 2, sensory re-weighting in postural control is not a new concept (cf. Black et al., 1983, 1988; Nashner et al., 1982). However, to our knowledge there presently exists in the literature only a single model of postural control that includes an explicit scheme for sensory re-weighting. The model of van der Kooij et al. (2001) proposes a general adaptive scheme for re-weighting sensory error signals in an optimal control model. The model was shown to have some success in accounting for changes in gain when fitting observed transfer functions to visual and support surface oscillations. Recent findings in our lab (cf. Carver, 2005), though, have revealed deficiencies in this model, and it is debatable whether proposing a model with specific mechanisms for sensory re-weighting is appropriate given our current state of knowledge. Of course, such a model would be invaluable in furthering our understanding of nervous system organization, as well as being beneficial as a potential tool for clinical diagnosis, but that remains to be achieved.

In our lab, we have approached the development of models in a different manner than mechanistic models such as that of van der Kooij et al. (2001), which generally

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[1] The results of the experiment detailed in this chapter have been published in Kiemel, Oie and Jeka (2006), which presents a detailed modeling analysis and interpretation of these data. Mr. Oie's contribution to that effort comprised experimental conceptualization and design, setup and conduct, and initial data analysis and interpretation, which was verified and extended by the modeling analysis presented in Kiemel et al. (2006).

apply established concepts such as Kalman filtering (e.g., van der Kooij et al., 1999, 2001) or Smith predictors (e.g., Morasso, 1999) in order to account for observed sway behavior. Our approach, instead, has been to develop descriptive models whose form and parameters are determined by fitting of experimental sway trajectories (cf. Kiemel et al., 2002). This is in contrast to mechanistic models, which often are used to reproduce measures such as gain, phase and variance that provide fewer constraints than reproducing the statistical properties of actual sway trajectories. Indeed, we know of no mechanistic model that has been rigorously shown to produce trajectories consistent with those observed experimentally. Developing descriptive models has the advantage of assuring one that all contributions to the postural system are accounted for if model trajectories are not statistically different from actual sway trajectories. This enables us to clearly identify the dynamic characteristics of postural behavior that must be produced by specific, proposed mechanisms.

Using such descriptive models, we have recently forwarded findings based upon fits of a linear 3rd-order model (Oie et al., 2002). Our results indicated that sensory re-weighting, and not changes in other parameters of the postural system, could account for changes in postural sway gain to oscillatory visual and somatosensory stimuli of different amplitudes. Thus, it is now our aim to develop a model of posture that implements a mechanism of sensory re-weighting for the multisensory integration required in postural control.

However, while sensory re-weighting is a generally well-accepted idea in the field of postural control, the findings of Oie et al. (2002) may be the most direct evidence for it as a mechanism in the sensorimotor integration for posture. Thus, little is yet known

about how such a mechanism operates nor how to formalize it in a model of posture. Rather than proposing a general adaptive scheme as in van der Kooij et al. (2001), our approach is to first identify empirical results that will provide important constraints on any proposed sensory re-weighting scheme.

In this first experiment, the question of how changes in stimulus amplitude affect the pattern of postural response gain across a range of stimulus frequencies was examined. Specifically, it was asked whether changes in gain changes in response to varying stimulus amplitudes are uniform across stimulus frequency using complex, sum-of-sines visual stimuli with frequencies ranging from 0.024-2.936 Hz at two different amplitudes.

A second question is the still open question of whether the postural system couples to visual position, as well as visual velocity. Velocity information is important in the use of vision of stance control (Dijkstra et al., 1994b; Jeka et al., 2000; Schöner, 1991; Stoffregen, 1986). However, some of our previous modeling efforts have also suggested the existence of position coupling (Jeka et al., 2000) or, alternatively, acceleration coupling (Oie et al., 2002). Expanding the stimulus frequency range in this experiment, with respect to previous studies, towards lower frequencies could allow the analysis of the transfer function of the postural response to visual motion to qualitatively assess the question of position coupling.

Method

Subjects

Eleven students (4 females, 6 males) at the University of Maryland participated in the study. Subjects ranged in age from 19-33 years and had no known musculoskeletal

injuries or neurological disorders that might have affected their ability to maintain balance. All subjects had normal vision or vision corrected to normal using contact lenses or eyeglasses. All subjects were given both oral and written task instructions and gave written consent according to guidelines implemented by the Internal Review Board at the University of Maryland before undergoing the experimental protocol.

Experimental setup

Figure 1 illustrates the 'moving room' paradigm employed in this study. Subjects stood with feet parallel and about 1 cm apart (standard Romberg) in front of a large, translucent screen (2.0 m x 1.0 m, Da-Lite Screen Company, Inc.) at a distance of 40 cm. The animated visual display that was used as the stimulus consisted of a pattern of 100 white triangles on a black background. Each triangle was approximately $0.2°$ x $0.3°$ x $0.2°$ on a side and was randomly positioned in an annulus between $10°$ and $45°$ of visual eccentricity. The hole in the middle of the stimulus array was made to suppress the visibility of aliasing effects, which would be most noticeable in the foveal region. Stimulus motion was always suggested in the anterior-posterior direction relative to the subject, and the center of the annulus, which was located at the focus of expansion in virtual space, was positioned at the approximate center of the subject's foveal region prior to data collection.
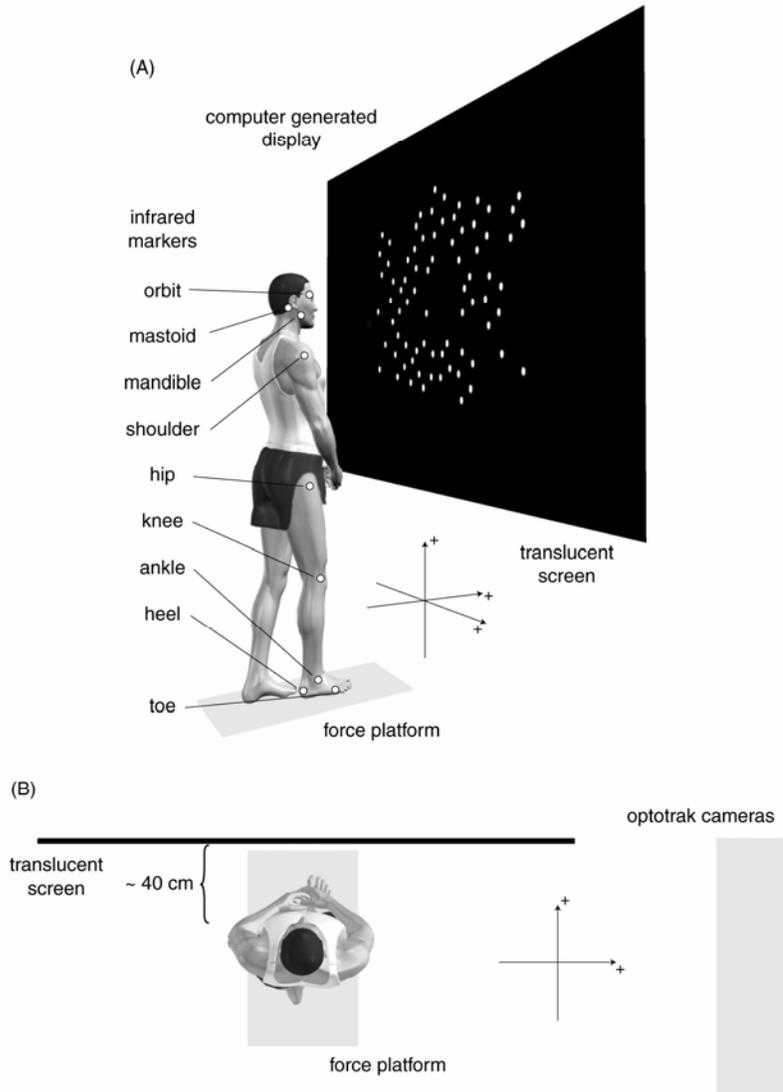
Figure 3.1. Experimental paradigm illustrating stance and marker placements.
Subjects stood about 40 cm from the display screen and wore goggles (not shown) that
restricted their peripheral vision such that no part of the screen's frame or other additional
visual reference cues were available.

The visual display was generated by a graphics workstation (Intergraph, Inc). at a

frame rate of 25 Hz. The display had a spatial resolution of 1024 x 768 pixels with a

vertical refresh rate of 75 Hz, and was rear-projected via a CRT projection system (ECP

4500, Electrohome, Inc.). The suggested position of the stimulus was updated by a

position voltage input specified by a custom D/A Labview signal generator running on a

separate personal computer (E-3400, Gateway, Inc.), and obtained by the visual display program via an A/D board (PC-MIO-16E, National Instruments, Inc.). Subjects wore goggles that limited their visual range to approximately 100° high x 120° wide, while allowing them to wear their prescription eyeglasses, if necessary. The goggles prevented subjects from seeing the edges of the screen or other potential visual cues relevant to stance control.

Subject motion was captured via an active infrared position tracking system (OptoTrak, Northern Digital, Inc.) at a sampling rate of 50 Hz. The OptoTrak cameras were positioned perpendicular to and to the right of the subject. A total of nine points on the body were measured on the right side of the body: toe (distal end of the fifth metatarsal), heel (lateral, posterior calcaneous), ankle (lateral malleolus), knee (lateral tibial tuberosity or approximate joint center), hip (greater trochanter), shoulder (acromion), mandilble, mastoid process and orbit (lateral, inferior protrusion of the frontal bone on the orbit of the eye). The stimulus generator signal and the actual visual display position (cm), as well as anterior-posterior (AP) and medial-lateral (ML) center-of-mass position measured using a force platform (Kistler), were also recorded at 50 Hz via an A/D unit synchronized with the OptoTrak system.

Postural sway measures

An estimate of the center-of-mass position trajectories was computed using a three-segment model based upon the position trajectories of the ankle, knee, hip and shoulder markers. The anthropometric standards published in Winter (1991) were used for the location of the segmental centers of mass:

$$X_{leg}(t) = x_{knee}(t) - 0.394(x_{knee}(t) - x_{ankle}(t))$$
$$Y_{leg}(t) = y_{knee}(t) - 0.394(y_{knee}(t) - y_{ankle}(t))$$
(3.1)

$$X_{thigh}(t) = x_{hip}(t) - 0.433(x_{hip}(t) - x_{knee}(t))$$
$$Y_{thigh}(t) = y_{hip}(t) - 0.433(y_{hip}(t) - y_{knee}(t))$$
(3.2)

$$X_{trunk}(t) = x_{hip}(t) + 0.626(x_{shoulder}(t) - x_{knee}(t))$$
$$Y_{trunk}(t) = y_{hip}(t) + 0.626(y_{shoulder}(t) - y_{knee}(t))$$
(3.3)

where $x_j(t)$ and $y_j(t)$ are the time-varying medial-lateral and anterior-posterior

positions of the ankle, knee, hip and shoulder, respectively. $X_j(t)$ and $Y_j(t)$ are the time-

varying medial-lateral and anterior-posterior positions of the segmental centers of mass

of the leg, thigh and trunk, respectively. The medial-lateral (X) and anterior-posterior

(Y) positions of the total-body center of mass were computed as a weighted sum of the

segmental centers of mass:

$$X(t) = 2*0.061X_{leg}(t) + 2*0.100X_{thigh}(t) + 0.678X_{trunk}(t)$$
$$Y(t) = 2*0.061Y_{leg}(t) + 2*0.100Y_{thigh}(t) + 0.678Y_{trunk}(t)$$
(3.4)

While both AP and ML center-of-mass and center-of-pressure positions were

obtained in this study, the analyses below focus only upon AP center-of-mass (COM)

motions, which were scaled to centimeters for comparison with the visual display

trajectories.

Experimental Design

Subjects were presented with sum-of-sines visual display motion in low and high

amplitude conditions. The sum-of-sines motion consisted of 10 sinusoids, with

frequencies ranging from 0.0244-2.9696 Hz, with each sinusoid beginning at 0° of phase.

The frequencies of the sinusoids were chosen as prime multiples of a base frequency to

avoid low-order harmonics. The amplitudes of the sinusoidal components were varied as 1/frequency to maintain a constant peak velocity across frequency, with the amplitude of each sinusoid in the high amplitude condition twice that of the respective sinusoid in the low amplitude condition. Stimulus (peak) velocity was kept constant across stimulus frequencies as the postural control system is known to be sensitive primarily to the velocity of environmental motion (cf., Kiemel et al., 2006). The amplitude at the highest frequency in the low and high amplitude conditions were 0.0175 cm and 0.035 cm, respectively.

Subjects performed 8 trials in the low amplitude condition and 3 trials in the high amplitude condition. All trials were 260 s in duration, with the sum-of-sines motion active for 250 s and 10 s of quiet stance with a static visual display collected prior to stimulus onset. The order of trials across conditions was randomized for each subject, though all subjects were presented first with a trial in the low amplitude condition. This was done to insure that subjects were familiarized with the experimental task first in the easier of the two conditions. It should be noted that, due to technical difficulties during data collection where measurements from one of the four body markers used in the computation of center of mass were lost and resulted in either the exclusion of the trial (n = 3) or truncation of the data (n = 3) at the end of the trial. This left one subject with 6 trials and another subject with 7 trials in the low condition. In the case of truncation, the data were zero-padded to maintain the same spectral resolution across all trials during analysis (see below).

Experimental Protocol

After subjects were given instructions and consented to participate in the experiment, they were asked to change into a short-sleeved shirt and shorts, without socks. Small infrared-emitting diodes (IREDs) were then attached to the subject at the body landmarks reported above. The wire leads of the IREDs were secured with cloth tape in order to avoid having them obstruct the view of the cameras. Once all markers were in place, the subject was again instructed about and asked to assume the required stance position for the experiment. The experimenter then positioned the center of the stimulus pattern at the approximate center of the subject's visual field.

The subject was then asked to sit and the overhead lights were turned off, with at least 5 minutes of rest taken before the start of the first trial in order to allow the subject's visual system to adapt to the low-light conditions. The overhead lights remained off throughout the remainder of the experimental session, though illumination from the computer monitors, a small desk lamp, and the visual display itself produced low-light conditions, rather than complete darkness. While full dark adaptation of the visual system requires at least 30-40 minutes, the rapid initial phase of this process, which occurs on the order of 2-3 minutes (cf. Bennett et al., 2002) was assumed to be sufficient for the current experimental conditions given the high-contrast stimuli employed. Further, no subjects reported any perceptual discomfort after only a few minutes in the low-light conditions.

Prior to each trial, the subject was asked to stand and assume the required position, with the experimenter, using a small handheld flashlight, assisting the subject with foot placement and insuring that the wire leads did not hamper the subject's motion. The foot position was marked on the force platform where the subject stood to maintain a

consistent position across trials. Once the subject was in position, the experimenter first

checked that all IREDs were visible by the OptoTrak cameras, then asked the subject to

signal that he/she was ready to begin the trial. Data collection was started, then after a

delay of at least 10 s, stimulus motion was started. Once the trial was complete, the

experimenter assisted the subject in sitting down, and at least 120 s of seated rest was

given. The total experimental session lasted approximately 120 m.

Analysis

Linear, spectral analysis was performed for each trial by computing the individual

Fourier transforms of the time series of postural displacements and of stimulus position.

For each trial, the transfer function or frequency-response function (FRF) at each of the

stimulus frequencies was computed by dividing the transform of the center-of-mass by

the transform of the stimulus, and then averaged across trials. The FRF is complex-

valued function; its absolute value is gain and its argument is phase. By definition, a

positive phase indicates that sway lead the visual motion.

To characterize the gains and phases of the sampled group, we used the absolute

value and argument of the average FRF across subjects in each condition to obtain group

gain and phase, respectively. For each condition and stimulus frequency, an F-statistic

was used to compute 95% confidence ellipses in the complex plane based on the

assumption that the real and imaginary parts of the FRF come from a bivariate normal

distribution. The range of absolute values and arguments for points on the boundary of

the ellipses were used to obtain conservative 95% confidence intervals for group gain and

group phase.

To compare gain and phase between the low- and high-amplitude conditions at each frequency, we computed the ratio $r = z_{high}/z_{low}$, where z_{high} and z_{low} are the mean FRF for the low-and high-amplitude conditions, respectively (cf. Kiemel et al., 2006). Similar to the above, a 95% confidence region, R, was computed in the complex plane for r and the range of absolute values and arguments were used to obtain 95% confidence intervals for the gain ratio and phase difference. The region, R, was defined as follows: for any possible r, let $p(r)$ be the P value from testing whether $z_{high} - r z_{low}$ is significantly different from zero using an F-test. Then, $R = [r : p(r) \geq 0.05]$. R is the complex analog of the Fieller confidence interval for the ratio of the two means (Miller, 1986).

Results

Previously, we (e.g., Jeka et al., 2000; Oie et al., 2002) and others (e.g., van Asten et al., 1988a; Dijkstra et al., 1994a,b; Peterka and Benolken, 1995; Soechting et al., 1979) have shown that postural sway responses to highly predictable, sinusoidal motions of the visual environment strongly reflect the structure of stimulus motion. In Figure 3.2A, we present an example of this effect, showing how postural sway responses to simple sinusoidal motion of the visual environment strongly reflect stimulus motion. By contrast, in the current experiment, the motion of the visual display was comprised of the addition of 10 unique sinusoidal components, and none of our subjects reported being able to predict the motion of the stimulus. In Figure 3.2B, the relationship between stimulus motion and postural response seems less evident, upon visual inspection. However, the averaged amplitude spectra shown in Figure 3.2C revealed peaks in the subject's postural sway responses at the stimulus frequencies, showing that the postural

63

response was indeed structured by the unique sinusoidal components of the stimulus. All subjects provided similar results.
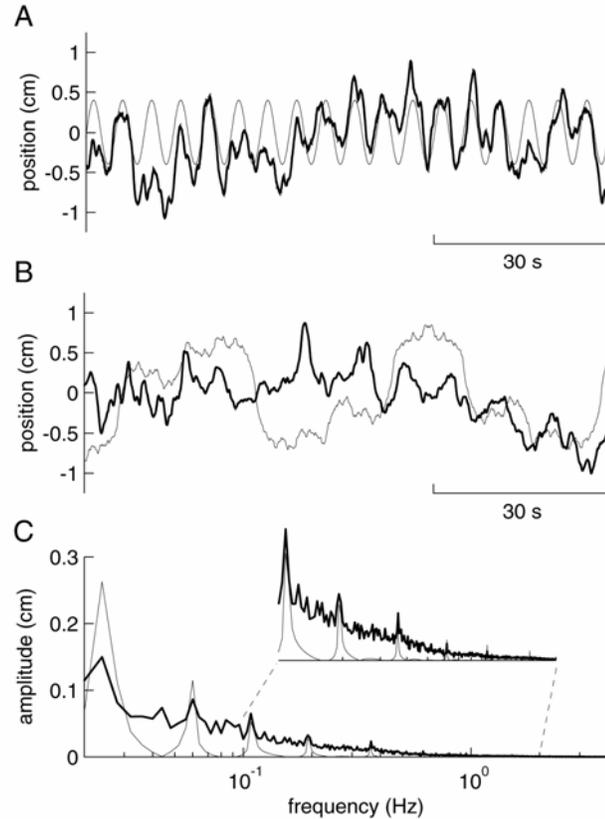

Figure 3.2. Exemplar trajectories and amplitude spectra. A) An exemplar trajectory illustrating CoM response (dark line) to a simple sinusoidal visual stimulus (light line). B) CoM response (dark line) to sum-of-sines visual motion (light line). C) Averaged amplitude spectra of CoM response (dark line)(n = 8) to sum-of-sines visual stimulus motion (light line).

Gain and Phase Functions

In Figure 3.3 (A and B), the group gain and phase response across all subjects is shown. As expected, gain (Figure 3.3A) was found to vary with stimulus frequency, with a maximum found to be in the range between 0.2-0.4 Hz, and with gains in the low amplitude condition found to be higher than those in the high amplitude condition. Gain was found to be significantly greater than zero ($p < 0.05$) for the eight lowest frequencies

(0.024 – 1.432 Hz)), indicating that a detectable response to stimulus motion. For the two

highest frequencies, 2.104 and 2.936 Hz, gain was not significantly greater than zero in at

least one of the conditions ($p > 0.05$).
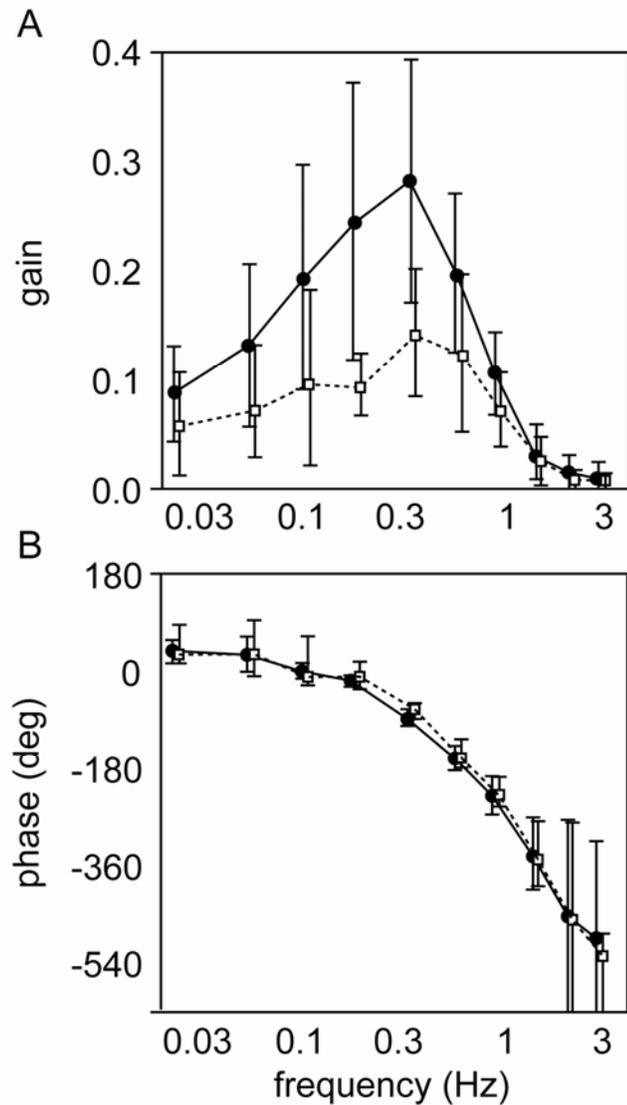
Figure 3.3. Group gain and phase functions. A) Mean gain across subjects for high amplitude (squares) and low amplitude (circles) conditions as a function of stimulus frequency. B) Corresponding mean phase across subjects. Errorbars indicate 95% confidence intervals.

Phase (Figure 3.3B) was also found to vary with stimulus frequency, starting out at a slight phase lead at low frequencies, and showing an increasing phase lag of about 360 deg as frequency increased from 0.024 to 1.432 Hz. At the two highest frequencies, phase could not be reliably estimated due to the difficulty in detecting a response to visual motion.
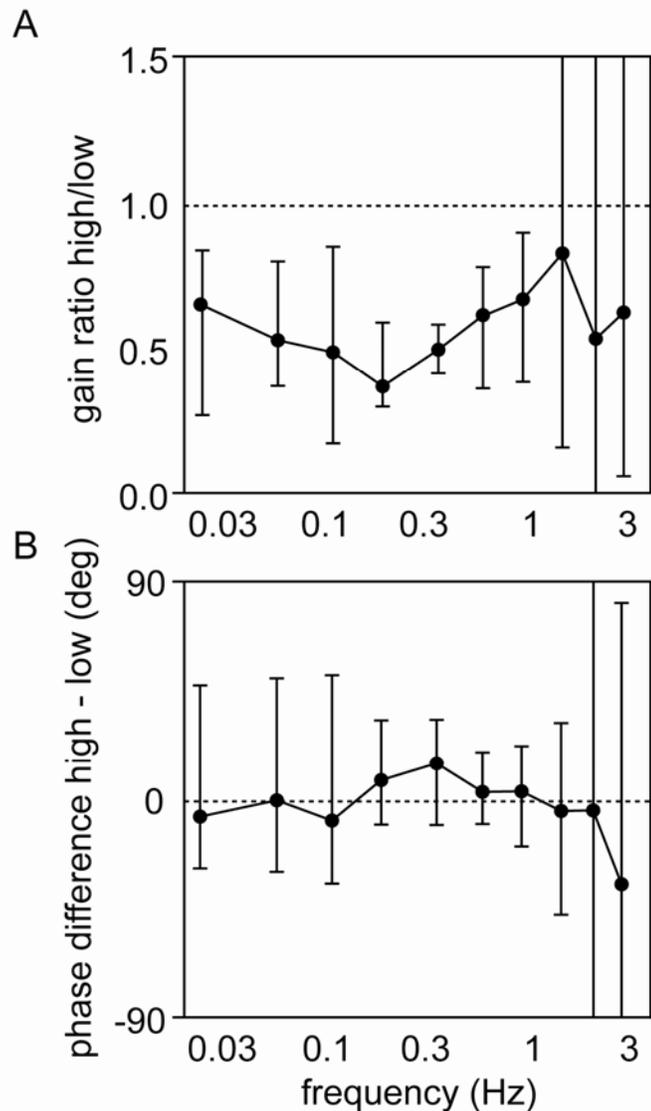

Figure 3.4. Gain ratio and phase difference. Functions describing the differences in postural response to motion of the visual scene between low- and high-amplitude conditions. Errorbars indicate 95% confidence intervals.

When visual motion amplitude was doubled in the high-amplitude condition, gain decreased significantly at all frequencies from 0.024 to 0.904 Hz (Figure 3.4 A). At all 10 frequencies, the high- to low-amplitude gain ratio was not significantly different from 0.5. A gain ratio of 0.5 corresponds to equal response amplitudes in both conditions. No significant differences in phase were detected between the two conditions (Figure 3.4 B).

Discussion[2]

One of the advantages of using sum-of-sines stimuli over different frequency sinusoids in different trials, as with the pseudorandom stimuli used in Peterka (2002), is that it allows one to estimate the transfer function at different frequencies simultaneously. Under these conditions, the dynamics of the postural system can be assumed to be the same across stimulus frequencies at a given amplitude. In this study, we utilized sum-of-sines techniques and observed changes in gain with stimulus amplitude that are consistent with previously observed changes in gain made in our laboratory (Oie et al., 2002) and by others (Peterka, 2002; Peterka and Benolken, 1995): In the low-amplitude condition, group gain was found to be significantly different from gain in the high-amplitude condition at frequencies between 0.024 and 0.904 Hz. These results are consistent with an interpretation of an adaptive sensory re-weighting mechanism that allows stance control under varying sensory conditions.

Doubling the amplitude of visual motion led to a change in gain of roughly one half. This indicates that the sway response amplitude remained roughly constant across conditions. Peterka and Benolken (1995) found that, when stimulus amplitude was

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[2] The results of this experiment were reported in Kiemel et al. (2006). The discussion presented here focuses only upon aspects related to multisensory re-weighting and position coupling addressed in this dissertation thesis.

increased, response amplitude initially increased but reached saturation, resulting in a plateau in gain at high motion amplitude. The current finding that the gain ratio across stimulus frequencies was not different from 0.5 suggests that the amplitudes used in this study were within this saturation region.

However, as has been argued previously, any amplitude dependent change in gain indicates some type of nonlinearity in the postural control system. Parameters of linear stochastic models fit to the postural sway trajectories in this study did not, however, provide strong evidence for position coupling of body sway to visual motion. Fifth-order, linear stochastic models were fit to COM trajectories using the maximum likelihood method, and used to estimate parameters of the autocovariance function of the residual sway (i.e., sway with the effect of stimulus input subtracted). Five model parameters were associated with the coupling of sway to visual motion. Of these, only the velocity coupling coefficient was found to be significantly positive for all subjects and conditions ($p < 0.05$). Its mean across subjects was significantly positive in both conditions ($p < 0.0002$) and was significantly higher in the low-amplitude condition than in the high-amplitude condition ($p = 0.001$).

Velocity coupling in the postural control system between visual motion and sway has been argued for based upon both theoretical analysis (Schöner, 1991) and empirical evidence (Dijkstra et al., 1994; Jeka et al., 2000). It should be noted, as well, that velocity coupling in posture is not limited to visual motion, but has also been found similarly with somatosensory input (Jeka et al., 1998a, 2004; Kiemel et al., 2002). The current findings support these previous results.

68

By contrast, none of the non-velocity related coupling coefficients exhibited a consistent sign across subjects, though for a substantial number of subjects, these coefficients were significantly different from zero ($p < 0.05$). For higher-order coefficients (i.e., acceleration and the 3rd and 4th derivatives of stimulus position), this was true for 8, 6 and 5 subjects, respectively. This was true, however, for only 2 of the 10 subjects in the case of the position coupling coefficient. The means of the position coupling coefficient were different from each other in the two conditions ($p = 0.045$), with the mean in the low-amplitude condition being significantly less than zero ($p = 0.021$) and the mean in the high-amplitude condition not significantly different from zero ($p = 0.67$).

Previously, Jeka et al. (2000) have argued for position coupling based upon a second-order model. Additionally, Jeka et al. (1998a) similarly argued for position coupling to somatosensory inputs. The results presented here with a more accurate fifth-order model provide only weak evidence for position coupling. However, it is important to consider that the lack of evidence for position coupling is based on a descriptive model; its interpretation depends upon consideration of a mechanistic model. For example, optimal control models such as those presented by Kiemel et al. (2002), Kuo (2005) and van der Kooij et al. (1999) generate estimates of body position and velocity based upon noisy sensor inputs, which are multiplied by feedback gains in order to specify the resultant motor command. For such a model, zero position coupling implies that the body state estimates are not based upon position of the visual scene, but only upon velocity and higher-derivative information. It does not imply, however, that the position feedback gain is zero.

69

Chapter 4: Experiment – The Dynamics of Sensory Re-weighting

In our previous investigations examining sensory re-weighting (Oie et al., 2001, 2002), including the preliminary results that I have presented in Chapter 3, my focus has been on characterizing how the transfer function of the postural control system depends upon stimulus amplitude. In order to provide the initial characterization of the sensory re-weighting mechanism for human postural control that represents a culmination to the body of work presented in this thesis we examined the question: What is the time scale over which sensory re-weighting occurs?

Introduction

The fact that we have multiple sensory modalities that are sensitive to different forms of physical energy and can provide information that is unique or redundant necessitates that our nervous systems estimate which sensory signals are relevant within a given sensory context. How we accomplish this multisensory integration has been the focus of several recent theoretical efforts (e.g., Anastasio, 2006; Pouget, 2006; Shams and Ma, 2006), which have argued that neural computation can be understood as probabilistic (i.e., Bayesian) in nature: Because neural systems are inherently noisy, their

sensory inputs cannot be strictly deterministic. It is postulated that neurons compute the conditional probability of the stimulus value (e.g., if a target is present or not within a neuron's receptive field), given the uncertainty in their sensory inputs (c.f., Anastasio and Patton, 2003, for an in-depth treatment of the Bayes' rule model to multisensory neurons in the deep superior colliculus).

The Bayesian framework can also be applied to the problem of estimating quantities that change stochastically with time. In the case of a linear stochastic system, Bayesian inference can be implemented using a Kalman filter. Kalman filters have been used, for example, in models of postural control of human upright stance (van der Kooij et al., 1999; Kiemel et al., 2002; Kuo, 2005). In these models, a Kalman filter continually estimates the body's position and velocity based on noisy inputs from multiple senses, and these estimates are used to generate appropriate motor commands to stabilize the continual deviations from the upright vertical that characterize postural behavior.

In the vast majority of experimental contexts at the neural and behavioral level, the Bayesian framework has been applied to paradigms in which sensory fusion is treated on a condition by condition basis (cf., Anastasio and Patton, 2003; Peterka, 2002; Kiemel et al., 2002). Sensory parameters are arranged discretely so that conditional probabilities can be calculated independently in each condition. Such paradigms, however, avoid the important question of how behaving animals continuously adapt to changing environmental conditions. For example, one common experimental technique in the postural domain is to have subjects stand within a visual "moving room". The walls of the laboratory move sinusoidally but the floor that the subject stands upon remains

motionless, creating conflicts between vision and the other senses (i.e. proprioception and the vestibular sense). The visual motion of the walls is initially small, making it difficult to distinguish self-motion from the motion of the room, leading to a strong postural response (gain on the order of 1). What happens if amplitude of the sinusoidal visual input doubles? A linear system depends linearly on its inputs, so doubling the amplitude of a sinusoidal input to a linear system would double the response at the frequency of the input. What in fact happens is that gain decreases dramatically, indicating a nonlinear process. One of the prevailing hypotheses is that this non-linear response reflects a decrease in coupling, or weighting to that particular sensory modality which is compensated at least partially by an increase in weighting to other sensory inputs in order to prevent a loss of balance (e.g., Carver et al., 2005; Keshner et al., 2004; Mahboobin et al, 2005; Oie et al., 2002; van der Kooij et al, 2001; however, see Mergner et al., 2003 for an alternative interpretation). The Bayesian framework has also been used to account for multisensory re-weighting (in postural control) through an adaptive Kalman filter (van der Kooij et al., 2001; Carver et al., 2005). However, because of the paucity of empirical research about the real-time properties of the multisensory re-weighting, namely, the dynamics of re-weighting, adaptive schemes are not motivated biologically. The present investigation tested a prediction of the Carver et al. (2005) model about the time course of re-weighting.

In the Carver et al. model, adaptation is based on minimizing the mean squared torque specified by the neural controller. As a consequence of this adaptation scheme (see Discussion), the Carver et al. (2005) model predicts a temporal asymmetry in response to changes in environmental motion. Specifically, if the amplitude of

environmental motion is suddenly changed from one value to another, the initial decrease in gain when environmental motion is increased is predicted to be faster than the initial increase in gain when environmental motion is decreased. Here, we present experimental results that are consistent with this prediction.

Method
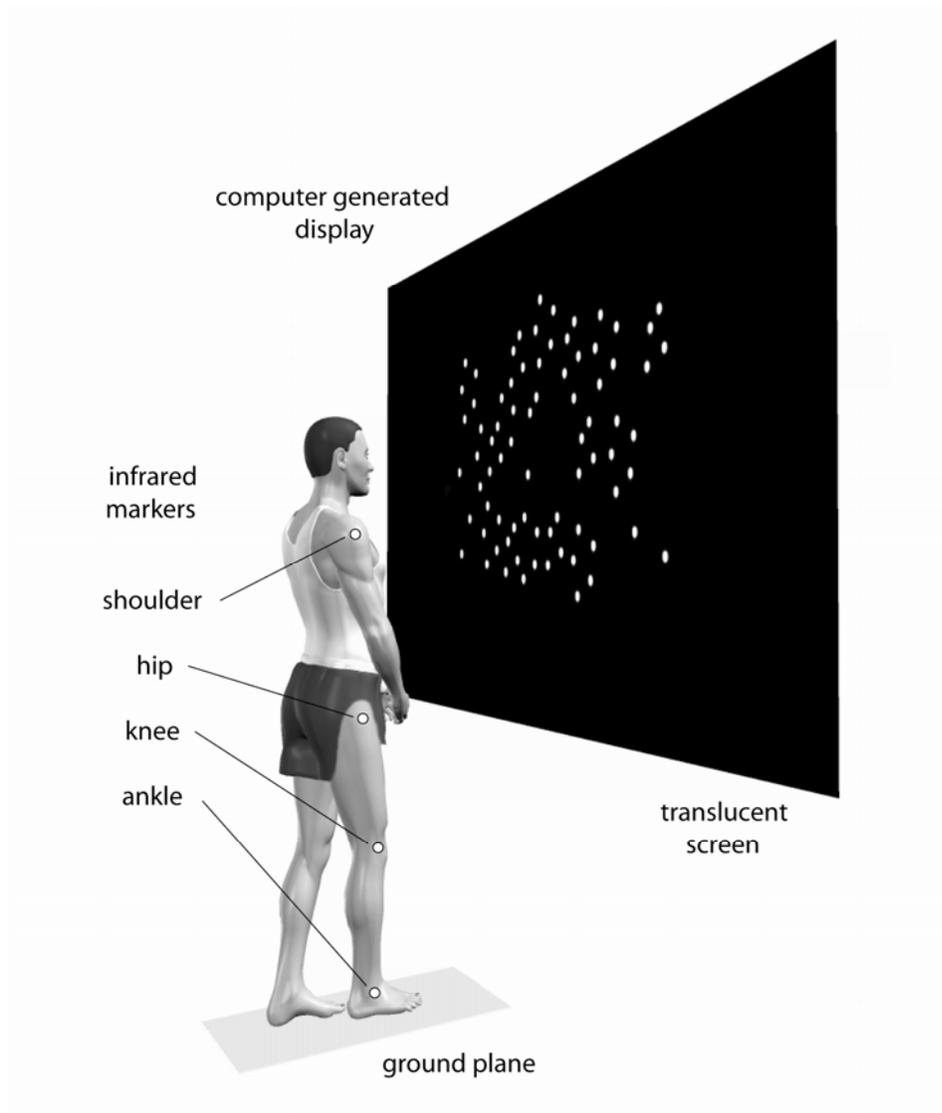
Figure 4.1. Experimental paradigm.

Subjects

Thirty participants (15 female, 15 male, mean age 20.9 (± 1.6) years of age) took part in this study. All participants had normal or corrected-to-normal vision, were free of any self-reported musculoskeletal or neurological disorders, and gave written consent to participate according to the guidelines implemented by the Internal Review Board of the University of Maryland.

Experimental Setup and Procedures

Participants were asked to stand quietly, approximately 0.5 m from a large translucent screen (2.0 m x 1.0 m, Da-Lite Screen Company, Inc., Warsaw, IN)(see Figure 4.1). A pattern of randomly positioned, white 2-D triangles (approximately 0.2º x 0.3º x 0.2º) in a front-parallel plane on a black background was rear projected onto the screen via a Direct Drive Image Light Amplifier (D-ILA) projector (JVC M15, JVC America, Wayne, NJ). The visual displays were generated using a desktop PC (Dell PWS650, Dell, Inc., Austin, TX) with a Wildcat4 7210 video adapter (3Dlabs US, Madison, AL) at a resolution of 1280 x 1024 pixels.

Large-scale, sinusoidal environmental motion was specified by varying the suggested position of the virtual 'wall' of triangles in a forward-backward direction relative to the participant. The focus of expansion of visual motion was positioned at the approximate center of the participant's foveal region prior to the start of data collection, and no triangles were placed near the focus of expansion to suppress the visibility of aliasing effects. Participants were asked to keep their head level, eyes open, gaze directed at the focus of expansion and to avoid locking their knees during the conduct of an experimental trial. Stimulus motion comprised a 0.4 Hz sinusoid whose amplitude was

changed twice within a 360 s trial, from 0.3 cm to 1.2 cm and back to 0.3 cm at 120 s and 180 s into the trial, respectively. Three trials were run for all participants.

It should be noted that the 0.4 Hz stimulus frequency was utilized as a compromise between temporal resolution and the robustness of the postural response to stimulus motion, which was the result of extensive pilot experimentation. Previous results (e.g., Dijkstra et al., 1994a, b; Jeka et al.., 2000; Oie et al., 2002) have shown that postural responses to sinusoidal visual motion are most consistent at a stimulus frequency of ~02 Hz, with increasing gain and phase variability as stimulus frequency is increased or decreased. However, it was thought that sensory re-weighting is a relatively fast process. In part, this was due to unpublished analyses in that showed little evidence of adaptive changes in postural responses at the beginning of experimental trials at the onset of visual stimulus motion. As a 0.2 Hz stimulus would allow estimation of cycle-by-cycle frequency response functions (FRF) every 5 s, an increase in stimulus frequency to 0.4 Hz was used to improve the temporal resolution without overly degrading the stability of the postural responses to visual stimulus motion.

Participants' postural responses to visual display motion were captured using an OptoTrak camera position tracking system (Northern Digital, Inc., Waterloo, ON, CA) at a sampling rate of 60 Hz. Markers were placed at the heel (posterior calcaneous), ankle (lateral malleolus), knee (lateral tibial tuberosity), hip (greater trochanter) and shoulder (acromion) on the right side of the body. Center-of-mass (COM) trajectories were estimated using a three-segment model based upon the trajectories of these markers (cf. Winter, 1991).

Analysis

To characterize how the postural response to visual scene motion varied as a function of time, we used the FRF from visual scene position to COM position at the stimulus frequency. As a compromise between accuracy and temporal resolution, we divided each trial into 72 5-s intervals (two stimulus cycles per interval) and computed the FRF for each interval. Each FRF was computed by dividing the Fourier transform of the COM trajectory by the Fourier transform of the stimulus trajectory. The FRF is complex-valued. The absolute value of the FRF is gain; the postural response amplitude divided by the stimulus amplitude. The argument of the FRF is phase, which indicates the temporal relationship between postural response and stimulus motion. A positive phase indicated that COM position lead stimulus position. In addition to the FRF, position and velocity variability of the residual sway response was computed as the standard deviation of the COM motion after the deterministic response of the postural response at the stimulus frequency was removed (cf., Jeka et al., 2000), over 60 s segments, with a time step of 0.167 s.

For each subject and time interval, the FRF was averaged across trials. In general, FRFs changed slowly with time except at the beginning of the trial and after the two switches in stimulus amplitude (see Results). To describe these slow changes, we fit FRFs by a linear function of the time-interval index over three separate time periods: before the first switch, between the first and second switches, and after the second switch. To avoid the effects of relatively fast changes in postural responses when sensory motion was initiated or changed, the first 6 time intervals (30 s) were excluded. We fit the FRFs by computing least-squares fits of their real and imaginary parts.

90

The linear fits were used to estimate the FRFs in the last time interval before each

switch and in the last time interval of the trial. We performed a statistical analysis on

these three estimated FRFs and the FRFs from the first time interval after each switch.

We averaged the resulting five FRFs across subjects and computed group gains and

phases as the absolute value and argument, respectively of the averaged FRFs. Null

hypotheses involving group gains and phases were tested under the assumption of

multivariate normality for the real and imaginary parts of the FRFs. For each null

hypothesis, group gains and phases for the constrained and unconstrained models were

estimated using the method of maximum likelihood, and Wilks' Λ, which is related to the

likelihood ratio, was tested using the same degrees of freedom as in linear regression

(Seber, 1984). For group gain and phase, we made comparisons for all pairs of time

intervals. To test for temporal asymmetry, we tested whether the changes at the two

switches summed to zero, that is, H_0: (b1-a1) + (b2-a2) = 0 (see Figure 4.2). A closed

testing procedure (Hochberg and Tamhane, 1987) was used to control the family-wise

Type I error rate at $\alpha = 0.05$ for all test on gains, and separately for all tests on phase.

Results

Figure 4.2 shows two examples of the mean cycle-to-cycle gain and phase

trajectories for different subjects (A-C and B-E, respectively). In general, subjects

exhibited similar qualitative changes in response to the changes in stimulus motion

amplitude. That is, gain decreased quickly when stimulus amplitude was increased at 120

s in the trial, and increased more slowly when stimulus amplitude was subsequently

decreased at 180s. Some individual differences were observed in the overall response to

stimulus motion; for example, compare the overall gain between the subjects' results in

Figures 2A and 2D, respectively. These individual differences are largely responsible for the inter-subject variability shown in the mean cycle-to-cycle gain and phase across all thirty subjects presented in Figure 4.3.

Across subjects, when visual motion amplitude was low ($t \leq 120$ s, $t \geq 180$ s), gain was observed to be higher than when visual motion amplitude was high (120 s $< t <$ 180 s), with phase showing an approximately constant phase of about -90º (see Figure 4.2). Pair-wise contrasts revealed significant differences between the estimated FRFs: b1 > b2 (p < 0.001) and b2 < b3 (p < 0.001), and no difference between b1 and b3 (p = 0.469). This result reproduces the characteristic gain-dependence of the postural response upon the amplitude of visual motion, where gain has been observed to be higher when stimulus amplitude was low, and lower when stimulus amplitude was high (e.g., Kiemel et al., 2006; Oie et al., 2000; Peterka and Benolken, 1995; Mergner, et al, 2003).
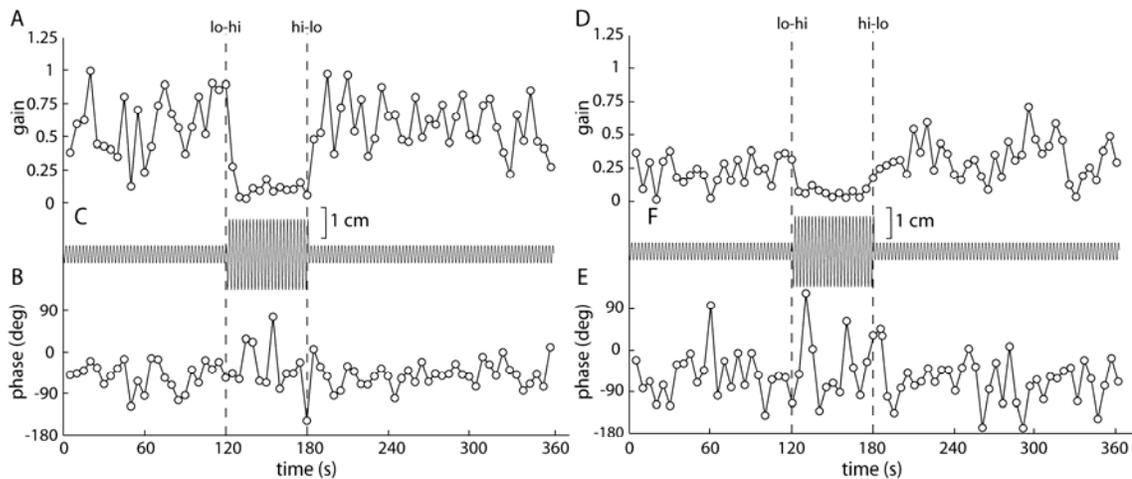

Figure 4.2. Examples of mean gain and phase responses of two subjects. Mean cycle-to-cycle gain (A & D, respectively) and phase (B & E, respectively) for two individual subjects.

When visual motion amplitude was either increased or decreased (at 120 s and 180 s, respectively. See Figure 4.2A and 4.2B), the resultant change in postural response

was different. Gain of the averaged FRFs showed a significant difference ($p < 0.001$) between time intervals b1 and a1, when visual motion amplitude was increased, indicating a significant decrease in gain within the first two cycles of stimulus motion. A significant change in phase was observed ($p = 0.041$). By contrast, no difference ($p = 0.518$) was observed between b2 and a2, when stimulus motion amplitude was subsequently decreased indicating that gain of the averaged FRF did not increase significantly within the first two cycles of stimulus motion after the decrease in stimulus motion amplitude. No change in phase was detected ($p = 0.471$).
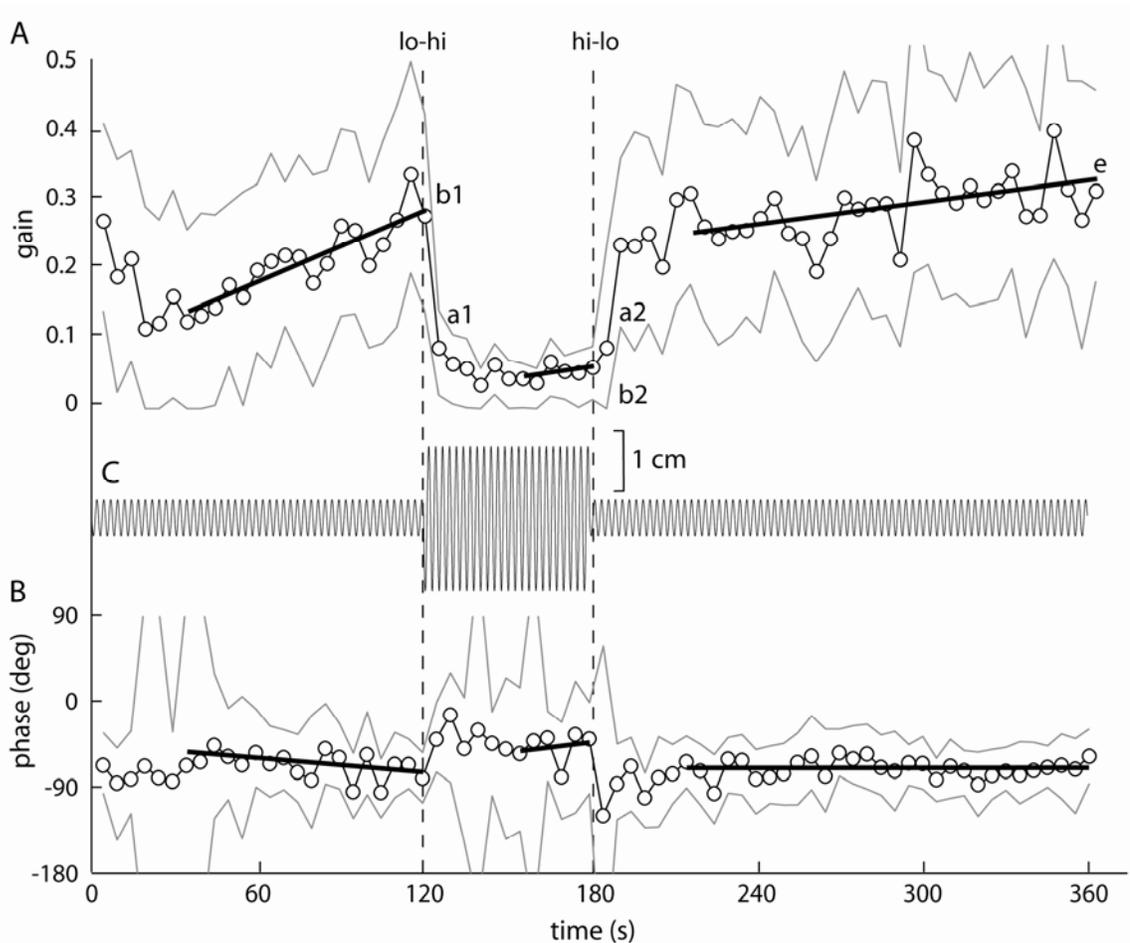

Figure 4.3. Group gain and phase trajectories and stimulus motion position. Mean (A) Gain and (B) phase across subjects. Dark lines indicate results of linear fits, which were used to estimate FRF values at b1, b2 and b3. Light lines indicate endpoints of conservative 95% confidence intervals (cf., Kiemel et al., 2006)

93

Testing more explicitly for temporal asymmetry, we tested whether the sum of the changes in FRFs at the two amplitude switches summed to zero. Results revealed a significant difference from zero in the gain of the summed FRFs ($p = 0.009$), indicating that the observed changes in FRFs over the same amount of time (i.e., 2 stimulus cycles) were significantly larger (i.e., faster) when stimulus motion increased versus when it decreased.

Finally, both position and velocity variability showed a significant increase when stimulus motion amplitude was increased (p's < 0.002)(see Figure 4.3). After stimulus motion amplitude was decreased (at 180 s), both position and velocity variability remained significantly higher (p's < 0.03) than during the initial portion of the trial prior to the initial increase in stimulus amplitude at 120 s.

Discussion

Sensory re-weighting as an adaptive process in the nervous system is not unique to the control of upright stance. Hypotheses of sensory re-weighting appear across many functional behaviors, including object perception and manipulation (Ernst and Banks, 2002), perception of full-body motion (Lambrey and Berthoz, 2003), and goal-directed reaching (Sober and Sabes, 2003, 2005). However, few studies have investigated the dynamics of the re-weighting process. Here we studied the time course of sensory re-weighting and found evidence of a temporal asymmetry, consistent with the predictions of an adaptive model (Carver et al., 2006).

The Carver et al. (2005) model contains an adaptive Kalman filter that uses noisy sensory measurements to estimate the body's position and velocity (see Introduction).

The relative weighting of visual and non-visual inputs in the Kalman filter is specified by an adaptive parameter, θ, which is continually adjusted to minimize a performance index J, the mean squared ankle torque specified by the neural controller. (This choice of J is not crucial; there are other choices that lead to qualitatively similar behavior.) J is minimized by changing θ at a rate proportional to $-dJ/d\theta$ (gradient descent).
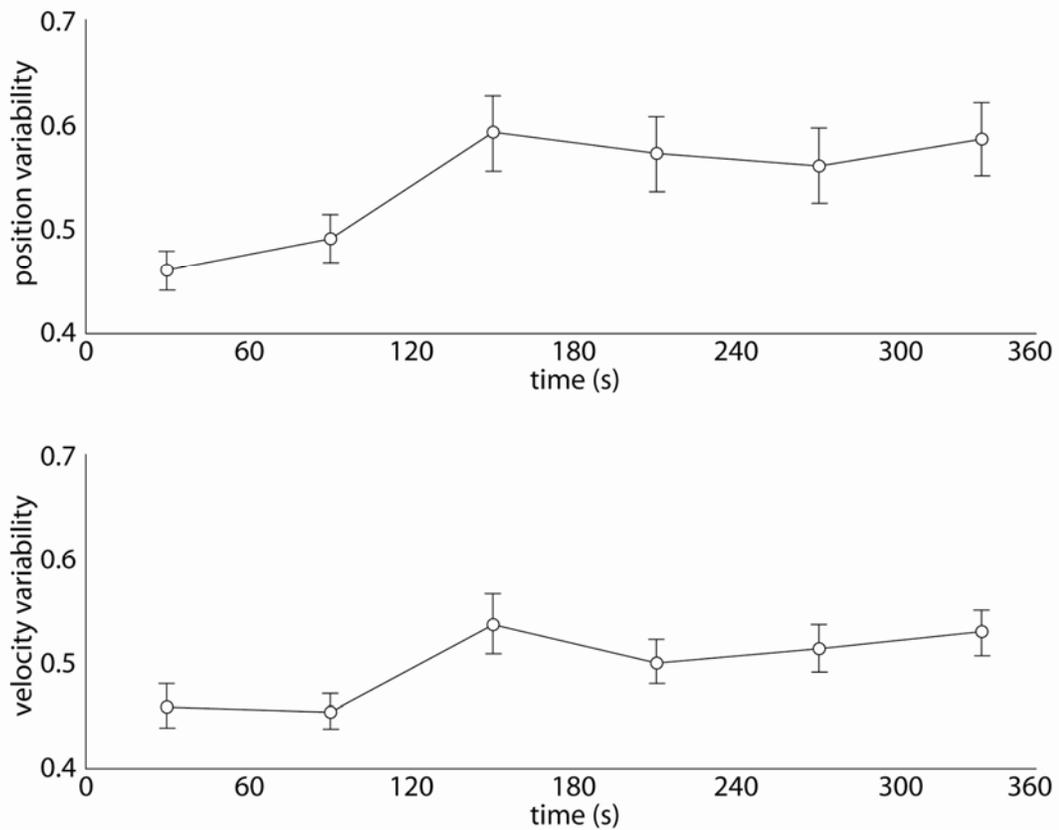
Figure 4.4. Position and velocity sway variability. Mean position (upper) and velocity (lower) variability across subjects, indicating the mean sway response after the induced effects of stimulus motion were removed over 60 s time intervals. Error bars indicate ± s.d.

The model's adaptive scheme leads to a temporal asymmetry like that reported here (Carver et al. 2006). When motion of the visual scene is small, adaptation leads to substantial weighting of both visual and non-visual inputs, since using all the available sensory information reduces the effect of sensory noise on sway and, thus, the need for

corrective ankle torques. When visual motion amplitude suddenly increases, the sway at the stimulus frequency suddenly increases, leading to a large increase in corrective ankle torques that is highly sensitive to changes in the adaptive parameter. As a result, the adaptive parameter changes quickly to down-weight vision and gain quickly decreases. Later, when visual motion amplitude suddenly decreases, there is only a small decrease in sway at the stimulus frequency, since gain is initially low. This small decrease in sway leads to a small decrease in corrective torques that is not very sensitive to changes in the adaptive parameter. As a result, the adaptive parameter changes slowly to up-weight vision and gain slowly increases.

The preceding description of the model's temporal asymmetry refers to the initial change in gain after a change in visual motion amplitude. In the model, the change in gain produced by a sudden change in visual motion amplitude is not exponential and, therefore, cannot be characterized by a single fixed time constant. Instead, changes in gain can be viewed as reflecting a changing time constant that depends on the current gain level. When gain is high, the time constant is small (fast); when gain is low the time constant is large (slow). Note that the time constant depends on the current gain level, not the direction in which gain is changing. For example, if visual motion amplitude is low and suddenly changed by a small amount, the model predicts that gain will quickly converge to a new level regardless of whether amplitude is increased or decreased.

The sway variability results were only partially consistent with the Carver et al (2005) model. The Carver model predicts the observed increase in sway variability as vision is down-weighted (120-180 sec - Fig 2). However, the predicted decrease in sway variability as vision is up-weighted (180-240 sec - Fig 2) was not observed. The latter

result is also not consistent with previous studies which found a consistent trade-off between re-weighting and variability (Allison et al., 2006). This trade-off reflects the degree of weighting to a stimulus versus the precision of estimating body dynamics. Large amplitude sensory inputs are 'down-weighted' to minimize responses that would threaten stability if, for example, coupling to vision remained high. However, the consequence of down-weighting vision is reduced sensory information available for estimation, leading to increased sway variability. Conversely, it is advantageous to 'up-weight' small amplitude sensory inputs because more information is available for estimation, leading to a reduction in sway variability. Strong coupling to small amplitude inputs does not threaten stability. While this scenario has been supported in previous studies in which gain and sway variability was averaged over 2-4 minute trials with constant-amplitude sensory stimuli (Allison et al., 2006), the dynamic measures used here indicate that overall stability does not behave similarly when the visual stimulus changes abruptly.

For example, perhaps the first adaptive model of stance control was that of van der Kooij et al. (2001), which proposed an internal model of body and sensor dynamics based on an optimal (Kalman) estimator, as well as an internal model of the dynamics of the environment. However, Carver et al (2005) have demonstrated that an internal model of the visual environment is not necessary to reproduce the amplitude-dependent gain and roughly constant phase that is typically observed with visually induced postural responses.

The observed temporal asymmetry in sensory re-weighting can also be evaluated from a functional perspective: Upright stance is inherently unstable, and the stance

control system must continuously respond to internal and external perturbations that could produce an injurious fall. In our paradigm, when visual motion amplitude is low, vision provides a relatively stable source of information for stance control. When visual motion amplitude is increased beyond the stability boundaries of upright stance, visual information will provide a poor source of information for stance control. Under such conditions, if gain to visual motion remains high, the large visual motion amplitude threatens balance, and the stance control system must diminish the visual weighting rapidly in order to maintain upright standing. On the other hand, if current visual motion amplitude is large and stance is already stable, decreasing visual motion amplitude does not threaten balance and adapting rapidly to the new sensory conditions is not critical to avoid falling. One may argue that slow up-weighting reflects a conservative CNS strategy. Rapid up-weighting may cause instability if the change in sensory conditions is transient. Slow up-weighting insures stronger coupling to only sustained changes in the sensory surround. Thus, the temporal asymmetry can be interpreted to reflect a scheme in which the nervous system commits resources to sensory re- weighting based upon a functional need. Balance control entails an inherent "cost function", minimizing fall-risk, which modulates adaptive processes such as sensory re-weighting, suggesting a cognitive component to the re-weighting process.

Conclusion

De Ruyter van Steveninck and colleagues have also recently shown evidence for sensory re-weighting at the level of neural coding (Brenner et al, 2000; Fairhall et al, 2001). The authors presented evidence of adaptive scaling of the transfer function of motion-sensitive neurons in the fly visual system based upon the variance of the visual

input, such that information is optimized across a wide range of sensory contexts, as well as a temporal asymmetry dependent upon whether variance increased or decreased. Adaptation of the sort demonstrated by Brenner et al (2000) and Fairhall et al (2001), as well as in the current study, where adaptation is based upon some statistical property of the sensory input necessitates that the nervous system estimates these statistics, at least implicitly. As pointed out by Tin and Poon (2005), the related concepts of estimation, adaptive control and internal models have been influential in furthering our understanding of processes of sensorimotor and multisensory integration. The present empirical results add to our understanding of adaptive processing by demonstrating that the temporal asymmetry observed in sensory re-weighting dynamics may be a general property of adaptive estimation in the nervous system.

Chapter 5: Summary and Conclusions

In order to survive in the wide range of sensory contexts that comprise our physical world, the nervous system employs adaptive mechanisms that optimize functional behaviors within a given sensory environment. The control of human bipedal stance requires that the nervous system obtain relevant information about the environment and the body's relationship with it from multiple sensory systems. This dissertation examines the question: How does the nervous system accomplish this when the sensory environment compromises the information available from a given sensory system (e.g., vision in dark versus light conditions or proprioception on stable versus compliant or slippery surfaces)?

In previous theoretical and empirical work, we have provided evidence of nonlinearities that are consistent with an hypothesis of sensory re-weighting: The nervous system adapts to changing sensory contexts by decreasing its dependence, or weighting, on the compromised system and increases its weighting of other inputs that provide the most reliable information for stance control in order to prevent a loss of balance. Here, empirical findings have been presented that further support the sensory re-weighting

hypothesis, and advance efforts towards characterizing by providing empirical results that provide important constraints on any proposed sensory re-weighting scheme.

First, postural responses to complex visual motion consisting of the sum of 10 different sinusoidal components, were measured at two different amplitudes. Changes in the gain of body sway to visual motion were consistent with the nonlinearities previously interpreted as evidence for sensory re-weighting. The observed changes in gain did not vary significantly as a function of stimulus frequency. Recall that, because the postural system has been shown to be primarily velocity-sensitive (cf., Kiemel et al., 2006), the components of the stimuli used in the study all had the same peak velocity within a condition and that the amplitude of each component was doubled in the high amplitude versus the low amplitude condition. That there was no dependence of the changes in gain upon frequency, then, indicated that the re-weighting process affected the response at all stimulus frequencies in an approximately equal fashion. This may be suggestive of a relatively simple mechanism for multisensory re-weighting, though the results of this study can not address questions of whether more complex interactions within the sensory re-weighting process may exist; for example, that changes in stimulus motion at one frequency might affect responses at some or all other frequencies.

Further, analyses (cf., Kiemel et al., 2006) that fit linear stochastic models directly to sway trajectories found 1) fifth-order dynamics, 2) strong evidence of velocity coupling and 3) little evidence for position coupling. While these results provide greater knowledge that provide important constraints to models of postural control, individual differences also provide further questions: While the majority of subjects exhibited similar patterns of in the fitted model structure and parameters (i.e., fifth-order dynamics,

101

strong velocity coupling, weak or no position coupling), a substantial number of subjects revealed significant coupling to higher-order aspects of stimulus motion, though the patterns of these coefficients were not the same across subjects. However, as models in this study were fit to trajectories of a single-point estimate of total body center-of-mass (CoM) motion, it is possible that the residual variance accounted for by the higher-order coupling coefficients may be due to, for example, inadequacies of a single-component model (i.e., based upon trajectories of a single-point estimate of CoM) to adequately capture the dynamics of the motion of a multi-link body or errors in the computation of CoM based upon a simple three-segment body model (cf., Winter, 1990).

Second, we found evidence indicating a temporal asymmetry in the sensory re-weighting process dependent upon the direction of the change in stimulus motion amplitude: a significant change in postural response gain was observed within two stimulus cycles (5 s) following a rapid increase in stimulus amplitude, whereas after a rapid decrease in stimulus amplitude no significant change in response was found within this time window. This temporal asymmetry was interpreted functionally: an increase in visual environmental motion may threaten balance, requiring a rapid down-weighting of vision if a strong dependence upon visual information would increase postural response beyond the stability boundaries of stance. Conversely, if stance is already stable in the face of large visual motion amplitude, a decrease in motion amplitude does not threaten balance and adapting rapidly to the new sensory conditions is not critical to avoid falling, and may even be maladaptive if changes in sensory conditions are only transient.

Again, open questions remain: First, it is unclear why in this study position and velocity variability did not decrease after the second change in stimulus amplitude

decreased visual motion (see Figure 4.4), despite the observation that gain did increase significantly. The consequence of down-weighting vision when visual motion becomes large is not only a de-coupling to the large visual displacement which would threaten balance if gain remains high, but also a reduction in sensory information available for estimation. As we have previously argued (cf., Kiemel et al., 2002), increases in sway variability are reflective of errors in estimation based upon its sensory inputs, and therefore we would predict the increase in sway variability that was observed in the current study. Conversely, it would also be advantageous to up-weight vision, even when small-amplitude vision is present, to increase information available for estimation, which would lead to a reduction in sway variability. The Carver et al. (2005) model also makes this prediction regarding sway variability. Further, recent empirical evidence in response to constant-amplitude stimulus motion for both healthy older and fall-prone older adults is also not consistent with the results presented here (Allison et al., 2006), though some possible explanations may exist: For example, the abrupt changes in visual stimulus motion used here may affect postural stability in different ways. A conservative response to a decrease in stimulus motion may be to compromise between greater sway variability and the probability that the reduction in motion amplitude is transient rather than enduring. The young, healthy adults in the current study may adopt a strategy that tolerates higher levels of sway variability than those of older individuals, and sway variability may decrease more slowly despite relatively more rapid increases in postural gain.

While the variability observed within subjects was quite large, individual differences in response were qualitatively observed (e.g., see Figure 4.2). Previously, we

have observed individual differences in, for example, gain and phase responses to the same stimulus motion (cf., Jeka et al., 1998, 2000; Oie et al., 2001, 2002). Therefore, the range of the temporal asymmetries observed in response to changes in stimulus motion will be an important constraint to future models of postural control. Indeed, the Carver et al. (2005) model makes further predictions about the nature of the observed temporal asymmetry. For example, the model does not predict a single time constant for sensory re-weighting, but rather that the temporal dynamics of the re-weighting process are dependent upon the system's current state. While the current results can not address this issue, it remains an open question whether such state-dependence of the time scale of re-weighting is correct or not.

Finally, the functional interpretation of the observed temporal asymmetry may have important implications to developing strategies for mitigating the potential for injurious falls, especially in clinical populations. The development of sensory training protocols to improve postural stability in the performance of activities of daily life may be integral to preventative and rehabilitative treatment programs, especially as the population ages.

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