POSTURAL SWAY AND SWAY-ADAPTATION DURING EXPOSURE TO OPTIC FLOW: THE EFFECT OF STIMULUS PERIODICITY AND CONCURRENT COGNITIVE TASKS

by

Mark Christopher Musolino

BS in Mechanical Engineering, Carnegie Mellon University, 1993

MS in Bioengineering, University of Pittsburgh, 1996

Submitted to the Graduate Faculty of

School of Engineering in partial fulfillment

of the requirements for the degree of

Doctor of Philosophy

University of Pittsburgh

2006

UNIVERSITY OF PITTSBURGH

SCHOOL OF ENGINEERING

This dissertation was presented

by

Mark Christopher Musolino

It was defended on

April 3, 2006

and approved by

J. Richard Jennings, Professor, School of Medicine, Psychiatry Department

Patrick J. Loughlin, Professor, Electrical and Computer Engineering Department

Patrick J. Sparto, Assistant Professor, Bioengineering Department

Mark S. Redfern, Professor, Bioengineering Department
Dissertation Director

POSTURAL SWAY AND SWAY-ADAPTATION DURING EXPOSURE TO OPTIC FLOW: THE EFFECT OF STIMULUS PERIODICITY AND CONCURRENT COGNITIVE TASKS

Mark Christopher Musolino, PhD

University of Pittsburgh, 2006

Stable upright stance is achieved through an active postural control process that requires the accurate integration of sensory feedback signals from the visual, graviceptive and proprioceptive systems. Previous studies have shown that this integration process may involve "reweighting", whereby the relative contributions of the various sensory signals are dynamically altered in order to minimize reliance on unreliable signals. In addition, evidence suggests that feedback control by itself cannot explain experimental observations of postural behavior. In light of these observations, the current study proposed that a predictive mechanism exists within the postural control system that can identify the highly repetitive pattern within a predictable sensory input, and can use this information to facilitate the sensory reweighting process.

The objectives of the current work were to: (1) uncover experimental evidence of such a predictive mechanism, through examination of postural sway responses in healthy young adults exposed to various types of predictable and unpredictable moving visual scenes; (2) examine how this predictive mechanism manifested itself in individuals who were particularly reliant on visual sensory information; and (3) determine if this predictive mechanism was influenced by cognitive tasks, which are thought to interact with the sensory reweighting process.

Data revealed that in healthy young adults predictable stimuli elicited improved sway performance compared to unpredictable stimuli, as indicated by significant decreases in both overall sway magnitude, and the time required for sensory reweighting to occur. This effect was enhanced during the performance of a concurrent cognitive task, but was not observed in visually dependent individuals, apparently due to an inability to perform sensory reweighting. Taken together, these observations support the existence of a predictive component to postural control that can alter the dynamic reweighting of sensory inputs during exposure to predictable stimuli. These findings may have implications for the design of experiments involving moving visual scenes, as well as for the treatment of individuals suffering from certain balance disorders.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

ANOVA	Analysis of Variance
A-P	Anterior-Posterior
BNAVE	Balance NAVE Automatic Virtual Environment
CNS	Central Nervous System
COP	Center of Pressure
dB	Decibels
DEP	(Visually) Dependent
DFT	Discrete Fourier Transform
Hz	Hertz
INDEP	(Visually) Independent
LCD	Liquid Crystal Display
PSUM	Periodic Sum-of-Sinusoids
PTFD	Positive Time Frequency Distribution
NPSUM	Non-Periodic Sum-of-Sinusoids
QS	Quiet Stance
RMS	Root mean square
RT	Reaction Time
SOS	Sum-of-Sinusoids
SVV	Subjective Visual Vertical

PREFACE

I offer a heartfelt thank you to everyone in the Human Movement and Balance Laboratory (HMBL) and the Medical Virtual Reality Center (MVRC). You folks are fantastic, and I can only hope that in the future I'm fortunate enough to again encounter such a creative, energetic and friendly group. As both friends and colleagues, you all have helped me achieve what I didn't think was possible. While I'm of course sorry to see our time together come to an end, I take comfort in knowing that our paths will cross again. Thank you again, and good luck.

A special thank you to Mark Redfern, the best boss that I have ever had. I have always admired and appreciated your willingness to go the extra mile to help others achieve their goals, and am constantly humbled by your ability to treat students and colleagues alike with the utmost respect. I hope that I can be a Mark Redfern to someone, somewhere down the road.

Thank you to my dissertation committee, for spending the time and energy to shape this work, from concept to final product. I sincerely appreciate your effort. Also, thanks to Adriana Escandon, Leigh Mahoney, Melissa Repine, Nikki Ross, Susan Strelinski, Theresa Yi and Amy Zhang and for their help with subject recruitment, data collection and technical assistance.

To my friends, both inside and outside of the lab, thanks for letting me be myself, for better or worse. I'm indebted to you for providing a source of relaxation and comic-relief that helped make the bad days bearable, and the good days…well…just that much better. A special shout out to Brian Moyer and Martijn Muller, who have journeyed this doctoral path together with me. Here's a collective pat on the back for us all. Now let's take a day off and enjoy life ;)

Lastly, to my mother and father, and to my dearest Elizabeth, thank you for your enduring love and support, and for giving me strength when I needed it most. I love you all more than you know. I dedicate this work, and all the ambition and hope that it represents, to you.

This work was supported by the Eye and Ear Foundation, as well as NIH grants R01-AG14116, R01-DC04435 and P30-DC05205.

1.0 INTRODUCTION

The work presented here is part of an ongoing effort to better understand the sensory processing mechanisms related to postural control. Despite a wealth of research in this area, several important questions remain unanswered. The motivation for the current study was to address one of these unknowns, namely whether or not the central nervous system (CNS) utilizes sensory prediction as part of the postural control process. We propose that a predictive mechanism exists within the postural control system that can identify the highly repetitive pattern within a periodic sensory input, and can use this information to facilitate sensory processing by predicting future sensory inputs. The present work describes our attempt to uncover evidence of such a mechanism, through examination of postural sway responses in healthy adults exposed to various types of periodic (i.e. "predictable") and non-periodic (i.e. "unpredictable") moving visual scenes.

A series of three experiments were performed to explore various behaviors that were expected to occur as a consequence of the proposed predictive mechanism. The first experiment examined whether or not periodic and non-periodic optic flow elicit significantly different postural responses. Evidence of postural sensitivity to stimulus periodicity would implicate a control process that is to some degree predictive in nature.

The second experiment examined whether or not predictive mechanisms contribute to the postural phenomenon of "adaptation", which is characterized by a within-trial decrease in the amplitude of sway in response to a sinusoidal oscillating visual stimulus. This adaptive behavior has been attributed to sensory re-weighting [Loughlin *et al.*, 1996], a process by which the relative contributions of individual sensory inputs change in response to alterations in the sensory environment. Evidence of a link between stimulus periodicity and postural adaptation would identify prediction as a contributing factor to sensory re-weighting.

The third experiment examined how the aforementioned behaviors (i.e. postural sway and sway adaptation in response to periodic and non-periodic optic flow) are influenced, if at all, by concurrent cognitive tasks. Prior studies have reported that cognitive resources are particularly important for the maintenance of postural stability when inputs from the various sensory pathways are not in agreement with one another [Redfern *et al.*, 2001], which is the case during exposure to optic flow. Moreover, in such "sensory conflict" conditions, sensory re-weighting and adaptation have been shown to occur [Loughlin *et al.*, 1996] [Peterka and Loughlin, 2004]. Therefore, this third experiment attempted to determine whether cognitive tasks interfere with this adaptive process.

2.0 BACKGROUND

2.1 POSTURAL CONTROL

The standing human is inherently unstable, and upright stance is achieved only through an active postural control process that counteracts the body's tendency to fall away from earth vertical. Although we perceive this ability to maintain stable upright stance as automatic and effortless, it in fact requires a substantial amount of highly coordinated sensory processing and motor control. This complex task can be represented as a series of distinct stages, a simple conceptual model of which is depicted graphically in Figure 1.

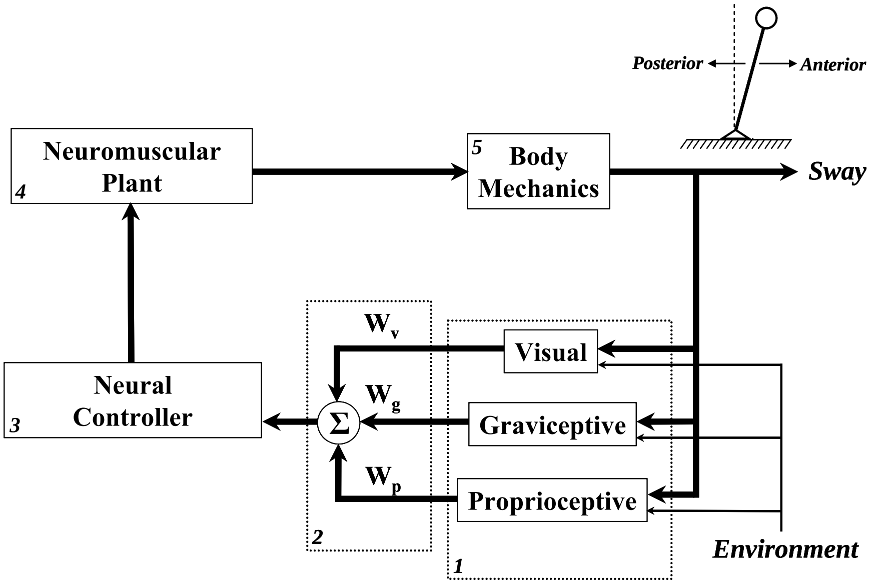


Figure 1 Schematic Diagram of Postural Control Feedback Loop. (1) visual, graviceptive and proprioceptive sensory channels that detect body motion, as well as environmental perturbations; (2) sensory integration component, including a channel weight for the visual (W_v), graviceptive (W_g) and proprioceptive (W_p) signals; (3) neural controller that governs corrective action ; (4) neuromuscular plant which generates muscle forces, that act upon (5) body mechanics (represented here as an inverted pendulum) in order to stabilize postural sway.

Visual, graviceptive, and proprioceptive sensory organs in the peripheral nervous system (PNS) can detect movements of the body, as well as any external events that might occur in the environment, and transmit this information along specialized pathways to the CNS. Signals from the individual sensory channels must then be combined, or “integrated”, in order to provide the control apparatus (i.e. “neural controller”) with a cohesive representation of the current postural state, so that the appropriate corrective action can occur. Evidence suggests that this integration process may involve the weighting of visual (W_v), graviceptive (W_g) and propricoeptive (W_p) sensory inputs, such that the relative contribution of each signal can be varied [Ernst and Bulthoff, 2004; Deneve and Pouget, 2004; Kording and Wolpert, 2004; Battaglia *et al.*, 2003;

Zupan *et al.*, 2002]. The neural controller and neuromuscular plant act together to generate muscular activity that interacts with body mechanics in order to stabilize sway. Together these stages comprise a feedback control system that utilizes an error-correction strategy to continuously drive the body toward earth vertical (which is assumed to be the ideal or preferred orientation). As the body drifts from vertical, the neural controller acts to counteract this movement in a manner that is proportional to the deviation from vertical, such that larger deviations will induce larger corrections. Numerous mathematical models of this postural feedback control process have been developed over the past two decades, and have provided evidence in support of this rather intuitive idea that postural stability requires feedback control [Mergner *et al.*, 2003; Mergner *et al.*, 2002; Peterka, 2002; Oie *et al.*, 2002; Kiemel *et al.*, 2002; Johansson *et al.*, 2001b; Johansson *et al.*, 2001a; van der Kooij *et al.*, 2001; Winter *et al.*, 2001; Maurer *et al.*, 2000; Fukuoka *et al.*, 1999; van der Kooij *et al.*, 1999; Morasso and Schieppati, 1999; Breniere and Ribreau, 1998; Winter *et al.*, 1998; Kuo, 1995; Pellionisz and Ramos, 1993; Collins and De Luca, 1993; Yang *et al.*, 1990; Barin, 1989; Johansson *et al.*, 1988; Maki *et al.*, 1987; Agarwal and Gottlieb, 1984b; Agarwal and Gottlieb, 1984a; Werness and Anderson, 1984; Nashner, 1972].

Despite their success both in characterizing various subsystems of the postural control loop, and in simulating particular experimental data, such studies have yet to offer a consensus view as to whether feedback control by itself is sufficient to produce postural stability, as some have suggested [Peterka, 2003; Peterka, 2002], or if instead feed-forward mechanisms are likely involved as well [Davidson *et al.*, 2002; Hay and Redon, 1999; Fitzpatrick *et al.*, 1996]. A variety of possible roles for feedforward processes have been posited, primarily in the motor control literature. These include the maintenance of stability in the presence of feedback delays, and the facilitation of sensorimotor learning [Blakemore and Sirigu, 2003; van der Kooij *et al.*, 2001; de Vlugt *et al.*, 2001; van der Kooij *et al.*, 1999]. It remains unclear, though, how the underlying mechanisms might operate, and how they interact with feedback processes to achieve postural stability. One possibility that has been suggested is that the CNS contains an *internal forward model* that can predict the consequences of motor commands [Blakemore and Sirigu, 2003; Wolpert *et al.*, 1998], and can provide timely estimates of new sensory information in the absence of actual sensory input due to temporal delays associated with feedback control. Note that the predictive capability of the internal forward model relies solely on the sensorimotor mapping that the model contains, and is not influenced by specific properties of the sensory stimulus. The possibility that feedforward mechanisms may play a part in postural stability was a motivating factor for the current work.

2.1.1 SENSORY INTEGRATION

A review of the various existing models of postural control reveals that many differ mainly in their description of the sensory integration component of the model, with some for example describing it as simple linear sum, while others offer some nonlinear characterization. This highlights two points, namely that sensory integration is a vital component of postural control, and also that there is no consensus view regarding the integration process. Not coincidentally, sensory integration is a focal point of the current work; not in the sense that it will be mathematically modeled, however, but instead from the perspective that certain features of the process might be deduced through examination of experimental data.

Sensory integration refers to the combining of incoming sensory information that the CNS performs in order to provide subsequent stages of the signal processing hierarchy with a coherent picture of the current state (e.g. position, velocity, etc.) of the body. The term "integration" is used conceptually, as opposed to mathematically, and merely indicates that visual, graviceptive and proprioceptive signals are combined in some manner. Exactly how or where this process occurs is not known, despite attempts to characterize this phenomenon at various scales of observation. For example, neurophysiologic studies have examined sensory integration at the neural level, through the use of intracellular recording techniques. Such studies have identified "multisensory neurons" that receive converging inputs from multiple sensory modalities, and whose output therefore represents the combined effect of the inputs it receives [Stein, 1998]. At the other end of the spectrum, on the larger scale, integration has been modeled in various ways: (1) as a simple linear additive process [Peterka, 2002; Jeka *et al.*, 2000; Hlavacka *et al.*, 1996]; (2) in a nonlinear fashion [Oie *et al.*, 2002; van der Kooij *et al.*, 2001; Oie *et al.*, 2001; Maurer *et al.*, 2000; van der Kooij *et al.*, 1999]; and (3) as a weighted summation wherein sensory inputs are weighted in either a task specific manner that favors signals which are more useful for a particular task, or a Bayesian manner (i.e. according to reliability) such that signals containing large variability contribute less to the output [Ernst and Bulthoff, 2004; Deneve and Pouget, 2004; Kording and Wolpert, 2004; Battaglia *et al.*, 2003; Zupan *et al.*, 2002]. For purposes of this study, we make no assumptions regarding the relative linearity of sensory integration, and instead are simply concerned with mechanisms that contribute to sensory re-weighting.

2.1.2 SENSORY REWEIGHTING

As mentioned above, sensory integration may involve the weighting of sensory signals, presumably as a means of favoring more relevant inputs, or of minimizing the influence of unreliable signals. Sensory reweighting is a term used to describe the process by which the weights of the various sensory channels are dynamically altered, either in response to changes in the sensory environment (e.g. an external perturbation of some type), or perhaps as a result of some internal influence (e.g. volition or expectation on the part of the subject). Such reweighting would seemingly provide the CNS with a degree of robustness, by offering the ability to accurately integrate sensory inputs under a wide variety of conditions. Findings from both experimental and modeling efforts have implicated such sensory re-weighting as a causal mechanism for various postural behaviors [Mahboobin *et al.*, 2005; Oie *et al.*, 2002; Day *et al.*, 2002; van der Kooij *et al.*, 2001; Maurer *et al.*, 2000; Ishida *et al.*, 1997], including resonance in sway responses following removal of certain sensory information [Peterka and Loughlin, 2004], and sway adaptation during exposure to sinusoidally oscillating optic flow [Loughlin and Redfern, 2001; Loughlin *et al.*, 1996]. This latter observation of sway adaptation in response to a periodic stimulus was a motivating factor for the current work. Loughlin et al. suggested that this sway adaptation, which is a gradual decrease in sway power during exposure to an optic flow stimulus, was the result of a reduction in visual channel weight prompted by sensory conflict among the various sensory signals [Loughlin and Redfern, 2001; Loughlin *et al.*, 1996]. Specifically, head movement induced by optic flow caused the visual system to underestimate sway amplitude, and therefore to produce an afferent signal that conflicted with graviceptive and proprioceptive signals. The decrease in visual weight would therefore have been an attempt by the CNS to minimize the contribution of this unreliable signal.

2.2 PROPOSED PREDICTIVE MECHANISM

In the current study, we offer an explanation for the observed adaptive behavior that is meant to complement, rather than replace, the very plausible 'sensory-conflict' explanation described above. Namely, we suggest that sway adaptation was the result both of sensory-conflict and of the predictable nature of the sinusoidal optic flow. In particular, we propose that postural control contains a predictive mechanism that is sensitive to the relative predictability of sensory inputs, such that highly predictable stimuli will activate this mechanism, while less predictable stimuli will not. Like the internal forward model described earlier, this predictive mechanism would be capable of estimating future sensory states, and of facilitating sensory integration by decreasing the time that is required to process information regarding future sensory inputs. We suggest, however, that the proposed mechanism is distinct from (but not necessarily independent of) the internal forward model, in that its predictive capability is affected by specific properties of the sensory stimulus. Interestingly, several prior postural studies have assumed that such predictive capability exists, and have purposely utilized unpredictable sensory stimuli in order to prevent the occurrence of any predictive behavior [Peterka, 2002; Johansson *et al.*, 2001b; Pavlik *et al.*, 1999]. None of these studies, however, cited existing evidence or provided any rationale to support this assumption. In contrast, the current study aimed specifically to uncover this very type of predictive behavior in postural responses.

With respect to sway adaptation, the *predictive mechanism is thought to facilitate the sensory re-weighting process*, and therefore facilitate sway adaptation as well. In particular, the predictive mechanism might exploit the repetitive nature of the sinusoidal visual stimulus in order to readily predict future visual input, which would presumably minimize the need to monitor newly arriving visual signals. One way for the CNS to achieve this would be to lower visual weight beyond that which is already occurring due to sensory conflict. This would in effect further reduce reliance on inaccurate visual afferent signals, and would produce an enhanced adaptation characterized by a more pronounced per-stimulus decrease in sway amplitude. *The purpose of the current study was to uncover evidence of such stimulus-dependent predictive behavior.* If indeed this predictive component of postural control exists, then one would expect to observe differences in postural responses to external perturbations that vary in their degree of predictability.

2.3 VISUAL INFLUENCES

Since the proposed predictive mechanism was expected to influence weighting of the visual channel in particular, it seemed appropriate to investigate how this process might have manifested itself not just in "normal" subjects, but also in a population known to be particularly dependent on vision. Findings from previous studies suggest that postural behavior during exposure to visual perturbations may be influenced by this type of sensitivity to visual stimuli [Isableu *et al.*, 1998; Isableu *et al.*, 1997; Nyborg, 1974]. As such, sway responses, and particularly sway adaptation, were examined in both "visually dependent" and "visually independent" subjects, with the dependent group composed of individuals who were thought to rely heavily on visual information for postural stability. Visual dependence was determined using the rod-and-frame test, as described by Isableu et al. [Isableu *et al.*, 1998; Isableu *et al.*, 1997] and Nyborg [Nyborg, 1974]. This procedure examines the subjective visual vertical (SVV), which represents a subject's ability to accurately identify earth vertical in an environment containing limited visual information, as described in detail in Isableu et al. [Isableu *et al.*, 1998;

Isableu *et al.*, 1997]. Briefly, subjects were seated in a dark room, equipped with a handheld device that controls the orientation of an illuminated rod situated directly in front of them, and instructed to align the rod with their perceived earth vertical. The difference (or error), in degrees, between the final position of the rod and true earth vertical is recorded and used to assess a subject's relative dependence on visual information, with errors above some threshold value being indicative of visual dependence.

2.4 COGNITIVE INFLUENCES

Previous studies that examined the influence of cognitive tasks on postural sway have suggested that sensory integration requires cognitive resources, or more specifically "attention", especially during challenging postural tasks that might induce sensory conflict [Teasdale and Simoneau, 2001; Redfern *et al.*, 2001]. Since sensory conflict has been identified as a precursor to sensory reweighting, *the possibility exists that attention may contribute to this reweighting process*. The term "attention" is typically used to refer to a selective process by which attended information is processed more efficiently than unattended information [Fernandez-Duque and Johnson, 2002]. From this perspective, the increased cognitive demands that would presumably be associated with sensory reweighting and the resolution of sensory conflict might require the enhanced information processing provided by attending to that task. If this were true, one might expect that performing a cognitive task during exposure to optic flow might interfere with the sensory reweighting process, since the cognitive task and postural task might be competing for shared resources, as suggested by the 'limited capacity' model of "attention" [Tombu and Jolicoeur, 2002; Fernandez-Duque and Johnson, 2002]. As such, the current study aimed to examine the interaction between “attention” and sensory reweighting, by examining sway responses during exposure to predictable and unpredictable optic flow, both with and without a concurrent cognitive task. Because reweighting has been identified as a possible causal mechanism for sway adaptation, any cognitive-task effect on sway would likely be observed in measures of sway adaptation.

Also, since “attention” is associated with enhanced processing of attended information, one might expect that the effect of a cognitive task on *visual* channel reweighting would depend on the sensory modality of the cognitive task. For example, attending to a *visual* task might be expected to *enhance* this reweighting, while attending to an auditory task might not enhance this visually-specific process. For this reason, both auditory and visual cognitive tasks were utilized in examining the interaction between “attention” and sensory reweighting.

3.0 OBJECTIVES

Based on the background information provided in the preceding section, the objectives of the current work were to: (1) uncover experimental evidence of a predictive mechanism in postural control, through examination of postural sway responses in healthy young adults exposed to various types of predictable and unpredictable moving visual scenes; (2) examine how the predictive mechanism manifested itself in individuals who were particularly reliant on visual sensory information; and (3) determine if the predictive mechanism was influenced by a cognitive task, which has been shown to interfere with sensory reweighting. The specific aims for each of these objectives are discussed in the next section.

4.0 SPECIFIC AIMS AND HYPOTHESES

4.1 SPECIFIC AIM #1

To experimentally examine the influence of visual stimulus periodicity on postural sway magnitude in healthy young adults. The hypotheses related to this specific aim were:

H1.1 Sway magnitudes, as measured by average stimulus-band power, would be lower in response to periodic stimuli compared to the non-periodic counterpart.

4.2 SPECIFIC AIM #2

To experimentally examine the influence of visual stimulus periodicity on postural sway magnitude and postural sway adaptation in visually dependent and visually independent healthy young adults. The hypotheses related to this specific aim were:

H2.1 Sway magnitudes, as measured by average stimulus-band power, would be lower in response to periodic stimuli compared to the non-periodic counterpart.

H2.2 Sway adaptation, as measured by the time constant of exponential decay, would be faster in response to periodic stimuli compared to the non-periodic counterpart.

H2.3 Sway magnitude and adaptation in response to periodic and non-periodic stimuli would be different in visually dependent and visually independent subjects.

4.3 SPECIFIC AIM #3

To experimentally examine the influence of both a concurrent cognitive task and visual stimulus periodicity on postural sway magnitude and postural sway adaptation. The hypotheses related to this specific aim were:

H3.1 Sway magnitudes, as measured by average stimulus-band power, would be lower in response to periodic stimuli compared to the non-periodic counterpart.

H3.2 Sway adaptation, as measured by the time constant of exponential decay, would be faster in response to periodic stimuli compared to the non-periodic counterpart.

H3.3 Sway in response to periodic stimuli would display faster adaptation and lower magnitude during a *visual* concurrent cognitive task, as compared to an auditory task.

H3.4 A concurrent cognitive task will cause a decrease in sway magnitude**.**

5.0 RESEARCH DESIGN AND METHODS

5.1 OVERVIEW

Three experiments were performed in order to accomplish the specific aims described previously in section 4. The various experiments shared a common methodology, namely examining postural sway responses in healthy young adults during exposure to spectrally similar periodic and non-periodic moving visual scenes. Differences among the experiments were limited to slight variations in the types of scene movements presented to subjects, and to the inclusion of a concurrent task in experiment #3. Other aspects of the experiments, including data collection and analysis, were essentially identical. Detailed descriptions of the methods employed in each experiment are included in the Methods section of the respective chapters (see experiments #1, #2, and #3).

Experiment #1 examined the *magnitude* of postural sway in healthy young adults exposed to spectrally similar periodic and non-periodic moving visual scenes. Experiment #2 expanded on the previous work by examining both sway *magnitude* and sway *adaptation*, in visually dependent and visually independent healthy young adults exposed to spectrally similar periodic and non-periodic optic flows. Experiment #3 was a further extension of these prior studies, and investigated how a concurrent cognitive task influenced the relationship between stimulus periodicity and postural sway that had been uncovered in experiments #1 and #2.

5.2 SUBJECT POPULATION

Each of the experiments examined healthy young adults between the ages of 21 and 35. Sample size differed among the three experiments. Experiment #1 was a preliminary study that was conducted on n=6 subjects. A statistical power analysis of this data indicated that at least n=15 subjects were required to observe significant differences in our chosen metrics, at the established statistical criteria levels we had established. Accordingly, sample sizes for experiments #2 and #3 were set at n=20 and n=16, respectively.

Subjects were recruited from the University of Pittsburgh and the greater Pittsburgh area, and received a comprehensive screening exam prior to entering the study. Exclusionary criteria included: (1) a history of vestibular or neurologic disease; (2) abnormalities on a physician-administered neurologic examination; (3) difficulties in standing that would prevent completion of the study; (4) binocular visual acuity (with corrective lenses) of worse than 20/40; (5) abnormal vestibular function (as measured by positional, caloric, and Earth-Vertical-Axis-Rotation tests); and (6) evidence of significant hearing loss. Subjects were also excluded from participation if they had been previously exposed to the types of visual scene perturbations that were used in these experiments. As such, each subject was eligible to participate in only one of the three experiments. All subjects provided informed consent to participate in this study.

5.3 EQUIPMENT

Tests were performed in the Balance NAVE Automatic Virtual Environment (BNAVE), a custom built virtual environment that creates an immersive visual surround by projecting computer generated images onto three adjoining screens [Jacobson J *et al.*, 2001]. The screens measure approximately 183cm x 213cm (width x height), and are arranged in front, to the left, and to the right of the viewer, such that they occupy the entire horizontal visual field. A contiguous image is projected onto the screens, and provides a full (180°) horizontal field of view. This visual scene extends onto the floor as well, but not to the ceiling (which is covered in black cloth), so the vertical field of view is thus limited to approximately 120°. A safety harness is incorporated into the BNAVE structure, in order to prevent a subject from falling in the event of a loss of balance. Data collection equipment includes a force platform (Neurocom, Inc., Clackamas OR) capable of measuring normal and shear forces at the foot-floor interface, via a group of four embedded load cells that output a voltage proportional to the force exerted on the load cell. This information is stored digitally, and then post-processed to yield foot center-of-pressure (COP) displacement values. In addition, a Fastrak electromagnetic tracking system (Polhemus Inc., Colchester VT) is used to collect information on motion of body segments during postural tasks. The system consists of a single stationary "base" that emits a magnetic field, as well as several mobile sensors, or "trackers", each of which contains an inductive coil, and is attached to the object whose movement is to be monitored. Motion between a tracker and the base induces a current in the tracker coil that is proportional to the relative displacement between the two objects. This system was used to measure movement of the head.

5.4 EXPERIMENTAL DESIGN

The experimental design is illustrated in Table 1 and Table 2. Experiments #1 and #2 involved only postural tasks. Experiment #3 utilized these same postural tasks, but included a concurrent cognitive task as well. Subjects stood on a fixed floor while viewing optic flow whose motion was driven by either a single sinusoid (TONE), a periodic sum-of-sinusoids (PSUM), or a non-periodic sum-of-sinusoids (NPSUM). Subjects also performed a single quiet stance trial without visual perturbation (NONE) prior to exposure to the moving visual scenes. In experiment #3, subjects performed a concurrent auditory or visual reaction-time task, and were also exposed to an additional visual condition in which a scene appeared on the BNAVE screens but remained stationary throughout the trial. Postural responses were quantified through measurements of foot center-of-pressure (COP) and head displacements. A full-factorial design across stimulus and cognitive-task conditions was necessary to address the hypotheses outlined earlier in section 4.

Table 1 Experimental design for experiments #1 and #2.

PLATFORM	VISUAL STIMULUS
Fixed	None, TONE, PSUM, NPSUM

Table 2 Experimental design for experiments #3.

PLATFORM	VISUAL STIMULUS	COGNITIVE TASK
Fixed	None, Stationary, TONE, PSUM, NPSUM	None, Auditory, Visual

6.0 EXPERIMENT 1: SPECTRALLY SIMILAR PERIODIC AND NON-PERIODIC OPTIC FLOWS EVOKE DIFFERENT POSTURAL SWAY RESPONSES

6.1 ABSTRACT

This study investigated the effect of optic flow periodicity on postural sway. Head and center-of-pressure (COP) displacements in response to an oscillating full-field bullseye-and-checkerboard pattern were recorded in six healthy adults. Scene movement was driven by one of five signals: (1) 0.1Hz sinusoid, (2) 0.3Hz sinusoid, (3) 0.5Hz sinusoid, (4) the periodic sum of these three sinusoids (PSUM), or (5) a non-periodic counterpart (NPSUM=0.1 + π/10 + 0.5 Hz). Sway response power at the various stimulus frequencies were compared (1) among the three single sinusoidal groups, and (2) between the two sum-of-sinusoid groups. Head and COP responses displayed similar spectral content, though sway magnitude was larger for the head. Sway responses to the moving scenes were significantly larger than those observed during quiet stance. Each sinusoidal moving scene evoked a strong response at the stimulus frequency, as well as increased sway at non-stimulus frequencies, primarily below 0.2Hz. For the sum-of-sinusoids stimuli, both PSUM and NPSUM signals elicited sway responses at each of their component frequencies. The amplitudes of these responses were similar to one another at 0.1Hz and 0.3Hz, but significantly different at 0.5Hz, with PSUM responses on average four times larger than those for NPSUM.

These findings indicate that spectrally similar periodic and non-periodic stimuli elicit quantitatively different sway responses. The observed behaviors may be due to postural sensitivity to the predictability of visual motion, or due to other nonlinear and/or time-varying mechanisms in the postural control system.

6.2 INTRODUCTION

The control of upright posture involves the continuous integration of afferent signals from the visual, vestibular and somatosensory systems. Despite the importance of this sensory integration in providing a sense of spatial orientation, and in contributing to the maintenance of balance, a clear picture of precisely how the central nervous system (CNS) actually combines and interprets incoming sensory signals has yet to emerge. This is due in part to an incomplete understanding of the feedforward (predictive) elements that may be part of this integration process. Many studies of postural control have focused on the feedback (corrective) mechanisms that are known to influence upright stance [Creath *et al.*, 2002; Day and Cole, 2002; Jeka *et al.*, 2000; Fukuoka *et al.*, 1999; Allum *et al.*, 1998; Bronstein and Buckwell, 1997; Fitzpatrick *et al.*, 1996; Peterka and Benolken, 1995], presumably because the sensory events that provide such feedback to the nervous system are observable, and therefore quantifiable. Some studies have concluded that feedback alone is sufficient to explain experimental observations of postural behavior [Peterka, 2003; Peterka, 2002], while others have reached the opposite conclusion [Fitzpatrick *et al.*, 1996].

Despite the lack of consensus regarding the exclusive role of feedback in postural control, such studies have nevertheless succeeded in uncovering a wealth of information regarding sensory contributions to postural control, including the characterization of individual sensory pathways, and evidence of adaptive phenomena such as sensory re-weighting [Peterka, 2002; Peterka and Benolken, 1995].

A variety of possible roles for predictive processes have been posited, primarily in the motor control literature. These include the maintenance of stability in the presence of feedback delays, and the facilitation of sensorimotor learning [Blakemore and Sirigu, 2003; van der Kooij *et al.*, 2001; van der Kooij *et al.*, 1999]. It remains unclear, though, how the underlying mechanisms might operate, and how they interact with feedback processes to achieve postural stability. One possibility that has been suggested is that the CNS contains an *internal forward model* that can predict the consequences of motor commands [Blakemore and Sirigu, 2003; Wolpert *et al.*, 1998]. The internal model captures the causal relationships between neuromuscular inputs and outputs, and is used in combination with an efference copy of the motor command in order to simulate subsequent sensory consequences. For example, an internal model could predict a future state (e.g. body position and/or velocity), given the current state and motor command. This mechanism would be useful, for instance, in providing timely estimates of new sensory information in the absence of actual sensory input due to temporal delays associated with feedback control. Note that the predictive capability of such an internal model relies solely on the sensorimotor mapping that the model contains, and is not influenced by specific properties of the sensory stimulus.

In this study, we proposed that postural control contains a predictive mechanism that is sensitive to the relative predictability of sensory inputs, such that highly predictable stimuli will activate this mechanism, while less predictable stimuli will not. Like the internal forward model described above, this predictive mechanism is capable of estimating future sensory states, and of facilitating sensory integration by decreasing the time that is required to process information regarding future sensory inputs. We suggest, however, that the proposed mechanism is distinct from (but not necessarily independent of) the internal forward model, in that its predictive capability is affected by specific properties of the sensory stimulus. The motivation for the present study was to uncover evidence of such stimulus-dependent predictive behavior. If indeed this predictive component of postural control exists, then we would expect to observe differences in postural responses to external perturbations that vary in their degree of predictability. With this in mind, *the purpose of this study was to investigate how the relative predictability of a moving visual scene influences the magnitude of postural sway*. Note that "predictable" is used here not in the statistical versus deterministic sense, but rather in terms of a periodicity or repetitive pattern that the CNS can readily discern.

Vision was chosen as the stimulus modality because it is easy to manipulate, and it's influence on posture has been extensively studied. It is well known that visual information contributes to posture, even during quiet stance, as evidenced by the fact that both amplitude and variability of spontaneous sway increase during eyes closed conditions [Prieto *et al.*, 1996]. The moving room paradigm is a useful investigative tool in that it allows the visual environment to be manipulated in a controlled manner, and produces a convincing sense of vection for the observer. Previous studies have demonstrated that moving visual scenes can elicit postural sway responses [Lee and Lishman, 1975; Lee and Aronson, 1974; Gibson, 1958], and that such responses are influenced by specific spatial and temporal properties of the optic flow, including geometric structure [van Asten *et al.*, 1988; Stoffregen, 1985], amplitude [Peterka, 2002; Dijkstra *et al.*, 1994b], velocity [Kiemel *et al.*, 2002; Dijkstra *et al.*, 1994a; Stoffregen, 1986; Lestienne *et al.*, 1977], frequency [Dijkstra *et al.*, 1994a; Lestienne *et al.*, 1977], and location in the field of view [Stoffregen *et al.*, 1987; Stoffregen, 1986; Brandt *et al.*, 1973].

Comparisons were made among sway responses to three types of antero-posterior (AP) optic flow stimuli: pure sinusoidal motion, a sum of three sinusoids with an obvious periodicity, and a sum of three sinusoids that exhibited no periodicity. *It was hypothesized that the periodic visual stimuli would elicit lower sway amplitudes compared to the non-periodic stimulus*. The rationale for this hypothesis, as alluded to earlier, was that predictive mechanisms in the CNS could exploit the repetitive nature of periodic stimuli in order to predict future visual inputs and/or subsequent periodic changes in body position and/or velocity, and that this predictive behavior could in turn promote postural stability. For example, reliance on visual afferents might be reduced (i.e. by lowering visual gain in the control loop), and/or additional corrective torque based on the predicted body motions could be generated, both of which could result in a reduction of sway compared to situations in which sensory perturbations and resulting body oscillations were not as repetitive and predictable.

6.3 METHODS

Postural sway responses to various moving visual scene perturbations were examined in six healthy young adults, ranging in age from 22-26 years (mean age = 24.5 yrs). Subjects had no history of neurological or balance-related dysfunction, and no previous exposure to visual scene perturbations in an experimental setting. All subjects provided informed consent to participate in this study, and the experimental protocol was approved by the Institutional Review Board at the

University of Pittsburgh. Tests were performed in the BNAVE, a custom built virtual environment that creates an immersive visual surround by projecting computer generated images onto three adjoining screens [Jacobson J *et al.*, 2001]; see Figure 2. The screens are approximately 183cm x 213cm (width x height), and are arranged in front, to the left, and to the right of the viewer. A contiguous image is projected onto the screens, and provides a full (180°) horizontal field of view. This visual scene extends onto the floor as well, but not to the ceiling (which is covered in black cloth), so the vertical field of view is thus limited to approximately 120°.

Figure 2 Subject viewing a bullseye-and-checkerboard pattern in the BNAVE virtual environment. Sway responses were recorded via a single force plate beneath the feet, and an electromagnetic tracking device located at the head. Subject is secured to the support structure by a safety harness.

6.3.1 VISUAL SCENES

The image presented to the subjects consisted of a "bullseye" pattern of six alternating black-and-white concentric rings (with each ring occupying 5° of visual arc), surrounded by a checkerboard of black-and-white squares (15cm per side), as shown in Figure 2. Previous studies have utilized similar patterns in a moving room paradigm to evoke postural responses in both healthy and patient populations [Borger *et al.*, 1999; Peterka and Benolken, 1995; Stoffregen, 1985].

The bullseye-and-checkerboard pattern oscillated toward and away from subjects in either a periodic ("predictable") or non-periodic ("unpredictable") fashion. Scene movement was driven by one of five signals (Figure 3): (1) ±8cm 0.1Hz sinusoid, (2) ±8cm 0.3Hz sinusoid, (3) ±8cm 0.5Hz sinusoid, (4) the periodic sum of these three sinusoids (PSUM = 0.1 + 0.3 + 0.5 Hz), or (5) a non-periodic counterpart ($0.1 + \pi/10 + 0.5$ Hz = NPSUM). Because the frequencies of the PSUM stimulus are integer multiples of each other, the stimulus is periodic, with period given by $T=1/0.1=10$ sec. For the NPSUM stimulus, component frequencies were chosen in order to produce a signal with frequency content nearly identical to that of the PSUM stimulus, but lacking a temporal periodicity. Since $\pi/10$ is not an integer multiple of 0.1 Hz, the NPSUM stimulus is not periodic and exhibits markedly different temporal characteristics than the PSUM stimulus, even though the spectra of the PSUM and NPSUM stimuli are very similar (see Figure 3). In addition, the sum-of-sinusoids signals were normalized such that their root-mean-square (RMS) was equal to that of the ±8cm single sinusoids; this ensured that peak amplitudes were similar among the five stimuli.

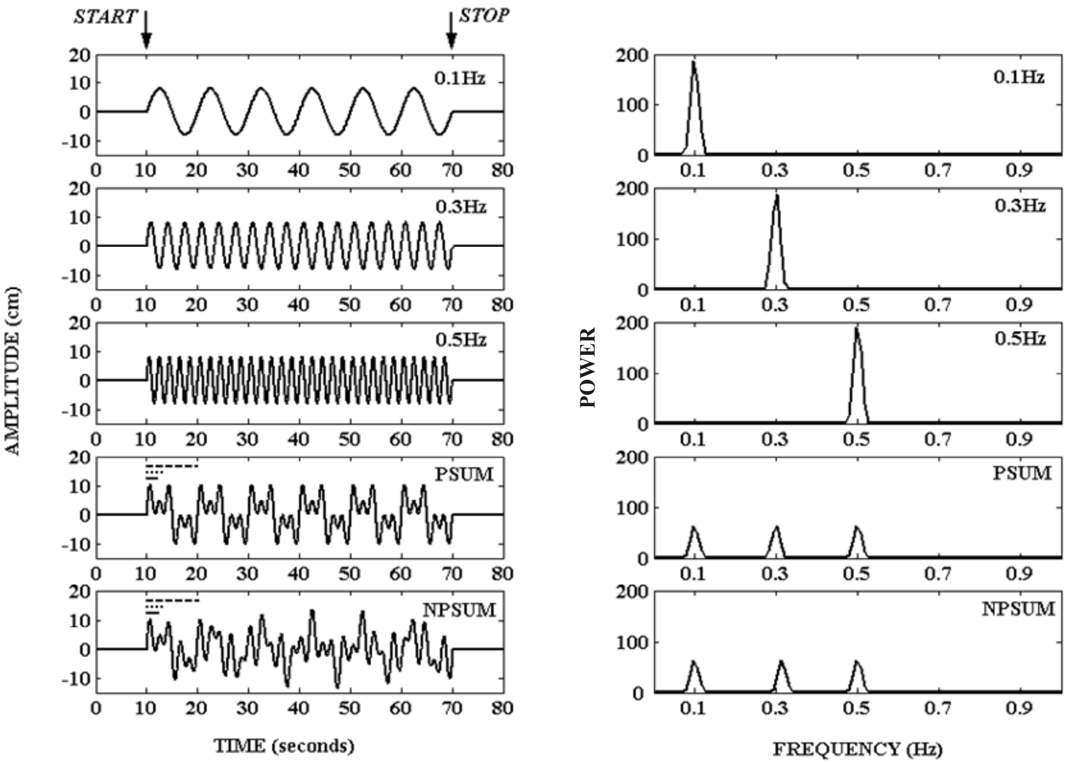


Figure 3 Time series' (left) and corresponding power spectra (right) for the five scene movements presented to subjects. Shown from top to bottom are 0.1Hz, 0.3Hz, 0.5Hz, PSUM (0.1 + 0.3 + 0.5Hz) and NPSUM (0.1 + π/10 + 0.5Hz). "Start" and "Stop" indicate times at which scene movement begins and ends, respectively. The set of three lines in the top left-hand corner of the PSUM and NPSUM time series plots represent the period (frequency $^{-1}$), in seconds, of the component sinusoids – 0.1Hz (dashed), 0.3Hz (dotted), and 0.5Hz (solid).

6.3.2 DATA COLLECTION

Subjects stood in an upright position 1.5 meters from the front screen, with arms folded across the chest, and with bare feet placed shoulder-width apart on a force platform (NeuroCom Inc., Clackamas OR). Image height was adjusted so that the bullseye center was located at eye level. Subjects were secured to the BNAVE support structure with a tether and harness. This safety line was sufficiently loose to afford subjects free range of motion, and did not hinder sway or provide sensory feedback regarding their body sway. Each of the five scene movements was presented once, in random order, to each subject. Prior to each trial, room lights were dimmed, and subjects were instructed to "stand comfortably and look straight ahead at the image on the screen." Trial duration was 80 seconds, and consisted of 60 seconds of scene movement preceded and followed by 10 seconds of no motion. A rest period of 2 minutes was provided between successive trials, during which time room lights were switched on, and subjects relaxed in a seated position. In addition, a 30-second quiet stance trial was performed prior to the moving scene trials, in order to record "baseline" spontaneous sway in the absence of visual perturbation (i.e. subjects viewed a blank screen during these baseline trials).

Postural responses were examined through measurements of head and center-of-pressure (COP) displacements. Head data were collected at 20Hz using a Polhemus Fastrak electromagnetic tracking system (Polhemus Inc., Colchester VT), with a single sensor located at the crown of the head. Foot force data were sampled at 100Hz via load cells embedded in the force platform, and post-processed in Matlab (The Mathworks Inc., Natick MA) to obtain COP values.

6.3.3 DATA PROCESSING

Data were high-pass filtered, down-sampled to 5 Hz, and zero-meaned. High-pass filtering was achieved through zero-phase implementation of a fourth order Chebyshev type II filter, with a cutoff frequency of 0.025 Hz, and a stop-band attenuation of 20 decibels (a decibel (dB) is a unit of measure often used for values that span several orders of magnitude, and is mathematically defined as $10*\log_{10}(\text{Power})$). The 3dB attenuation point for the high-pass filter occurred at approximately 0.03Hz, and frequencies above 0.07Hz were not attenuated at all. This high-pass filter removed the dominant DC and very low frequencies observed in postural sway position data, and facilitated the identification of sway responses to the low frequency (0.1 Hz) component of the stimuli.

Filtered data were then examined using Fourier analysis, in order to estimate spectral densities for head and COP response signals, for both the quiet-stance baseline trial and moving scene trials. This was achieved through the calculation of windowed periodograms using the discrete Fourier transform (DFT). Spectral estimation was performed on only the 60-second moving scene portion of each trial (i.e. the first and last 10 seconds of data were removed prior to Fourier analysis). The 60-second data segments were multiplied by a Hanning window (a smooth function that tapers gradually to zero [1975]) prior to performing the DFT, in order to minimize edge effect artifacts that can arise during the Fourier transform. The squared-magnitude of the DFT was computed to produce an estimate of sway response power, at frequency intervals of 0.01Hz, spanning DC through 2.5Hz. Of particular interest was response power at each of the stimulus frequencies: 0.1 Hz, 0.3 Hz, and 0.5 Hz. These were obtained by calculating the average power across seven frequency bins (bin size = 0.01Hz) at and around each of the stimulus frequencies. The averaging was performed because subject responses to a particular stimulus frequency didn't necessarily occur exactly at that frequency. This yielded a "stimulus-band" power equal to the average power at a given stimulus frequency ± 0.03Hz. These frequency-band power metrics were used as the means of comparison (1) among the three single sinusoidal groups (0.1,0.3,0.5Hz), and (2) between the two sum-of-sinusoid groups (PSUM, NPSUM). Responses to moving scenes were compared to those for quiet stance, in order to separate contributions of optic flow from those due purely to spontaneous sway. A full factorial repeated measures ANOVA was utilized to test how the main effect of stimulus type (i.e. PSUM, NPSUM, 0.1Hz, 0.3Hz, or 0.5Hz) contributed to the observed differences in stimulus-band power. Data distributions were tested for normality using the Shapiro-Wilk W test, and log-transformed to achieve normality when necessary. The significance level was set at $p = 0.05$ for both primary and post-hoc (Tukey's HSD) comparisons. Unless otherwise noted, any statistical differences described in the text or indicated in figures with an asterisk, correspond to a significance level of $p<0.05$.

6.4 RESULTS

6.4.1 GENERAL SWAY RESPONSES

Subjects responded strongly to each of the five visual stimuli. Movements of the head and COP were in phase with one another for all trials, as revealed by visual inspection of time series data. Response amplitudes were largest at the head (between 1cm and 2cm) and lowest for COP, as shown in the time-series plots in Figure 4. Except for absolute power levels, the corresponding spectral densities were very similar up to approximately 0.5Hz. These findings indicated that subjects had swayed predominantly as an inverted pendulum, which is consistent with previous findings of postural sway [Peterka, 2003; Peterka, 2002].

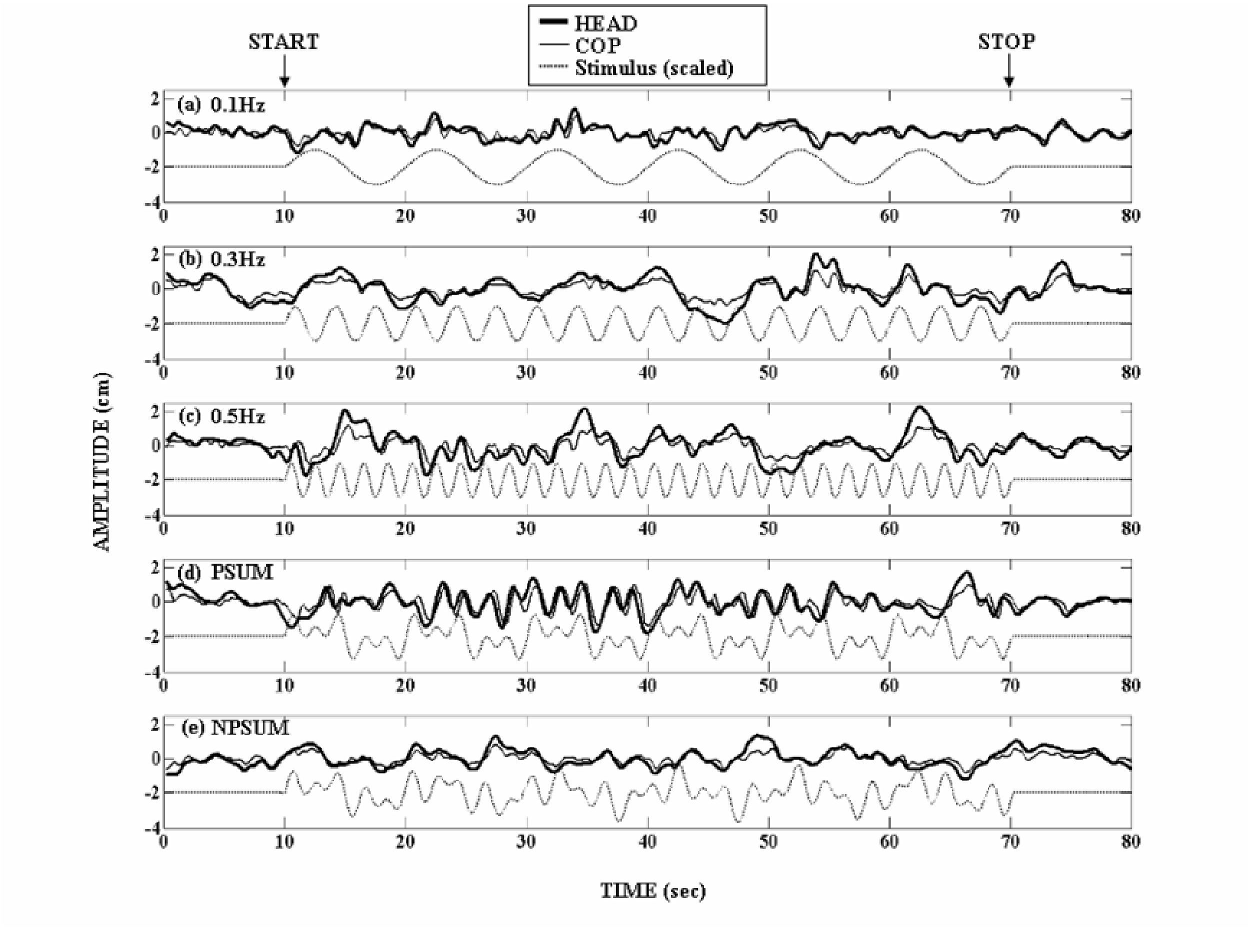


Figure 4 Time series' of Head and COP responses for a single subject (s08). Shown from top to bottom are (a) 0.1Hz, (b) 0.3Hz, (c) 0.5Hz, (d) PSUM (0.1 + 0.3 + 0.5Hz), and (e) NPSUM (0.1 + π/10 + 0.5Hz). Data for the stimuli (dotted line) are included for comparison; for clarity, they have been scaled by a factor of 8, and shifted down by 2cm. "Start" and "Stop" indicate times at which scene movement begins and ends, respectively.

Both the quiet stance and moving scene sway responses displayed power that was highest at low frequencies (i.e. below 0.1Hz), and that generally decreased across the spectrum, with minimum values occurring at frequencies above 0.5Hz, as shown for head motion in Figure 5 (COP responses, though not shown, were very similar). Quiet stance sway power was spread across a band of frequencies from DC to approximately 0.3Hz, which is typical for spontaneous sway. The moving scene responses were characterized by larger sway amplitudes in this same frequency range, and substantial power at the stimulus frequency (or frequencies, for the sum-of-sinusoids) as well. Both single sinusoid and sum-of-sinusoid motion elicited sway responses that were consistently larger than those observed during quiet stance. This effect was least evident at 0.1Hz (Figure 5 and Figure 6). Note that if comparing Figure 5 and Figure 6, keep in mind that the bar plot values shown in Figure 6 represent the average power across a narrow range of frequencies near the stimulus frequency (as indicated by the arrows shown at the top of Figure 5a), while the spectral densities in Figure 5 represent raw (i.e. not averaged) power at a given frequency.

6.4.2 RESPONSES TO SINGLE SINUSOIDS

Each of the single sinusoids evoked sway not only at the stimulus frequency, but also across a band of frequencies ranging from DC to approximately 0.5Hz (Figures 5a-c, Figure 6a). In all cases, frequencies that were not present in the stimulus appeared in the response. This effect was pronounced for the 0.3 and 0.5Hz stimuli, while less apparent for the 0.1Hz stimulus.

Moving scene responses were larger than those during quiet stance. The 0.3Hz and 0.5Hz stimuli produced sway in the 0.1Hz frequency band (0.07 to 0.13 Hz) that was at least two times (3dB) larger than that for quiet stance (Figure. 6a); these differences were significant. Sway in the 0.1Hz band in response to the 0.1Hz stimulus was smaller than sway in the 0.1Hz band in response to both the 0.3Hz and 0.5Hz stimuli, though still almost two times (3dB) larger than the corresponding quiet stance value.

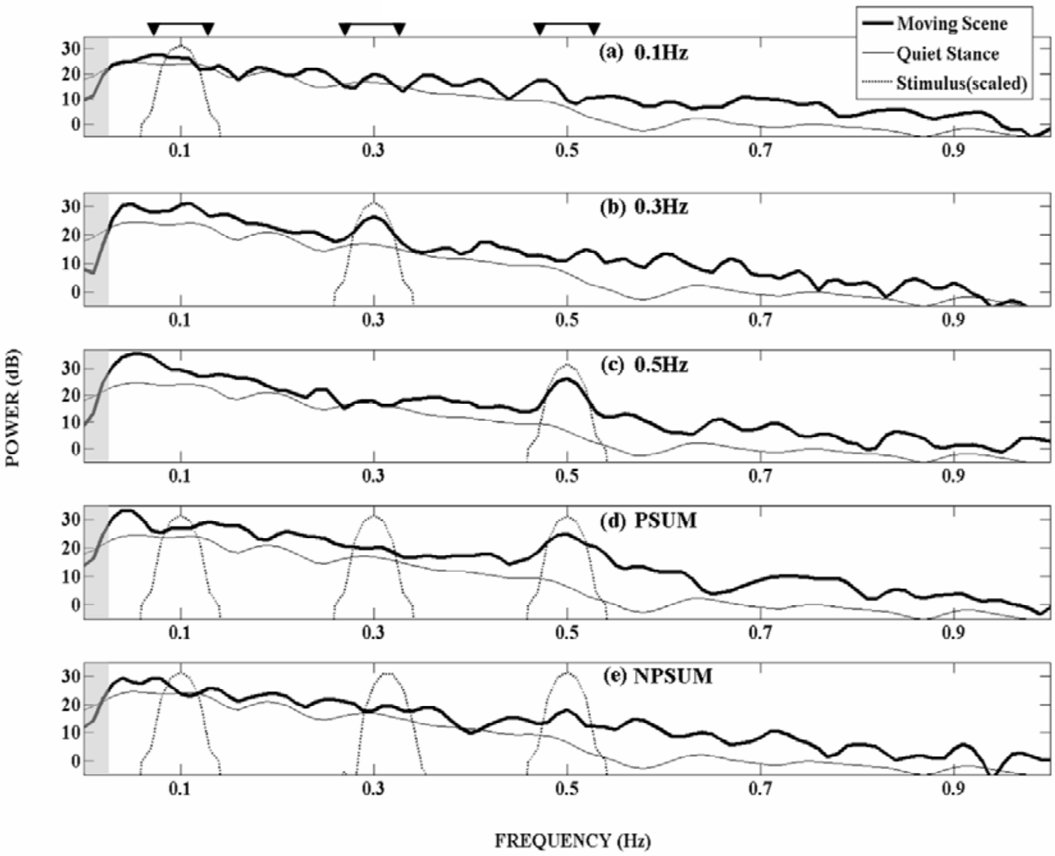


Figure 5 Ensemble power spectra of Head responses to the five scene movements (MS Response). Values are the average across n=6 subjects. Shown from top to bottom are (a) 0.1Hz, (b) 0.3Hz, (c) 0.5Hz, (d) PSUM (0.1 + 0.3 + 0.5Hz), and (e) NPSUM (0.1 + π/10 + 0.5Hz). Spectra for the stimuli (dotted line) and quiet-stance (QS) baseline response (thin solid line) are included for comparison. Stimulus power values have been scaled, for clarity (see Figure 2 for actual values). Note that the absence of power below 0.025Hz is due to the data having been high-pass filtered, as represented by the shaded area. Arrows indicate the regions over which power values were averaged to yield the "stimulus-band" values that are shown in the Figure 6 bar plots (see *Data Processing* section for details).

Sway power in the 0.3Hz band (0.27 to 0.33 Hz) was significantly larger in response to the 0.3Hz sinusoid, as compared to that during quiet stance (7dB difference), as well as compared to that in response to the 0.1Hz and 0.5Hz stimuli (4dB differences in both cases); see Figure 6a. Similarly, sway in the 0.5Hz band (0.47 to 0.53 Hz) was largest in response to the

0.5Hz stimulus, with power significantly larger (by approximately 8dB) than that for responses to the 0.1Hz and 0.3Hz sinusoids. In addition, quiet stance power in the 0.5Hz band was significantly lower (by between 7dB and 15dB) than the corresponding response power to any of the sinusoids (Figure. 6a). These trends, including significant differences, were observed in the COP data as well.

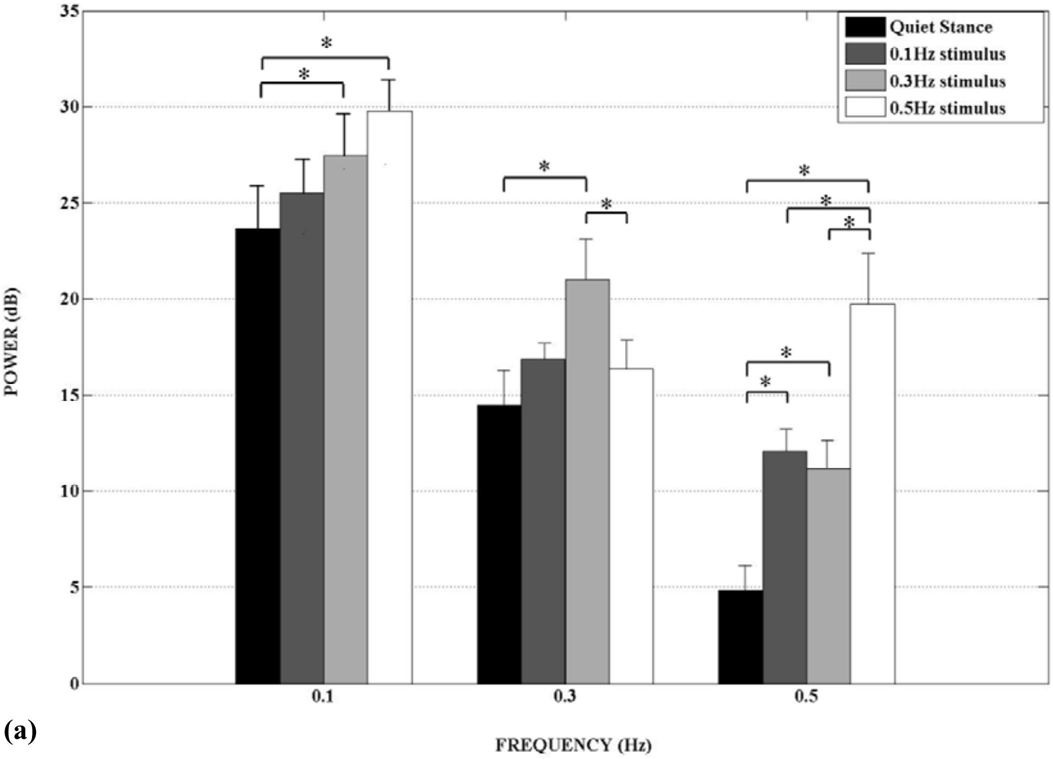


Figure 6 Ensemble head sway response power at each of the stimulus frequencies for (a) the three single sinusoidal stimulus trials, and (b) the two sum-of-sinusoids stimulus trials. Quiet stance baseline values are shown for comparison. Values plotted are the mean +/- std error (in decibels) for all subjects (n=6). Asterisks denote statistically significant differences (p<0.05).

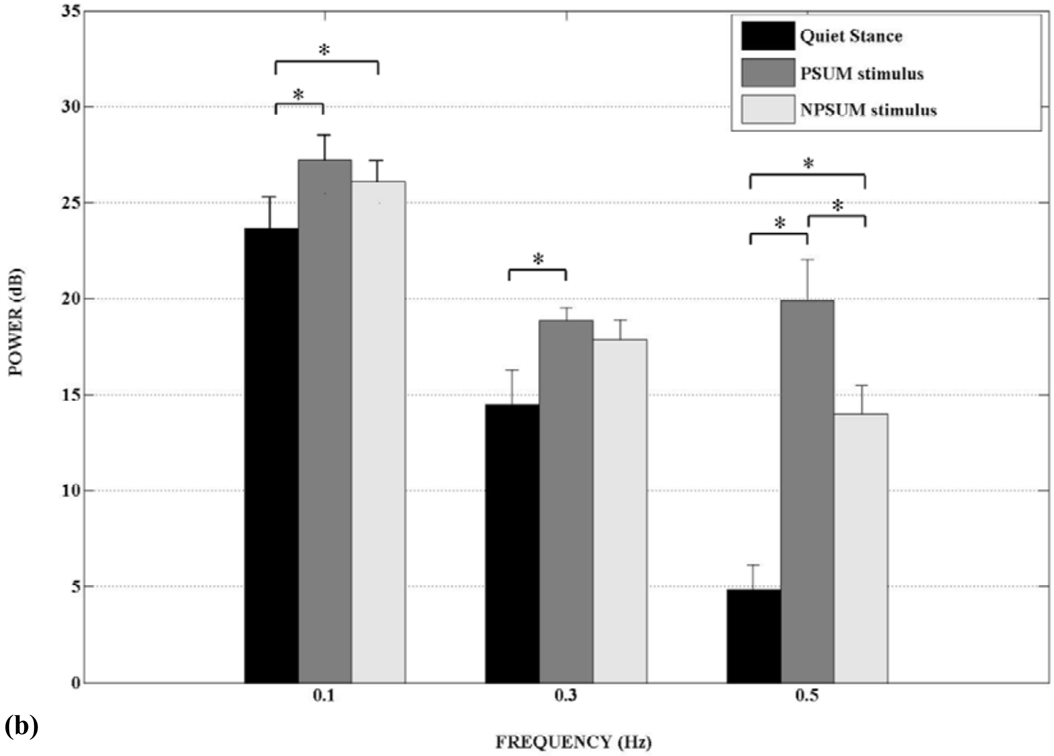


Figure 6 (continued) – part (b)

6.4.3 RESPONSES TO SUM-OF-SINUSOIDS

For the sum-of-sinusoids stimuli, both the periodic (PSUM) and non-periodic (NPSUM) signals elicited sway at each of their three component frequencies (Figures 5d-e, Figure 6b). PSUM and NPSUM response amplitudes were nearly identical to one another in the 0.1Hz and 0.3Hz bands, but significantly different in the 0.5Hz band, with PSUM larger than NPSUM by over 6dB (Figure 6b). These trends in the 0.5Hz band were clearly observed in four of the six subjects (Figure 7). In addition, group mean responses were significantly larger (by at least 3dB) than quiet stance values at each of the stimulus frequencies, with the difference being particularly large (10dB or more) in the 0.5Hz band (Figure 6b). As in the case of the single sinusoidal stimuli, these trends, including significant differences, were observed in the COP data as well.

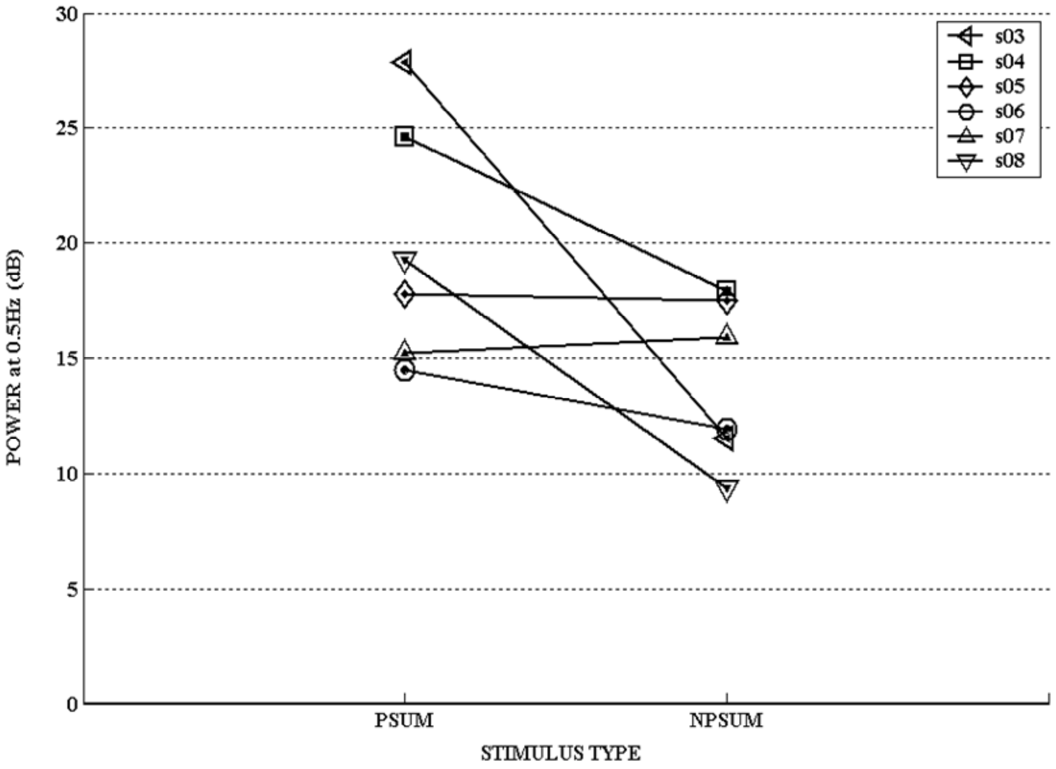


Figure 7 Individual subject head sway response power at 0.5Hz for the sum-of-sinusoids stimulus trials (PSUM and NPSUM). Subjects are identified by number, as shown in the legend (e.g. 's03' = subject 3). These individual values, when averaged, yield the group means depicted in the corresponding bar plots in Figure 6.

6.5 DISCUSSION

This study investigated the effect of optic flow periodicity on postural sway, in an attempt to uncover evidence of the existence of a predictive component to postural control. The main finding was that the PSUM and NPSUM sum-of-sinusoids stimuli elicited sway responses that were similar to one another at 0.1Hz and 0.3Hz, but significantly different at 0.5Hz, with PSUM responses on average four times larger than those for NPSUM. This effect was observed in four of six subjects, and indicates that spectrally similar periodic and non-periodic stimuli can elicit quantitatively different sway responses. This finding was contrary to the original hypothesis that PSUM values would be *lower* than NPSUM values. Nevertheless, the fact that the PSUM and NPSUM stimuli evoked significantly different responses suggests that postural control may indeed be sensitive to optic flow periodicity. However, this sensitivity was not accompanied by an attenuation of sway in response to periodic optic flow, as had been expected for the predictive process that we proposed. Further investigation is necessary to fully explore possible underlying mechanisms for the current findings, some of which are discussed below.

Previous findings in other sensorimotor systems have shown that the CNS can discern sensory stimuli based on periodicity. For example, Barnes et al. [Barnes *et al.*, 2000], in examining ocular pursuit in healthy adults, have observed that exposure to sinusoidal visual inputs enhances visual tracking performance during subsequent exposure to similar sinusoidal stimuli. The authors suggested that the CNS is capable of detecting periodicity, and proposed a model of predictive control in which velocity information could be sampled, stored and subsequently replayed as an anticipatory pattern of movement. In addition, a number of similar studies have reported that the predictability of a moving visual stimulus affects the gain and phase of the smooth pursuit component of eye velocity [Larsby *et al.*, 1988; Collewijn and Tamminga, 1984; St. Cyr and Fender, 1969; Michael and Melvill Jones, 1966]. For example, Larsby et al. [Larsby *et al.*, 1988] exposed subjects to both single-sinusoidal and pseudorandom target motion at frequencies ranging from 0.2Hz to 2Hz, and observed significantly higher gain in response to single-sinusoidal stimuli, as compared to pseudorandom stimuli, at frequencies similar to those used in the current study. Predictability effects have also been observed outside of the visual domain. For example, Nelson et al. [Nelson *et al.*, 2004] recently reported that (1) motor responses to single sinusoidal vibrotactile perturbations were faster and more accurate than responses to random perturbations; and that (2) both the amount and location of activation in the cerebral cortex were different between responses to these predictable and unpredictable stimuli. Based on these observations, the authors suggested that exposure to predictable stimuli caused subjects to rely less on sensory feedback and more on feedforward control. These findings indicate that the CNS, especially the visual system, is sensitive to stimulus periodicity, and provide evidence in support of the current observations.

In addition to differences between PSUM and NPSUM responses, we also observed (1) sway power at non-stimulus frequencies, and (2) strong responses at 0.5Hz, in both the single-sinusoid and sum-of-sinusoid data. Changes in the overall distribution of spectral power in response to single-frequency sinusoidal perturbations have been observed previously [van Asten *et al.*, 1988; Dichgans and Brandt, 1978; Lestienne *et al.*, 1977]. Two possible explanations for increased sway at non-stimulus frequencies are: (1) the system is responding in a nonlinear fashion, and (2) the system is not time-invariant, but rather changes in response to external perturbations. Such nonlinearities and time-variations have been observed previously. For example, Lestienne et al. found that sway was proportional to the logarithm of moving scene velocity [Lestienne *et al.*, 1977], while Peterka and Benolken reported saturation in postural sway responses to increasing amplitude of scene movement [Peterka and Benolken, 1995]. Such logarithm-like saturation nonlinearities would generate harmonics of a sinusoidal stimulus [Victor and Shapley, 1980]. Our results are partially consistent with this, in that the 0.1 Hz single sinusoidal stimulus evoked significantly greater sway at 0.5Hz compared to quiet stance; the 0.1Hz stimulus did not, however, produce a similar increase at 0.3 Hz. In addition, previous studies have uncovered time varying behavior such as “sensory re-weighting”, whereby the relative contributions of the various sensory systems change over time in response to external perturbations [Peterka and Loughlin, 2004; Peterka, 2002]. Sensory re-weighting can lead to increased sway power at lower frequencies, if the sensory gains decrease in response to a perturbation [Peterka and Loughlin, 2004]. In the current study, it may be that in response to visual perturbations, sensory re-weighting occurred such that the “visual gain” of the system was reduced, leading to a change in the overall distribution of spectral power relative to quiet stance. The observation of increased sway power below 0.2 Hz in response to sinusoidal perturbations at higher frequencies is consistent with this aspect of postural control. Several studies have examined such time-varying postural behavior, using time-frequency methods that quantify how spectral power of the sway response changes throughout the duration of a trial [Loughlin *et al.*, 2003; Loughlin and Redfern, 2001; Loughlin *et al.*, 1996; Schumann *et al.*, 1995]. Preliminary application of such methods to the current data uncovered clear evidence of a time-varying response in numerous trials, notably a within-trial decrease in the amplitude of sway at the stimulus frequency. This effect has been previously reported by Loughlin et al. [Loughlin *et al.*, 2003; Loughlin and Redfern, 2001; Loughlin *et al.*, 1996], who implicated the aforementioned sensory re-weighting as a possible mechanism for this adaptive behavior.

With respect to the strong responses at 0.5Hz, the data show that stimulus-band response power generally increased with stimulus frequency. For example, in response to the single sinusoids, the greatest increase in sway relative to quiet stance was at 0.5 Hz, while the smallest increase was at 0.1 Hz; the latter being not significantly different from quiet stance power at 0.1 Hz. The sum-of-sinusoids data also exhibited the largest response, relative to quiet stance, at 0.5 Hz. This noticeable sway at such a high frequency was a surprising observation, considering that it is seldom reported for healthy adults. One possible explanation is that the virtual testing environment utilized in the current study, which presented full-field luminous scenes via computer generated images and LCD projection cameras, provided visual stimuli that were much more compelling than those used in previous studies. Moreover, the consistently large responses at 0.5Hz suggest that velocity may be a salient feature of the visual stimulus, since the 0.5Hz sinusoid had the highest velocity of the three sinusoidal frequencies (amplitudes were identical among sinusoids, and therefore velocity increased proportionately to frequency). Such postural sensitivity to visual stimulus velocity has been reported previously [Kiemel *et al.*, 2002; Dijkstra *et al.*, 1994a; Lestienne *et al.*, 1977].

6.6 CONCLUSION

This study found differences in sway responses to spectrally similar periodic and non-periodic moving visual stimuli. Specifically, periodic optic flow evoked larger sway amplitudes compared to non-periodic optic flow of equal total power and nearly identical spectral content. Previous findings in other sensorimotor systems suggest that this effect may be due to the visual system's sensitivity to signal periodicity [Barnes *et al.*, 2000; Larsby *et al.*, 1988], and therefore may not be unique to postural control. In addition, we observed increases in low frequency sway relative to quiet stance sway in response to sinusoidal moving scene perturbations, regardless of the stimulus frequency. This finding is consistent with time-varying aspects of postural control, in particular the sensory re-weighting hypothesis [Peterka and Loughlin, 2004; Peterka, 2002]. Future studies are planned to more fully investigate these findings and to develop models of the underlying mechanisms.

7.0 EXPERIMENT 2: POSTURAL SWAY ADAPTATION DURING INITIAL EXPOSURE TO PERIODIC AND NON-PERIODIC OPTIC FLOWS

7.1 ABSTRACT

We propose that postural control contains a predictive component that is sensitive to stimulus periodicity, such that periodic sensory inputs will produce lower sway than will non-periodic inputs. Results from an initial study refuted this hypothesis, showing that sway power in a group of six healthy adults was significantly *larger* in response to a *periodic* sum-of-sinusoids (SOS) optic flow stimulus, compared to a spectrally similar non-periodic counterpart, but only at the highest component frequency of the SOS stimuli (0.5Hz) [Musolino *et al.*, 2006]. The objective of the current study was to determine whether this behavior would be reproduced in a larger group of subjects, and for a wider variety of SOS optic flow stimuli. Twenty subjects (13F, 7M ; age 21-35) were exposed to ten different full-field bullseye-and-checkerboard optic flow stimuli, presented in random order: four single sinusoids (0.1, 0.3, 0.5, 0.7Hz), three different periodic combinations of these sinusoids (PSUM), and three non-periodic combinations (spectrally similar to the periodic signals) in which the 0.3Hz component was replaced by a sinusoid with a frequency of π/10 Hz (NPSUM). Head and center-of-pressure (COP) sway response power at the various stimulus frequencies were compared among the different stimulus groups. In addition, subjects were separated into "visually dependent" (DEP) and "visually independent" (INDEP) groups, based on subjective visual vertical (SVV) data collected using the rod-and-

frame test. As had been seen previously, head and COP responses were similar enough in both magnitude and phase to suggest that subjects swayed as an inverted pendulum. Also, we again observed strong responses at the stimulus frequency, as well as significant sway power at non-stimulus frequencies. With regard to the relationship between responses to PSUM and NPSUM stimuli, differences again appeared only at the highest frequency component of the SOS stimulus. A new, and unexpected, finding in this study was a strong trial effect, in which sway power for trial 1 was significantly larger than that for trials 2 through 10. Interestingly, differences between the PSUM and NPSUM groups existed only during this first trial. Moreover, these differences were influenced by subjects' visual dependence. Specifically, DEP subjects swayed more in response to PSUM stimuli as compared to NPSUM stimuli, while INDEP subjects displayed the opposite behavior. There were no differences between PSUM and NPSUM groups for trials 2-10. Time-frequency analysis revealed evidence of *adaptation* (i.e. a within-trial decline in sway amplitude at the stimulus frequency) in trial 1. Subjects responded strongly during initial exposure to optic flow, but the amplitude of this response decreased substantially during trial 1, and remained at an attenuated level for subsequent trials. Further, the rate at which adaptation occurred was fastest for INDEP subjects exposed to PSUM stimuli, and slowest for DEP subjects exposed to PSUM stimuli. These findings suggest that periodic and non-periodic optic flow stimuli do indeed evoke quantitatively different sway responses, and that this can be attributed to differences in the rate of adaptation during initial exposure to these stimuli. Such behavior is consistent with the existence of a predictive component to postural control that is capable of reducing visual gain during exposure to periodic optic flow.

7.2 INTRODUCTION

Many previous examinations of postural control have focused on the feedback mechanisms that are known to influence upright stance [Peterka, 2003; Peterka, 2002; Day and Cole, 2002; Creath *et al.*, 2002; Jeka *et al.*, 2000; Fukuoka *et al.*, 1999; Allum *et al.*, 1998; Bronstein and Buckwell, 1997; Fitzpatrick *et al.*, 1996; Peterka and Benolken, 1995]. Some of these studies have concluded that feedback alone is sufficient to explain experimental observations of postural behavior [Peterka, 2003; Peterka, 2002], while others suggest that feedforward mechanisms must be involved as well [Fitzpatrick *et al.*, 1996]. A variety of possible roles for predictive processes have been posited, primarily in the motor control literature. These include the maintenance of stability in the presence of feedback delays, and the facilitation of sensorimotor learning [Blakemore and Sirigu, 2003; van der Kooij *et al.*, 2001; van der Kooij *et al.*, 1999]. It remains unclear, though, how the underlying mechanisms might operate, and how they interact with feedback processes to achieve postural stability. One possibility that has been suggested is that the CNS contains an internal forward model that can predict the consequences of motor commands [Blakemore and Sirigu, 2003; Wolpert *et al.*, 1998]. The internal model captures the causal relationships between neuromuscular inputs and outputs, and is used in combination with an efference copy of the motor command in order to simulate subsequent sensory consequences. For example, an internal model could predict a future state (e.g. body position and/or velocity), given the current state and motor command. This mechanism would be useful, for instance, in providing timely estimates of new sensory information in the absence of actual sensory input due to temporal delays associated with feedback control. Note that the predictive capability of such an internal model relies solely on the sensorimotor mapping that the model contains, and is not influenced by specific properties of the sensory stimulus.

In this study, it is proposed that postural control contains a predictive mechanism that is sensitive to the relative predictability of sensory inputs, such that highly predictable stimuli will activate this mechanism, while less predictable stimuli will not. Like the internal forward model described above, this predictive mechanism would be capable of estimating future sensory states, and of facilitating sensory integration by decreasing the time that is required to process information regarding future sensory inputs. It is suggested, however, that the proposed mechanism is distinct from (but not necessarily independent of) the internal forward model, in that its predictive capability is affected by specific properties of the sensory stimulus. If indeed this predictive component of postural control exists, then one would expect to observe differences in postural responses to external perturbations that vary in their degree of predictability. With this in mind, our motivation was to uncover evidence of such stimulus-dependent predictive behavior. Specifically, this work examined how the relative predictability of a moving visual scene influences postural sway. Note that "predictable" is used here not in the statistical versus deterministic sense, but rather in terms of a periodicity or repetitive pattern that the central nervous system (CNS) can readily discern.

In a previous study in our laboratory [Musolino *et al.*, 2006], comparisons were made among sway responses to two types of antero-posterior (AP) full-field oscillatory optic flow stimuli: a sum of sinusoids (SOS) with an obvious periodicity, and a spectrally similar SOS that exhibited no periodicity. We had hypothesized that the periodic visual stimulus would elicit lower sway amplitudes compared to the non-periodic stimulus. The rationale for this hypothesis, as alluded to earlier, was that predictive mechanisms in the CNS could exploit the repetitive nature of a periodic stimulus in order to predict future visual inputs, and that this predictive behavior could in turn promote postural stability. For example, reliance on visual afferents might be reduced, perhaps by lowering visual gain in the postural control loop, which would effectively attenuate the visual signal that is driving the postural system, and thereby cause a reduction in the sway response. The results of this study did not support our hypothesis, and instead showed that sway power in a group of six healthy adults was significantly larger in response to the periodic SOS compared to the non-periodic SOS, but only at the highest component frequency of the stimuli (0.5Hz). Other findings from this study included: a consistently strong response at 0.5Hz, suggesting a sensitivity to stimulus velocity [Kiemel *et al.*, 2002; Dijkstra *et al.*, 1994a; Lestienne *et al.*, 1977]; sway power at non-stimulus frequencies, implying a non-linear response [van Asten *et al.*, 1988; Dichgans and Brandt, 1978; Lestienne *et al.*, 1977]; sway amplitudes of approximately ±2cm in response to stimulus amplitudes of ±8cm, indicative of a saturation type non-linearity, as described by Peterka and Benolken [Peterka and Benolken, 1995]; and evidence of "adaptation", a within-trial decrease in the amplitude of sway at the stimulus frequency, as observed previously by Loughlin et al. [Loughlin *et al.*, 2003; Loughlin and Redfern, 2001; Loughlin *et al.*, 1996]. These findings supported the notion of postural sensitivity to the predictability of visual motion, but a clear picture of this phenomenon was obscured by other findings that implicated various nonlinear and/or time-varying mechanisms in the postural control system. As such, the objective of the current study was to determine whether the aforementioned behaviors would be reproduced in a larger group of subjects, and for a wider variety of SOS optic flow stimuli. Specifically, the following questions were to be addressed:

1. Would differences again be observed between periodic and non-periodic SOS groups? If so, would they be the same as in our previous study, or instead support our hypothesis?

2. Would subjects again respond strongly to the highest component frequency in a SOS stimulus, regardless of the whether that frequency is 0.3Hz, 0.5Hz or 0.7Hz?
3. How would sway amplitudes in response to a ±8cm stimulus compare to those in response to the substantially lower stimulus amplitude of ±4cm?
4. Would adaptation be observed in any of the sway responses? If so, would this adaptation be different for responses to periodic stimuli compared to those for non-periodic stimuli?

7.3 METHODS

Postural sway responses to various moving visual scene perturbations were examined in twenty healthy young adults, ranging in age from 21-35 years (mean age = 26). Subjects had no history of neurological or balance-related dysfunction, and no previous exposure to visual scene perturbations in an experimental setting. All subjects provided informed consent to participate in this study, and the experimental protocol was approved by the Institutional Review Board at the University of Pittsburgh. Tests were performed in the Balance Near Automatic Virtual Environment (BNAVE), a custom built virtual reality system that creates an immersive visual surround by projecting computer generated images onto three adjoining screens [Jacobson J *et al.*, 2001]. The screens are approximately 183cm x 213cm (width x height), and are arranged in front, to the left, and to the right of the viewer. A contiguous image is projected onto the screens, and provides a full (180°) horizontal field of view. This visual scene extends onto the floor as well, but not to the ceiling (which is covered in black cloth), so the vertical field of view is thus limited to approximately 120°.

7.3.1 VISUAL SCENES

The image presented to the subjects consisted of a “bullseye” pattern of six alternating black-and-white concentric rings (with each ring occupying 5° of visual arc), surrounded by a checkerboard of black-and-white squares (15cm per side) [Musolino *et al.*, 2006]. Previous studies have utilized similar patterns in a moving room paradigm to evoke postural responses in both healthy and patient populations [Borger *et al.*, 1999; Peterka and Benolken, 1995; van Asten *et al.*, 1988]. The bullseye-and-checkerboard pattern oscillated toward and away from subjects in either a periodic (“predictable”) or non-periodic (“unpredictable”) fashion. Scene movement was driven by one of ten signals (Figure 8): (1) 0.1Hz sinusoid, (2) 0.3Hz sinusoid, (3) 0.5Hz sinusoid, (4) 0.7Hz sinusoid, (5) three different periodic sums of these three sinusoids ($PSUM_{13}$ = 0.1 + 0.3Hz ; $PSUM_{135}$ = 0.1 + 0.3 + 0.5Hz; $PSUM_{1357}$ = 0.1 + 0.3 + 0.5 + 0.7Hz), and (6) three non-periodic counterparts ($NPSUM_{13}$ = 0.1 + π/10Hz; $NPSUM_{135}$ = 0.1 + π/10 + 0.5Hz; and $NPSUM_{1357}$ = 0.1 + π/10 + 0.5 + 0.7Hz). Because the frequencies of the PSUM stimuli are integer multiples of each other, these stimuli are periodic, with period given by $T=1/0.1=10$ sec. For the NPSUM stimuli, component frequencies were chosen in order to produce signals with frequency content nearly identical to that of the corresponding PSUM stimuli, but lacking a temporal periodicity. Since π/10 is not an integer multiple of 0.1 Hz, the NPSUM stimuli are not periodic and exhibit markedly different temporal characteristics than the PSUM stimuli, even though the spectra of corresponding PSUM and NPSUM stimuli are very similar (see Figure 8).

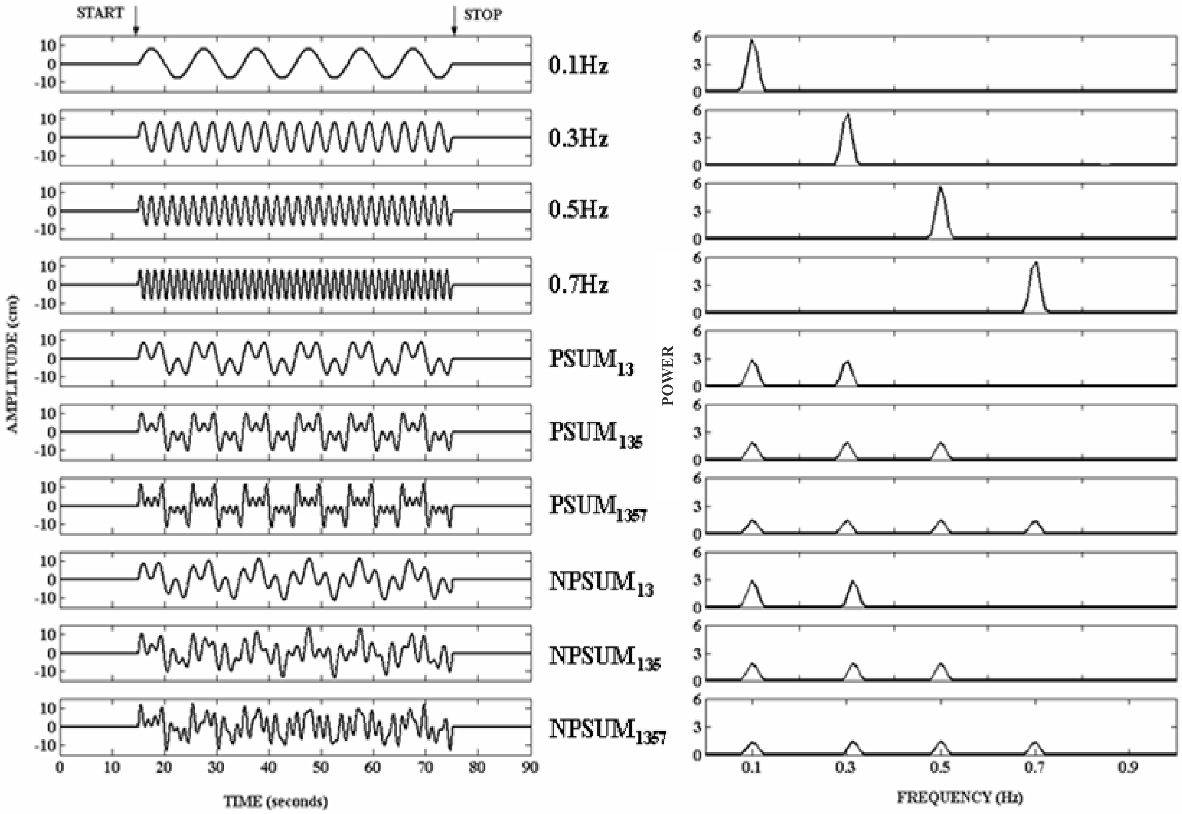


Figure 8 Time series' (left) and corresponding power spectra (right) for the ten scene movements presented to subjects. Shown from top to bottom are 0.1Hz, 0.3Hz, 0.5Hz, 0.7Hz, PSUM$_{13}$ (0.1 + 0.3Hz), PSUM$_{135}$ (0.1 + 0.3 + 0.5Hz), PSUM$_{1357}$ (0.1 + 0.3 + 0.5 + 0.7Hz), NPSUM$_{13}$ (0.1 + π/10Hz), NPSUM$_{135}$ (0.1 + π/10 + 0.5Hz), and NPSUM$_{1357}$ (0.1 + π/10 + 0.5 + 0.7Hz). "Start" and "Stop" indicate times at which scene movement begins and ends, respectively.

In addition, the sum-of-sinusoids signals were normalized such that their root-mean-square (RMS) was equal to that of the single sinusoids; this ensured that peak amplitudes and total input power were the same among the ten stimuli. Twelve of the twenty subjects were exposed to ±8cm amplitude stimuli, as in the previous study, while the remaining subjects viewed stimuli with an amplitude of only ±4cm.

7.3.2 DATA COLLECTION

Subjects stood in an upright position 1.5 meters from the front screen, with arms folded across the chest, and with bare feet placed shoulder-width apart on a force platform (NeuroCom Inc., Clackamas OR). Image height was adjusted so that the bullseye center was located at eye level. Subjects were secured to the BNAVE support structure with a tether and harness. This safety line was sufficiently loose to afford subjects free range of motion, and did not hinder sway or provide sensory feedback regarding their body sway. Each of the ten scene movements was presented once, in random order, to each subject. Prior to each trial, room lights were dimmed, and subjects were instructed to "stand comfortably and look straight ahead at the image on the screen." Trial duration was 90 seconds, and consisted of 60 seconds of scene movement preceded and followed by 15 seconds of no motion. A rest period of 3 minutes was provided between successive trials, during which time room lights were switched on, and subjects relaxed in a seated position. In addition, a 60-second quiet stance trial was performed prior to the moving scene trials, in order to record "baseline" spontaneous sway in the absence of visual perturbation (i.e. subjects viewed a blank screen during these baseline trials).

Postural responses were examined through measurements of head and center-of-pressure (COP) displacements. Head data were collected at 20Hz using a Polhemus Fastrack electromagnetic tracking system (Polhemus Inc.), with a single sensor located at the crown of the head. Foot force data were sampled at 100Hz via load cells embedded in the force platform, and post-processed in Matlab (The Mathworks Inc.) to obtain COP values.

7.3.3 DATA PROCESSING

Data were high-pass filtered, down-sampled to 5 Hz, and zero-meaned. High-pass filtering was achieved through zero-phase implementation of a fourth order Chebyshev type II filter, with a cutoff frequency of 0.025 Hz, and a stop-band attenuation of 20 decibels (a decibel (dB) is a unit of measure often used for values that span several orders of magnitude, and is mathematically defined as $10*\log_{10}(\text{Power})$). The 3dB attenuation point for the high-pass filter occurred at approximately 0.03Hz, so that frequencies above 0.07Hz were not attenuated at all. This high-pass filter removed the dominant DC and very low frequencies observed in postural sway position data, and facilitated the identification of sway responses to the low frequency (0.1 Hz) component of the stimuli.

Filtered data were then examined using Fourier analysis, in order to estimate spectral densities for head and COP response signals, for both the quiet-stance baseline trial and moving scene trials. This was achieved through the calculation of windowed periodograms using the discrete Fourier transform (DFT). Spectral estimation was performed on only the 60-second moving scene portion of each trial (i.e. the first and last 15 seconds of data were removed prior to Fourier analysis). The 60-second data segments were multiplied by a Hanning window (a smooth function that tapers gradually to zero [1975]) prior to performing the DFT, in order to minimize edge effect artifacts that can arise during the Fourier transform. The squared-magnitude of the DFT was computed to produce an estimate of sway response power, at frequency intervals of 0.01Hz, spanning DC through 2.5Hz. Of particular interest was response power at each of the stimulus frequencies: 0.1 Hz, 0.3 Hz, 0.5 Hz, and 0.7 Hz. These were obtained by calculating the average power across seven frequency bins (bin size = 0.01Hz) at and around each of the stimulus frequencies. This yielded a “stimulus-band” power equal to the average power at a given stimulus frequency ± 0.03Hz. These frequency-band power metrics were used as the means of comparison (1) among the four single sinusoidal groups, and (2) among the six sum-of-sinusoid groups. Responses to moving scenes were compared to those for quiet stance, in order to separate contributions of optic flow from those due purely to spontaneous sway.

7.3.4 SWAY ADAPTATION ANALYSIS

Changes in sway amplitude throughout each trial were determined by examining the time-varying spectrum of sway position, as obtained through the use of time-frequency analysis, as described by Cohen [Cohen, 1989; Cohen and Posch, 1985] and Loughlin et al. [Loughlin *et al.*, 1994]. This technique combines the time-frequency information from multiple spectrograms (short-time Fourier transforms) computed with various window lengths, to obtain an improved estimate of time-varying spectral power, denoted by P(t, ω) where t=time and ω =frequency, compared to that provided by a single spectrogram. Of particular interest was the time-varying response power at the stimulus frequency, P(t), which was calculated as shown in equation (1) below:

$$\mathrm{P(t)} = \sum_{\omega=Fs-0.03Hz}^{\omega=Fs+0.03Hz} P(t,\omega)\text{, where Fs = stimulus frequency} \qquad (1)$$

This time series was visually examined for evidence of sway adaptation. Whether or not adaptation occurred was determined subjectively on a trial-by-trial basis, as opposed to being based on any strict quantitative criteria, statistical or otherwise. This approach was possible because there were relatively few adaptation trials, and because it was rather obvious when P(t) displayed adaptive characteristics. For example, the decline in sway power shown in Figure 14 was typical for an adaptation trial, whereas non-adaptation trials displayed no such drop in sway power over time. For cases in which adaptation occurred, the time series, P(t), was fit with an exponential curve of the form $Ae^{-t/\tau} + B$, and the following parameters were extracted:

A = pre-adaptation magnitude of stimulus-band sway response to the moving scene
B = post-adaptation magnitude of stimulus-band sway response to the moving scene
τ = time constant of the exponential decay

Choosing a region over which the time series would be fit with an exponential curve contained a degree of subjectivity. Responses among subjects were not consistent: there were transients, delayed responses, and power did not necessarily decrease monotonically following the initial response. As such, the selection of fit boundaries was done on a trial by trial basis, as opposed to applying some automated algorithm to each trial. The starting point for curve fitting was chosen as the point of maximum power within a ten second window following the onset of scene movement. If this maximum power corresponded to an obviously transient event that was not representative of the overall response, then a more appropriate point in the same ten second region was used instead. The choice of ten seconds was not arbitrary. We had assumed that the primary sway response would occur during exposure to the first full cycle of a given stimulus, and ten seconds corresponded to the period of the lowest component frequency (0.1 Hz) in any of the stimuli. The end point for the curve fit was chosen as the point at which sway power returned to the pre-response magnitude, and remained at that level for at least ten seconds. Any increase in power after ten seconds was considered to be a secondary response. Fitting an exponential curve to the portion of the power-versus-time data series bounded by these beginning and end points provided a means of quantifying the adaptation process, by yielding both the time constant of decay, as well as the per-stimulus decline in sway magnitude.

7.3.5 EXAMINATION OF SUBJECT VISUAL DEPENDENCE

Findings from previous studies suggest that postural behavior during exposure to visual perturbations may be influenced by a subject's relative sensitivity to visual stimuli [Isableu *et al.*, 1998; Isableu *et al.*, 1997; Nyborg, 1974]. This "visual dependence" was examined in the current subject population via the rod-and-frame test, as described by Isableu et al. [Isableu *et al.*, 1998; Isableu *et al.*, 1997] and Nyborg [Nyborg, 1974]. This procedure examines the subjective visual vertical (SVV), which represents a subject's ability to accurately identify earth vertical in an environment containing limited visual information. Subjects are seated in a dark room, equipped with a handheld device that controls the orientation of a 2.4cm wide illuminated rod situated directly in front of them, and instructed to align the rod with their perceived earth vertical. The initial orientation of this rod is 40 degrees clockwise (CW) or counterclockwise (CCW) from earth vertical. Subjects perform this alignment under two different conditions. In the "Frame" condition, the illuminated rod is surrounded by an illuminated square frame (90cm x 90cm) oriented 23 degrees CW or CCW from earth vertical. In the "Disc" condition, the illuminated rod is surrounded by a randomly arranged field (90cm diameter) of variously sized illuminated dots that rotates in the CW or CCW direction at 30 degrees per second. The difference (or error), in degrees, between the final subject-adjusted position of the rod and true earth vertical is recorded for these various conditions, and used to assess a subject's relative dependence on visual information. The method used in this study to categorize subjects as visually dependent (DEP) or visually independent (INDEP) based on SVV data was borrowed from Isableu et al. [Isableu *et al.*, 1998; Isableu *et al.*, 1997]. For each subject, the mean "unsigned" deviation from vertical (in degrees) is calculated for both the Frame and Disc trials. The median value of these scores among all subjects is then determined, and subjects with scores well *above* this median are considered visually DEP, while subjects whose scores are well *below* the median are categorized as visually INDEP. For this study, the DEP and INDEP thresholds were 5.29 degrees and 1.28 degrees respectively. This visual dependence was included as a variable in the statistical analysis to determine whether visually DEP and INDEP groups exhibited different sway behaviors.

7.3.6 STATISTICAL ANALYSIS

A mixed-factor repeated measures ANOVA was utilized to examine the effects of stimulus type (STIM: PSUM, NPSUM, Single Sinusoid), stimulus amplitude (AMP: 4cm, 8cm) and visual dependence (VIS: DEP, INDEP) on total sway power, on sway power at each of the stimulus frequencies (i.e. "stimulus-band power") and on the sway adaptation time constant (τ). Data distributions were tested for normality using the Shapiro-Wilk W test, and log-transformed to achieve normality when necessary. The significance level was set at $p = 0.05$ for both primary and post-hoc (Tukey's HSD) comparisons.

7.4 RESULTS

7.4.1 GENERAL SWAY RESPONSES

Subjects responded strongly to each of the ten visual stimuli. Movements of the head and COP were in phase with one another for all trials, as revealed by visual inspection of time series data. Response amplitudes were in the range of 1cm to 2cm, with values for the head larger than those for COP below 0.5Hz, as shown in the time-series plot in Figure 9 (the plots show the responses of a single subject during just one trial, but are representative of responses for all subjects). Except for absolute power levels, the corresponding spectral densities of head and COP responses were very similar up to approximately 0.7Hz. These findings indicated that subjects had swayed predominantly as an inverted pendulum, which is consistent with previous findings of postural sway [Peterka, 2003; Peterka, 2002]. Because of the strong similarities among head and COP responses, the remaining results presented are limited to head data, with the occasional reference to COP when appropriate. Unless stated otherwise, all results presented for the head data, including significant differences, were observed in the COP data as well. In addition, no significant differences were observed in total sway power ($F_{1,860}$=0.670, p=0.4133) between the ±4cm and ±8cm stimulus amplitude groups, so these data were pooled together for all subsequent analyses.

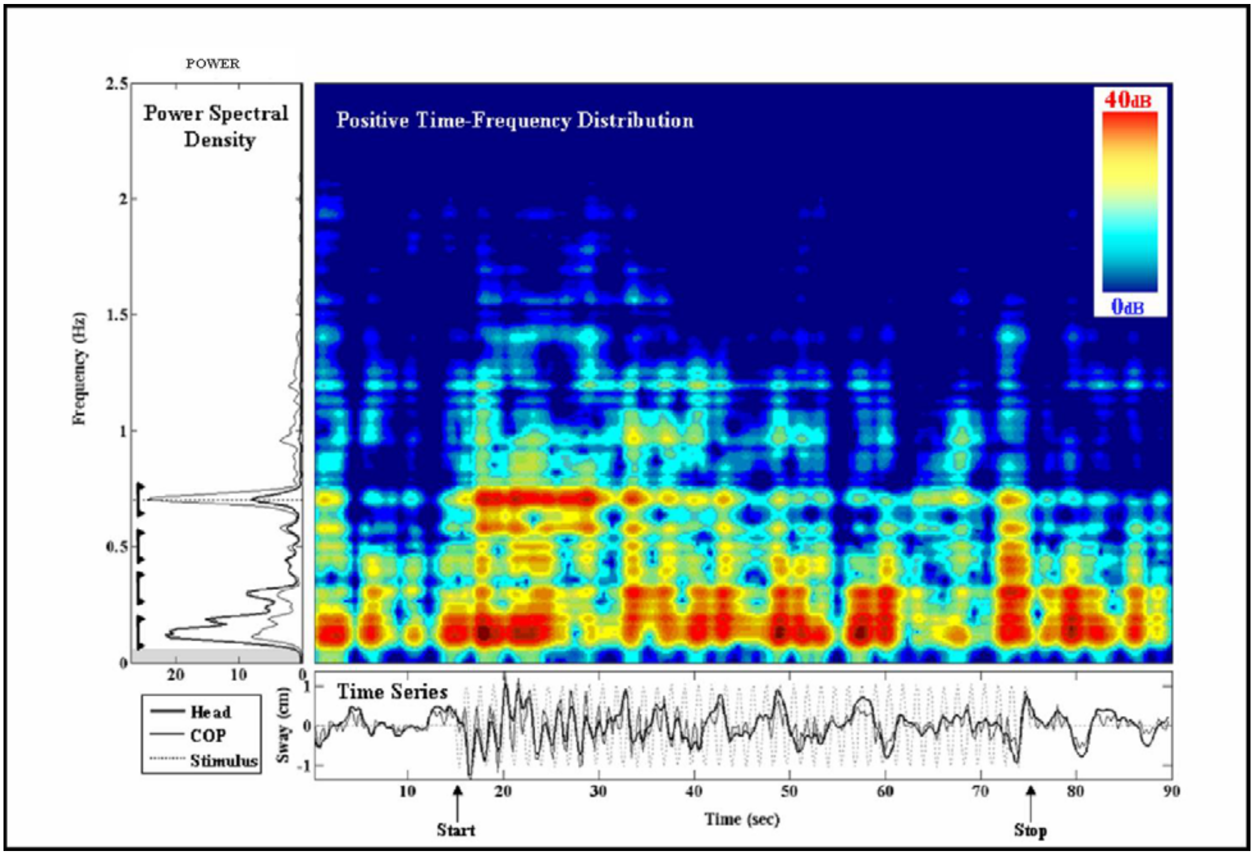


Figure 9 Time series, power spectral density, and positive-time frequency distribution (PTFD) of Head responses for one trial (trial #1, 0.7Hz stimulus) for a single subject (s204). Time series and power spectral density data for the COP response is shown for comparison. Time series data for the stimuli (dotted line) are also included for comparison; for clarity, they have been scaled by a factor of 8. "Start" and "Stop" indicate times at which scene movement begins and ends, respectively. For the power spectral density, the dotted line indicates stimulus frequency. Note that the absence of power below 0.05Hz is due to the data having been high-pass filtered, as represented by the shaded area. Arrows indicate the regions over which power values were averaged to yield the "stimulus-band" values that are shown in the Figure 11 bar plots (see *Data Processing* section for details).

Both the quiet stance (QS) and moving scene sway responses displayed power that was highest at low frequencies (i.e. below 0.1Hz) and that generally decreased across the spectrum, as shown for head motion in the power spectral density plot of Figure 9. COP data in this same figure was an exception to this trend in that there was a very large response at 0.7Hz. Quiet stance sway power was spread across a band of frequencies from DC to approximately 0.3Hz, which is typical for spontaneous sway. The moving scene responses were characterized by larger sway amplitudes in this same frequency range, and substantial power at the stimulus frequency (or frequencies, for the sum-of-sinusoids) as well. Both single sinusoid and sum-of-sinusoid stimuli elicited sway responses that were consistently larger than those observed during QS (Figure 10). This difference between moving scene power and QS power was significant for each of the ten moving scene stimuli ($F_{10,720}$=7.55, p<0.0001).

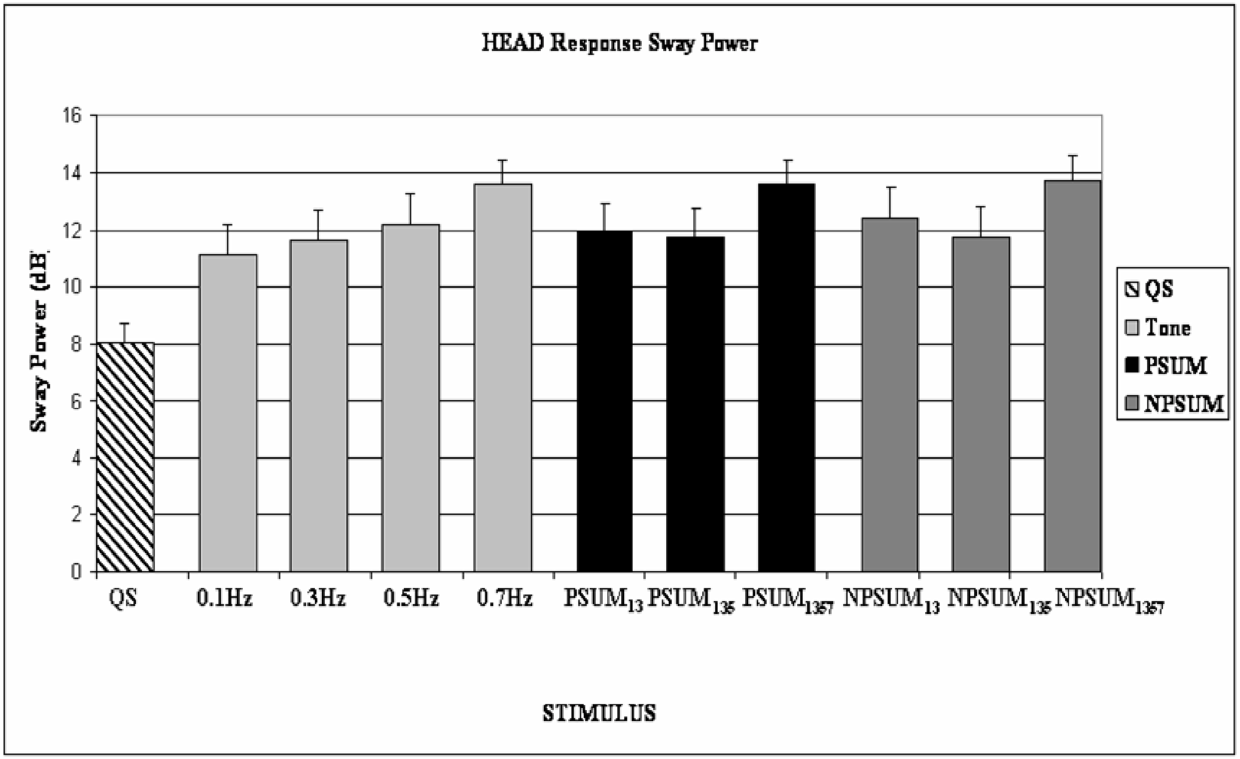


Figure 10 Ensemble total head sway power responses to the ten optic flow stimuli. Quiet stance baseline values are shown for comparison. Values shown are the mean +/- std error (in dB) for all subjects (n=20). $PSUM_{13}$ = 0.1 + 0.3Hz ; $PSUM_{135}$ = 0.1 + 0.3 + 0.5Hz; $PSUM_{1357}$ = 0.1 + 0.3 + 0.5 + 0.7Hz; $NPSUM_{13}$ = 0.1 + π/10Hz; $NPSUM_{135}$ = 0.1 + π/10 + 0.5Hz; $NPSUM_{1357}$ = 0.1 + π/10 + 0.5 + 0.7Hz. Note that the values are averaged across all frequencies, and therefore represent total output power.

This increase in sway power relative to QS was more pronounced for stimuli with higher frequency components. For example, the 0.1Hz sinusoidal stimuli produced sway responses whose total power output was 3dB larger ($p=0.019$) than that for QS, while the 0.7Hz stimuli elicit responses almost 6dB larger ($p<0.0001$) than that for QS (note that total power is the power across all frequencies, and is equal to the area under the power spectral density curve, such as that shown in Figure 9). The same trend was observed in the sum-of-sinusoids trials ($PSUM_{1357} > QS$: $p<0.0001$; $NPSUM_{1357} > QS$: $p<0.0001$), indicating that total sway power was largest for stimuli that contained the highest component frequency (0.7Hz in this case), which is consistent with findings from our previous study [Musolino *et al.*, 2006].

7.4.2 PSUM VERSUS NPSUM RESPONSES

This analysis addressed the hypotheses that (1) PSUM stimuli were expected to produce lower sway power and faster adaptation rates, as compared to NPSUM stimuli, and that (2) sway power and adaptation rates would be different between visual DEP and visual INDEP groups. Differences between responses to PSUM and NPSUM stimuli were observed only in a limited set of experimental conditions. As seen in Figure 10, total sway power (i.e. power averaged across all frequencies) was not significantly different between spectrally similar PSUM and NPSUM groups (i.e. $PSUM_{13} = NPSUM_{13}$, $PSUM_{135} = NPSUM_{135}$, and $PSUM_{1357} = NPSUM_{1357}$). Similarly, stimulus-band power (i.e. average power at a given stimulus frequency ± 0.03Hz) at each of the stimulus frequencies was not significantly different between PSUM and NPSUM groups (Figure 11).

Close inspection of responses across the ten trials uncovered an unexpectedly strong trial effect in which total sway power for trial 1 was on average 2dB larger than that for trials 2 through 10 (Figure 12). Because this difference was significant ($F_{1,720}$=60.69, p<0.0001), subsequent comparisons among the various stimulus and visual dependence groups were performed separately for trial 1 and trials 2 through 10.

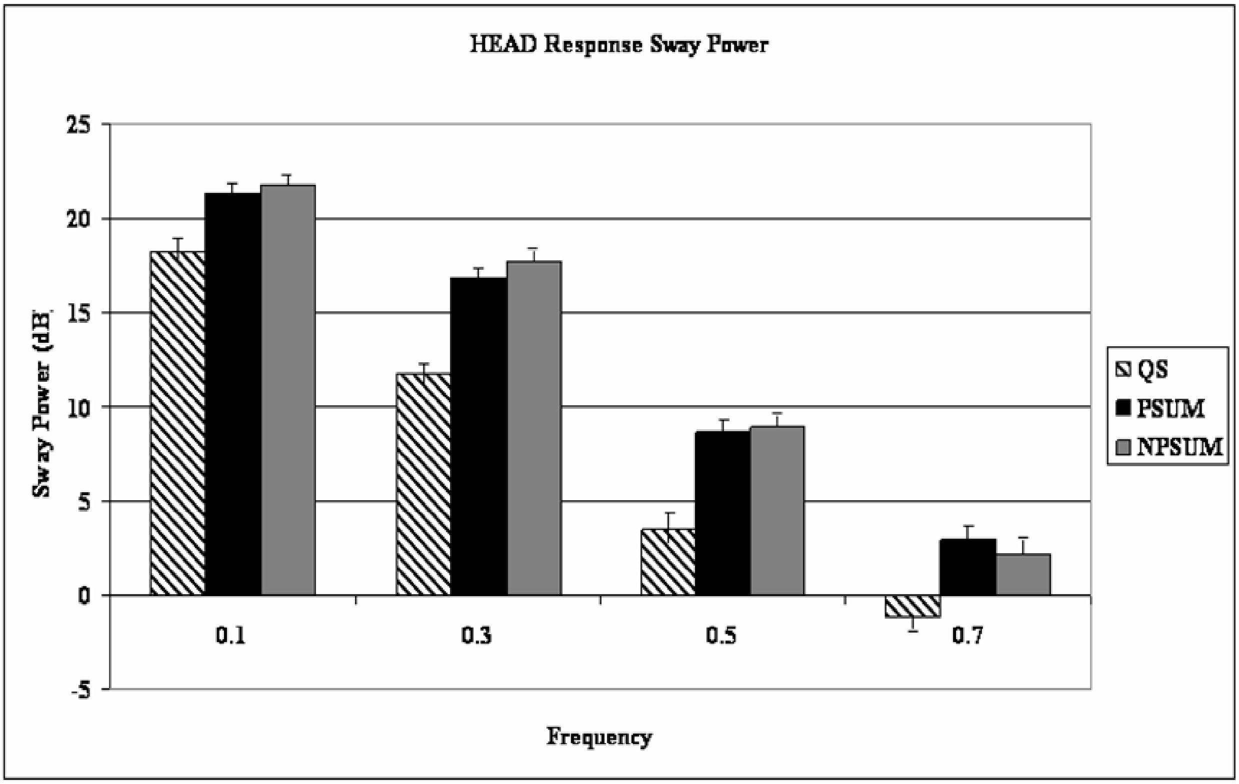


Figure 11 Ensemble head sway response power at each of the stimulus frequencies for both the sum-of-sinusoids and single tone stimulus trials. The PSUM group includes responses to all three periodic SOS stimuli ($PSUM_{13}$, $PSUM_{135}$, and $PSUM_{1357}$). Likewise, the NPSUM label represents responses to $NPSUM_{13}$, $NPSUM_{135}$, and $NPSUM_{1357}$. Quiet stance baseline values are shown for comparison. Values plotted are the mean +/- std error (in dB) for all subjects (n=20).

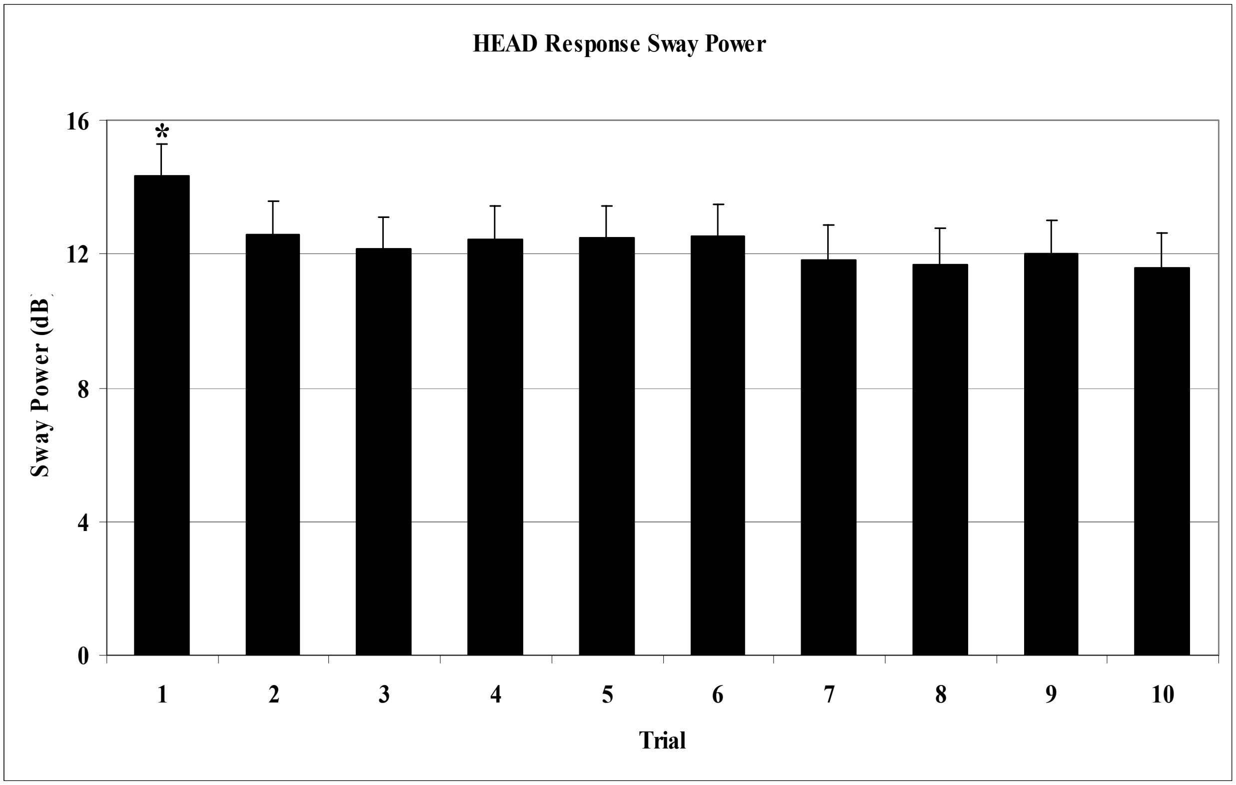


Figure 12 Ensemble head sway response power for trials 1 through 10. Values plotted are the mean +/- std error (in dB) for all subjects (n=20). Asterisk denotes a statistically significant difference ($p<0.05$). Note that the values are averaged across all frequencies (0.1, 0.3, 0.5, and 0.7Hz) and all stimulus types (Tones, PSUM, and NPSUM).

Substantial differences between responses to PSUM and NPSUM stimuli were observed only in the 0.7Hz frequency band, and only during the first trial. This was in contrast to response power at the other stimulus frequencies (i.e. 0.1Hz, 0.3Hz and 0.5Hz), where values for PSUM and NPSUM groups were not significantly different for any trial. The absence of a difference between PSUM and NPSUM responses at 0.5Hz was inconsistent with the earlier observation in experiment #1, in which sway power at 0.5Hz was significantly larger for the PSUM group compared to the NPSUM group.

The different responses at 0.7Hz to PSUM and NPSUM stimuli during trial 1 were influenced by subject visual dependence (Figure 13). Seventeen of the twenty subjects participated in SVV testing. Of these, five were determined to be visually INDEP, while the remaining twelve were categorized as visually DEP, according to the methods described earlier. The interaction between the effects of visual dependence and trial manifested itself as markedly different behavior between the DEP and INDEP groups in response to the PSUM and NPSUM stimuli. Specifically, in DEP subjects sway power was close to 10dB larger in response to PSUM stimuli compared to NPSUM stimuli (Figure 13), a finding that is similar to what had been observed in our previous study. In contrast, INDEP subjects exhibited response power nearly 10dB *lower* for the PSUM optic flow compared the NPSUM counterpart, a finding that is consistent with the hypothesis that periodic stimuli would produce lower sway compared to non-periodic stimuli. However, these observations were based on a very limited subset of the data, specifically only first trials that involved a PSUM or NPSUM stimulus. This consisted of only eight observations, with a sample size of n=2 in each of the four groups, as shown in Figure 13. Because of these very small sample sizes, the significance of differences in sway power among the groups could not be statistically determined.

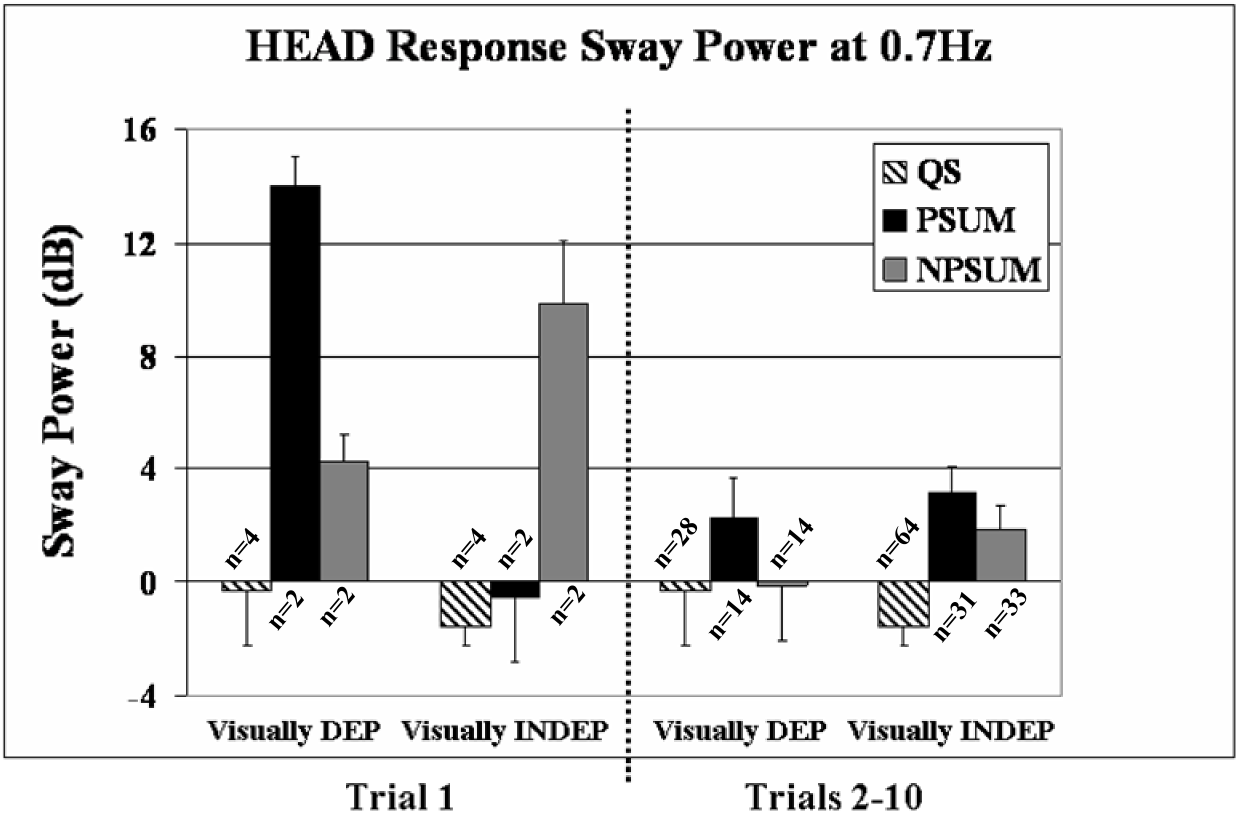


Figure 13 Ensemble head sway response power at 0.7Hz for visually dependent (DEP) and independent (INDEP) subjects exposed to PSUM and NPSUM stimuli during trial 1 and trials 2 through 10. Values plotted are the mean +/- std error (in dB). Quiet stance baseline values are shown for comparison. Asterisk denotes a statistically significant difference ($p<0.05$). The number of observations for each group are shown for reference (e.g. n=2).

7.4.3 SWAY ADAPTATION

Time-frequency analysis revealed evidence of a within-trial decline in sway amplitude at the stimulus frequency (i.e. *adaptation*) during trial 1, an example of which is shown in Figure 9. Notice in the time-frequency distribution of Figure 9 that sway power at the stimulus frequency (0.7Hz) gradually declines, or adapts, within 25 seconds following the onset of stimulus motion, and remains at this lower level for the remainder of the trial. This example is representative of the adaptation that was observed in numerous trials. Thus, subjects responded strongly during initial exposure to optic flow, but the amplitude of this response decreased substantially during trial 1, and remained at an attenuated level for subsequent trials.

Thirteen of twenty subjects exhibited adaptation during trial 1. Of these thirteen first trials, eight involved a sum-of-sinusoids stimulus that contained a 0.7Hz component, such that the primary sway response and subsequent adaptation occurred at this frequency. The adaptive response in these eight trials was quantified by fitting an exponential curve (i.e. $Ae^{-t/\tau} + B$) to the power-versus-time data at 0.7Hz, as shown in Figure 14 (and described in the Methods section). This process yielded adaptation parameters A (pre-adaptation sway power), B (post-adaptation sway power), and τ (time constant of exponential decay), which were then compared among DEP, INDEP, PSUM and NPSUM groups. The exponential curve-fits provided a reasonably good approximation of the adaptive response, with R^2 values for the curve-fits ranging roughly from 0.50 to 0.90.

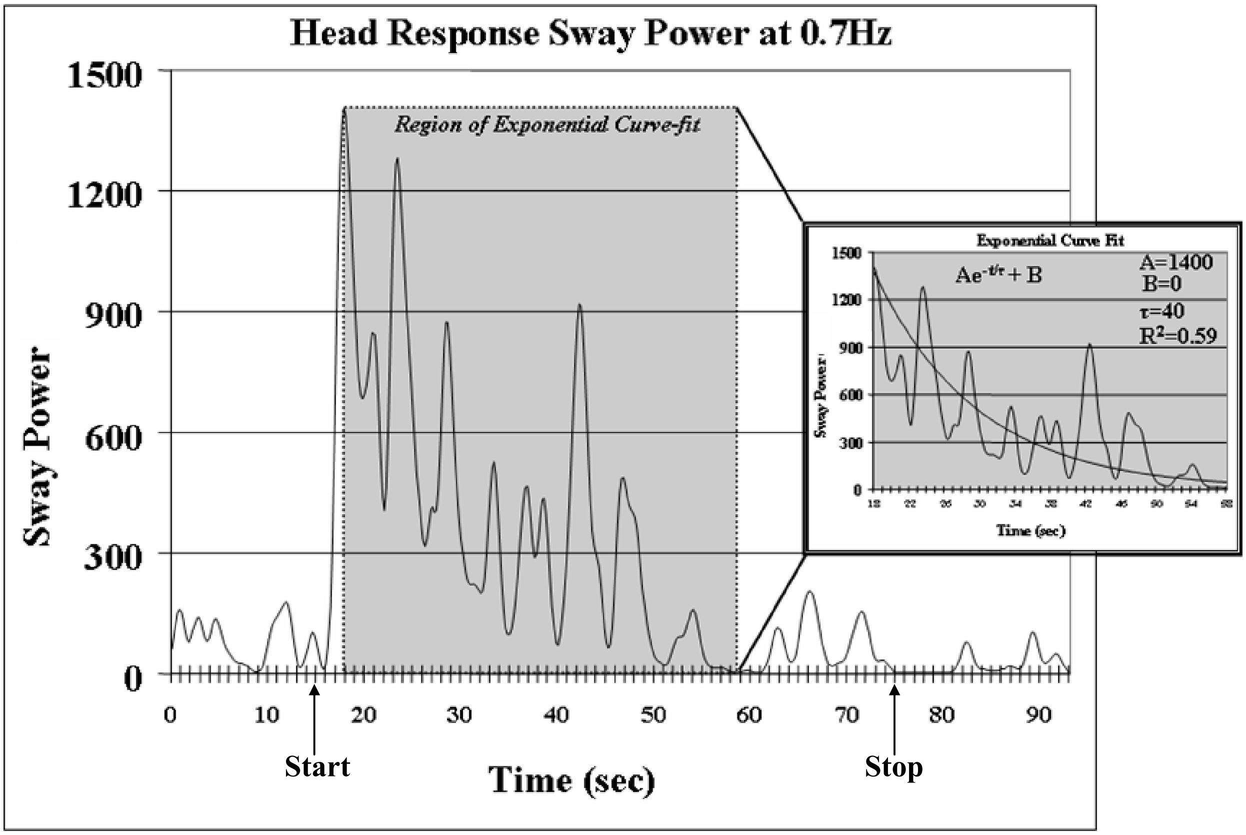


Figure 14 Head sway power versus time for a single adaptation trial, together with the corresponding exponential curve fit that was used to determine the adaptation parameters, A, B, and τ. R^2 is the 'goodness-of-fit' statistic for the exponential curve fit. Data shown is for one subject, but is representative of adaptation seen in many first trials. "Start" and "Stop" indicate times at which scene movement begins and ends, respectively

As seen in Figure 15, values for 'A' were between 7dB and 10dB higher for trial 1 compared to trials 2-10. This difference was significant ($F_{1,79}$=7.44, p=0.008), indicating that *initial* sway response power dropped significantly following initial exposure to a moving visual stimulus. Further, within both trial 1 and trials 2-10, 'A' was very similar among DEP and INDEP subjects for both PSUM and NPSUM stimuli. The differences among groups (i.e. DEP versus INDEP, and PSUM versus NPSUM) were not statistically significant within trial 1 or within trials 2 through 10. In addition, values for 'B' were essentially zero in all responses that exhibited adaptation, meaning that sway power after adaptation had occurred was equal to sway power that existed prior to exposure to optic flow. As such, ‘B’ was excluded from subsequent analyses. These observations regarding ‘A’ and ‘B’ indicated that the large differences in stimulus-band power between PSUM and NPSUM groups in trial 1 (Figure 24a) could not be fully explained by differences in ‘A’ or ‘B’ between the groups, but instead must be at least partly the result of differences in the rate of adaptation, as captured by the time constant τ.

The rate at which adaptation occurred was not the same among groups (Figure 16). The time constant (τ) was fastest for subjects who displayed the lowest stimulus-band sway power (INDEP subjects during initial exposure to PSUM stimuli) and slowest for the group that exhibited the highest responses (DEP subjects during initial exposure to PSUM stimuli). Time constant values were not significantly different between DEP and INDEP groups, or between PSUM and NPSUM groups. The significance of the interaction between visual dependence and visual stimulus could not be statistically examined due to the very small sample sizes involved. However, the observation that both stimulus-band power and the adaptation time constant (τ) displayed similar trends among the various stimulus and visual dependence groups suggests the possibility that a correlation exists between these two parameters. These findings are summarized in Figure 17, which shows exponential curves based on the values for A and τ in Figure 15 and Figure 16. Note that values for the barplots shown in the inset of Figure 17 are approximately equal to the area under the corresponding exponential curve.

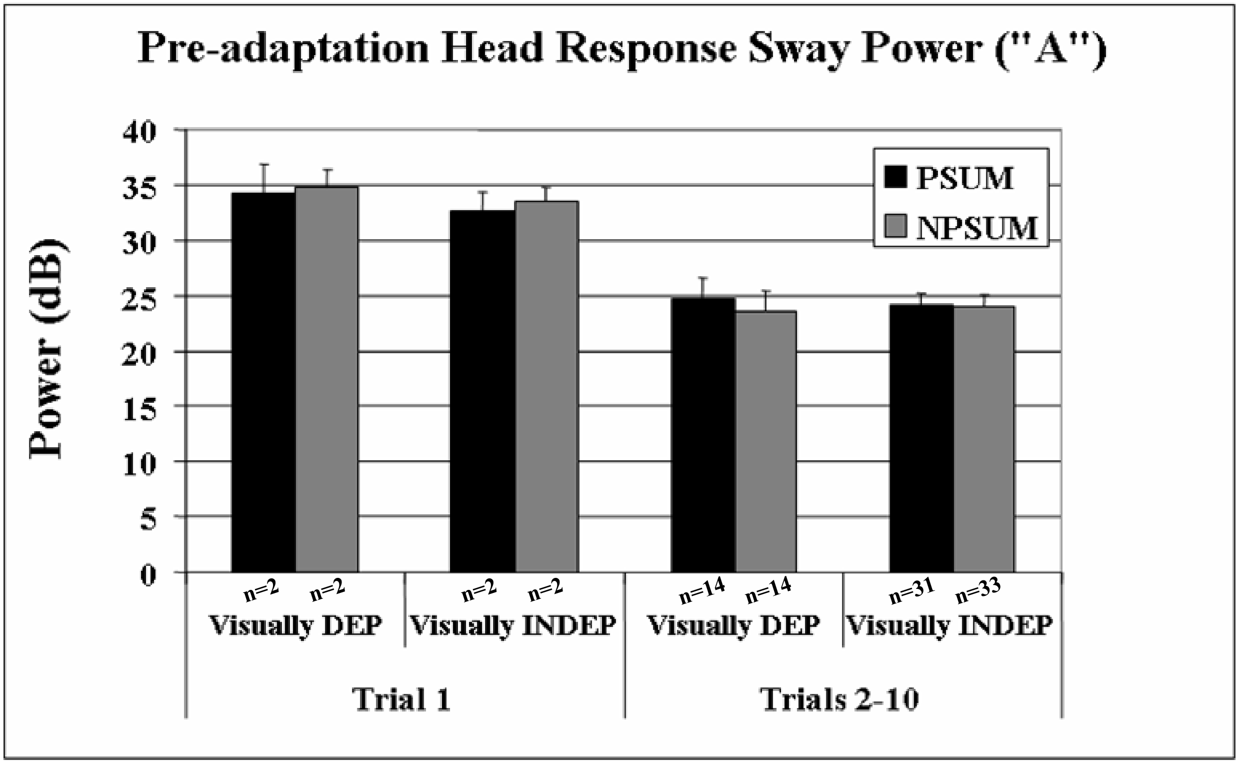


Figure 15 Pre-adaptation head sway power (A) for visually dependent (DEP) and independent (INDEP) subjects exposed to PSUM and NPSUM stimuli during trial 1 and trials 2 through 10. Values plotted are the mean +/- std error (in dB). Sample sizes are shown for each groups (e.g. n=2).

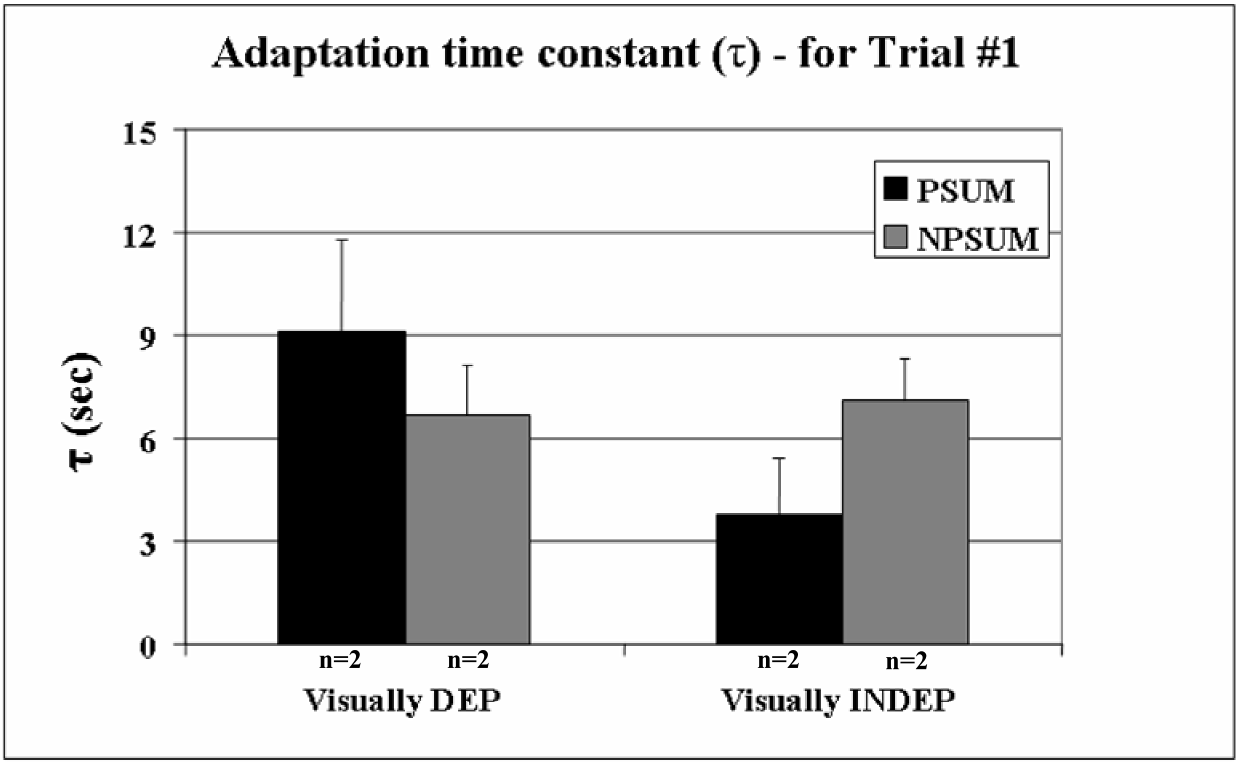


Figure 16 Head sway power adaptation time constant (τ) during trial 1, for visually dependent (DEP) and independent (INDEP) subjects exposed to PSUM and NPSUM stimuli. Values plotted are the mean +/- std error (in seconds). Sample sizes are shown for each groups (e.g. n=2).

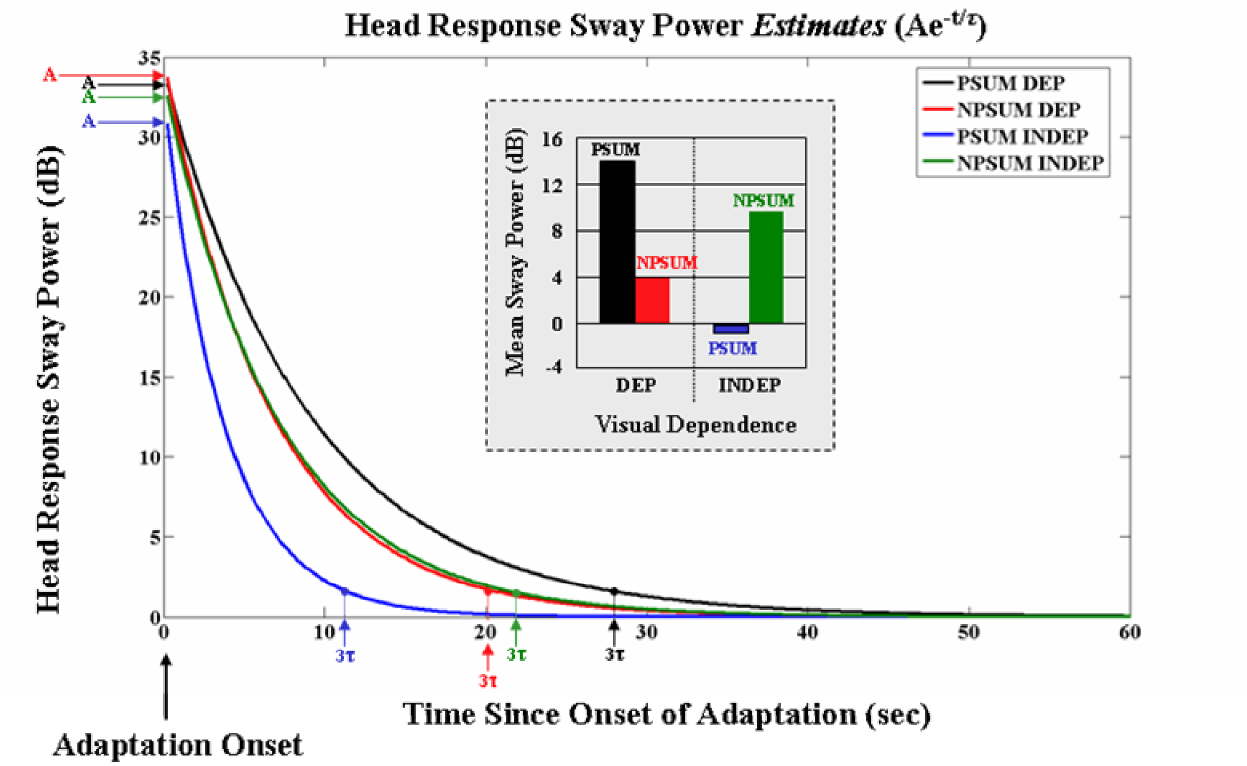


Figure 17 Estimates of head sway power versus time during trial 1, for visually dependent (DEP) and independent (INDEP) subjects exposed to PSUM and NPSUM stimuli. Curves were generated by substituting the appropriate values for the adaptation parameters (shown in Figure 15 and Figure 16) into the equation $Ae^{-t/\tau} + B$. Recall that 'B' was found to equal zero for all trials. The area under each curve corresponds to the bar plot values in Figure 13, which are shown in the inset for comparison. The point at which sway power has decreased by 99% from it's initial value (i.e. "3τ") is shown for reference.

Overall, these data do not provide strong support either for or against the hypothesis of lower sway power and faster adaptation rates in response to PSUM stimuli, but the trends in the data may be interpreted as favoring the hypothesis. Likewise, the observed trends are consistent with the hypothesis that sway power and adaptation rates would be different among visually DEP and INDEP groups, but the data cannot be interpreted as providing strong support either for or against this hypothesis.

7.5 DISCUSSION

7.5.1 MAIN FINDINGS

This study investigated the effect of optic flow periodicity on postural sway, in an attempt to uncover evidence of the existence of a predictive component to postural control. The main finding of the current study was that spectrally similar periodic and non-periodic oscillatory optic flow elicited quantitatively different sway responses in visually DEP and INDEP subjects during initial exposure to these moving stimuli. Specifically, during trial 1, visually DEP subjects swayed *more* in response to periodic stimuli, while visually INDEP subjects displayed the opposite behavior. Time-frequency analysis revealed evidence of sway *adaptation* in trial 1, indicating that subjects responded strongly during initial exposure to optic flow, but the amplitude of this response decreased substantially during trial 1, and remained at an attenuated level for subsequent trials. This notion of reduced sensitivity to subsequent visual stimuli was supported by the fact that values for the initial, or "pre-adaptation", sway response power (A) were significantly lower in trials 2 through 10, compared to trial 1. Further, the rate at which adaptation occurred was fastest for those who displayed the lowest mean sway power (i.e. visually INDEP subjects exposed to periodic stimuli), and slowest for the group that exhibited the highest responses (i.e. visually DEP subjects exposed to periodic stimuli). *These findings suggest that periodic and non-periodic oscillatory optic flow stimuli do indeed evoke quantitatively different sway responses, and that this can be attributed to differences in the rate of adaptation during initial exposure to these stimuli.* Such behavior is consistent with the existence of a predictive component to postural control that is capable of reducing visual gain during exposure to periodic optic flow.

7.5.2 SWAY ADAPTATION

The association between the proposed predictive mechanism and sway adaptation can be understood within the context of the sensory re-weighting process. Previous findings indicate that this dynamic regulation of sensory channel gains occurs during sensory conflict conditions [Peterka and Loughlin, 2004; Loughlin *et al.*, 1996]. For example, during exposure to optic flow, visual inputs are inaccurate (as compared to somatosensory and graviceptive inputs) and may be attenuated in order to maintain stability by reducing the contribution of erroneous information. This concept of weighting input signals according to their reliability has been examined previously, most often as a form of Bayesian integration, whereby signals containing large variability contribute less to the output [Ernst and Bulthoff, 2004; Deneve and Pouget, 2004; Kording and Wolpert, 2004; Battaglia *et al.*, 2003; Zupan *et al.*, 2002].

Within the context of postural control, sensory re-weighting has been implicated as one possible cause of postural sway adaptation [Loughlin *et al.*, 1996]. Specifically, the inaccurate visual information produced by exposure to optic flow is thought to yield a decrease in visual channel gain, as described above, which in turn acts to attenuate the visual input that is driving the system. The subsequent decrease in postural sway might be considered a *baseline adaptation* that is expected to occur during exposure to optic flow in general, regardless of the specific properties (e.g. periodicity) of the visual stimulus. We have proposed that a predictive mechanism in the postural control loop has the ability to facilitate the sensory re-weighting process, and therefore the ability to influence sway adaptation as well. In particular, the predictive mechanism would exploit the repetitive nature of periodic visual stimuli in order to readily predict future visual input, which would presumably minimize the need to monitor newly arriving visual signals. One way for the CNS to achieve this would be to lower visual gain in the control loop beyond that which has already occurred as part of the baseline adaptation. This would in effect further reduce reliance on inaccurate visual afferent signals, and would produce a *facilitated adaptation* characterized by a more pronounced decrease in sway response.

As such, we expected that sensory re-weighting and subsequent sway adaptation would occur in response to both periodic and non-periodic visual stimuli, but that the effect would be larger for periodic inputs. This facilitated adaptation would have two distinct, but related, measurable effects as compared to baseline adaptation. First, adaptation of the sway response would begin earlier and/or occur more rapidly in response to the periodic stimuli. Second, this would produce a larger per-stimulus reduction in sway amplitude, which when measured by a summary statistic such as root-mean-square (RMS) or mean sway power, would appear as lower sway amplitude.

The findings of the current study are for the most part consistent with this explanation. For example, visually INDEP subjects adapted twice as fast to a periodic sum-of-sinusoids compared to a non-periodic counterpart, and this produced a significantly lower mean stimulus-band sway power. However, differences in the starting time of adaptation were not observed in this group, which suggests that the proposed predictive mechanism influences the rate, but not the onset time, of adaptation. Results for the visually DEP subjects are not as easily interpreted. Upon initial inspection, it appears that our hypothesis was not supported by the data for visually DEP subjects, since their adaptation times were *slower* for periodic stimuli compared to non-periodic stimuli. One possible explanation for this behavior is that the proposed predictive mechanism is not active in visually DEP subjects, perhaps because the associated decrease in visual channel gain would be detrimental to individuals who rely heavily on visual information for postural stability. As such, the adaptation observed in visually DEP subjects would therefore be unrelated to visual stimulus periodicity, and instead be the result only of sensory re-weighting induced by sensory-conflict. In other words, visually DEP subjects might exhibit baseline adaptation, but not facilitated adaptation. If this were true, adaptation in visually DEP subjects should be similar in response to both the periodic and non-periodic stimuli, since it is independent of any predictive mechanism. It is unclear whether or not the current data support this interpretation. Note in Figure 16 that the adaptation time constant in visually DEP subjects was three seconds different between periodic and non-periodic groups. If this difference were significant, it would strongly suggest that the proposed predictive mechanism is active in visually DEP subjects. If, however, the temporal aspects of adaptation were the same for these two groups, then we might reasonably conclude that the observed adaptive decay represents only baseline adaptation. Unfortunately, the small sample size for this observation (n=4) did not provide enough statistical power to determine if this three second difference was significant.

Another comparison that may prove insightful would be that of adaptation rate between visually DEP and visually INDEP subjects exposed to non-periodic stimuli. Since non-periodic inputs don't activate the proposed predictive mechanism, subjects exposed to these stimuli should exhibit baseline, but not facilitated, adaptation, regardless of relative visual dependence. Therefore, these two groups would be expected to have very similar rates of adaptation. This is indeed what the data revealed, as seen in Figure 16. Again, the difference cannot be shown to be statistically significant, but both the mean and standard error in the two groups are similar enough to suggest that there is no difference.

Overall, these findings indicate that exposure to non-periodic optic flow yields a baseline adaptation in all subjects, while exposure to periodic optic flow produces a faster, or facilitated, adaptation only in visually INDEP individuals. Such behavior is consistent with the existence of a predictive component to postural control that is capable of reducing visual gain during exposure to predictable optic flow.

7.5.3 COMPARISONS TO PREVIOUS STUDY

This study aimed in part to answer several questions prompted by our first experiment. These questions are addressed below.

1. *Would differences again be observed between periodic and non-periodic SOS groups? If so, would they be the same as in our previous study, or instead support our hypothesis?*

In fact, both of these behaviors were observed, but in distinct subject populations, and only during initial exposure to the optic flow stimulus. Specifically, findings from our previous study [Musolino *et al.*, 2006] were reproduced in visually DEP subjects, while behaviors consistent with the stated hypothesis were observed in visually INDEP subjects. As explained earlier, these apparently conflicting behaviors have been attributed to differences in how the proposed predictive mechanism is manifested in these particular subject populations.

In visually DEP subjects, who are particularly reliant on vision, we suggest that the predictive mechanism is not active under any circumstances, because the resulting decrease in visual channel weight would adversely affect their postural stability. We therefore would expect visually DEP subjects to show similar responses to both types of optic flow stimuli, regardless of its relative periodicity. As we have shown already, this is not what was observed. Instead, the periodic stimuli produced noticeably larger sway as compared to the non-periodic stimulus. It's possible that this behavior is a natural consequence of the coupled oscillation [Strogatz and Stewart, 1993; Schoner *et al.*, 1992] that occurs between the subject and the periodic stimulus, and might have been observed in visually INDEP subjects as well if it were not for the influence of the predictive mechanism that we believe is active in that population. From this perspective, findings in the visually DEP group are not necessarily at odds with the existence of a predictive component to postural control.

In contrast, in visually INDEP individuals, who are presumably no more dependent on vision than on any other sensory information, the predictive mechanism is not hindered in an way. It therefore manifests itself completely during exposure to periodic optic flow, producing an enhanced, or facilitated sway adaptation, and a corresponding decrease in overall sway power compared to responses to non-periodic stimuli.

2. *Would subjects again respond strongly to the highest component frequency in a SOS stimulus, regardless of the whether that frequency is 0.3Hz, 0.5Hz or 0.7Hz?*

As in the previous study, strong responses consistently occurred at the highest frequency component for each of the SOS stimulus. This was particularly true of responses to stimuli that contained a 0.7Hz sinusoid. That is, when the highest stimulus frequency was 0.7Hz, the largest increase in total sway power with respect to quiet stance was observed in the 0.7Hz frequency band of the response, while the corresponding increase in power above and beyond that for quiet stance was much smaller in the 0.5Hz and 0.3Hz frequency bands (see Figure 10). Since velocity increases with frequency for sinusoids of identical amplitude, such strong responses to the 0.7Hz component implies that subjects were sensitive to stimulus velocity, as had been suggested in our earlier study. Such postural sensitivity to visual stimulus velocity has been reported previously [Kiemel *et al.*, 2002; Dijkstra *et al.*, 1994a; Lestienne *et al.*, 1977]. The relative lack of sway power in the 0.3Hz and 0.5Hz frequency bands seems to indicate a masking effect, whereby subjects were disproportionately influenced by the 0.7Hz stimulus component, even though the energy in the input signal was spread equally across the various component frequencies. In addition, this noticeable sway at such a high frequency was a surprising observation, considering that it is seldom reported for healthy adults. One possible explanation is that the virtual testing environment utilized in the current study, which presented full-field luminous scenes via computer generated images and LCD projection cameras, provided visual stimuli that were much more compelling than those used in previous studies.

3. *How would sway amplitudes in response to a ±8cm stimulus compare to those in response to the substantially lower stimulus amplitude of ±4cm?*

The decision to utilize two different stimulus amplitudes was motivated by our observation in the previous study that sway amplitudes in response to ±8cm stimuli rarely exceeded ±2cm. Earlier work by Peterka and Benolken had suggested that such sub-unity output-to-input gains indicate that the postural control system has exceeded some saturation threshold, and is operating in a non-linear fashion [Peterka and Benolken, 1995]. The addition of ±4cm stimuli to the protocol for the current study was an attempt to determine if stimulus amplitudes that were substantially lower than ±8cm would elicit similar responses. As mentioned in the results section, responses for the ±4cm trials were not significantly different than those for the ±8cm trials, suggesting that even ±4cm stimuli evoked sway responses indicative of a saturation non-linearity. While it is unclear how this 'amplitude effect' influences the behaviors that were observed in the current study, it would seem prudent to utilize even lower stimulus amplitudes in future experiments, in an effort to eliminate such a substantial output-to-input attenuation.

4. *Would adaptation be observed in any of the sway responses? If so, would this adaptation be different for responses to periodic stimuli compared to those for non-periodic stimuli?*

As discussed in detail earlier in this section, sway adaptation was indeed observed in numerous trials, primarily during initial exposure to the optic flow stimuli. The rate of adaptation was approximately three seconds different between periodic and non-periodic stimulus groups, but the statistical significance of this difference could not be ascertained. Moreover, the effect of stimulus periodicity on adaptation rates appeared to interact with the relative visual dependence status of the subject population, such that visually INDEP individuals displayed lower sway in response to periodic optic flow, while visually DEP subjects did not.

7.5.4 PREVIOUS STUDIES OF STIMULUS PERIODICITY

The current findings are supported by previous studies of other sensorimotor systems, which have reported that the CNS can discern sensory stimuli based on periodicity. For example, Barnes et al. [Barnes *et al.*, 2000], in examining ocular pursuit in healthy adults, have observed that exposure to sinusoidal visual inputs enhances visual tracking performance during subsequent exposure to similar sinusoidal stimuli. The authors suggested that the CNS is capable of detecting periodicity, and proposed a model of predictive control in which velocity information could be sampled, stored and subsequently replayed as an anticipatory pattern of movement. In addition, a number of similar studies have reported that the predictability of a moving visual stimulus affects the gain and phase of the smooth pursuit component of eye velocity [Larsby *et al.*, 1988; Collewijn and Tamminga, 1984; St. Cyr and Fender, 1969; Michael and Melvill Jones, 1966]. Larsby et al. [Larsby *et al.*, 1988] exposed subjects to both pure-sinusoidal and pseudorandom target motion at frequencies ranging from 0.2Hz to 2Hz, and observed significantly higher gain in response to pure-sinusoidal stimuli, as compared to pseudorandom stimuli, at frequencies similar to those used in the current study. Predictability effects have also been observed outside of the visual domain. For example, Nelson et al. [Nelson *et al.*, 2004] recently reported that (1) motor responses to pure sinusoidal vibrotactile perturbations were faster and more accurate than responses to random perturbations; and that (2) both the amount and location of activation in the cerebral cortex were different between responses to these predictable and unpredictable stimuli. Based on these observations, the authors suggested that exposure to predictable stimuli caused subjects to rely less on sensory feedback and more on feedforward control. These findings indicate that the CNS, especially the visual system, is sensitive to stimulus periodicity, and provide evidence in support of the current observations.

7.6 CONCLUSION

The current study reproduced various observations from our previous study [Musolino *et al.*, 2006], including (1) significantly different sway responses to periodic and non-periodic stimuli; (2) consistent responses at the highest component frequency of the stimuli; and (3) significant response power at non-stimulus frequencies. More importantly, several interesting new findings were reported, including (1) significantly higher sway responses during trial 1 as compared to trials 2 through 10; (2) postural sway adaptation during initial exposure to optic flow; and (3) differences in sway responses between visually DEP and INDEP subjects. We conclude that periodic and non-periodic optic flow stimuli evoke quantitatively different sway responses, and that this can be attributed to differences in the rate of adaptation during initial exposure to these stimuli. Such behavior is consistent with the existence of a predictive component to postural control that is capable of reducing visual gain during exposure to periodic optic flow. Future studies are planned to more fully investigate these findings and to develop models of the underlying mechanisms.

8.0 EXPERIMENT 3: THE INFLUENCE OF CONCURRENT COGNITIVE TASKS ON POSTURAL SWAY ADAPTATION DURING EXPOSURE TO PERIODIC AND NON-PERIODIC OPTIC FLOWS

8.1 ABSTRACT

Two previous in-house studies have provided evidence in support of our proposal that the postural control system contains a predictive component that can facilitate dynamic re-weighting of sensory inputs in response to periodic moving visual stimuli [Musolino *et al.*,] [Musolino *et al.*, 2006]. Specifically, the data have shown that periodic and non-periodic oscillatory full-field optic flow stimuli evoke quantitatively different sway responses, and that this can be attributed to differences in the rate of sway adaptation during initial exposure to these stimuli. In addition, other studies have suggested that cognitive resources are required for this type of sensory re-weighting to occur, particularly during the type of sensory conflict condition that exists during exposure to optic flow [Redfern *et al.*, 2001].

In light of this, the purpose of the current study was to examine the influence of concurrent cognitive tasks on postural sway during exposure to periodic and non-periodic optic flow. In particular, this study explored the interaction between cognitive task effects and predictive-mechanism effects on sway adaptation. We hypothesized that performing a visual simple reaction time (RT) task would facilitate processes occurring within the visual system and therefore enhance sway adaptation, while an auditory simple RT task would have the opposite effect and hinder this adaptive process. Sixteen subjects (11F, 5M; age 21-35 yrs) performed an

auditory or visual simple RT task, during exposure to one of four different full-field bullseye-and-checkerboard optic flow stimuli: a single sinusoid (0.3 Hz), a periodic sum-of-sinusoids (PSUM=0.1+0.3+0.5Hz), a spectrally similar non-periodic counterpart (NPSUM=0.1+π/10+0.5Hz), and a fourth condition in which the scene remained stationary for the entire 90 second trial. Visual and auditory tasks were performed on separate days. For each visit, the visual stimuli were shown twice, once in combination with a cognitive task, and once without a task, yielding a total of 8 randomized trials. Head and center-of-pressure (COP) sway response power at the various stimulus frequencies were compared among the different groups.

Results showed that sway responses during a cognitive task were significantly lower compared to sway for the no-task condition, regardless of whether the task was auditory or visual. Moreover, cognitive tasks elicited different sway responses among PSUM and NPSUM groups. Specifically, responses to PSUM and NPSUM stimuli were similar during no-task trials, but significantly different for trials in which a cognitive task was performed. Further, PSUM sway power was lower than NPSUM sway power for visual task trials, but higher than NPSUM values for auditory tasks. These trends were supported by data from adaptation trials, which revealed that adaptation rates were significantly faster in response to PSUM stimuli, as compared to NPSUM stimuli. These findings (1) indicate that concurrent cognitive tasks cause a reduction in sway response, and (2) are consistent with the existence of a sensory reweighting process that is sensitive to optic flow periodicity, and that can be influenced by cognitive tasks.

8.2 INTRODUCTION

Two previous in-house studies have provided evidence in support of our proposal that the postural control system contains a predictive component that can facilitate dynamic re-weighting of sensory inputs in response to periodic moving visual stimuli [Musolino *et al.*,] [Musolino *et al.*, 2006]. While predictive mechanisms have been examined previously, these discussions have been limited to prediction as a means of improving performance of the motor control system. For example, it has been suggested that the central nervous system (CNS) contains an internal forward model that can predict the consequences of motor commands [Blakemore and Sirigu, 2003; Wolpert *et al.*, 1998]. This internal model captures the causal relationships between neuromuscular inputs and outputs, and is used in combination with an efference copy of the motor command in order to simulate subsequent sensory consequences and predict a future state (e.g. body position and/or velocity). This mechanism would be useful, for instance, in providing timely estimates of new sensory information in the absence of actual sensory input due to temporal delays associated with feedback control. Another example of prediction in motor control has been provided by Barnes et al., who examined ocular pursuit in healthy adults, and observed that exposure to sinusoidal visual inputs enhances visual tracking performance during subsequent exposure to similar sinusoidal stimuli [Barnes *et al.*, 2000]. The authors suggested that the CNS is capable of detecting periodicity, and proposed a model of predictive control in which velocity information could be sampled, stored and subsequently replayed as an anticipatory pattern of movement. These studies promote the idea that prediction in the CNS exists to enhance performance of some motor task.

In contrast, the predictive mechanism that we propose is thought to influence only sensory processes, namely re-weighting and integration of sensory inputs. Sensory re-weighting has been explored previously, as a form of Bayesian integration in which the weighting of a signal is proportional to the reliability of that signal [Ernst and Bulthoff, 2004; Deneve and Pouget, 2004; Kording and Wolpert, 2004; Battaglia *et al.*, 2003; Zupan *et al.*, 2002], and as a sensory integration mechanism within postural control [Peterka and Loughlin, 2004; Peterka, 2002; Jeka *et al.*, 2000] [Oie *et al.*, 2002; van der Kooij *et al.*, 2001; Oie *et al.*, 2001; Maurer *et al.*, 2000; van der Kooij *et al.*, 1999]. Within this postural context, sensory reweighting has been implicated as a cause of sway adaptation, a phenomenon in which sinusoidal optic flow elicits a sway response at the stimulus frequency whose amplitude decreases throughout exposure to this stimulus [Loughlin and Redfern, 2001; Loughlin *et al.*, 1996]. This effect has been attributed to a decrease in weighting of the visual channel that occurs because visual information during exposure to optic flow conflicts with sensory afferent signals from other sensory systems.

While it is clear that sensory re-weighting is an attempt to minimize the influence of unreliable sensory information so that postural stability can be maintained in the face of challenging sensory environments, the mechanism by which this occurs is unknown. One possibility is that predictive processes are at least partly responsible for sensory re-weighting and subsequent sway adaptation. We have proposed that postural control contains a predictive component that is sensitive to stimulus periodicity, such that periodic sensory inputs will produce lower sway than will non-periodic inputs. Results from previous studies in our laboratory have been mostly consistent with this hypothesis, showing that periodic and non-periodic oscillatory full-field optic flow stimuli evoked quantitatively different sway responses, and that this may have been due to differences in the rate of sway adaptation during initial exposure to these stimuli [Musolino *et al.*,] [Musolino *et al.*, 2006]. That is, a per-stimulus decrease in sway power occurred during first exposure to optic flow, and the rate at which this adaptation occurs was faster in response to periodic visual stimuli as compared to the non-periodic case (note: this behavior was observed in subjects who were shown to be visually independent, as described by [Isableu *et al.*, 1998; Isableu *et al.*, 1997]). In particular, non-periodic optic flow elicited what we have termed a *baseline adaptation,* that was due solely to sensory re-weighting caused by the sensory conflict conditions that exist during exposure to optic flow. In contrast, periodic optic flow evoked a *facilitated adaptation,* characterized by a more pronounced per-stimulus decrease in sway power, that reflected the combined effect of baseline adaptation and the proposed predictive mechanism. We attributed both forms of adaptation to decreases in visual channel gain in the postural control loop.

In addition, it has been suggested that the sensory re-weighting process requires cognitive resources, particularly during sensory conflict conditions, when inputs from various sensory systems are not in agreement [Redfern *et al.*, 2001]. In light of this, it would be useful to examine how cognitive tasks influence sway during exposure to optic flow, an environment that is known to induce sensory conflict. As such, the purpose of this study was to explore the interaction between the effects of a cognitive task and the effects of the proposed predictive mechanism on sensory re-weighting and sway adaptation during exposure to periodic and non-periodic optic flow. We hypothesized that performing a visual cognitive task would facilitate processes occurring within the visual system and therefore enhance sensory reweighting and subsequent sway adaptation, while an auditory cognitive task would have the opposite effect and hinder this adaptive process.

8.3 METHODS

Postural sway responses to various moving visual scene perturbations were examined in sixteen healthy young adults, ranging in age from 21-35 years (mean age = 25 yrs). Subjects had no history of neurological or balance-related dysfunction, and no previous exposure to visual scene perturbations in an experimental setting. All subjects provided informed consent to participate in this study, and the experimental protocol was approved by the Institutional Review Board at the University of Pittsburgh. Tests were performed in the Balance Near Automatic Virtual Environment (BNAVE), a custom built virtual reality system that creates an immersive visual surround by projecting computer generated images onto three adjoining screens [Jacobson J *et al.*, 2001]. The screens are approximately 183cm x 213cm (width x height), and are arranged in front, to the left, and to the right of the viewer. A contiguous image is projected onto the screens, and provides a full (180°) horizontal field of view. This visual scene extends onto the floor as well, but not to the ceiling (which is covered in black cloth), so the vertical field of view is thus limited to approximately 120°.

8.3.1 VISUAL SCENES

The image presented to the subjects consisted of a "bullseye" pattern of six alternating black-and-white concentric rings (with each ring occupying 5° of visual arc), surrounded by a checkerboard of black-and-white squares (15cm per side) [Musolino *et al.*, 2006]. Previous studies have utilized similar patterns in a moving room paradigm to evoke postural responses in both healthy and patient populations [Borger *et al.*, 1999; Peterka and Benolken, 1995; van Asten *et al.*, 1988]. The bullseye-and-checkerboard pattern oscillated toward and away from subjects in either a periodic ("predictable") or non-periodic ("unpredictable") fashion. Scene movement was driven by one of three signals (Figure 18): (1) ±4cm 0.3Hz sinusoid, (2) a periodic sums of three ±4cm sinusoids (PSUM = 0.1 + 0.3 + 0.5Hz, and (3) a spectrally similar non-periodic counterpart (NPSUM = 0.1 + π/10 + 0.5Hz. There was also a fourth visual scene, in which the bullseye-and-checkerboard pattern remained stationary throughout the trial. Because the frequencies of the PSUM stimulus are integer multiples of each other, this stimulus is periodic, with period given by T=1/0.1=10 sec. For the NPSUM stimulus, component frequencies were chosen in order to produce a signal with frequency content nearly identical to that of the corresponding PSUM stimulus, but lacking a temporal periodicity. Since π/10 is not an integer multiple of 0.1 Hz, the NPSUM stimulus is not periodic and exhibits markedly different temporal characteristics than the PSUM stimulus, even though the spectra of corresponding PSUM and NPSUM stimuli are very similar (see Figure 18). In addition, the sum-of-sinusoids signals were normalized such that their root-mean-square (RMS) was equal to that of the single sinusoid; this ensured that peak amplitudes were similar and total input power identical among the three stimuli.

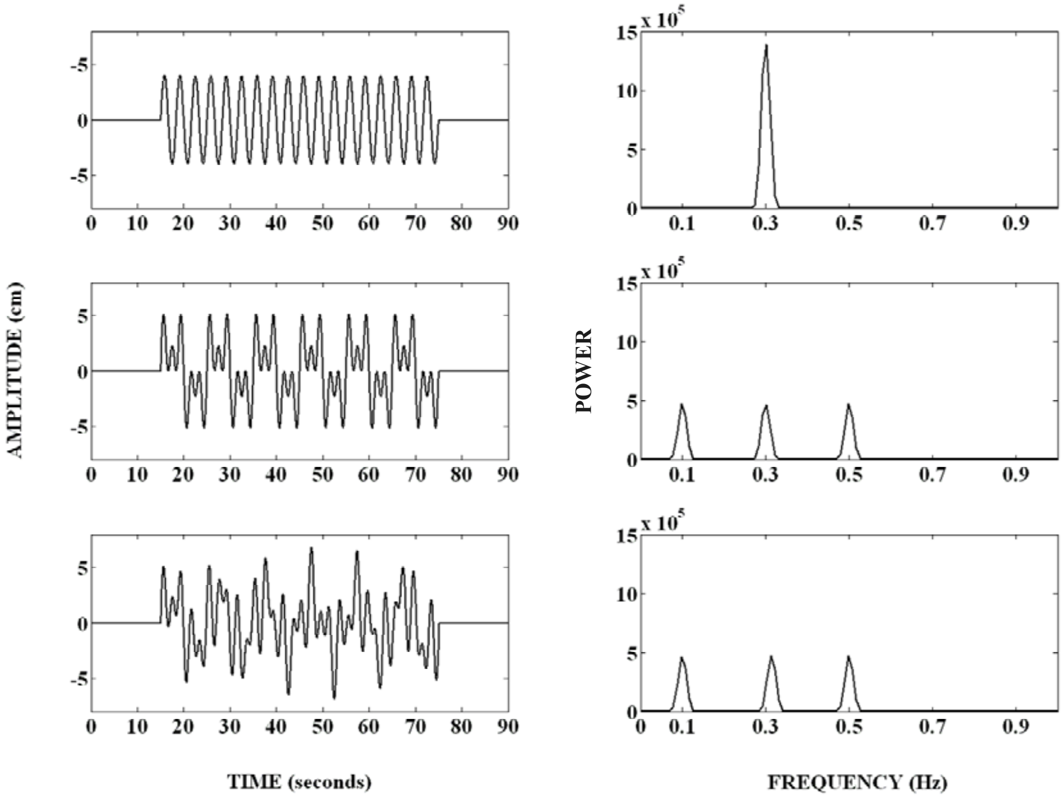


Figure 18 Time series' (left) and corresponding power spectra (right) for the three scene movements presented to subjects. Shown from top to bottom are 0.3Hz, PSUM (0.1 + 0.3 + 0.5Hz), and NPSUM (0.1 + π/10 + 0.5Hz). "Start" and "Stop" indicate times at which scene movement begins and ends, respectively.

8.3.2 COGNITIVE TASKS

In some trials, subjects performed either an auditory or visual simple reaction time (RT) task during exposure to the moving visual stimulus. Both types of tasks required subjects to respond, with the click of a button held in the dominant hand, to transient changes in a task stimulus. The visual task stimulus consisted of a white triangle superimposed on the center of the black bullseye, that moved in synchrony with the surrounding scene. The white-on-black color scheme was utilized for maximum contrast. At randomly timed intervals of between 1 and 3 seconds, the triangle briefly changed to a rectangle, then back to a triangle (Figure 19). Similar inter-stimulus timing has been successfully used in a previous in-house study of the interaction between cognitive tasks and posture [Redfern *et al.*, 2001]. The cognitive tasks commenced at time t=0 seconds, prior to the onset of scene movement at time t=15 seconds, such that subjects engaged the reaction time task before the postural task. Subjects were instructed to "*Stand comfortably and look straight ahead. Respond as quickly as possible when you notice the triangle change to a rectangle. We will monitor your reaction time. It's okay to make mistakes, but please keep errors to a minimum*." Reaction time was not measured, but presenting this impression was necessary in order to effectively capture the effect of the cognitive task on postural sway. For the trials in which a visual task was not performed, the triangle object was continuously presented (i.e. it did not include any transient changes).

The auditory task stimulus consisted of a constant tone at 560Hz, that at randomly timed intervals of between 1 and 3 seconds was combined with another tone at 1120Hz. These two tones are related harmonically, and have a frequency difference that is highly detectable. The superimposed tone at 1120Hz had a duration of 250msec in order to assure a clear sense of tonality, while still being a discrete temporal event compared to the constant tone at 560Hz. Tones were presented stereophonically at a sound pressure level (SPL) of 80dB, via disposable foam ear inserts worn by subjects. To maintain consistency with visual task trials, the moving visual scenes for all auditory trials included an unchanging triangle object at the center of the bullseye pattern. As in the visual task trials, subjects were instructed to respond as quickly as possible to a change in the task stimulus, while attempting to keep errors to a minimum.

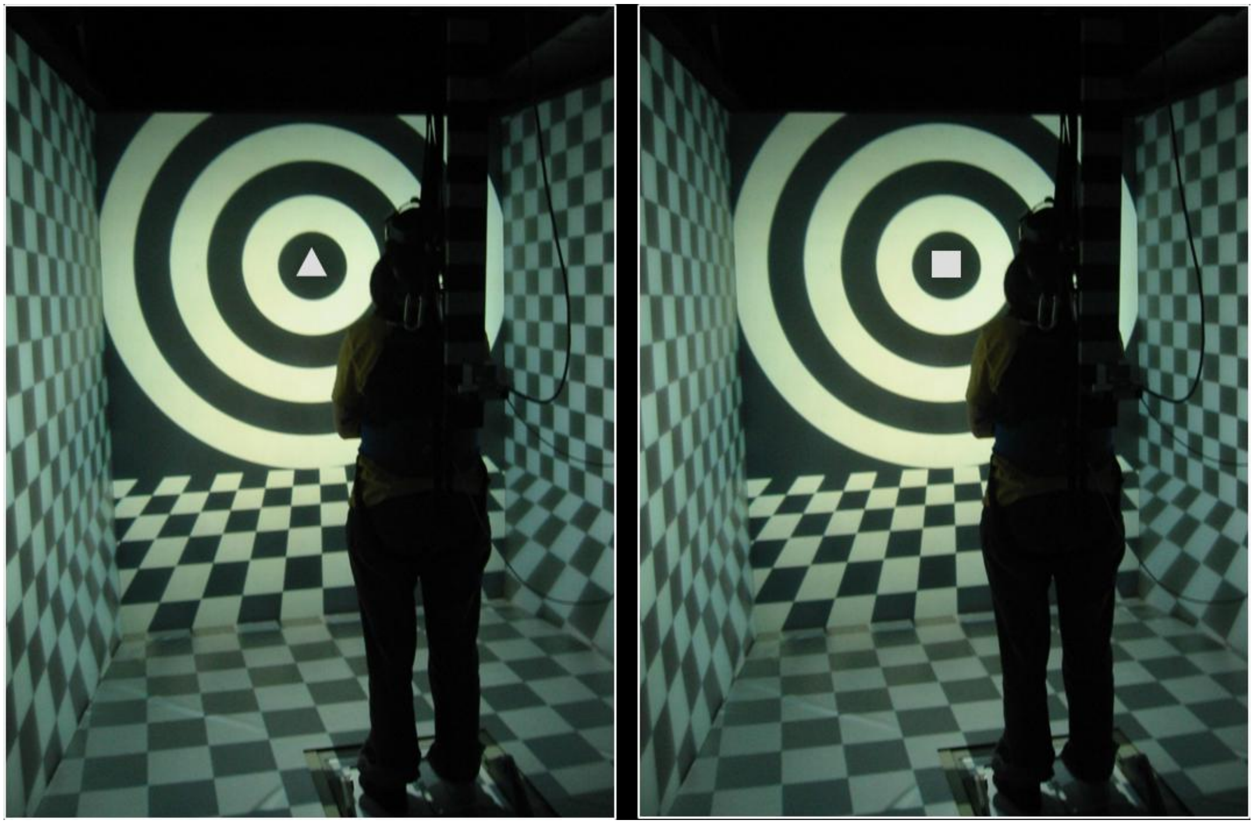


Figure 19 Subject performing a reaction time task while viewing the bullseye-and-checkerboard pattern in the BNAVE virtual environment. Subject was instructed to respond as quickly as possible, with the click of a button held in the dominant hand, to randomly-timed transient changes in the centrally located object (i.e. from a triangle to a square). Sway responses were recorded via a single force plate beneath the feet, and an electromagnetic tracking device located at the head. Subject was secured to the support structure by a safety harness.

8.3.3 DATA COLLECTION

Data were collected on two separate days. During each visit, subjects were exposed to eight different combinations of visual stimulus and cognitive task (4 visual stimuli * 2 task conditions), as shown in Table 3. Visual and auditory cognitive tasks were presented on separate days, in a randomized fashion, so that half of the subject population encountered auditory tasks on day 1, while the remaining subjects were presented with visual tasks first. Trial one was a “dummy” trial that consisted of a 0.3Hz sinusoidal moving visual stimulus, with no cognitive task. Exposing every subject to an identical initial stimulus was an attempt to eliminate the confounding influence of a “trial effect” that had been observed in our previous study, in which sway amplitudes during initial exposure to optic flow were significantly larger than those during subsequent exposures [Musolino *et al.*, 2006].

Table 3 Stimulus-task combinations presented to subjects on each of two testing days

Trial #	Visual Stimulus	Cognitive Task (yes/no)
1	0.3Hz sinusoid	no
2 – 9 (randomized)	Stationary	no
	0.3Hz sinusoid	no
	PSUM	no
	NPSUM	no
	Stationary	yes
	0.3Hz sinusoid	yes
	PSUM	yes
	NPSUM	yes

Following trial 1, the eight stimulus-task combinations were presented once, in random order, in trials 2 through 9. For each trial, subjects stood in an upright position 1.5 meters from the front screen, with arms folded across the chest, and with bare feet placed shoulder-width apart on a force platform (NeuroCom Inc., Clackamas OR). For trials that included a cognitive task, subjects held a small cylindrical push-button device in the dominant hand. Image height was adjusted so that the bullseye center was located at eye level. Subjects were secured to the BNAVE support structure with a tether and harness. This safety line was sufficiently loose to afford subjects free range of motion, and did not hinder sway or provide sensory feedback regarding their body sway. Prior to each trial, room lights were dimmed, and subjects were instructed to “stand comfortably and look straight ahead at the image on the screen.” Trial duration was 90 seconds, and consisted of 60 seconds of scene movement preceded and followed by 15 seconds of no motion. A rest period of 3 minutes was provided between successive trials, during which time room lights were switched on, and subjects relaxed in a seated position. In addition, a 60-second quiet stance (QS) trial was performed prior to the moving scene trials, in order to record "baseline" spontaneous sway in the absence of visual perturbation (i.e. subjects viewed a blank screen during these baseline trials).

Postural responses were examined through measurements of head and center-of-pressure (COP) displacements. Head data were collected at 20Hz using a Polhemus Fastrack electromagnetic tracking system (Polhemus Inc.), with a single sensor located at the crown of the head. Foot force data were sampled at 100Hz via load cells embedded in the force platform, and post-processed in Matlab (The Mathworks Inc.) to obtain COP values.

8.3.4 DATA PROCESSING

Data were high-pass filtered, down-sampled to 5 Hz, and zero-meaned. High-pass filtering was achieved through zero-phase implementation of a fourth order Chebyshev type II filter, with a cutoff frequency of 0.025 Hz, and a stop-band attenuation of 20 decibels (a decibel (dB) is a unit of measure often used for values that span several orders of magnitude, and is mathematically defined as 10*log10(Power)). The 3dB attenuation point for the high-pass filter occurred at approximately 0.03Hz, so that frequencies above 0.07Hz were not attenuated at all. This high-pass filter removed the dominant DC and very low frequencies observed in postural sway position data, and facilitated the identification of sway responses to the low frequency (0.1 Hz) component of the stimuli.

Filtered data were then examined using Fourier analysis, in order to estimate spectral densities for head and COP response signals, for both the quiet-stance baseline trial and moving scene trials. This was achieved through the calculation of windowed periodograms using the discrete Fourier transform (DFT). Spectral estimation was performed on only the 60-second moving scene portion of each trial (i.e. the first and last 15 seconds of data were removed prior to Fourier analysis). The 60-second data segments were multiplied by a Hanning window (a smooth function that tapers gradually to zero [1975]) prior to performing the DFT, in order to minimize edge effect artifacts that can arise during the Fourier transform. The squared-magnitude of the DFT was computed to produce an estimate of sway response power, at frequency intervals of 0.01Hz, spanning DC through 2.5Hz. Of particular interest was response power at each of the stimulus frequencies: 0.1 Hz, 0.3 Hz, and 0.5 Hz. These were obtained by calculating the average power across seven frequency bins (bin size = 0.01Hz) at and around each of the stimulus frequencies. This yielded a "stimulus-band" power equal to the average power at a given stimulus frequency ± 0.03Hz. These frequency-band power metrics were used as the means of comparison among the various visual stimulus and cognitive task conditions. Responses to moving scenes were also compared to those for quiet stance, in order to separate contributions of optic flow from those due purely to spontaneous sway.

8.3.5 SWAY ADAPTATION ANALYSIS

Changes in sway amplitude throughout each trial were determined by examining the time-varying spectrum of sway position, obtained through the use of time-frequency analysis, as described by Cohen [Cohen, 1989; Cohen and Posch, 1985] and Loughlin et al. [Loughlin *et al.*, 1994]. This technique combines the time-frequency information from multiple spectrograms (short-time Fourier transforms) computed with various window lengths, to obtain an improved estimate of time-varying spectral power, denoted by P(t, ω) where t=time and ω =frequency, compared to that provided by a single spectrogram. Of particular interest was the time-varying response power at the stimulus frequency, P(t), which was calculated as shown in equation (1) below:

$$P(t) = \sum_{\omega=Fs-0.03Hz}^{\omega=Fs+0.03Hz} P(t,\omega), \text{ where Fs = stimulus frequency} \qquad (1)$$

This time series was visually examined for evidence of sway adaptation. Whether or not adaptation occurred was determined subjectively on a trial-by-trial basis, as opposed to being based on any strict quantitative criteria, statistical or otherwise. This approach was possible because there were relatively few adaptation trials, and because it was rather obvious when P(t) displayed adaptive characteristics. For example, the decline in sway power shown in Figure 14 was typical for an adaptation trial, whereas non-adaptation trials displayed no such drop in sway power over time. For cases in which adaptation occurred, the time series, P(t), was fit with an exponential curve of the form $Ae^{-t/\tau} + B$, and the following parameters were extracted:

A = pre-adaptation magnitude of stimulus-band sway response to the moving scene

B = post-adaptation magnitude of stimulus-band sway response to the moving scene

τ = time constant of the exponential decay

Choosing a region over which the time series, P(t), was fit with an exponential curve contained a degree of subjectivity. Sway responses among subjects were not consistent: there were transients, delayed responses, and power did not necessarily decrease monotonically following the initial response. As such, the selection of fit boundaries was done on a trial by trial basis, as opposed to applying some automated algorithm to each trial. The starting point for curve fitting was chosen as the point of maximum power within a ten second window following the onset of scene movement. If this maximum power corresponded to an obviously transient event that was not representative of the overall response, then a more appropriate point in the same ten second region was used instead. The choice of ten seconds was not arbitrary. We had assumed that the primary sway response would occur during exposure to the first full cycle of a given stimulus, and ten seconds corresponded to the period of the lowest component frequency (0.1 Hz) in any of the stimuli. The end point for the curve fit was chosen as the point at which sway power returned to the pre-response magnitude, and remained at that level for at least ten seconds.

Any increase in power after ten seconds was considered to be a secondary response. Fitting an exponential curve to the portion of the power-versus-time data series bounded by these beginning and end points provided a means of quantifying the adaptation process, by yielding both the time constant of decay, as well as the per-stimulus decline in sway magnitude.

8.3.6 STATISTICAL ANALYSIS

A mixed-factor repeated measures ANOVA was utilized to examine the effects of stimulus type (STIM: NPSUM, PSUM, Stationary) and task condition (TASK: No Task, Auditory, Visual) on total sway power, on sway power at each of the stimulus frequencies (i.e. “stimulus-band power”) and on the sway adaptation time constant (τ).

Data distributions were tested for normality using the Shapiro-Wilk W test, and log-transformed to achieve normality when necessary. The significance level was set at $p = 0.05$ for both primary and post-hoc (Tukey's HSD) comparisons.

8.4 RESULTS

8.4.1 GENERAL SWAY RESPONSES

As observed in previous optic flow studies in our laboratory, subjects responded strongly to each of the moving visual stimuli. Peak-to-peak excursions of the head ranged from approximately 1cm to 4cm, with those for COP slightly lower. Sway magnitude was generally smallest for trials in which the scene appeared but remained stationary, slightly larger during quiet stance (QS), and largest during exposure to the moving visual scenes (Figure 20 and Figure 22). Among responses to the various moving scenes, sway was largest for the 0.3Hz "dummy" trial (i.e. trial #1), and lower for both the sum-of-sinusoids and the remaining 0.3Hz sinusoid trials.

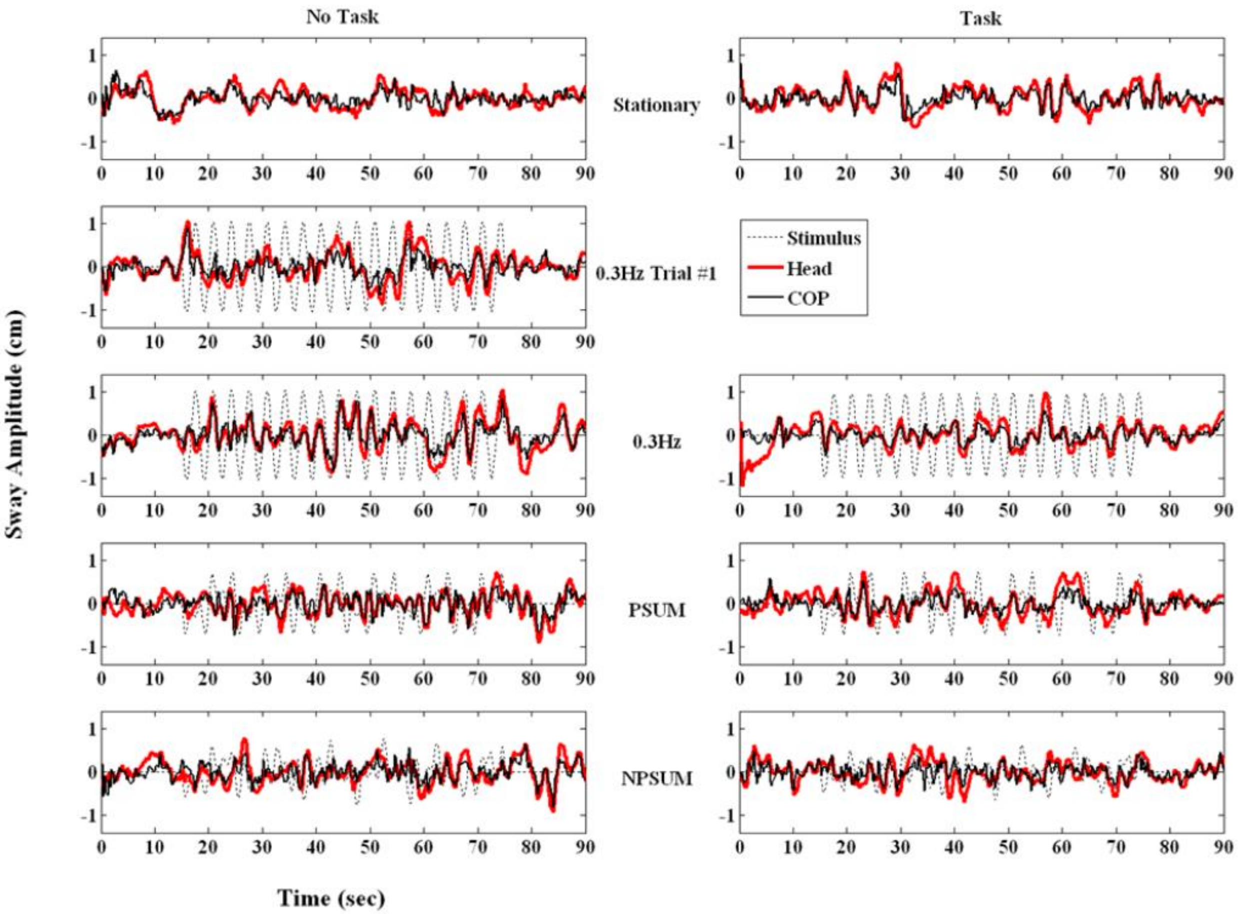


Figure 20 Ensemble time-series of Head (red) and COP (black) sway responses for the various visual and task conditions. Values shown are the average of first and second visits (i.e. auditory and visual days) for n=16 subjects. From top to bottom are Stationary scene, 0.3Hz Trial #1 (for No Task condition only), 0.3Hz sinusoid, PSUM (0.1 + 0.3 + 0.5Hz), and NPSUM (0.1 + π/10 + 0.5Hz). Responses for Task and No Task trials are displayed separately, on the right and left hand sides of the figure, respectively. Stimulus values are shown for comparison, and have been scaled for clarity.

Movements of the head and COP were in phase with one another for all trials, as revealed by visual inspection of time series data (Figure 20 and Figure 21). Head responses were larger than those for COP below 0.5Hz, as shown in the power spectral density plots in Figure 21 and Figure 22. Except for absolute power levels, the corresponding spectral densities of head and COP responses were very similar up to approximately 0.7Hz. These findings indicated that subjects had swayed predominantly as an inverted pendulum, which is consistent with previous findings of postural sway [Peterka, 2003; Peterka, 2002]. Because of the strong similarities among head and COP responses, the remaining discussion was limited to head data, with the occasional reference to COP when appropriate. Unless stated otherwise, all results presented for the head data, including significant differences, were observed in COP data as well.

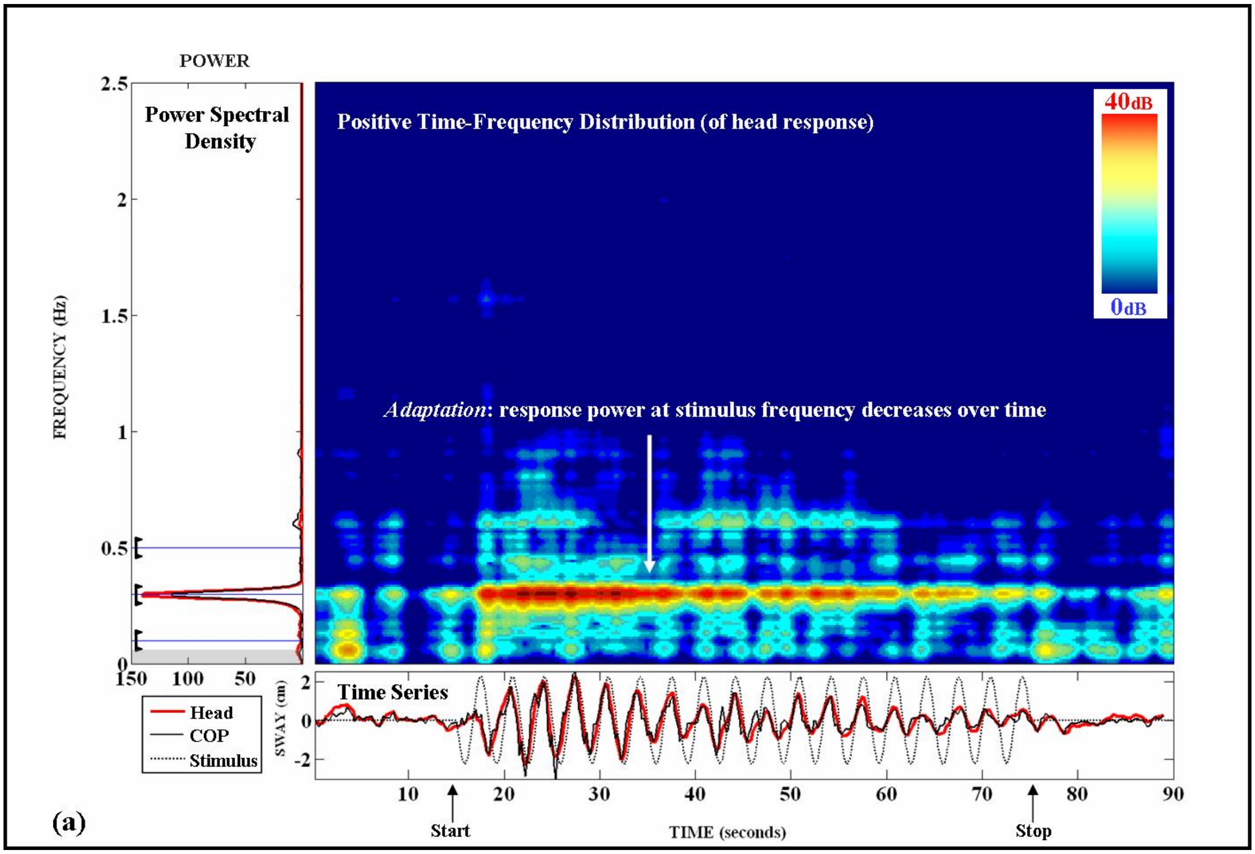


Figure 21 Time series, power spectral density, and positive-time frequency distribution (PTFD) of head responses of a single subject (s245) for two separate trials: (a) trial #1, 0.3Hz stimulus, auditory task day, no task; and (b) trial #2, PSUM stimulus, auditory task day, no task. Time series and power spectral density data for the COP response is shown for comparison. Time series data for the stimuli (dotted line) are also included for comparison; for clarity, they have been scaled by a factor of 2. "Start" and "Stop" indicate times at which scene movement begins and ends, respectively. For the power spectral density, the dotted line indicates stimulus frequency. Note that the absence of power below 0.05Hz is due to the data having been high-pass filtered, as represented by the shaded area. Arrows indicate the regions over which power was averaged to yield "stimulus-band" values, such as those shown in the bar plots in Figure 23b, Figure 24a, Figure 25a-b, and Figure 26a-c (see *Data Processing* section for details). Data shown is representative of responses for most subjects.

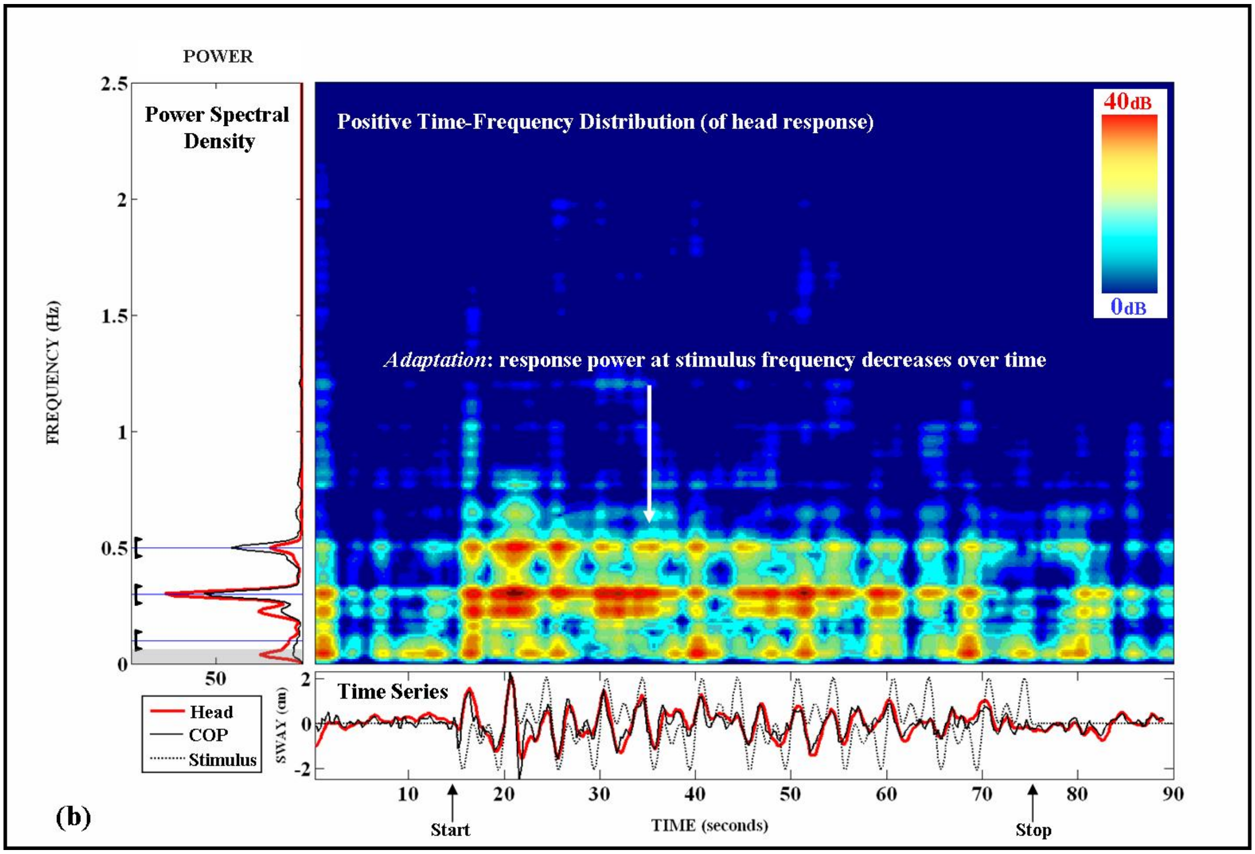


Figure 21 (continued) – part (b)

Both the quiet stance and moving scene sway responses displayed power that was usually largest at low frequencies (i.e. below 0.1Hz) and that generally decreased across the spectrum, as shown for head and COP motion in the power spectral density plots of Figure 22. Note that the data shown in Figure 21a was an exception to this rule, in that responses at the 0.3Hz stimulus frequency were particularly large for that subject, and therefore much larger than power at lower frequencies. The data in Figure 21a has been included to highlight the salient features of sway adaptation, which was particularly apparent in this case. Quiet stance sway power was spread across a band of frequencies from DC to approximately 0.4Hz, which is typical for spontaneous sway. The moving scene responses were characterized by larger sway amplitudes in this same frequency range, and substantial power at the stimulus frequencies as well. As expected, both single sinusoid and sum-of-sinusoid motion elicited sway responses that were consistently larger than those observed during quiet stance. These gains in power relative to quiet stance increased with frequency, with the smallest relative increase occurring at 0.1Hz, and the largest relative increase occurring at 0.5Hz. Also, sway during exposure to the stationary scene was generally lower than that for quiet stance (Figure 22).

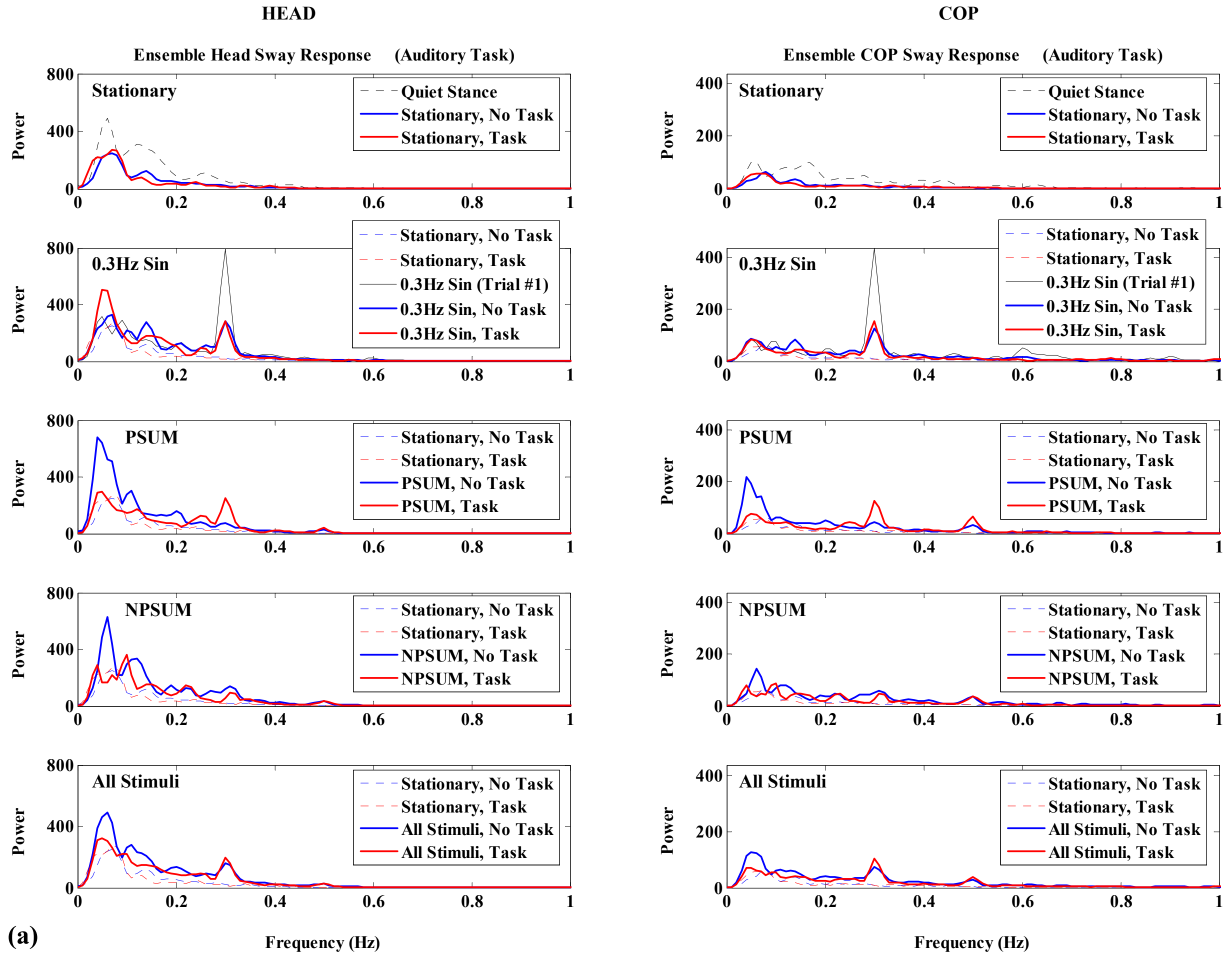
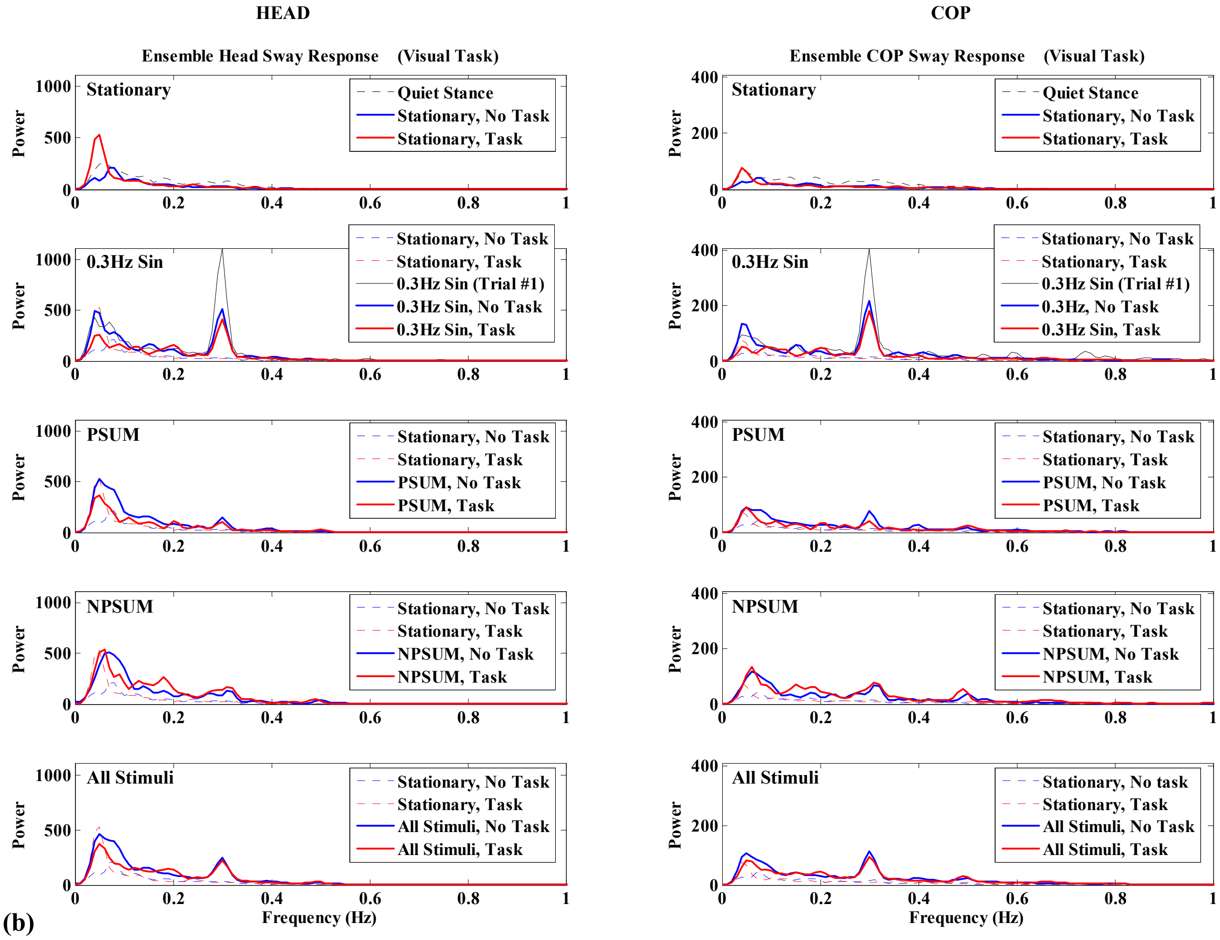
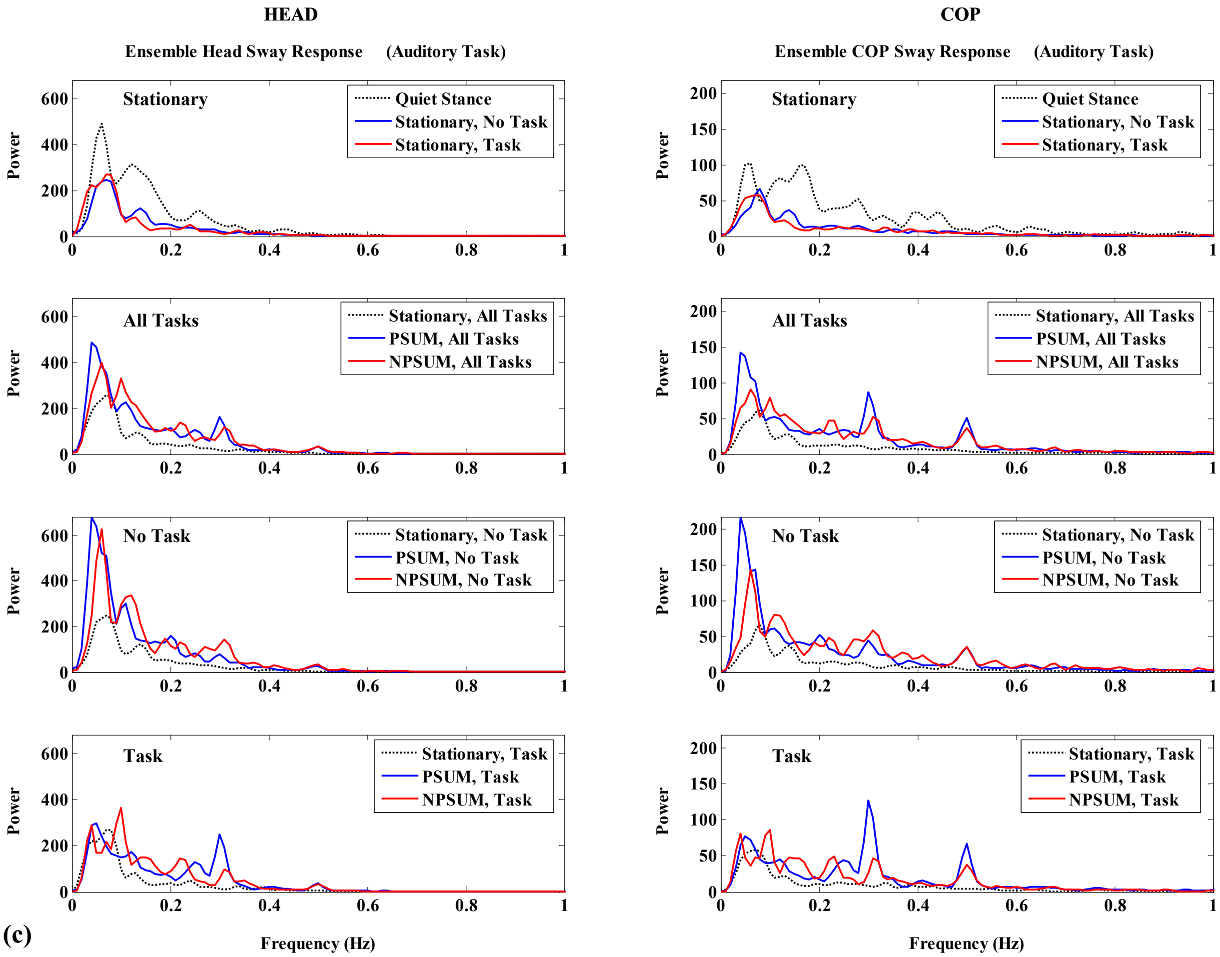


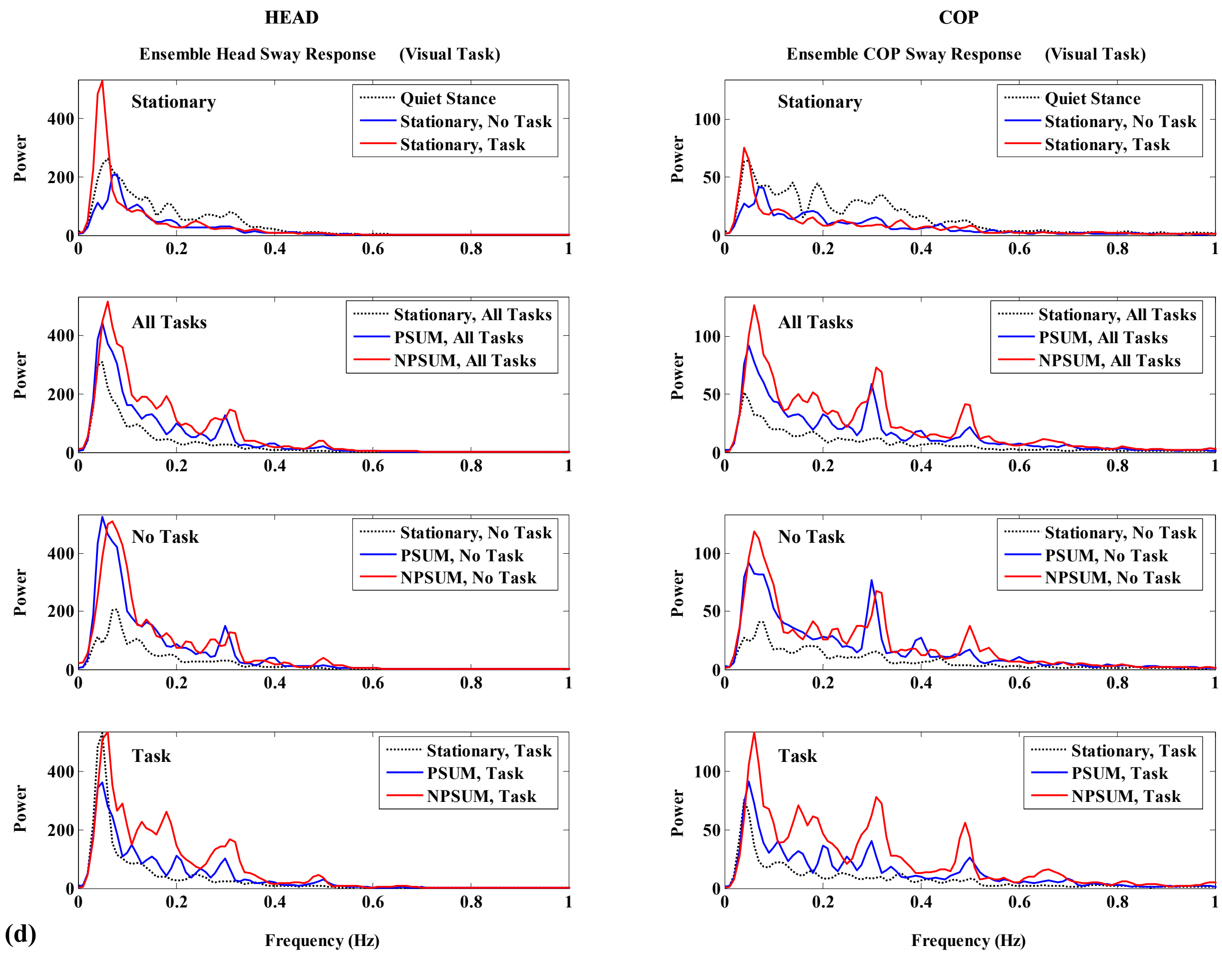
Figure 22 Ensemble power spectral densities of Head (left) and COP (right) sway responses for the various stimulus and task conditions. Values shown are the average across n=16 subjects. Values for Quiet Stance baseline and Stationary scene are shown in (a) through (d) for comparison. PLOTS (a) and (b): Values for Task (red line) versus No Task (blue line) conditions during (a) auditory and (b) visual trials in response to the various optic flow stimuli -- from top to bottom are Stationary scene, 0.3Hz sinusoid, PSUM (0.1 + 0.3 + 0.5Hz), and NPSUM (0.1 + π/10 + 0.5Hz). The bottom plot in (a) and (b) represents the average across all optic flow stimulus types. PLOTS (c) and (d): Responses to PSUM and NPSUM stimuli for (c) auditory and (d) visual Task and No Task trials. “All Tasks” represents both Task and No Task conditions.


HEAD
COP
Ensemble Head Sway Response (Visual Task)
Ensemble COP Sway Response (Visual Task)
Stationary
Quiet Stance
Stationary, No Task
Stationary, Task
0.3Hz Sin
Stationary, No Task
Stationary, Task
0.3Hz Sin (Trial #1)
0.3Hz Sin, No Task
0.3Hz Sin, Task
0.3Hz, No Task
PSUM
PSUM, No Task
PSUM, Task
NPSUM
NPSUM, No Task
NPSUM, Task
All Stimuli
Stationary, No task
All Stimuli, No Task
All Stimuli, Task
Power
1000
500
0
400
200
0
0.2
0.4
0.6
0.8
1
Frequency (Hz)

(b)


HEAD
Ensemble Head Sway Response (Auditory Task)
COP
Ensemble COP Sway Response (Auditory Task)
Stationary
Quiet Stance
Stationary, No Task
Stationary, Task
All Tasks
Stationary, All Tasks
PSUM, All Tasks
NPSUM, All Tasks
No Task
Stationary, No Task
PSUM, No Task
NPSUM, No Task
Task
Stationary, Task
PSUM, Task
NPSUM, Task
Power
0
200
400
600
50
100
150
0.2
0.4
0.6
0.8
1
Frequency (Hz)

(c)



(d)

8.4.2 TRIAL EFFECT

As expected, total sway power for trial 1 was significantly larger than that for each of trials 2 through 9 ($F_{8,718}$=8.63, p<0.001)(Figure 23a). Based on findings from the previous experiment, this trial effect was thought to be the result of sway adaptation. Since adaptation in the current study was observed at both 0.3Hz and 0.5Hz, we therefore examined the effect of trial on sway power at each of the stimulus frequencies. When viewed in this way, the trial effect displayed a different trend at each frequency (Figure 23b). The strongest effect existed at 0.3Hz, with values for stimulus-band power during trial 1 between 1.5 dB and 3.5 dB larger than those for subsequent trials. Values for trial 1 were significantly larger than those for trials 2 through 9 ($F_{1,143}$=10.11, p=0.002). A similar, but smaller, effect was observed at 0.5Hz, with decreases in power of no more than 2.5 dB; note that this decrease occurred after trial 2, not trial 1, since stimuli containing a 0.5Hz sinusoid were not presented until trial 2. Stimulus-band power at 0.5Hz for trial 2 was not significantly different than stimulus-band power at 0.5Hz *averaged across trials 3 through 9*. In terms of individual pair-wise comparisons between trial 2 and each of trials 3 through 9, a significant difference was observed only for trial 8 (p=0.036). No trial effect was seen at 0.1Hz.

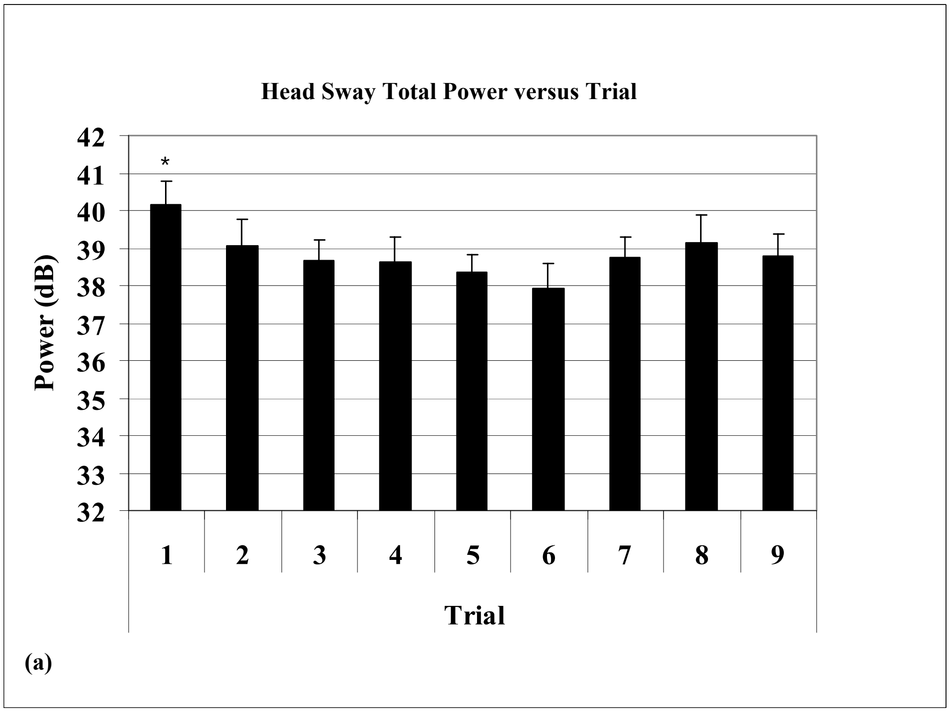
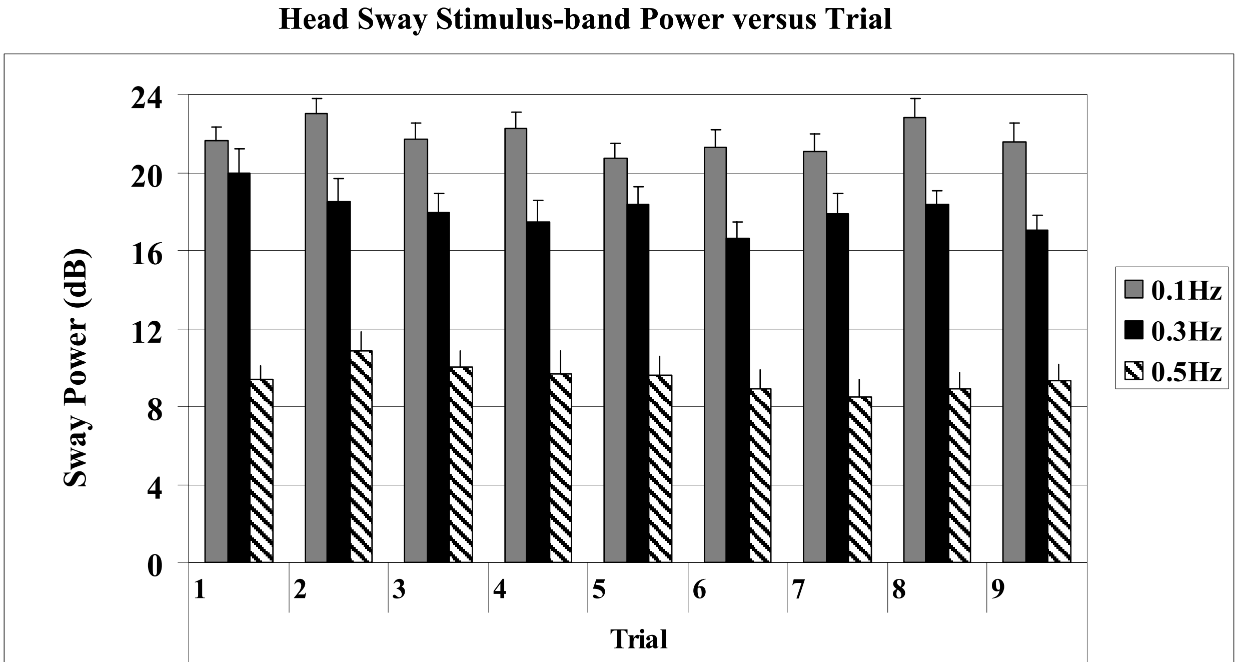


Figure 23 Ensemble head sway response power for trials 1 through 9. (a) Total power, averaged across all frequencies (0.1, 0.3 and 0.5Hz). (b) Stimulus-band power at each stimulus frequency. Values plotted are the mean +/- std error (in dB) for all subjects (n=16). Asterisk denotes a statistically significant difference (p<0.05) between the highlighted value and all subsequent values at that frequency. Note that the values are averaged across all optic flow stimuli (Stationary, PSUM, and NPSUM).



(b)									
▒ 0.1Hz	21.63	23.01	21.72	22.25	20.70	21.26	21.06	22.82	21.57
■ 0.3Hz	$\boxed{19.93}^{*}$	18.50	17.96	17.49	18.33	16.60	17.87	18.34	17.03
▧ 0.5Hz	9.39	10.87	9.99	9.66	9.61	8.90	8.48	8.91	9.33

Figure 23 (continued) – part (b)

8.4.3 SWAY ADAPTATION

Time-frequency analysis revealed sway adaptation, as evidenced by within-trial decreases in sway amplitude at the stimulus frequency (Figure 21). Notice in the time-frequency distribution of Figure 21a that sway power at the stimulus frequency (0.3Hz in this case) gradually declined following the onset of stimulus motion. In contrast to our previous study, in which adaptation occurred at a single frequency (0.7Hz) and only during trial #1, adaptation in this study was observed at multiple frequencies and in numerous trials, but always at the *highest* frequency for a given stimulus. That is, for the 0.3Hz sinusoid, adaptation was seen in the 0.3Hz frequency band of the response, while for the sum-of-sinusoids stimuli, subjects displayed adaptive responses at 0.5Hz instead. Adaptation was not observed in the 0.1Hz frequency band of any response.

The incidence of adaptation was not the same for all subjects. Four of the sixteen subjects did not display adaptation in any of the eighteen trials they performed over two separate visits. Of the remaining twelve subjects, two adapted just once, eight adapted twice, and two adapted more than two times (Table 4b). These trends in adaptation were mostly consistent with the observed trial effects, in that adaptation was followed by decreased sway power in subsequent trials. For example, eight of the fourteen cases of adaptation at 0.3Hz occurred during trial #1 (Table 4a), after which point sway power at 0.3Hz decreased for four consecutive trials (Figure 23b). The remaining six cases of adaptation at 0.3Hz were spread across trials 3 through 8, but were not accompanied by a noticeable drop in sway power in any subsequent trials. As for adaptation at 0.5Hz (i.e. in response to the SOS stimuli), there were sixteen total occurrences. Four of these were observed during initial exposure to SOS stimuli in trial #2. This was followed by lower sway power at 0.5Hz in all of the remaining trials (Figure 23b) Another six cases of adaptation at 0.5Hz occurred during trial #5, and this also corresponded to a noticeable decrease in sway power at 0.5Hz in subsequent trials (Figure 23b).

Table 4a Incidence of Sway Adaptation at 0.3Hz and 0.5Hz, Across All Subjects (notation represents # of *actual* adaptation trials / # of *possible* adaptation trials)

Trial	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	***Total***
Incidence of Adaptation at 0.3Hz	**8**/32	**0**/32	**2**/32	**1**/32	**2**/32	**0**/32	**0**/32	**1**/32	**0**/32	***14**/288*
Incidence of Adaptation at 0.5Hz	**0**/32	**4**/32	**2**/32	**0**/32	**6**/32	**0**/32	**3**/32	**0**/32	**1**/32	***16**/28*
Total	***8**/32*	***4**/32*	***4**/32*	***1**/32*	***8**/32*	***0**/32*	***3**/32*	***1**/32*	***1**/32*	**30**/*288*

Table 4b Incidence of sway adaptation at different frequencies and in multiple trials

	Trials in which adaptation occurred on *auditory* task day				Trials in which adaptation occurred on *visual* task day				
	No Task		Task		No Task		Task		
Subject	**0.3Hz**	**0.5Hz**	**0.3Hz**	**0.5Hz**	**0.3Hz**	**0.5Hz**	**0.3Hz**	**0.5Hz**	**Total # of trials**
230	-	-	-	5	-	-	-	2	**2**/18
231	-	-	-	-	-	-	-	-	**0**/18
232	-	-	-	-	-	-	-	-	**0**/18
233	-	-	-	-	-	-	-	5	**1**/18
234	-	-	-	-	1	3	-	-	**2**/18
235	1	-	-	5	-	-	-	-	**2**/18
236	-	-	-	-	1	9	-	-	**2**/18
237	-	5	-	-	-	2	-	-	**2**/18
238	-	7	-	-	1	-	-	-	**2**/18
239	8	-	-	-	3	-	-	-	**2**/18
240	-	-	5	-	1	2	-	3	**4**/18
241	-	-	-	7	-	-	-	-	**1**/18
242	-	-	-	-	-	-	-	-	**0**/18
243	1	-	-	-	1	-	-	-	**2**/18
244	-	-	-	-	-	-	-	-	**0**/18
245	1,4	5	3	2,7	1	-	-	5	**8**/18
Total # of trials	**5**/48	**3**/32	**2**/32	**5**/32	**7**/48	**4**/32	**0**/32	**4**/32	***30***/288
	8/80		**7**/64		**11**/80		**4**/64		
	15/144				**15**/144				

With the exception of subject #245, no subject adapted at 0.3Hz more than once during a single visit (Table 4b). This is consistent with our previous finding, in which adaptation occurred only once for a given series of a trials [Musolino *et al.*,]. However, there were cases in which adaptation was observed multiple times in a single testing session. In four of the six instances of such multiple adaptation (subjects 234, 235 236, and 245 [visual]), the adaptive behavior was observed two times: first at 0.3Hz, then at 0.5Hz (Table 4b). Another subject (240 [visual]) displayed adaptive behavior in three trials, first at 0.3Hz, followed by two instances at 0.5Hz. In the remaining case of multiple adaptation (subject 245 [auditory]), adaptation occurred numerous times at both 0.3Hz and 0.5Hz. So, for cases in which adaptation was observed more than once, adaptation occurred first at 0.3Hz, then at 0.5Hz.

Due to what appears to be a frequency specificity to adaptation, the use of a 0.3Hz "dummy" trial #1 did not have the intended effect of eliminating adaptation during subsequent trials. Since adaptation was not limited to trial #1, it was no longer useful to compare 'trial 1' to 'non-trial 1' data, as had been done in the previous study (see experiment #2). A more appropriate comparison to make instead was between 'adaptation' trials and 'non-adaptation' trials. Because adaptation occurred at a specific frequency, these comparisons were made based on measures of *stimulus-band* sway power (as opposed to *total* sway power). This provided a means of examining the effect of adaptation on sway responses during post-adaptation trials.

In addition, the adaptive responses were quantified by fitting an exponential curve to the power-versus-time data at 0.5Hz, as shown in Figure 14 (and described in *section 8.3.5*) for curve-fits to stimulus-band power at 0.7Hz. The exponential curve-fits provided a reasonably good approximation of the adaptive response, with r^2 values for the curve-fits ranging roughly from 0.50 to 0.90. This process yielded adaptation parameters A (pre-adaptation sway power), B (post-adaptation sway power), and τ (time constant of exponential decay). Values for A were compared between PSUM and NPSUM groups for adaptation versus non-adaptation trials, while values for τ (which existed only for adaptation trials) were compared between PSUM and NPSUM groups for each of the task conditions (No Task, Auditory and Visual).

8.4.4 PSUM VERSUS NPSUM RESPONSES

This analysis addressed the hypotheses that PSUM stimuli were expected to produce faster adaptation rates and lower sway power, as compared to NPSUM stimuli. Since the largest sway responses relative to quiet stance occurred at 0.5Hz, as did sway adaptation, comparisons between PSUM and NPSUM groups focused on differences in sway measures at this frequency. Stimulus-band sway power at 0.5Hz was lower in the PSUM group compared to the NPSUM group, for both adaptation and non-adaptation trials (Figure 24a). The difference of approximately 1dB in non-adaptation trials was not significant. Likewise, the near 3dB difference between the PSUM and NPSUM groups during adaptation trials was not significant.

With respect to adaptation parameters, pre-adaptation power (A) at 0.5Hz showed similar trends as that for stimulus-band power at 0.5Hz. Namely, lower values for the PSUM group compared to the NPSUM group in adaptation trials (Figure 24b), but overall no significant differences between PSUM and NPSUM groups for both adaptation and non-adaptation trials. In addition, values for ‘B’ were essentially zero in all responses that exhibited adaptation, meaning that sway power after adaptation had occurred was equal to sway power that existed prior to exposure to optic flow. As such, ‘B’ was excluded from subsequent analyses. These observations regarding ‘A’ and ‘B’ indicated that the 3dB difference in stimulus-band power between PSUM and NPSUM groups during adaptation trials (Figure 24a) could not be fully explained by differences in ‘A’ or ‘B’ between the groups, but instead must be at least partly the result of differences in the rate of adaptation, as captured by the time constant τ.

The rate at which adaptation occurred was not the same between these PSUM and NPSUM groups; it was over 3 seconds faster in subjects who had displayed adaptation during exposure to the PSUM stimuli (Figure 24c). As in the case of both stimulus-band power and pre-adaptation power at 0.5Hz for adaptation trials, this difference was not significant. However, the observation that both stimulus-band power and the adaptation time constant (τ) trended lower for the PSUM group compared to the NPSUM group suggests the possibility that a correlation exists between these two parameters. As such, the data do not provide strong support either for or against the hypothesis of lower sway power and faster adaptation rates in response to PSUM stimuli, but the trends in the data may be interpreted as favoring the hypothesis.

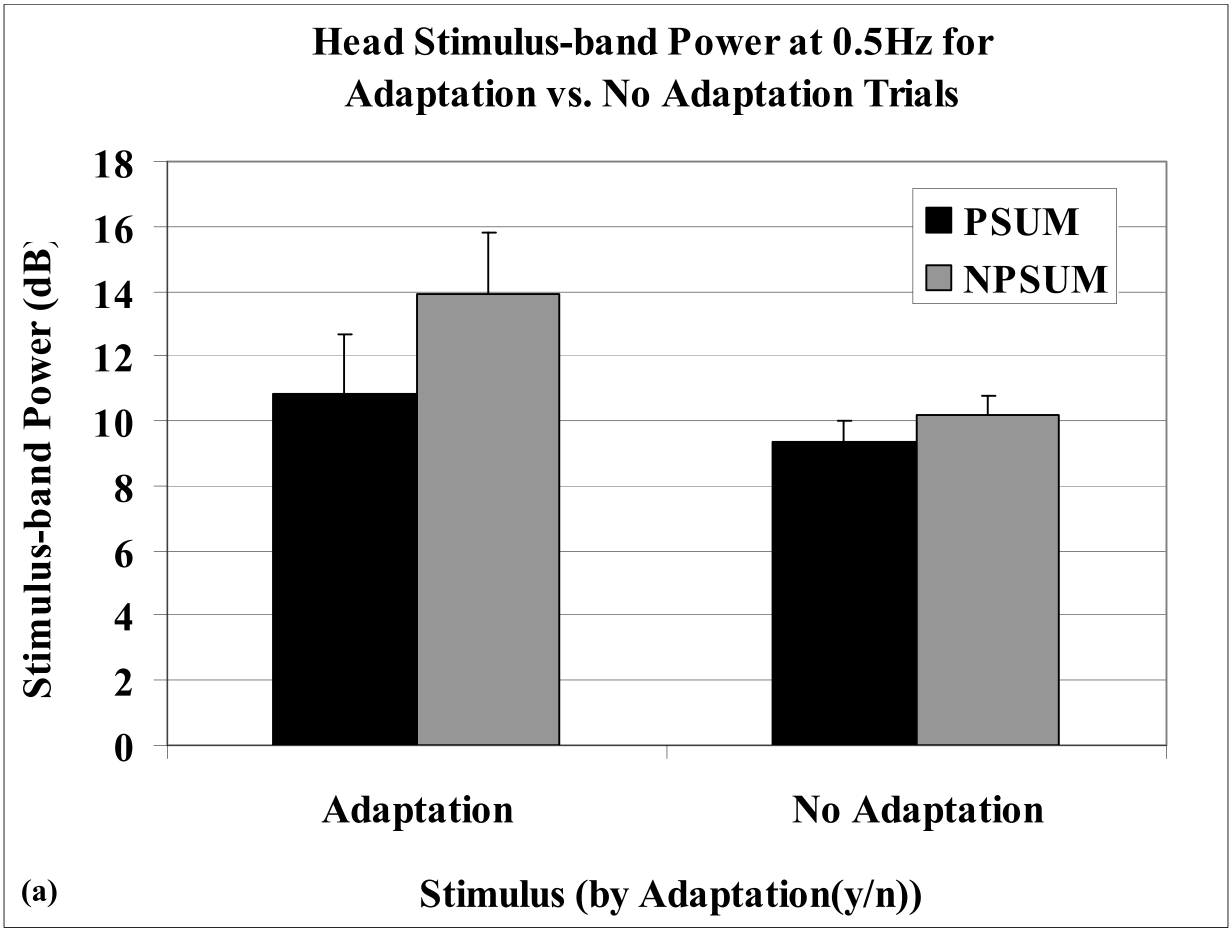
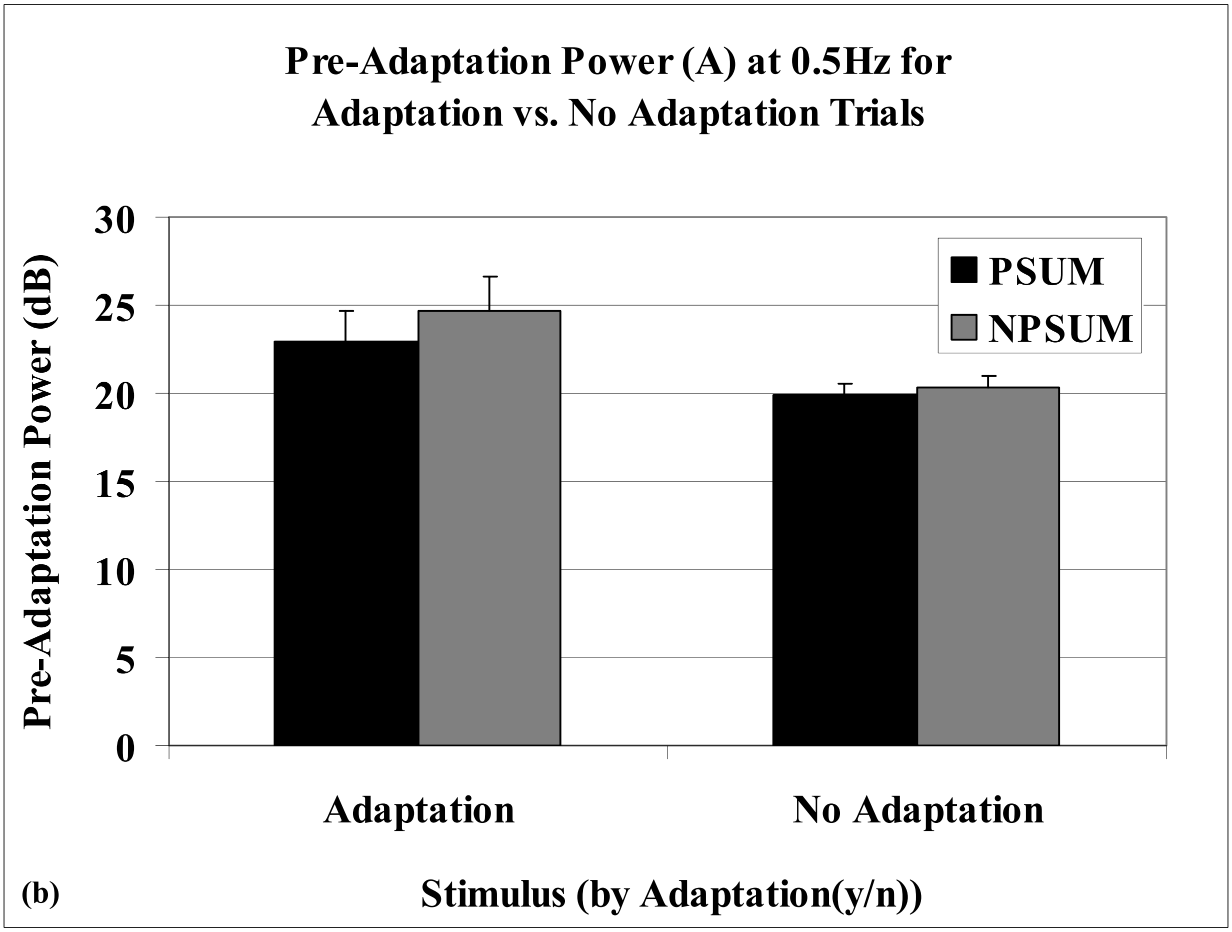
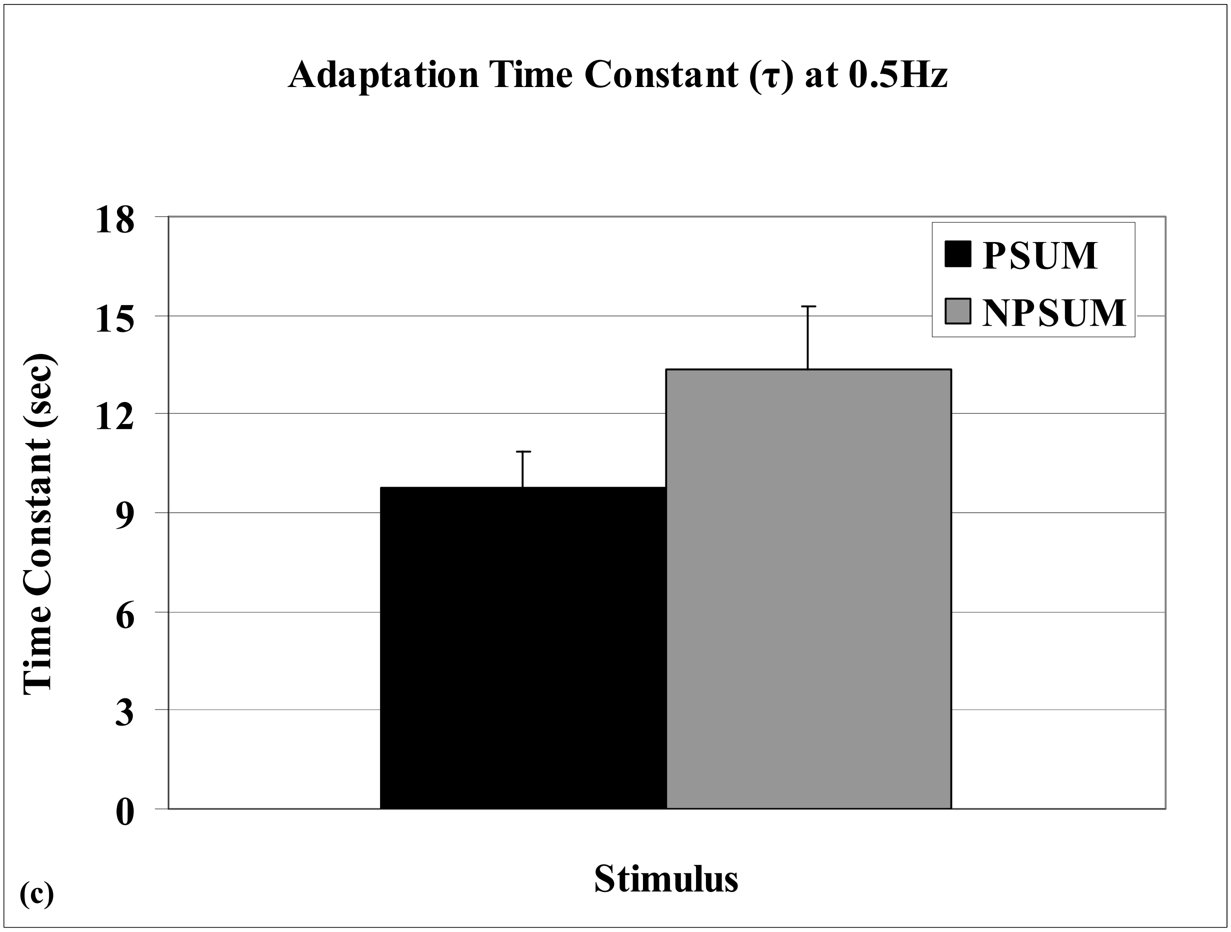


Figure 24 Head sway responses to PSUM and NPSUM stimuli: (a) Stimulus-band power at 0.5Hz, compared among adaptation and non-adaptation trials; (b) Pre-adaptation power (A) at 0.5Hz, compared among adaptation and non-adaptation trials; (c) Adaptation time constant (τ) for adaptation trials. Values plotted are the mean +/- std error.


Pre-Adaptation Power (A) at 0.5Hz for Adaptation vs. No Adaptation Trials
30
25
20
15
10
5
0
Pre-Adaptation Power (dB)
■ PSUM
▨ NPSUM
Adaptation
No Adaptation
(b)
Stimulus (by Adaptation(y/n))



8.4.5 INFLUENCE OF COGNITIVE TASKS

This analysis addressed the hypotheses that concurrent cognitive tasks would cause reductions in overall sway response power, and that visual tasks would enhance sway adaptation, while auditory tasks would not. Total sway power for the head was significantly lower ($F_{1,750}$=18.29, p<0.001) for trials involving a cognitive task (38.95 ± 0.30 dB), compared to trials without a task (38.47 ± 0.32 dB). Note that this total sway power represents the average across the optic flow stimuli of interest, namely Stationary, PSUM and NPSUM. When the Task versus No Task comparison was performed separately for each stimulus type, the same significant difference stated above (i.e. Task < No Task) was observed for both PSUM (38.76 ± 0.30 dB < 39.61 ±

0.35 dB, p=0.003) and NPSUM (38.91 ± 0.40 dB < 39.90 ± 0.33 dB, p<0.001) groups, while the Stationary group displayed the *opposite* behavior, with sway power for the Task condition larger than those for the No Task condition (36.67 ± 0.35 dB > 36.20 ± 0.28 dB). This difference approached significance (p=0.08).

Data in Figure 22 suggest that the influence of cognitive tasks was a function of frequency, cognitive task type, and optic flow stimulus type. For example, decreases in sway that were observed in cognitive task trials seemed to occur primarily at low frequencies, typically below 0.2Hz, as seen in the spectral density plots of Figure 22a and Figure 22b. A significant difference ($F_{1,186}$=7.16, p=0.008) in stimulus-band sway power between Task and No Task trials was observed at 0.1Hz (Figure 25a), indicating that the significant task effect noted above was due mainly to task-induced decreases in sway power at low frequencies. In some instances, this low frequency decrease was accompanied by *increases* in sway power at higher frequencies for cognitive task trials, but no significant differences in stimulus-band sway power at 0.3Hz or 0.5Hz were observed (Figure 25a).

Note that the data in Figure 25a represents values that have been averaged across optic flow stimulus groups (i.e. PSUM and NPSUM) and across cognitive task modalities (i.e. auditory and visual). When the task modalities were considered separately, both the auditory (p=0.036) and visual (p=0.028) groups exhibited the aforementioned significant decrease in stimulus-band power at 0.1Hz (Figure 25b). Differences in stimulus-band sway power were also observed at 0.5Hz, with visual task values *larger* than those for both auditory task and no task groups. This difference was not significant for either comparison, but approached significance (p=0.09) in the case of the No Task condition (Figure 25b). Together, these findings support the hypothesis that concurrent cognitive tasks would cause reductions in overall sway response power.

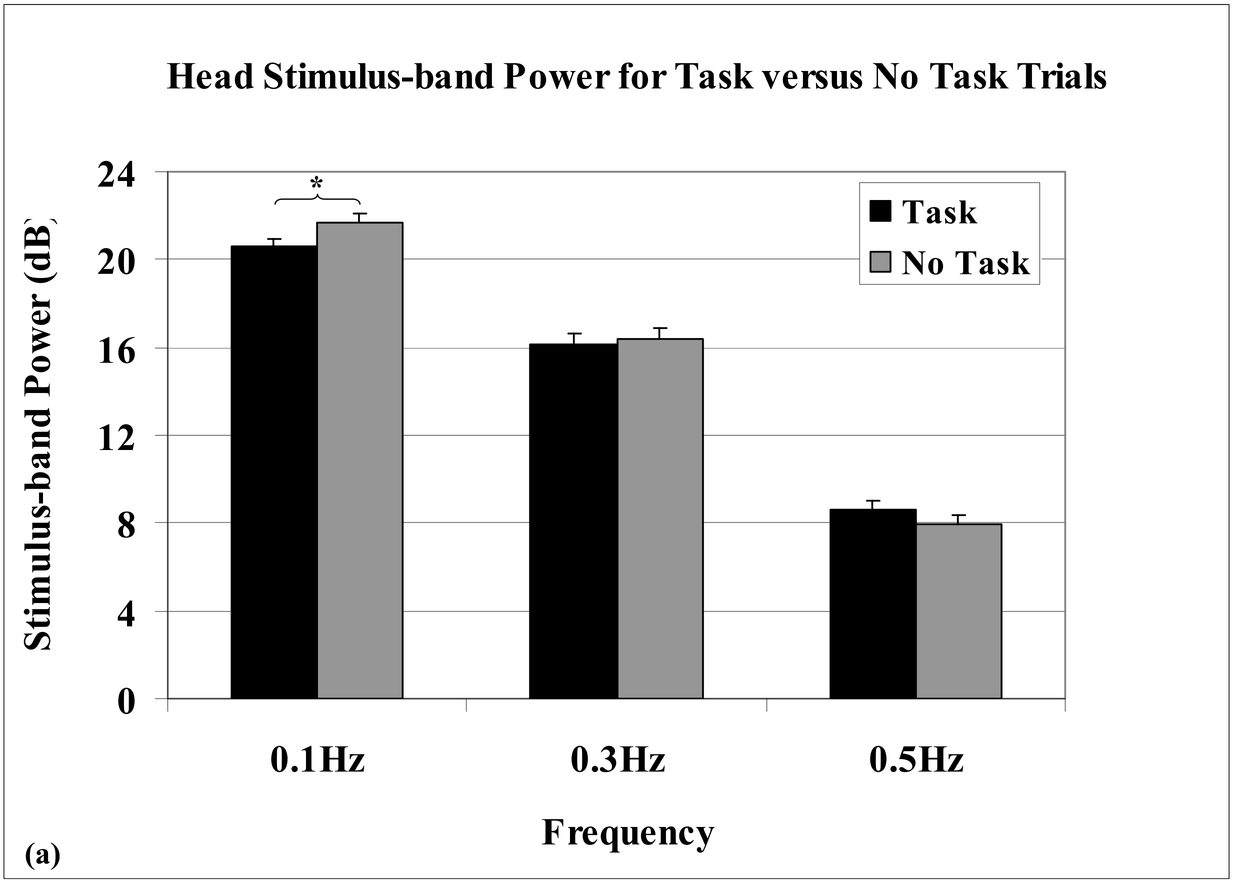
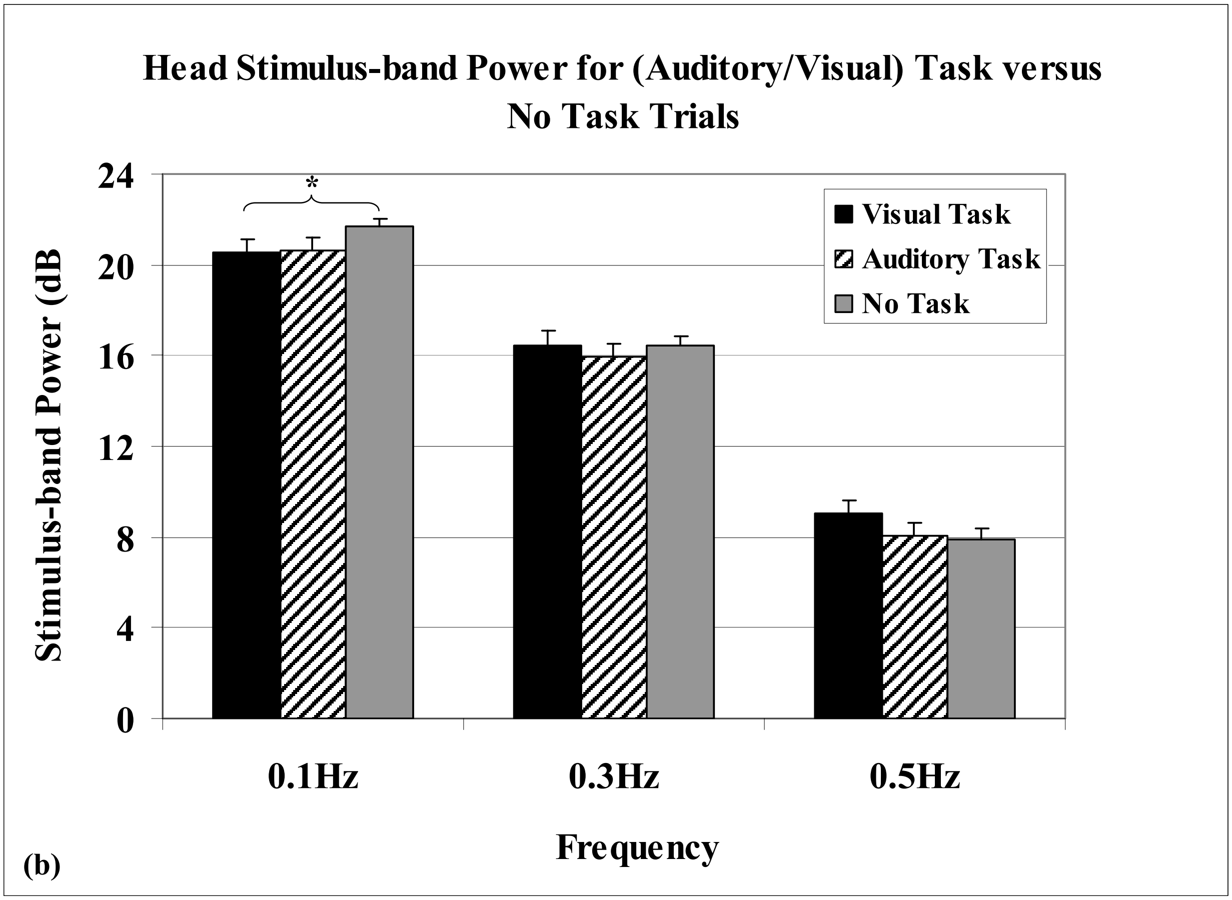


Figure 25 Stimulus-band power for head sway responses during Task and No-task trials: (a) auditory and visual task values combined; (b) auditory and visual task values shown separately. Values plotted are the mean +/- std error (in dB). Note that these values represent responses across visual stimulus type (i.e. PSUM and NPSUM).



In addition, an interaction between cognitive task modality and optic flow stimulus type was observed, in which the effect of the auditory and visual cognitive tasks was different for the PSUM and NPSUM stimuli. For instance, the bottom two plots in Figure 22d clearly show that performing a *visual* cognitive task produced noticeably lower sway power across the entire frequency spectrum during exposure to PSUM optic flow, as compared to NPSUM stimuli. This difference was significant ($F_{1,185}$=3.80, p=0.05) only at 0.5Hz (Figure 26d). In contrast, the corresponding plots in Figure 22c reveal the opposite behavior for *auditory* cognitive task trials, in that PSUM responses were *larger* than those for the NPSUM group.

This difference approached significance ($F_{1,185}$=2.95, p=0.088) at 0.3Hz (Figure 26c). Note that PSUM and NPSUM responses during the No Task condition were not significantly different from one another at any of the frequency bands (Figure 26).

With respect to the Stationary visual scene condition, performing a concurrent cognitive task caused an *increase* in total sway power compared to the No Task condition. This difference was significant (p=0.04) only in the case of the visual task (Figure 26a). When viewed at the level of stimulus-band sway power at each of the stimulus frequencies, the relationship among the auditory task, visual task and No Task groups during exposure to the Stationary stimulus was different at each frequency. At 0.1Hz, values for the auditory task groups were large than those for the No Task and visual task groups (Figure 26b). At 0.3Hz, both auditory task and visual task values were lower compared to No Task values (Figure 26c). At 0.5Hz, both auditory task and visual task groups displayed larger sway than the No task group (Figure 26d), which was consistent with the trend observed for total sway power. None of these differences were significant.

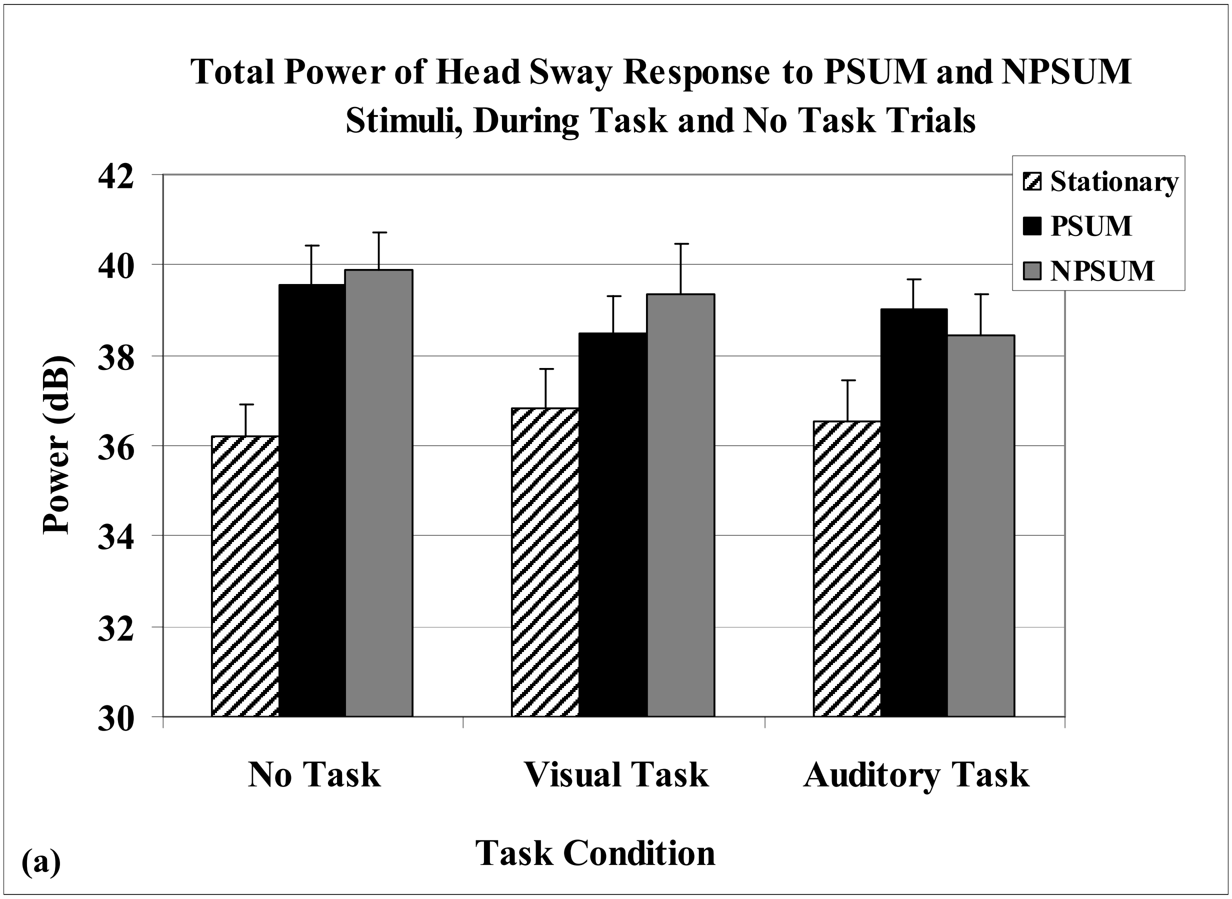
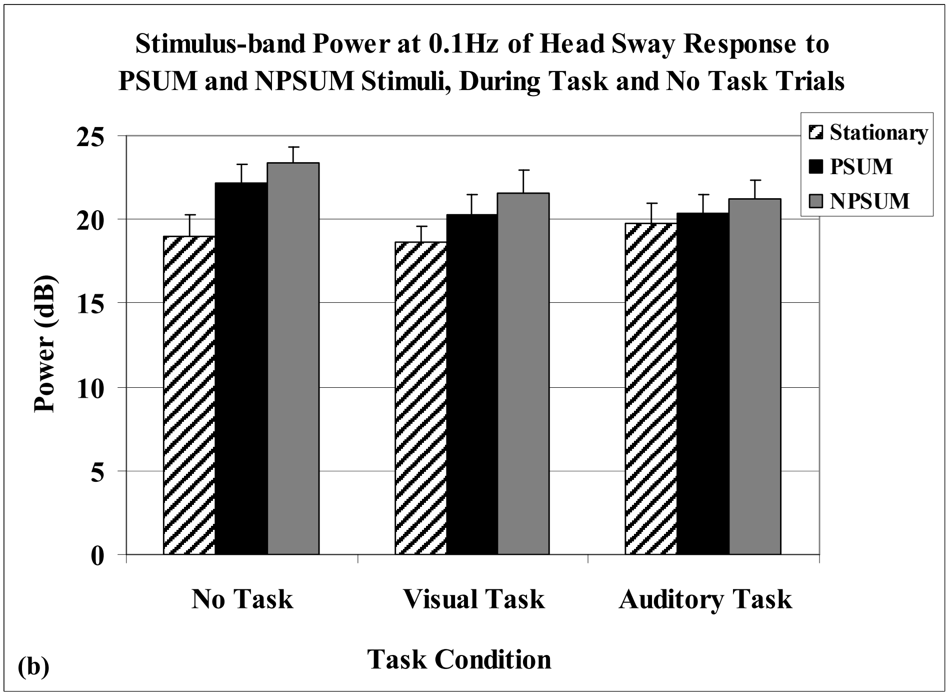
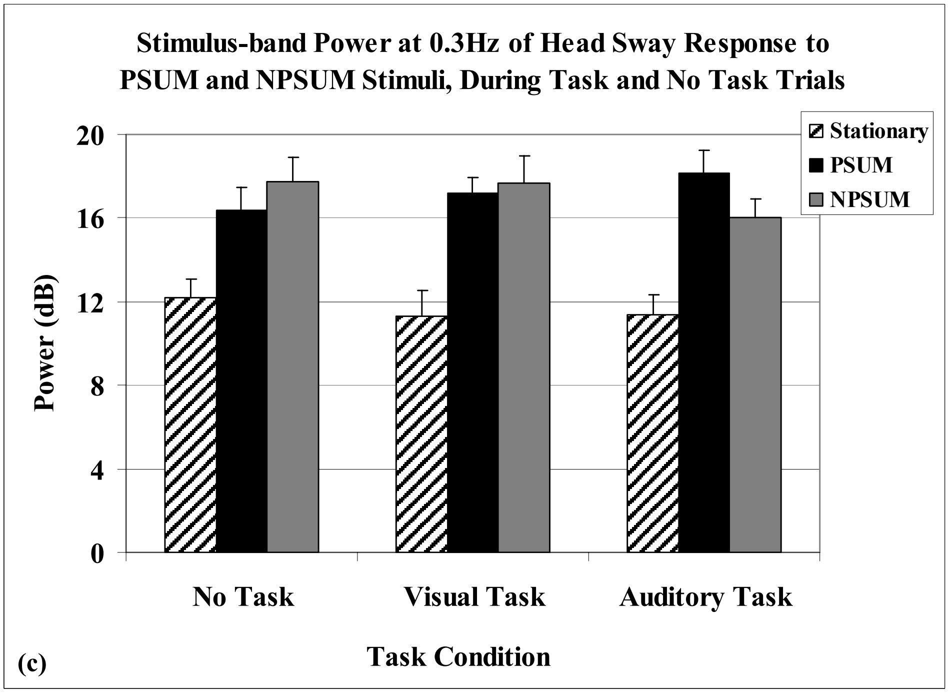
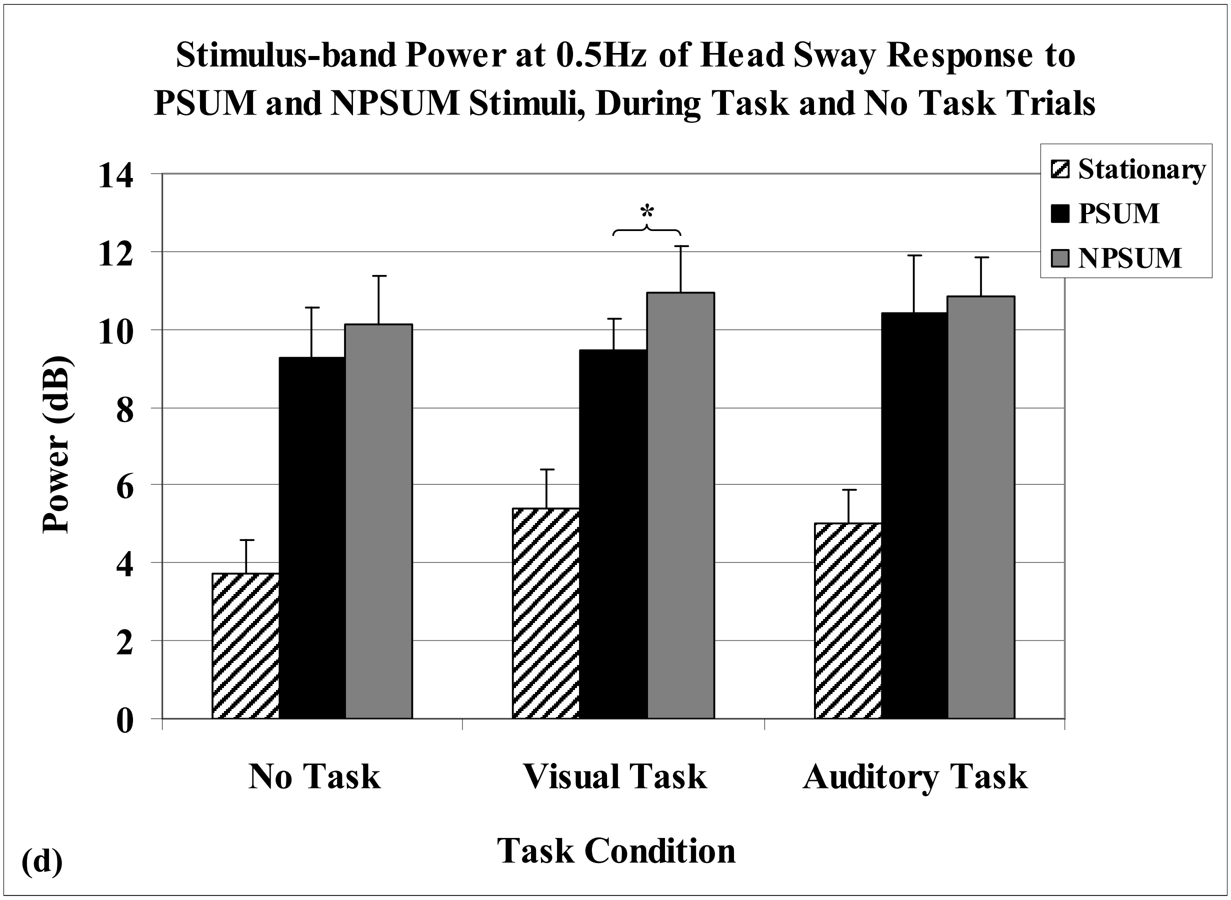


Figure 26 Head (a) total sway power, and stimulus-band power at (b) 0.1Hz, (c) 0.3Hz, and (d) 0.5Hz in response to PSUM and NPSUM stimuli for the various cognitive task conditions. Values plotted are the mean +/- std error. Values for Stationary scene are shown for comparison.


Stimulus-band Power at 0.1Hz of Head Sway Response to PSUM and NPSUM Stimuli, During Task and No Task Trials
▨ Stationary
■ PSUM
■ NPSUM
Power (dB)
0
5
10
15
20
25
No Task
Visual Task
Auditory Task
Task Condition
(b)


Stimulus-band Power at 0.3Hz of Head Sway Response to PSUM and NPSUM Stimuli, During Task and No Task Trials
▨ Stationary
■ PSUM
■ NPSUM
Power (dB)
0
4
8
12
16
20
No Task
Visual Task
Auditory Task
Task Condition
(c)



The incidence of adaptation was roughly equal between Task and No Task trials, and also among auditory-task and visual-task trials (Table 4b). This relative equity among Task and No Task groups suggested that cognitive tasks did not contribute to adaptation. At the same time, however, the fact that the PSUM group displayed adaptation and was also influenced by the visual cognitive task suggested that the cognitive task may indeed have contributed to adaptation in the PSUM group. The data in Figure 27 show that the rate of adaptation at 0.5Hz among PSUM and NPSUM groups was nearly identical for both No Task and auditory Task conditions, but was faster in the PSUM group for visual Task.

At the same time, however, time constant values were lowest for the No Task condition and highest for the visual Task condition. Note, however, that this data represents only a handful of observations (i.e. n=1 or n=2 per group), so the statistical significance of these differences could not be determined.

Overall, these data indicate that cognitive tasks generally produced lower sway in response to PSUM stimuli compared to NPSUM stimuli, but offer limited insight into whether or not this behavior was due to differences in adaptation rates between the groups. As such, the findings only partially support the hypothesis that an interaction would exist between cognitive task modality and optic flow stimulus type, such that visual tasks would enhance the differences in sway power and adaptation rates that were observed between PSUM and NPSUM groups.

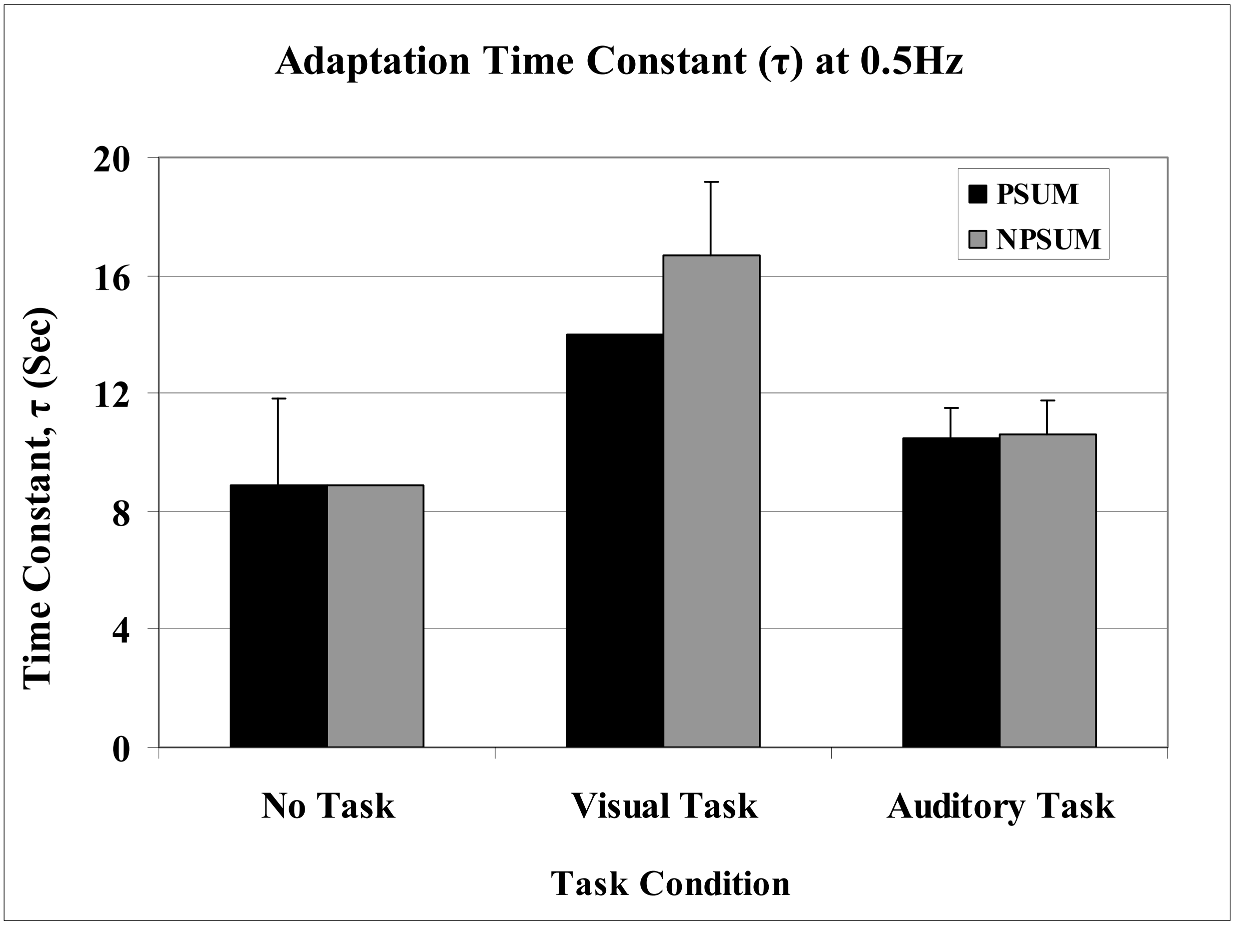


Figure 27 Sway adaptation time constants for head responses to PSUM and NPSUM stimuli during the various task conditions. Values plotted are the mean +/- std error. Bars without a std error value represent just a single observation (i.e. n=1).

8.5 DISCUSSION

8.5.1 MAIN FINDINGS

This study investigated the influence of a concurrent cognitive task on postural sway, during exposure to periodic and non-periodic oscillating optic flow. The objective was to determine whether or not a cognitive task modulates the previously observed effects of optic flow periodicity on postural sway [Musolino *et al.*, 2006]. The main finding of this study was that performing a cognitive task evoked lower sway responses compared to the no-task condition. This effect was observed for both auditory and visual cognitive tasks. This finding is in agreement with previous studies which have shown that performing cognitive tasks produces lower sway responses [Ehrenfried *et al.*, 2003; Dault *et al.*, 2001b; Dault *et al.*, 2001a; Teasdale and Simoneau, 2001; Vuillerme *et al.*, 2000; Fearing, 1924].

In addition, performance of a cognitive task while viewing oscillating optic flow caused subjects to respond differently as compared to viewing optic flow alone. Moreover, sway responses were affected not only by the presence or absence of a task, but also by the sensory modality of the task, as well as by the relative periodicity of the moving visual scene. For instance, as had been observed previously, periodic optic flow evoked lower sway amplitudes than non-periodic optic flow in the absence of a cognitive task. In the presence of a visual concurrent cognitive task, however, this effect was more pronounced. In contrast, an auditory cognitive task produced the opposite behavior, in which responses to periodic optic flow were larger than those to non-periodic stimuli.

Note that a task-induced decrease in sway is at odds with the ‘limited capacity’ model of attention [Fernandez-Duque and Johnson, 2002; Sanders, 1997], which argues that concurrent attention tasks would interfere with postural performance and cause a decrease in postural stability, which is typically associated with an increase in postural sway. The alternate view is that the decreases in sway observed in many studies of the cognitive influences on posture may in fact be indicative of increased postural stability that reflects a change in control strategy. In particular, the postural system might employ increased stiffness as a means of ensuring postural stability in the presence of the increased demands associated with a concurrent cognitive task [Dault *et al.*, 2001b; Dault *et al.*, 2001a]. An increase in stiffness, which physiologically may be achieved through increased co-contraction of gastrocnemius and anterior tibialis musculature, would be expected to cause a decrease in sway magnitude, but an increase in the frequency of sway oscillation [Winter *et al.*, 1998]. Findings in the current study are partly consistent with this. For example, as seen in Figure 22a, Figure 22b and Figure 25b, cognitive tasks were associated with decreases in sway power at low frequencies (which accounts for 95% of overall sway power), but with increases in sway power at some higher frequencies. Taken together, these observations provide some support for the idea that an increased stiffness control strategy is responsible for the observed decreases in sway while performing concurrent cognitive tasks.

8.5.2 ADAPTATION IN MULTIPLE TRIALS AND VARIOUS FREQUENCIES

In a previous study, we observed adaptation in a single trial (trial #1) and at a single frequency (0.7Hz). In contrast, the current study uncovered adaptation in multiple trials (including trial #1) and at two different frequencies (0.3Hz and 0.5Hz). The occurrence of adaptation in multiple trials throughout the experiment was likely the result of two separate, but related, factors: (1) the ineffectiveness of the 0.3Hz dummy trial, and (2) an apparent frequency specificity of the adaptation process. Adaptation during trial #1 occurred in only eight of thirty-two possible cases (16 subjects * 2 testing days), meaning that in the remaining twenty-four cases adaptation was possible in subsequent trials. Adaptation indeed occurred in subsequent trials, but at 0.5Hz instead of 0.3Hz. As such, adaptation in response to the 0.3Hz sinusoid occurred during initial exposure to this stimulus, but not after. This is consistent with previous findings [Musolino *et al.*,]. Adaptation at 0.5Hz was observed in numerous trials, primarily during trials #2 and trial #5, together with decreases in mean sway power in subsequent trials. The adaptation during trial #2, which in this case corresponded to initial exposure to a 0.5Hz sinusoidal frequency component, was also consistent with findings from our previous study [Musolino *et al.*,]. Adaptation during trial #5, however, was an unexpected observation. At first it was thought that this behavior perhaps reflected a second wave of adaptation that occurred after the effects of the initial adaptation had subsided, with the time between the two adaptive responses representing something akin to a refractory period. Closer inspection, though, revealed that adaptation at 0.5Hz in both trial #2 and trial #5 was observed not in any single subject, but rather only in behavior for the entire subject population. Therefore, this dual adaptation appears to simply indicate that some subjects did not adapt until trial #5. This in itself is intriguing, as it indicates that adaptation does not necessarily occur during initial exposure to optic flow. The data in Table 4b support this, revealing several cases of subjects adapting for the first time well after initial exposure.

Despite the fact that adaptation at one frequency did not necessarily prevent subsequent adaptation at a different frequency, there appeared to be a "directionality" to this phenomenon, such that the subsequent adaptation occurred only at a *higher* frequency. That is, adaptation at 0.3Hz was in some cases followed by adaptation at 0.5Hz, whereas adaptation at 0.5Hz was never followed by adaptation at 0.3Hz. This may be related to what we have termed a "velocity sensitivity" to oscillating optic flow, whereby subjects who are exposed to a stimulus that contains multiple frequencies respond primarily to the highest frequency component of that stimulus. This is considered a velocity effect because velocity increases with frequency for sinusoids of equal amplitude (such as those used in our experiments), so that the highest frequency corresponds to the highest velocity. This "directionality" might explain why adaptation in the current study occurred at two separate frequencies, while adaptation in our previous study was observed at only a single frequency. The current study had purposely exposed all subjects to a 0.3Hz sinusoidal stimulus in trial #1, in hopes of limiting adaptation to this trial. This “dummy” trial did not have the intended effect, as evidenced by the occurrence of adaptation in later trials. This subsequent adaptation, however, occurred more often than not at the higher frequency of 0.5Hz, and was never observed at the lower frequency of 0.1Hz. In contrast, in the earlier experiment, a majority of first trials had by chance included a stimulus that contained the highest frequency component used in the study, a 0.7Hz sinusoidal component. Sway responses and adaptation during trial #1 therefore occurred at 0.7Hz. The “directionality” of adaptation may have then prevented subsequent adaptation from occurring at any of the other frequencies, all of which were lower than 0.7Hz.

8.5.3 RATES OF ADAPTATION

Adaptation rates observed at 0.3Hz were slower than those at 0.5Hz, which themselves were slow compared to the rates seen at 0.7Hz in our previous experiment (Figure 28). This raises the possibility that adaptation rates are a function of the frequency at which adaptation is occurring. If adaptation is the result of prediction, as we hypothesize, then this frequency dependent behavior may be related to the temporal aspect of the predictive process. For example, if the predictive mechanism requires N number of cycles of a periodic stimulus to occur in order to produce a predictive estimate, then the time required for prediction (and therefore presumably for adaptation as well) would decrease with increases in stimulus frequency. That is, a 0.7Hz sinusoid, with a period of T = 1/0.7 = 1.43 seconds would require 1.43*N seconds for prediction, whereas 0.5Hz and 0.3Hz sinusoids would require 2*N and 3.33*N cycles, respectively. That predictive behavior may be linked to the temporal aspect of a sinusoidal stimulus has been reported previously by Bahill and McDonald, who showed that accurate tracking of sinusoidal moving targets occurs within the first ½ cycle of exposure [Bahill and McDonald, 1983]. This, however, might have implications more for the onset time of adaptation than for the rate of adaptation once that process has begun. Another possibility is that lower frequencies are perhaps associated with longer adaptation times because sway power is larger at lower frequencies, so that it simply takes more time for power to decrease to pre-response levels (i.e. for B to reach a value of zero). However, if the purpose of adaptation is assumedly to ensure postural stability, then this explanation does not make sense. Instead, one would expect rates of adaptation to be faster at low frequencies, which contain more power, such that sway magnitude would be lowered more quickly. From this perspective, the "N-cycle" paradigm is a more plausible explanation for the decrease in adaptation rates with frequency.

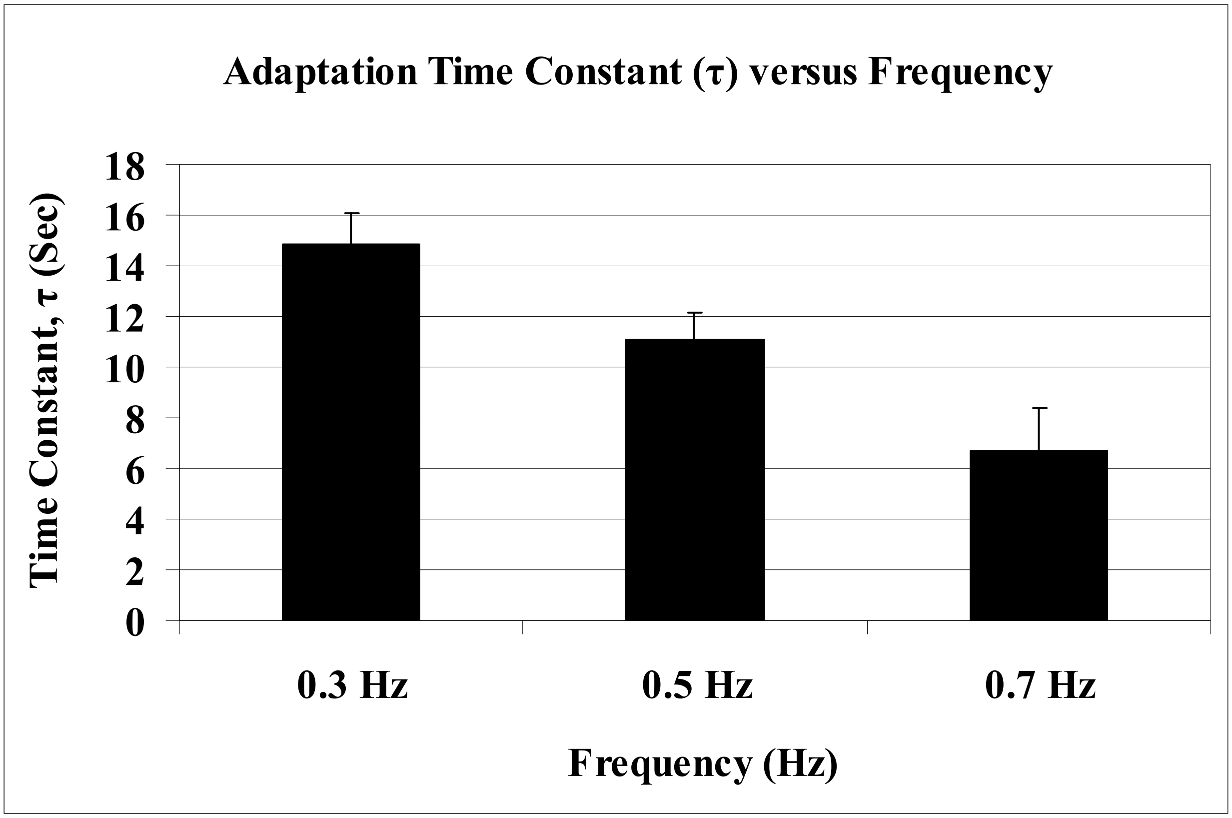


Figure 28 Adaptation time constant (Tau) versus frequency. Values at 0.7Hz are from a previous experiment. Note that these values represent responses across stimulus type, task type, task condition, and trial. Values plotted are the mean +/- std error (in dB).

In addition, note that the adaptation time constant (τ) represents the time at which stimulus-band sway power has decreased by approximately 67% from the initial, pre-adaptation value (i.e. "A"). Values for τ can be misleading if they are mistakenly interpreted as the total time required for adaptation to occur. A more accurate metric of the time at which sway power has been reduced to post-adaptation level (i.e. "B") is the "3τ" point, which corresponds to a 99% reduction in sway power. For example, based on the values for τ shown in Figure 16, the total time required for adaptation at 0.7Hz to occur ranged from approximately twelve to twenty-seven seconds. For a sixty second optic flow trial, this fifteen second difference represents a full

25% of the trial duration. With respect to the period of oscillation of a 0.7Hz sinusoidal component (T = 1/0.7Hz ~ 1.43 sec), which is the frequency at which this adaptation occurred, fifteen seconds represents over ten full cycles of oscillation. From this perspective, differences in τ of just several seconds may in fact represent substantial differences in adaptation rates.

Comparisons to adaptation rates reported by others is difficult because of a scarcity of data. Only one such report has been uncovered thus far, and that involved postural sway adaptation in response to galvanic stimulation [Johansson *et al.*, 2001b]. Values for the time constant of decay in that case were in the range of 40-50ms, which is several times larger than those observed in the current study. It is worth noting that the authors in that study chose to use pseudorandom stimuli, specifically in order to avoid, in their words, “anticipative (i.e. feedforward) responses”. Based on the findings presented in the current study, the noticeably slower adaptation rates in the Johansson paper are probably due in part to the use of unpredictable stimuli.

8.5.4 CONCEPTUAL MODEL

The results presented here are thought to reflect the interaction between two separate processes: (1) a predictive mechanism that is sensitive to visual stimulus periodicity, and (2) a cognitive task effect that can modulate visual information processing. Recall that the proposed predictive mechanism is believed to produce a *facilitated* adaptation in response to periodic stimuli, which represents an enhancement of the *baseline* adaptation that occurs during exposure to any type of optic flow, regardless of periodicity. A conceptual model of the influences of both cognitive tasks and the proposed predictive mechanism on sensory reweighting and sway behavior is shown in Figure 29a. Though this has not been explicitly stated thus far, note that optic flow produces an increase in sway compared to quiet stance (represented by thick black arrow in

Figure 29a), such that any reductions in sway caused by sensory reweighting (due to either sensory conflict (green arrow in Figure 29a), prediction (blue arrow in Figure 29a) or cognitive tasks (red arrow in Figure 29a)), are counteracted in part by this optic-flow induced increase in sway.

Performing a *visual* attention task is thought to *enhance* the effects of the predictive mechanism, because of an increase in resources devoted to visual processes during the visual attention task. That is, attending to a visual task will enhance processing of visual information. Several previous reports provide evidence to support this, showing that attention to a visual task modulates neural activity in various locations throughout the visual cortex, and can influence visual processing that is specific to motion detection [Felisberti and Zanker, 2005; Ress *et al.*, 2000; Alais and Blake, 1999; Treue and Maunsell, 1996; Lankheet and Verstraten, 1995]. This interaction between the predictive mechanism and the cognitive task is expected to have similar, but not equal, effects for periodic and non-periodic visual stimuli. In the case of periodic optic flow, in which the predictive mechanism is expected to produce facilitated adaptation, the increased visual processing associated with a visual attention task will act to further accelerate sway adaptation, yielding even faster adaptation times and lower mean sway power. For non-periodic optic flow, when the predictive mechanism is not active, and only baseline adaptation occurs, the effects of the visual task will again accelerate the adaptation process. Because the starting point in this case is only baseline adaptation, though, the overall effect will not be as great as that for periodic stimuli.

In contrast, performing an *auditory* attention task is thought to *reduce* the effects of the predictive mechanism, because of a decrease in resources devoted to visual processes during the auditory attention task. That is, attending to an auditory task would impair the processing of visual information, which in this case should slow any reduction in visual channel weight that is occurring, whether it were associated with either baseline adaptation or facilitated adaptation.

The data are consistent with this conceptual model, as most readily seen in the COP plots in Figure 22c and Figure 22d. Figure 29b presents the data from Figure 26a in a format appropriate for comparison to the expected behaviors displayed in Figure 29a. Though significant differences were not observed in the Figure 29b data, the trends in PSUM versus NPSUM values for the various cognitive task conditions are consistent with those expected based on the conceptual model shown in Figure 29a. These findings indicate that cognitive tasks do indeed influence postural responses to periodic and non-periodic optic flow, and that this may be related to differences in the rates of sway adaptation in the various stimulus and task conditions.

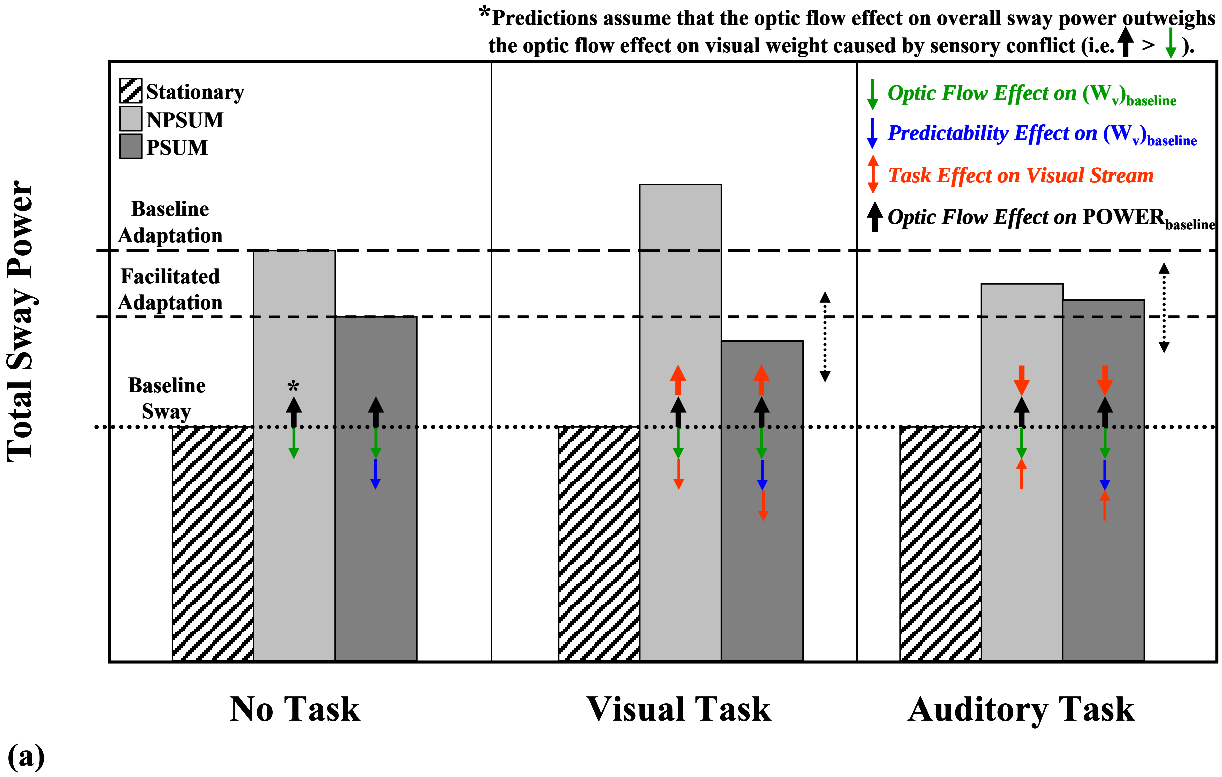
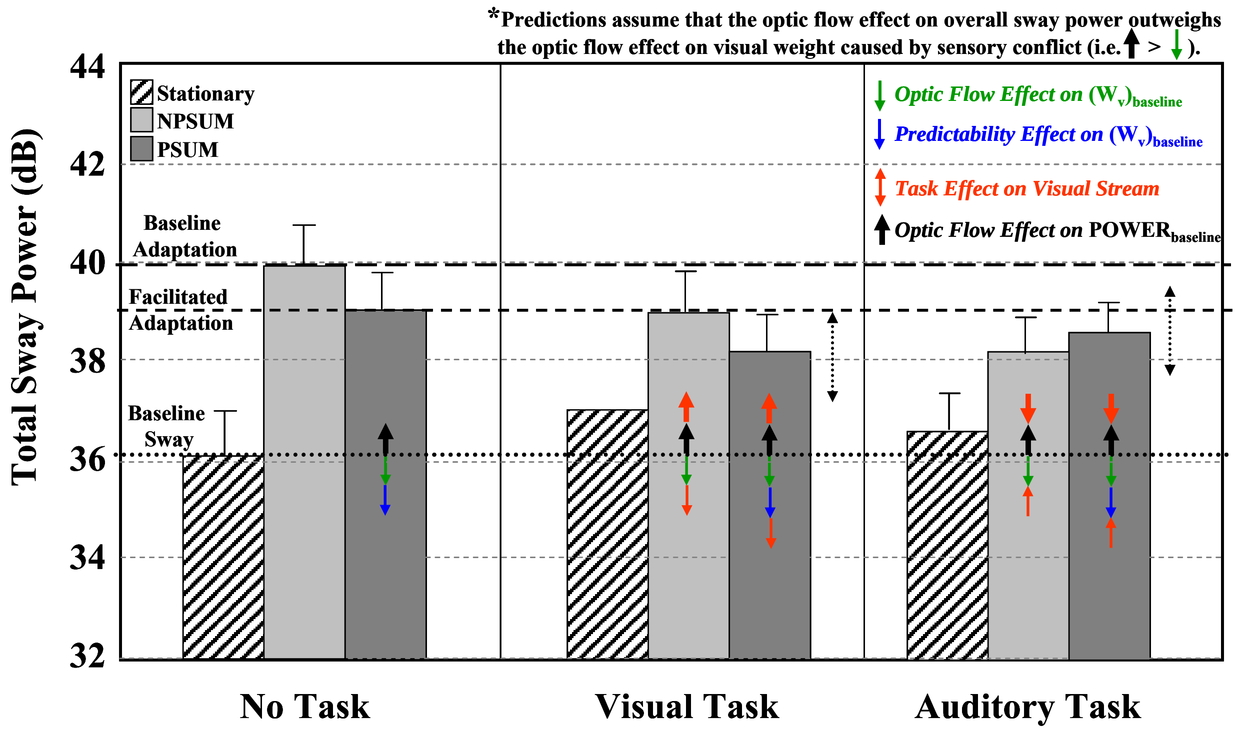


Figure 29 (a) Conceptual diagram of the interaction among the effects of optic flow, sensory prediction and cognitive tasks, and their influence on both visual channel weight and overall sway power. (b) Head response data from Figure 26a, in a format for comparison to Figure 29a. Values plotted in (b) are the mean +/- std error (in dB). Direction of arrow indicates change in power caused by the respective mechanism. Green arrow represents decrease in visual weight caused by optic-flow induced sensory conflict. Blue arrow represents decrease in visual weight caused by predictive mechanism in response to predictable stimuli. Red arrow represents effect of cognitive task on information processing in the visual stream: up/down signifies increases/decreases in visual weight (thin arrow) or sway power (thick arrow). Black arrow represents increase in sway power, compared to quiet stance condition, caused by exposure to optic flow; arrow is thicker to indicate that this optic flow effect on sway power outweighs the effect of any other single mechanism. Dotted arrow-lines next to PSUM bar for visual and auditory tasks indicates that the value for this bar depends on the relative strength of each of the various counteracting effects. See body text for a detailed description.



(b)

8.6 CONCLUSIONS

The current study reproduced various observations from previous studies [Musolino *et al.*, 2006], including (1) postural sway adaptation during exposure to optic flow; (2) significantly different sway responses to periodic and non-periodic stimuli; and (3) consistent responses at the highest component frequency of the stimuli. More importantly, several interesting new findings were reported, including (1) decreases in sway magnitude during cognitive tasks; (2) modulation of stimulus periodicity effects on sway by concurrent cognitive tasks; and (3) sway adaptation in multiple trials and at multiple frequencies. These findings provide further evidence that differences in sway responses to periodic and non-periodic optic flow stimuli are due to differences in rates of sway adaptation during exposure to these stimuli. Such behavior is consistent with the existence of a predictive component to postural control that is capable of reducing visual gain during exposure to periodic optic flow. Moreover, these predictive effects on visual channel gain can apparently be modulated by the influence of cognitive tasks. Future studies are planned to more fully investigate these findings and to develop models of the underlying mechanisms.

9.0 CLOSING DISCUSSION

9.1 SUMMARY OF FINDINGS

The series of experiments presented in this work have shown that periodic and non-periodic full-field oscillating optic flow evoke quantitatively different postural sway responses in healthy young adults, as observed in measures of both sway magnitude and sway adaptation. This effect was due primarily to a difference in the rate at which the sway response adapted during initial exposure to these stimuli, a behavior which has been attributed to a sensory reweighting process aimed at reducing visual channel weight. Specifically, non-periodic stimuli produced what has been termed a baseline adaptation, while periodic stimuli evoked a faster, facilitated adaptation. Moreover, this effect was observed in visually independent subjects, but not in visually *dependent* subjects, who presumably were particularly reliant on visual information. The absence of a predictive effect in the visually dependent group was attributed to an inability of these subjects to reduce visual channel weight, presumably because such reductions would adversely affect postural stability in this population.

In addition, the performance of a cognitive task during exposure to optic flow caused a general decrease in postural sway magnitude, regardless of whether that task was auditory or visual. However, an interaction existed between this cognitive task effect and the predictive mechanism effect, such that visual tasks enhanced the reductions in sway and adaptation elicited by periodic stimuli, while auditory tasks did not.

Overall, these findings have provided evidence to support the existence of a predictive component to postural control that can promote sensory reweighting during exposure to periodic optic flow. The following sections will discuss possible mechanisms for the observed behaviors, as well as limitations of this study, and ideas for future work.

9.2 POSSIBLE MECHANISMS FOR OBSERVED BEHAVIORS

It is difficult to say with certainty that reductions in visual channel weight were responsible for the sway adaptation and reductions in overall sway power that have been observed in response to periodic stimuli. The results thus far provide only indirect evidence in support of our claim that a predictive mechanism in the postural control system can induce changes in visual channel weight. As will be discussed later in the Future Work section, we plan to perform computer simulations based on a linearized inverted pendulum feedback control model developed by Peterka [Peterka, 2002]. The purpose of these simulations will be to quantify changes in visual channel weight for the various stimulus-response combinations in this study. Decreases in visual channel weight for trials involving periodic stimuli would implicate sensory re-weighting as a causal mechanism for sway adaptation.

Previous findings, mainly from studies of the visual system, provide ample evidence in support of the notion that predictive mechanisms influence behavior during exposure to moving visual stimuli. For instance, Barnes et al. have amassed a wealth of data over the past two decades that demonstrate rather convincingly that the visual smooth pursuit system can generate predictive eye movements in response to sinusoidal moving targets. These authors have suggested that the CNS is capable of detecting periodicity, and have proposed a model of predictive control in which velocity information can be sampled, stored and subsequently replayed as an anticipatory pattern of movement [Barnes and Paige, 2004; Barnes *et al.*, 2004; Bennett and Barnes, 2004; Barnes *et al.*, 2002; Barnes *et al.*, 2000; Barnes and Donelan, 1999; Wells and Barnes, 1999; Barnes and Grealy, 1992a; Barnes and Grealy, 1992b; Barnes and Asselman, 1991b; Barnes and Asselman, 1991a; Barnes and Ruddock, 1989; Barnes *et al.*, 1987; Barnes and Gresty, 1973].

Bahill and McDonald have offered similar insight, but employed a slightly different approach than Barnes et al., in that they incorporated non-sinusoidal periodic waveforms into their smooth pursuit tracking experiments. The main finding of their work is that subjects tracked target movement with near zero-latency and minimal position error within a ¼ cycle of initial exposure to sinusoidal and parabolic stimuli [Bahill and McDonald, 1983]. Performance on tracking tasks that involved target movement which had been generated by a cubic function, a sawtooth curve, or a pseudo-random sequence was noticeably worse. The authors claimed that subjects must have used some type of prediction in order to so quickly and accurately track the sinusoidal and parabolic movements – indeed, subjects hadn't even seen one half-cycle of these stimuli, but performed very well – and that this predictive capability was understandable since sinusoidal and parabolic motion are common in nature. Similarly, the authors argued that poor performance while tracking cubic, sawtooth, and pseudorandom waveforms was likely due to the fact that such movements are uncommon enough in the natural environment that our visual system lacked the opportunity or necessity to develop relevant predictive mechanisms.

In addition, a variety of similar studies have reported that the predictability of a moving visual stimulus affects the gain and phase of the smooth pursuit component of eye velocity [Larsby *et al.*, 1988; Collewijn and Tamminga, 1984; St. Cyr and Fender, 1969; Michael and

Melvill Jones, 1966]. Overall, there is ample evidence that the visual pursuit system utilizes prediction while tracking a target that is moving across the visual field. It is unclear, though, whether or not this mechanism, or something similar to it, might exist for visual motion detection that is unrelated to a pursuit task, such as the full-field oscillating optic flow visual stimulus that was utilized in the current study.

Predictability effects have also been observed outside of the visual domain. For example, Nelson et al. [Nelson *et al.*, 2004] reported that (1) motor responses to pure sinusoidal vibrotactile perturbations were faster and more accurate than responses to random perturbations; and that (2) both the amount and location of activation in the cerebral cortex were different between responses to these predictable and unpredictable stimuli. Based on these observations, the authors suggested that exposure to predictable stimuli caused subjects to rely less on sensory feedback and more on feedforward control.

In addition, it has already been suggested that the proposed predictive mechanism is distinct from the internal forward model that others have promoted [Blakemore and Sirigu, 2003; Wolpert *et al.*, 1998], in that the predictive capability of the proposed predictive mechanism is dependent on the particular characteristics of a stimulus, whereas the internal forward model instead uses a pre-existing (i.e. previously learned) input-output mapping for prediction. From this perspective, its plausible that these two mechanisms provide different functions for sensorimotor control. For example, the internal forward model affords the CNS a means of learning new sensory-motor mappings that can improve *long-term* sensorimotor performance.

In contrast, the proposed predictive mechanism cannot provide this learning benefit, and instead may serve the purpose of predicting future sensory inputs in order to improve *short-term* performance on sensorimotor tasks. As such, the internal forward model and the proposed predictive mechanism might provide complementary functionality to the CNS.

9.3 LIMITATIONS OF STUDY

9.3.1 SCENE MOVEMENT

Sum-of-sinusoids (SOS) may not have been the ideal stimulus choice for the current experimental paradigm. The SOS stimuli were chosen in order to expose subjects to spectrally similar optic flow that had different temporal characteristics. The potential problem with such stimuli, which contained component frequencies that are integer multiples of one another, is that they may evoke responses at harmonic frequencies due to nonlinear interactions among the sinusoidal components of the input [Victor and Shapley, 1980]. The current sway responses did in fact display behaviors which indicate that this type of harmonic response had occurred. For instance, there were numerous cases in which an optic flow stimulus containing multiple sinusoids (e.g. at 0.1Hz, 0.3Hz, and 0.5Hz) produced output power at non-stimulus harmonic frequencies outside the spectral range of typical postural responses (e.g. at 0.6Hz, 0.9Hz and 1.2Hz). Examples of this can be seen in Figure 9 (at 1.2Hz) and in Figure 21a (at 0.6Hz and 0.9Hz).

In seeking an alternative to the SOS signals, we had in fact attempted to create "predictable" and "unpredictable" scene movement in another way, but with only limited success [Musolino *et al.*,]. Specifically, scene motions were driven by "tone-in-noise" (TIN) time series' consisting of a ± 8cm single sinusoid (0.3Hz) combined with band-passed Gaussian white noise, at various signal-to-noise ratios (SNR): (1) single sinusoid, (2) 12 dB, (3) 6 dB, (4) 3 dB, (5) 0 dB, and (6) pure noise. We hypothesized that sway magnitude would decrease with SNR of the visual stimulus. The rationale was that as the sinusoidal component in the moving scene decreased (relative to noise), so too would the response elicited by the sinusoid. We also believed that a SNR threshold existed, below which subjects would no longer respond to the sinusoid. The results did not support this hypothesis. Subjects responded strongly to the sinusoid when presented in isolation, as expected, and in agreement with previous findings [Loughlin *et al.*, 1996; van Asten *et al.*, 1988]. However, the presence of noise in the visual stimulus, even when its relative power was 16 times less than that in the sinusoid (i.e. SNR of 12dB), produced sway responses that were significantly lower in magnitude and noticeably lacking a component at the stimulus frequency. In the absence of consistent and strong sway responses, it was not possible to draw conclusions regarding the influence of stimulus periodicity on postural sway responses. We therefore ruled out using such TIN stimuli, and instead utilized the SOS approach.

9.3.2 BNAVE ENVIRONMENT

Technical limitations limited the spatial resolution that could be achieved with the LCD projection system, and this caused jitter in some scene movements, particularly in the peripheral portion of the visual field during low frequency scene oscillations (i.e. 0.1Hz). In light of findings that have indicated postural sensitivity to peripheral optic flow [Stoffregen *et al.*, 1987; Jasko *et al.*,], this jitter may have influenced subjects in unintended ways.

Further, for trials in experiment #3 that included an object superimposed on the center of the bullseye, the object and bullseye did not move in perfect synchrony, such that there existed some amount of relative motion between the two. This too was the result of technical limitations in the BNAVE system. This may have provided useful feedback to subjects regarding relative motion between them and the scene, which has been identified as an important means by which the postural control system receives information regarding self-motion [Kelly *et al.*, 2005; Bronstein and Buckwell, 1997]. In this way, the slight lack of synchrony between the object and surrounding scene may have acted as an unintended source of useful visual information, that allowed subjects to minimize the destabilizing effects of oscillating optic flow field.

9.3.3 SMALL SAMPLE SIZES

We must take care in interpreting some of the current results, since they have been derived from relatively small sample sizes. For example, the significant differences observed between PSUM and NPSUM groups in experiment #1 were based on two trials of data for each of six subjects – that's a total of just twelve samples. Indeed, statistical power for this observation was approximately 0.45, well below the commonly accepted standard of 0.8. To remedy this, sample sizes for experiment #2 and experiment #3 were determined via a power analysis of the data from experiment #1. The results suggested that a sample size of at least n=15 was necessary to observe a 3db difference in stimulus-band power at 0.5Hz between the PSUM and NPSUM groups, at the p=0.05 level with statistical power of 0.8. Despite having met this recommended subject quota (i.e. n=20 for experiment #2, and n=16 for experiment #3), we were nevertheless still faced with issues of inadequate sample sizes because some of the key comparisons were carried out on a subset of the total subject pool. For example, the observation in experiment #2 that PSUM and NPSUM stimuli evoked different responses in visually DEP and INDEP subjects during initial exposure to optic flow, was based on data from only six of twenty total subjects. Moreover, the related findings regarding the sway adaptation parameters ‘A’ and ‘τ’ were likewise based on data for these same six subjects. To remedy this problem in future work, we must make an effort to design our experiment more appropriately.

9.3.4 ACCURACY OF ADAPTATION CURVE FITTING

The adaptation curve-fitting procedure that was performed in experiments #2 and #3 contained a certain level of subjectivity. The portion of the power-versus-time data series that was fit with an exponential decay curve was chosen manually. While it was relatively easy to determine where the maximal initial response occurred, it was not always clear when adaptation began. Likewise, choosing a point that accurately reflected the end of adaptation was challenging, especially in cases in which there appeared to be a secondary response (albeit often a transient one) following adaptation.

In addition, an exponential decay did not always accurately represent the experimental data, as evidenced by R^2 values as low as 0.5 (values on the high end approached 0.9). This information was not used to exclude parameters that had been obtained from poorly fit data, so even when R^2 indicated a poor fit, values for A and T were still extracted and included in group averages. We chose to use exponential decay for fitting purposes because it is a behavior commonly observed in natural processes. This, of course, does not guarantee that it was the right choice. Though our results suggest that adaptation is not necessarily accurately modeled as an exponential decay, it is important to note that the low R^2 values were due in large part to what were essentially transient outliers in the data. We attempted to circumvent this problem by utilizing power-versus-time data that had been smoothed via low pass filtering, but abandoned this approach once it became clear that the filtering process removed transients in the data that were in fact useful in determining beginning and ending points for the curve-fit.

9.4 FUTURE WORK

The series of experiments presented in this work have been a first attempt at uncovering experimental evidence of a predictive mechanism in the postural control system. While some interesting findings have been observed, they have often been based on only a small subset of the subject population. This has happened because during the course of testing we have discovered confounding factors that were unknown prior to the experiments, and therefore unaccounted for in the experimental design. From this perspective, this set of experiments has served as a useful first step in developing a more sound methodology for future experiments. Of primary importance for future work will be the accurate classification of subjects prior to data collection. For instance, the *a priori* separation of subjects based on visual dependency will make it easier to manipulate sample sizes to achieve a balanced experimental design, and will ensure that the effect of visual dependence does not confound the data. In addition, larger sample sizes will be required for studies that examine sway adaptation, as this behavior has been observed in only about 75% of the subject populations involved in this study.

Moreover, despite several interesting findings in this study, numerous questions remain unanswered. To list just a few examples: might sway adaptation be due to some mechanism other than sensory reweighting? Are the different responses to predictable and unpredictable stimuli necessarily due to a predictive mechanism in the CNS? Are the behaviors observed in this study unique to postural responses to visual stimuli, or might they be observed in other activities or evoked by stimuli in other sensory modalities? Such unknowns suggest potential areas of future inquiry, some of which are discussed below.

9.4.1 SWAY ADAPTATION DURING SWAY REFERENCED CONDITIONS

Sway referencing the floor on which a subject stands is a common method that is employed in postural studies aimed at examining sensory reweighting and its effects on postural stability. Sway referencing is thought to maintain the ankle angle at roughly 90 degrees during sway, and therefore to eliminate any proprioceptive feedback to the CNS that would normally occur when a subjects sways in the A-P direction. In the context of this study, the ability to remove proprioceptive feedback will allow us to examine sway adaptation during this altered condition. Since sensory reweighting has been implicated as a possible source of sway adaptation, especially during conditions of sensory conflict, it will useful to see how the lack of proprioceptive inputs influences sensory reweighting and subsequent adaptation. This type of data has in fact already been collected, during both experiments #1 and #2, but not yet analyzed.

9.4.2 STIMULUS-RESPONSE PHASE RELATIONSHIPS

Examination of the time-series data in this study clearly showed that when subjects responded to an optic flow stimulus, sway occurred predominantly at the driving frequency. In the case of the SOS stimuli, the increase in sway above quiet stance values was largest at the frequency corresponding to the highest frequency component of the stimulus. However, subjects exhibited various behaviors that suggested they were not phase-locked with the stimulus. Responses appeared to come in-and-out of phase throughout the trial, and in some cases exhibited abrupt reversals in phase. Also, there were transient responses in which subjects appeared to follow a stimulus closely for just a few seconds, as well as delayed responses in which sway responses first occurred many seconds after stimulus onset. Further, there was no apparent pattern to the phase behavior, which implies that there is a random aspect to the sway response, in the sense that it may never quite reach a steady state. An investigation of these phase relationships would be useful for several reasons. First, it may provide insight into the underlying processes governing postural control, in a manner similar to the work of Dijkstra et al. [Dijkstra *et al.*, 1994b; Dijkstra *et al.*, 1994a]. Second, it may offer another means of examining whether or not the proposed predictive mechanism behaves as we have suggested. For instance, it has already been shown that the temporal aspects of sway adaptation are different in response to periodic and non-periodic stimuli. Perhaps a similar difference exists in the timing of sway responses in general, such as smaller phase differences between response and stimulus during exposure to *periodic* optic flow. Examining sway responses in this manner would be useful in determining the validity of our hypotheses.

9.4.3 PREDICTION IN OTHER SENSORY MODALITIES

The current study reported per-stimulus declines in the amplitude of postural sway during exposure to predictable and unpredictable *visual* stimuli. To the best of our knowledge, similar findings have not yet appeared in the literature. However, others have provided evidence of adaptive postural responses to stimuli presented in *non-visual* sensory modalities, including the vestibular system via galvanic stimulation [Fransson *et al.*, 2003b; Johansson *et al.*, 2001b], and the proprioceptive system via vibratory stimulation of lower leg musculature [Fransson *et al.*, 2003b; Fransson *et al.*, 2003a; Fransson *et al.*, 2000]. Interestingly, these studies utilized unpredictable stimuli specifically in order to avoid predictive behavior on the part of subjects, but provided no evidence or rationale for this decision. These findings suggest that postural sway adaptation is not necessarily a visually-evoked phenomenon, and provide an impetus for future work aimed at exposing subjects to both predictable and unpredictable *non-visual* stimuli. One possibility would be to stimulate the proprioceptive system through active platform rotations (as opposed to passive platform rotations associated with sway-referencing). Peterka has utilized this approach in examining sway responses to pseudorandom (i.e. unpredictable) stimuli, but did not report any evidence of sway adaptation [Peterka, 2002]. Overall, these findings indicate that it would be useful to examine postural sway and sway adaptation during exposure to both predictable and unpredictable platform rotations, perhaps even in combination with the various visual perturbations and cognitive tasks that were utilized in the current study.

9.4.4 MATHEMATICAL MODEL SIMULATIONS

The work presented here was purely experimental in scope. Considering that the focal point of this study is a biologically-rooted sensorimotor process, it makes sense to have examined real world behaviors produced by this process. However, despite experimental observation having uncovered some intriguing findings, this approach is nevertheless limited in it's ability to identify causal mechanisms. Mathematical model simulations, on the other hand, are better suited to this task, and are a useful complement to experimentation. For this reason, we plan to utilize model simulations in order to quantitatively examine sensory reweighting in a manner that is not possible through experimentation. These simulations will use experimentally collected postural sway data to calculate values for the weight of the visual channel, a parameter which we have suggested is responsible for numerous experimentally observed behaviors.

We hope to determine whether or not the changes in visual channel weight that have been implicated as a contributing factor to sway adaptation can be accurately simulated by the model.

The simulations are based on the linearized inverted-pendulum postural feedback control model developed by Peterka [Peterka, 2002]. This model has been used to successfully simulate a wide variety of experimentally observed behaviors, including the stabilogram diffusion analysis of Collins & DeLuca [Peterka, 2000; Collins and De Luca, 1993], and sensory-reweighting [Peterka and Loughlin, 2004]. Based on these successful implementations, we are confident that Peterka's model is suitable for the current objective. This model was developed to produce system outputs (e.g. sway position as indicated by ankle angle in degrees), typically for comparison to experimentally observed sway. This process would help determine if the underlying model was accurate. For purposes of the current study, the model would be operate in an inverse sense, in that estimates of model parameters will be determined based on inputs and outputs fed to the model. That is, the model will be used to determine a set of model parameter values that best explains the observed input-output relationship. Parameters in the Peterka model include a channel weight for the graviceptive (W_g), proprioceptive (W_p), and visual (W_v) systems; values for the proportional (K_P), integral (K_I), and derivative (K_D) components of the neural PID controller; and a system time delay (Td).

Of particular interest for the current study is the value of the visual channel weight, W_v. The goal of the simulation process will be to calculate W_v based on the stimulus and response signals from each of the 288 trials (16 subjects x 9 trials/day x 2 days) that were performed, and to determine if these values for Wv are consistent with our hypotheses.

For example, if values for Wv turn out to be significantly lower for trials involving predictable stimuli compared to unpredictable stimuli, this would support the notion that a predictive mechanism contributed to reductions in visual channel weight.

9.4.5 SEATED TRACKING TASKS

The postural behaviors displayed in this study have been attributed to sensory re-weighting induced by a predictive mechanism within the CNS. However, the possibility exists that the current observations may instead have been the result of some learning effect, whereby subjects learned or memorized a stimulus pattern over time, and adapted their behavior accordingly. In order to investigate this possibility, a third testing visit was included in the experiment #3 protocol, during which subjects performed a seated tracking task that required them to mirror the same visual motions that they had seen previously while standing (see section 8.3.1 *Visual Scenes* for details), using a mouse controlled with their dominant hand. Subjects were not provided with real-time visual feedback regarding their tracking performance, and at the conclusion of the testing session were queried about their ability to identify patterns in the moving scenes. This experiment was designed to examine whether or not any type of learning was occurring during exposure to periodic and non-periodic oscillating optic flow. For example, improved tracking performance in response to periodic stimuli compared to non-periodic stimuli, especially during trials in which subjects claimed to have noticed a pattern in the visual scene movement, might be interpreted as evidence that subjects had learned this pattern and were therefore able to predict the movements that they had been asked to track. Improved tracking performance in cases when a subject was aware of the patterned movement would be considered an example of *explicit* learning, while improvements in the absence of such subject awareness might indicate *implicit* learning [Aizenstein *et al.*, 2004; Thornton and Fernandez-Duque, 2000]. Tracking task data has been collected for each of the sixteen subjects that participated in experiment #3. These data have not yet been analyzed, but in the future will be examined using the stimulus-response phase relationships described earlier in section 9.4.2.

Further, findings from this tracking task may help determine if the predictive effect that was observed during postural trials is unique to posture, or if instead it is a mechanism common to all visual sensorimotor control processes. For example, if predictive effects were also observed on the seated tracking task, this would suggest that prediction is a property of the visual system in general, and was observed within a postural context likely because standing subjects had been exposed to a visual stimulus.

In addition, Collins and Barnes have shown that working memory plays a role in storing velocity information about a moving visual stimulus, for use in subsequent prediction of that stimulus [Collins and Barnes, 2005]. A similar effect was reported in a non-visual capacity by Dave and Margolish, who found that sensorimotor vocal learning was guided by neural activity that uses long sensory memories for predictive purposes [Dave and Margoliash, 2000]. This raises the question of whether prediction, as it is believed to occur in the current experimental paradigm, is related to memory or simply to perception instead. For example, if the proposed predictive mechanism utilizes working memory in order to identify a pattern in a periodic stimulus (i.e. by storing several cycles of the stimulus), then we might expect a memory task to interfere with this process. If this were the case, then decrements in the effect of the proposed mechanism (e.g. slower adaptation rates) while performing a memory task would suggest that the predictive mechanism utilizes memory, and that the observed effects were the result of interference between the memory task and the postural task.

In general, the concept that memory may be required for sensory prediction suggests a potential future direction to pursue, namely to incorporate a memory task into the current experimental protocol.

9.4.6 EXAMINATIONS OF OLDER ADULTS AND PATIENT POPULATIONS

This study examined postural sway behaviors related to sensory reweighting in healthy young adults. There is evidence, however, that sensory reweighting may be influenced by both aging and disease, particularly during the performance of a concurrent cognitive task [Teasdale and Simoneau, 2001; Redfern *et al.*, 2001; Marsh and Geel, 2000; Shumway-Cook and Woollacott, 2000]. As such, it would be useful to perform the experiments described in this work on older adults and on individuals with certain sensory impairments, in order to determine if the influences of cognitive tasks and of the proposed predictive mechanism are manifested differently in these populations, compared to healthy young adults. For example, we might expect that sway adaptation would be slower in individuals with an impaired capacity for sensory reweighting.

9.5 KEY CONTRIBUTIONS

This study has provided several novel findings which are valuable from both research and clinical perspectives. First, the data have clearly shown that healthy young adults respond differently to periodic and non-periodic moving visual scenes. This finding provides evidence in support of the existence of a predictive component to postural control that can facilitate reweighting of sensory inputs during exposure to predictable moving visual scenes. While sensitivity to stimulus periodicity has been previously observed in studies of visual sensorimotor control [Kiemel *et al.*, 2002; Dijkstra *et al.*, 1994a; Lestienne *et al.*, 1977], the current observation that this phenomenon can apparently manifest itself in postural sway responses is a new and potentially useful finding (as discussed below in the final paragraph of this section).

Second, this study has revealed for the first time that the performance of a cognitive task during exposure to oscillating optic flow causes a *reduction* in postural sway responses, regardless of whether the task is presented in the auditory or visual modality. This observation is similar to that seen previously for the case of unperturbed spontaneous sway [Ehrenfried *et al.*, 2003; Dault *et al.*, 2001b; Dault *et al.*, 2001a; Teasdale and Simoneau, 2001; Vuillerme *et al.*, 2000; Fearing, 1924]. That such decreases in sway occur during concurrent cognitive tasks, regardless of whether or not a sensory perturbation exists, suggests that this postural behavior reflects a basic change in postural control to a strategy that is "tighter" [Dault *et al.*, 2001b; Dault *et al.*, 2001a] and perhaps less reliant on sensory feedback. Moreover, an interaction existed between this cognitive task effect and the aforementioned predictive effect, such that visual tasks produced lower sway in response to predictable visual stimuli, while auditory tasks had the opposite effect. Considering that visual cognitive tasks are known to enhance information processing in the visual system, this finding provides even further evidence that decreases in sway during exposure to predictable scenes is likely the result of a facilitated reduction in visual channel weight that is driven by the proposed predictive mechanism.

Third, a trial effect among responses to optic flow was observed, in which sway magnitude during initial exposure to optic flow was significantly larger than that during subsequent exposure to comparable stimuli. This effect was determined to be the result of a per-stimulus reduction in sway amplitude at the primary response frequency (i.e. "adaptation").

Moreover, the rate at which this adaptive behavior occurred was faster when the visual stimulus was predictable, indicating the adaptive process was likely being affected by the proposed predictive mechanism. Though such sway adaptation had been observed in a previous in-house study [Loughlin *et al.*, 1996], neither the trial effect nor it's connection to adaptation and/or predictive mechanisms have yet been reported in the literature.

Fourth, the relationship among prediction, adaptation and the trial effect discussed above was not the same in visually dependent and visually independent populations. Dependent subjects, who presumably are particularly reliant on visual information, exhibited markedly slower adaptation rates as compared to their independent counterparts. This behavior implied that the ability to reduce visual channel weight was impaired in individuals who depend heavily on vision for postural stability. This too was a finding that has not been reported previously.

These latter two findings have implications for the design of experiments involving exposure to optic flow. For example, the observation that visually dependent and visually independent subjects displayed markedly different behaviors suggests that classifying individuals according to visual dependency is necessary in order to eliminate the confounding influence of this effect. Similarly, experimenters who utilize the optic flow paradigm should take care to account for the type of trial effect that was observed in both experiment #2 and experiment #3, either through appropriate experimental design or through data analysis.

From a clinical perspective, some of the current findings may offer insight into treatment methods for patients suffering from specific balance disorders. One example is that of visual vertigo, a condition in which individuals who have increased visual dependence and difficulty in resolving conflict among visual, graviceptive and proprioceptive information experience dizziness in the presence of visual perturbations [Guerraz *et al.*, 2001]. Findings from a portion of the current study that examined sway behavior in such visually dependent subjects, under conditions that are known to induce sensory conflict, indicate that moving visual environments which contain a strong temporal pattern may have a potentially destabilizing effect in this population, while visual movements without such patterns may not be destabilizing. This observation may provide a means of improving clinical desensitization therapy which is aimed at mitigating the effects of visual vertigo.

10.0 CONCLUSIONS

This study examined postural sway responses in healthy young adults during exposure to periodic and non-periodic oscillating optic flow, in some cases coupled with a concurrent cognitive task, in an attempt to uncover experimental evidence of a predictive component to postural control. A series of three experiments produced several novel findings, including: (1) sway adaptation during initial exposure to oscillating optic flow; (2) improved sway performance in response to periodic stimuli compared to non-periodic stimuli, as indicated by significant decreases in both overall sway magnitude, and the time required for sway adaptation to occur; (3) a general reduction in sway during exposure to optic flow while performing a concurrent cognitive task; and (4) an interaction between the predictive mechanism and the cognitive task, such that visual tasks enhanced the influence of the predictive mechanism. Overall, these observations support the existence of a predictive component to postural control that can alter the dynamic reweighting of sensory inputs during exposure to predictable stimuli. These findings may have implications for the design of experiments involving optic flow stimuli, as well as for the treatment of individuals suffering from certain balance disorders.

BIBLIOGRAPHY

Agarwal GC and Gottlieb, GL . Mathematical modeling and simulation of the postural control loop--Part II. [Review] [374 refs]. *Critical Reviews in Biomedical Engineering* **11**[2]. 1984a.

Agarwal GC and Gottlieb, GL . Mathematical modeling and simulation of the postural control loop. Part III. [Review] [328 refs]. *Critical Reviews in Biomedical Engineering* **12**[1]. 1984b.

Aizenstein HJ, Stenger VA, Cochran J, Clark K, Johnson M, Nebes RD, and Carter CS (2004) Regional brain activation during concurrent implicit and explicit sequence learning. *Cereb Cortex* **14,** 199-208.

Alais D and Blake R (1999) Neural Strength of Visual Attention Gauged by Motion Adaptation. *Nature Neuroscience* **22,** 1015-1018.

Allum JH, Bloem. B.R., Carpenter, MG, Hulliger, M, and Hadders-Algra, M . Proprioceptive control of posture: a review of new concepts [Review]. *Gait & Posture* **8**, 214-242. 1998.

Bahill TA and McDonald JD (1983) Smooth Pursuit Eye Movements in Response to Predictable Target Motions. *Vision Research* **23,** 1573-1583.

Barin K . Evaluation of a generalized model of human postural dynamics and control in the sagittal plane. *Biological Cybernetics* **61**[1]. 1989.

Barnes GR and Gresty MA (1973) Characteristics of eye movements to targets of short duration. *Aerosp Med* **44,** 1236-40.

Barnes GR, Donnelly SF, and Eason RD (1987) Predictive velocity estimation in the pursuit reflex response to pseudo-random and step displacement stimuli in man. *J Physiol* **389,** 111-36.

Barnes GR and Ruddock CJ (1989) Factors affecting the predictability of pseudo-random motion stimuli in the pursuit reflex of man. *J Physiol* **408,** 137-65.

Barnes GR and Asselman PT (1991a) The assessment of predictive effects in smooth eye movement control. *Acta Otolaryngol Suppl* **481,** 343-7.

Barnes GR and Asselman PT (1991b) The mechanism of prediction in human smooth pursuit eye movements. *J Physiol* **439,** 439-61.

Barnes GR and Grealy MA (1992a) The role of prediction in head-free pursuit and vestibuloocular reflex suppression. *Ann N Y Acad Sci* **656,** 687-94.

Barnes GR and Grealy MA (1992b) Predictive mechanisms of head-eye coordination and vestibulo-ocular reflex suppression in humans . *J Vestib Res* **2,** 193-212.

Barnes GR and Donelan SF (1999) The remembered pursuit task: evidence for segregation of timing and velocity storage in predictive oculomotor control. *Exp Brain Res* **129,** 57-67.

Barnes GR, Barnes DM, and Chakraborti SR (2000) Ocular pursuit responses to repeated, single-cycle sinusoids reveal behavior compatible with predictive pursuit. *J Neurophysiol* **84,** 2340-55.

Barnes GR, Schmid AM, and Jarrett CB (2002) The role of expectancy and volition in smooth pursuit eye movements. *Prog Brain Res* **140,** 239-54.

Barnes GR, Collins CJ, and Arnold LR (2004) Predicting the duration of ocular pursuit in humans. *Exp Brain Res*.

Barnes GR and Paige GD (2004) Anticipatory VOR Suppression Induced by Visual and Nonvisual Stimuli in Humans. *J Neurophysiol* **92,** 1501-11.

Battaglia P, Jacobs R, and Aslin R (2003) Bayesian integration of visual and auditory signals for spatial localization. *J Opt Soc Am A* **20,** 1391-1397.

Bennett SJ and Barnes GR (2004) Predictive smooth ocular pursuit during the transient disappearance of a visual target. *J Neurophysiol* **92,** 578-90.

Blakemore SJ and Sirigu A (2003) Action prediction in the cerebellum and in the parietal lobe. *Exp Brain Res* **153,** 239-45.

Borger LL, Whitney, SL, Redfern, MS, and Furman, JM . The influence of dynamic visual environments on postural sway in the elderly. *Journal of Vestibular Research* **9**[3], 197-205. 1999.

Brandt T, Dichgans J, and Koenig E (1973) Differential Effects of Central versus Peripheral Vision on Egocentric and Exocentric Motion Perception. *Exp Brain Res* **23,** 471-489.

Breniere Y and Ribreau, C . A double-inverted pendulum model for studying the adaptability of postural control to frequency during human stepping in place. *Biological Cybernetics* **79**[4], 337-45. 1998.

Bronstein AM and Buckwell D (1997) Automatic control of postural sway by visual motion parallax. *Exp Brain Res* **113,** 243-8.

Cohen L and Posch T (1985) Positive Time-Frequency Disribution Functions. *IEEE Trans Acoust Speech Sig Proc* **ASSP-33,** 31-38.

Cohen L (1989) Time-Frequency Distributions -- A Review. *Proceedings of the IEEE* **77,** 941-981.

Collewijn H and Tamminga E (1984) Human Smooth and Saccadic Eye Movements During Voluntary Pursuit of Different Target Motions on Different Backgrounds. *J Physiol* **351,** 217-250.

Collins CJS and Barnes GR (2005) Scaling of smooth anticipatory eye velocity in response to sequences of discrete target movements in humans. *Experimental Brain Research* 404-413.

Collins JJ and De Luca, CJ . Open-loop and closed-loop control of posture: a random-walk analysis of center-of-pressure trajectories. *Experimental Brain Research* **95**[2], 308-18. 1993.

Creath R, Kiemel T, Horak F, and Jeka JJ (2002) Limited control strategies with the loss of vestibular function. *Exp Brain Res* **145,** 323-33.

Dault MC, Frank JS, and Allard F (2001a) Influence of a Visuo-spatial, Verbal and Central Executive Working Memory Task on Postural Control. *Gait & Posture* **14,** 110-116.

Dault MC, Geurts ACH, Mulder TW, and Duysens J (2001b) Postural Control and Cognitive Task Performance in Healthy Participants While Balancing on Different Support Surface Configurations. *Gait & Posture* **14,** 248-255.

Dave AS and Margoliash, D . Song Replay During Sleep and Computational Rules for Sensorimotor Vocal Learning. *Science* **290**, 812-816. 2000.

Davidson PR, Jones, RD, Andreae, JH, and Sirisena, HR . Simulating closed- and open-loop voluntary movement: a nonlinear control-systems approach. *IEEE Transactions on Biomedical Engineering* **49**[11], 1242-52. 2002.

Day BL, Guerraz M, and Cole J (2002) Sensory interactions for human balance control revealed by galvanic vestibular stimulation. *Adv Exp Med Biol* **508,** 129-37.

Day BL and Cole J (2002) Vestibular-evoked postural responses in the absence of somatosensory information. *Brain* **125,** 2081-8.

de Vlugt E, van der Helm, FC, Schouten, AC, and Brouwn, GG . Analysis of the reflexive feedback control loop during posture maintenance. *Biological Cybernetics* **84**[2], 133-41. 2001.

Deneve S and Pouget A (2004) Bayesian multisensory integration and cross-modal spatial links. *Journal of Physiology - Paris* **98,** 249-258.

Dichgans J and Brandt T (1978) Visual-vestibular interaction: effects on self-motion perception and postural control. In *Handbook of Sensory Physiology* (Edited by Held R., Leibowitz H., and Teuber H.) Springer, Berlin Heidelberg New York.

Dijkstra TM, Schoner G, Giese MA, and Gielen CC (1994a) Frequency dependence of the action-perception cycle for postural control in a moving visual environment: relative phase dynamics. *Biol Cybern* **71,** 489-501.

Dijkstra TM, Schoner, G, and Gielen, CC . Temporal stability of the action-perception cycle for postural control in a moving visual environment. *Experimental Brain Research* **97**[3], 477-86. 1994b.

Ehrenfried T, Guerraz M, Thilo KV, Yardley L, and Gresty MA (2003) Posture and mental task performance when viewing a moving visual field. *Cogn Brain Res* **17,** 140-53.

Ernst M and Bulthoff H (2004) Merging the senses into a robust percept. *TRENDS in Cognitive Sciences* **8,** 162-169.

Fearing FS (1924) An Experimental Study of the Effect of Controlled and Uncontrolled Attention Upon Sway. *Comparative Psychology* **v,** 1-24.

Felisberti F and Zanker JM (2005) Attention Modulates Perception of Transparent Motion. *Vision Research* **45,** 2587-2599.

Fernandez-Duque D and Johnson ML (2002) Cause and Effect Theories of Attention: The Role of Conceptual Metaphors. *Review of General Psychology* **6,** 153-165.

Fitzpatrick R, Burke D, and Gandevia SC (1996) Loop gain of reflexes controlling human standing measured with the use of postural and vestibular disturbances. *J Neurophysiol* **76,** 3994-4008.

Fransson P, Johansson R, Hafstrom A, and Magnusson M (2000) Methods for evaluation of postural control adaptation. *Gait Posture* **12,** 14-24 .

Fransson PA, Johansson R, Tjernstrom F, and Magnusson M (2003a) Adaptation to vibratory perturbations in postural control. *IEEE Eng Med Biol Mag* **22,** 53-7.

Fransson PA, Hafstrom A, Karlberg M, Magnusson M, Tjader A, and Johansson R (2003b) Postural control adaptation during galvanic vestibular and vibratory proprioceptive stimulation. *IEEE Trans Biomed Eng* **50,** 1310-9.

Fukuoka Y, Tanaka, K, Ishida, A, and Minamitani, H . Characteristics of visual feedback in postural control during standing. *IEEE Transactions on Rehabilitation Engineering* **7**[4], 427-34. 1999.

Gibson J (1958) Visually Controlled Locomotion and Visual Orientation in Animals. *Br J Psychol* **49,** 182-194.

Guerraz M, Yardley L, Bertholon P, Pollak L, Rudge P, Gresty MA, and Bronstein AM (2001) Visual Vertigo: Symptom Assessment, Spatial Orientation and Postural Control. *Brain* **124,** 1646-1656.

Hay L and Redon, C . Feedforward versus feedback control in children and adults subjected to a postural disturbance. *Experimental Brain Research* **125**, 153-162. 1999.

Hlavacka F, Mergner, T, and Krizkova, M . Control of the body vertical by vestibular and proprioceptive inputs. *Brain Research Bulletin* **40**[5-6], 431-4; discussion 434-5. 1996.

Isableu B, Ohlmann, T, Cremieux, J, and Amblard, B . Selection of spatial frame of reference and postural control variability. *Experimental Brain Research* **114**, 584-589. 1997.

Isableu B, Ohlmann T, Cremieux J, and Amblard B (1998) How dynamic visual field dependence-independence interacts with the visual contribution to postural control. *Human Movement Science* **17,** 367-391.

Ishida A, Imai S, and Fukuoka Y (1997) Analysis of the posture control system under fixed and sway-referenced support conditions. *IEEE Trans Biomed Eng* **44,** 331-6.

Jacobson J, Redfern MS, Furman JM, Whitney SL, Sparto PJ, Wilson JB, and Hodges LF (2001) Balance NAVE; A Virtual Reality Facility for Research and Rehabilitation of Balance Disorders. In *Proceedings of the Virtual Reality Software and Technology Meeting*.

Jasko J, Loughlin P, Redfern M, and Sparto P The Role of Central and Peripheral Vision in the Control of Upright Posture During Anterior-Posterior Optic Flow. In *Proceedings of the 27th Annual Meeting of the American Society of Biomechanics*.

Jeka JJ, Oie, KS, and Kiemel, T . Multisensory information for human postural control: integrating touch and vision. *Experimental Brain Research* **134**[1], 107-25. 2000.

Johansson R, Magnusson M, and Akesson M (1988) Identification of human postural dynamics. *IEEE Trans Biomed Eng* **35,** 858-69.

Johansson R, Magnusson M, Fransson PA, and Karlberg M (2001a) Multi-stimulus multi-response posturography. *Math Biosci* **174,** 41-59.

Johansson R, Fransson PA, and Magnusson M (2001b) Identification of Adaption in Human Postural Control Using GARCH Models. In *Proceedings of the 40th IEEE Conference on Decision and Control*.

Kelly JW, Loomis JM, and Beall AW (2005) The Importance of Perceived Relative Motion in the Control of Posture. *Experimental Brain Research* **161,** 285-292.

Kiemel T, Oie KS, and Jeka JJ (2002) Multisensory fusion and the stochastic structure of postural sway. *Biol Cybern* **87,** 262-77.

Kording KP and Wolpert DM (2004) Bayesian integration in sensorimotor learning. *Nature* **427,** 244-7.

Kuo AD (1995) An optimal control model for analyzing human postural balance. *IEEE Trans Biomed Eng* **42,** 87-101.

Lankheet MJ and Verstraten FA (1995) Attentional Modulation of Adaptation to Two-component Transparent Motion. *Vision Research* **35,** 1401-1412.

Larsby B, Thell J, Moller C, and Odkvist L (1988) The effect of stimulus predictability and age on human tracking eye movements. *Acta Otolaryngol* **105,** 21-30.

Lee D and Aronson E (1974) Visual Proprioceptive Control of Standing Human Infants. *Perception Psychophys* **15,** 529-532.

Lee D and Lishman J (1975) Visual Proprioceptive Control of Stance. *J Human Movement Studies* **1,** 87-95.

Lestienne F, Soechting J, and Berthoz A (1977) Postural readjustments induced by linear motion of visual scenes. *Exp Brain Res* **28,** 363-84.

Loughlin PJ, Redfern, MS, and Furman, JM . Time-varying characteristics of visually induced postural sway. [Review] [36 refs]. *IEEE Transactions on Rehabilitation Engineering* **4**[4], 416-24. 1996.

Loughlin PJ and Redfern, MS . Spectral characteristics of visually induced postural sway in healthy elderly and healthy young subjects. *IEEE Transactions on Neural Systems & Rehabilitation Engineering* **9**[1], 24-30. 2001.

Loughlin PJ, Redfern, MS, and Furman, JM . Nonstationarities of postural sway.[erratum appears in IEEE Eng Med Biol Mag. 2003 May-Jun;22(3):14]. [Review] [53 refs]. *IEEE Engineering in Medicine & Biology Magazine* **22**[2], 69-75. 2003.

Loughlin P, Pitton J, and Atlas L (1994) Construction of Positive Time-Frequency Distributions. *IEEE Trans Sig Proc* **42,** 2697-2705.

Mahboobin A, Loughlin PJ, Redfern MS, and Sparto PJ (2005) Sensory re-weighting in human postural control during moving scene perturbations. *Experimental Brain Research* **167,** 260-267.

Maki BE, Holliday, PJ, and Fernie, GR . A posture control model and balance test for the prediction of relative postural stability. *IEEE Transactions on Biomedical Engineering* **34**[10]. 1987.

Marsh AP and Geel SE (2000) The Effect of Age on the Attentional Demands of Postural Control. *Gait & Posture* **12,** 105-113.

Maurer C, Mergner, T, Bolha, B, and Hlavacka, F . Vestibular, visual, and somatosensory contributions to human control of upright stance. *Neuroscience Letters* **281**[2-3], 99-102. 2000.

Mergner T, Maurer C, and Peterka RJ (2002) Sensory contributions to the control of stance: a posture control model. *Adv Exp Med Biol* **508,** 147-52.

Mergner T, Maurer C, and Peterka RJ (2003) A multisensory posture control model of human upright stance. *Prog Brain Res* **142,** 189-201.

Michael J and Melvill Jones G (1966) Dependence of Visual Tracking Capability on Stimulus Predictability. *Vision Res* **6,** 707-716.

Morasso PG and Schieppati, M . Can muscle stiffness alone stabilize upright standing? *Journal of Neurophysiology* **83**, 1622-1626. 1999.

Musolino MC, Loughlin PJ, and Redfern MS Effects of 'Tone-in-Noise' Moving Visual Scenes on Postural Sway. In *The 26th Annual Meeting of the American Society of Biomechanics*.

Musolino MC, Loughlin PJ, Sparto PJ, and Redfern MS Postural Sway Adaptation During Initial Exposure to Periodic and Non-Perioidic Optic Flow. In *The 29th Annual Meeting of the American Society of Biomechanics*.

Musolino MC, Loughlin PJ, Sparto PJ, and Redfern MS (2006) Spectrally Similar Periodic and Non-periodic Optic Flows Evoke Different Postural Responses. *Gait & Posture* **23,** 180-188.

Nashner LM . Vestibular postural control model. *Kybernetik* **10**[2]. 1972.

Nelson A, Staines W, and McIlroy W (2004) Tactile Stimulus Predictability Modulates Activity in a Tactile-Motor Cortical Network. *Exp Brain Res* **154,** 22-32.

Nyborg H (1974) A method for analysing performance in the rod-and-frame test. I. *Scand J Psychol* **15,** 119-123.

Oie KS, Kiemel T, and Jeka JJ (2001) Human multisensory fusion of vision and touch: detecting non-linearity with small changes in the sensory environment. *Neurosci Lett* **315,** 113-6.

Oie KS, Kiemel T, and Jeka JJ (2002) Multisensory fusion: simultaneous re-weighting of vision and touch for the control of human posture. *Brain Res Cogn Brain Res* **14,** 164-76.

Oppenheimer A and Schafer R (1975) *Digital Signal Processing*. Prentice-Hall International, London.

Pavlik AE, Inglis, JT, Lauk, M, Oddsson, L, and Collins, JJ . The effects of stochastic galvanic vestibular stimulation on human postural sway. *Experimental Brain Research* **124**[3], 273-80. 1999.

Pellionisz AJ and Ramos, CF . Geometrical approach to neural net control of movements and posture. [Review] [64 refs]. *Progress in Brain Research* **97**, 245-56. 1993.

Peterka RJ and Benolken, MS . Role of somatosensory and vestibular cues in attenuating visually induced human postural sway. *Experimental Brain Research* **105**[1], 101-10. 1995.

Peterka RJ . Postural control model interpretation of stabilogram diffusion analysis. *Biological Cybernetics* **82**[4], 335-43. 2000.

Peterka RJ (2002) Sensorimotor integration in human postural control. *J Neurophysiol* **88,** 1097-118.

Peterka RJ (2003) Simplifying the complexities of maintaining balance. *IEEE Eng Med Biol Mag* **22,** 63-8.

Peterka RJ and Loughlin PJ (2004) Dynamic regulation of sensorimotor integration in human postural control. *J Neurophysiol* **91,** 410-23.

Prieto T, Myklebust J, Hoffmann R, Lovett E, and Myklebust BM (1996) Measures of Postural Steadiness: Differences Between Healthy Young and Elderly Adults. *IEEE Trans Biomed Eng* **43,** 956-966.

Redfern MS, Jennings JR, Martin C, and Furman JM (2001) Attention influences sensory integration for postural control in older adults. *Gait Posture* **14,** 211-6.

Ress D, Backus BT, and Heeger DJ (2000) Activity in Primary Visual Cortex Predicts Performance in a Visual Detection Task. *Nature Neuroscience* **3,** 940-945.

Sanders AF (1997) A Summary of Resource Theories from a Behavioral Perspective. *Biological Psychology* **45,** 5-18.

Schoner G, Kopecz K, Spengler F, and Dinse HR (1992) Evoked oscillatory cortical responses are dynamically coupled to peripheral stimuli. *Neuroreport* **3,** 579-82.

Schumann T, Redfern, MS, Furman, JM, el-Jaroudi, A, and Chaparro, LF . Time-frequency analysis of postural sway. *Journal of Biomechanics* **28**[5], 603-7. 1995.

Shumway-Cook A and Woollacott M (2000) Attentional Demands and Postural Control: The Effect of Sensory Context. *Journal of Gerontology: MEDICAL SCIENCES* **55A,** M10-M16.

St. Cyr G and Fender D (1969) Nonlinearities of the Human Oculomotor System: Time Delays. *Vision Res* **9,** 1491-1503.

Stein BE (1998) Neural Mechanisms for Synthesizing Sensory Information and Producing Adaptive Behaviors. *Experimental Brain Research* **123,** 124-135.

Stoffregen TA . Flow structure versus retinal location in the optical control of stance. *Journal of Experimental Psychology: Human Perception & Performance* **11**[5], 554-65. 1985.

Stoffregen TA (1986) The role of optical velocity in the control of stance. *Percept Psychophys* **39,** 355-60.

Stoffregen TA, Schmuckler, MA, and Gibson, EJ . Use of central and peripheral optical flow in stance and locomotion in young walkers. *Perception* **16**[1], 113-9. 1987 .

Strogatz SH and Stewart, I . Coupled oscillators and biological synchronization. [Review] [5 refs]. *Scientific American* **269**[6], 102-9. 1993.

Teasdale N and Simoneau M (2001) Attentional Demands for Postural Control: the Effects of Aging and Sensory Reintegration. *Gait & Posture* **14,** 203-210.

Thornton IM and Fernandez-Duque D (2000) An implicit measure of undetected change. *Spat Vis* **14,** 21-44.

Tombu M and Jolicoeur P (2002) All-or-none Bottleneck versus Capacity Sharing Accounts of the Psychological Refractory Period Phenomenon. *Psychological Research* **66,** 274-286.

Treue S and Maunsell JH (1996) Attentinal Modulation of Visual Motion Processing in Cortical Areas MT and MST. *Nature* **382,** 539-541.

van Asten WN, Gielen CC, and Denier van der Gon JJ (1988) Postural adjustments induced by simulated motion of differently structured environments. *Exp Brain Res* **73,** 371-83.

van der Kooij H, Jacobs, R, Koopman, B, and Grootenboer, H . A multisensory integration model of human stance control. *Biological Cybernetics* **80**[5], 299-308. 1999.

van der Kooij H, Jacobs, R, Koopman, B, and van der Helm, F . An adaptive model of sensory integration in a dynamic environment applied to human stance control. *Biological Cybernetics* **84**[2], 103-15. 2001.

Victor J and Shapley R (1980) A Method of Nonlinear Analysis in the Frequency Domain. *Biophys J* **29,** 459-484.

Vuillerme N, Nougier V, and Teasdale N (2000) Effects of a Reaction Time Task on Postural Control in Humans. *Neuroscience Letters* **291,** 77-80.

Wells SG and Barnes GR (1999) Predictive smooth pursuit eye movements during identification of moving acuity targets. *Vision Res* **39,** 2767-75.

Werness SA and Anderson, DJ . Parametric analysis of dynamic postural responses. *Biological Cybernetics* **51**[3]. 1984.

Winter DA, Patla, AE, Prince, F, Ishac, M, and Gielo-Perczak, K . Stiffness control of balance in quiet standing. *Journal of Neurophysiology* **80**[3], 1211-21. 1998.

Winter DA, Patla, AE, Rietdyk, S, and Ishac, MG . Ankle muscle stiffness in the control of balance during quiet standing. *Journal of Neurophysiology* **85**[6], 2630-3. 2001.

Wolpert DM, Miall RC, and Kawato M (1998) Internal models in the cerebellum [Review]. *Trends in Cognitive Sciences* **2,** 338-347.

Yang JF, Winter, DA, and Wells, RP . Postural dynamics in the standing human. *Biological Cybernetics* **62**[4]. 1990.

Zupan L, Merfeld D, and Darlot C (2002) Using sensory weighting to model the influence of canal, otolith and visual cues on spatial orientation and eye movements. *Biological Cybernetics* **86,** 209-230.