

Copyright

by

**TARA MELAINE RUTTLEY**

**2007**

**The Dissertation Committee for Tara Melaine Ruttley Certifies that this is the approved version of the following dissertation:**

**THE ROLE OF BODY LOAD-REGULATING MECHANISMS IN GAZE  
STABILIZATION DURING LOCOMOTION**

**Committee:**

---

Jacob J. Bloomberg, Ph.D., Supervisor

---

Ronita L. Cromwell, Ph.D.

---

Galen D. Kaufman, D.V.M., Ph.D.

---

Golda A. Kevetter-Leonard, Ph.D

---

Ajitkumar Mulavara, Ph.D.

---

**Dean's Signature**

**THE ROLE OF BODY LOAD-REGULATING MECHANISMS IN GAZE  
STABILIZATION DURING LOCOMOTION**

**by**

**Tara Melaine Ruttley, B.S., M.S.**

**Dissertation**

Presented to the Faculty of the Graduate School of

The University of Texas Medical Branch

in Partial Fulfillment

of the Requirements

for the Degree of

**Doctor of Philosophy**

**The University of Texas Medical Branch**

**February, 2007**

## **Dedication**

*“We choose to go to the moon in this decade and do the other things, not because they are easy, but because they are hard, because that goal will serve to organize and measure the best of our energies and skills, because that challenge is one that we are willing to accept, one we are unwilling to postpone, and one which we intend to win, and the others, too.”*

*-John Fitzgerald Kennedy*

## **Acknowledgements**

Surprisingly, this is probably the toughest piece of this dissertation for me to write, simply because I am terrible at properly expressing my gratitude to all of the people who have supported me throughout obtaining this degree. Foremost, I absolutely must thank my husband, who has been at my side for eighteen years and shares everything with me, including an interest in this study. His support and love has helped make me the person I am today. Thank you to my mom and dad who have supported my decisions to continue my education over and over, wondering when it will all end. I would like to thank my mentor, Dr. Jacob Bloomberg for his patience, guidance and time spent with me on this project, which was above and beyond any previous experiences I have had with a mentor. A special, sincere gratitude to my committee members: Drs. Ronita Cromwell, Galen Kaufman, Golda Leonard, and Ajitkumar Mulavara, for taking a true interest in ensuring that my research was a learning experience of quality value, and for support beyond what I believe is expected of committee members. I would like to acknowledge the members of the Bloomberg laboratory for teaching me techniques, offering advice, and sharing a love for the space program over the past 3 years. I truly cannot find the words to properly thank my management at the Johnson Space Center, especially my Branch Chief Lisa Hammond, for supporting my intense school schedule and my rants about stressful school and work schedule because you believed in my education. Thanks to the Neuroscience and Cell Biology Department for their support over the years. To everyone else, I couldn't possibly list here...I hope you know who you are.

**THE ROLE OF BODY LOAD-REGULATING MECHANISMS IN GAZE  
STABILIZATION DURING LOCOMOTION**

Publication No. \_\_\_\_\_

Tara Melaine Ruttley, PhD.

The University of Texas Medical Branch, 2007

Supervisor: Jacob J. Bloomberg

The whole body acts as a gaze stabilization system: head-torso activity and lower body movement are coordinated to provide a stable retinal image during locomotion. Body loading is a fundamental parameter that modulates motor output during locomotion, and is especially important for controlling the generation of stepping patterns, dynamic balance, and termination of locomotion. Increased body weight support (BWS) during locomotion results in an immediate reorganization of locomotor control, such as a reduction in stance and double support duration and decreased hip, ankle, and knee angles during the gait cycle. Until now, no studies have investigated how gaze control systems respond to adaptive modification in the body load sensing system. The goal of this research is to determine the role of body load-regulating mechanisms in gaze control during locomotion. The general hypothesis behind the proposed research is that body load-regulating mechanisms contribute to gaze stabilization, and adaptive changes in these load-regulating mechanisms will require reorganization in the full-body gaze control system so that visual acuity can be maintained during locomotion.

To support the hypothesis of this study, head-torso coordination, lower limb movement patterns, and gait cycle timing were evaluated before and after a 30-minute adaptation session during which subjects walked on a treadmill at 5.4 km/hr with 40% body weight support (BWS). Before and after the adaptation period, head-torso and lower limb 3D kinematic data were obtained during locomotion using a video-based motion analysis system, and gait cycle timing parameters were collected by foot switches positioned under the heel and toe of the subjects' shoes. The predominant changes observed in the subjects were a result of adaptive modification in the body load-regulating mechanisms and included increased head movements, increased knee and ankle flexion, and increased stance, stride, and double support time, with no change in dynamic visual acuity. Therefore, it is evident that just 30 minutes of 40% BWS during locomotion was enough sensory conflict to induce adaptive modifications in the sensory systems that contribute to locomotor control, and these modifications represent an overall reorganization of vestibular-somatosensory interactions in the full-body integrated gaze stabilization system.

# Table of Contents

<b>List of Tables .....</b>	<b>xi</b>
<b>List of Figures.....</b>	<b>xii</b>
<b>Chapter 1: Introduction</b>	<b>1</b>
1.1 Background and Significance .....	1
The Role of Load in Posture and Locomotor Control .....	1
Effects of Load Adaptation on Motor Systems.....	9
Full-Body Contribution to Gaze Control During Locomotion ...	12
Vestibular - Somatosensory Interactions .....	20
1.2 Specific Aims.....	24
Specific Aim I.....	24
Specific Aim II:.....	25
Specific Aim III: .....	26
<b>Chapter 2: Materials and Methods</b>	<b>27</b>
2.1 Subjects.....	27
2.2 Testing Conditions.....	27
Integrated Treadmill Locomotion Protocol .....	27
Adaptation Protocol .....	28
2.3 Data Collection .....	29
Dynamic Visual Acuity (DVA) .....	29
Kinematics .....	33
Gait Cycle Timing.....	34
2.4 Data Analysis.....	37
Dynamic Visual Acuity (DVA) .....	37
Kinematics .....	38
Measuring Head Reflexive Control Mechanisms.....	38
Measuring Total Movement At Heel Strike.....	39
Gait Cycle Timing.....	40
2.5 Statistical Analyses .....	45

Sample Size.....	45
Data Analysis.....	45
<b>Chapter 3: Results</b>	<b>48</b>
3.1 Dynamic Visual Acuity.....	48
3.2 Changes in the Head Reflexive Control Bandwidths .....	48
3.3 Total Movement Changes in the Heel Strike Window .....	66
Upper Body Changes.....	66
Lower Body Changes.....	71
3.4 Changes in Gait Cycle Timing.....	75
3.5 Variable Relationships.....	80
3.6 Summary of Results.....	86
<b>Chapter 4: Discussion</b>	<b>88</b>
4.1 Specific Aim I: Prolonged BWS Locomotion Causes Adaptive Modification of Body Load Sensing Mechanisms That Alter Head Reflexive Control and Torso Movement.....	91
Prolonged BWS Locomotion Results in Hyperresponsive Vestibular Activity .....	91
Torso Movement Changes are Indicative of Altered Vestibular Activity .....	96
4.2 Specific Aim II: Prolonged BWS Locomotion Causes Adaptive Modification of Body Load Sensing Mechanisms That Alter Lower Body Kinematics .....	98
Adaptive Modification of Body Load Sensing Mechanisms Causes Changes in Lower Limb Coordination that may Aid in Gaze Stabilization .....	98
4.3 Specific Aim III: Prolonged BWS Locomotion Causes Adaptive Modification of Body Load Sensing Mechanisms That Alter Gait Cycle Timing.....	100
Adaptation of Body Load Sensors During BWS Locomotion Induces Changes in Stability Requirements.....	101
4.4 Adaptive Recovery.....	102
4.5 Vestibular – Somatosensory Convergence .....	104
4.6 Caveats and Forward Work .....	110
4.7 Conclusions.....	113

**References**

**115**

**VITA**

**127**

## List of Tables

<b>Table 2.3.1. Kinematic Markers and Locations.</b> .....	36
<b>Table 3.5.1. Pearson Correlations Between Movements</b> .....	82
<b>Table 3.5.2. Pearson Correlations Between Movements and Gait Cycle Timing</b> .....	84
<b>Table 3.5.3. Pearson Correlations Between Movements in Heel Strike Window</b> .....	85
<b>Table 3.6.1. Summary of Changes following 30 min of 40% BWS.</b> .....	87

## List of Figures

<b>Figure 1.1.1. Multiple Sensory Systems Contribute to Gaze Control and Locomotion.</b> .....	2
<b>Figure 1.1.2 Compensatory Head Pitch Movements.</b> .....	13
<b>Figure 1.1.3. The Integrated Gaze Stabilization System</b> .....	19
<b>Figure 2.2.1. Laboratory Treadmill Configurations</b> .....	31
<b>Figure 2.3.1. Dynamic Visual Acuity Assessment (DVA) display</b> .....	32
<b>Figure 2.3.2. Kinematic Marker Placement.</b> .....	35
<b>Figure 2.3.3. Foot-switch.</b> .....	37
<b>Figure 2.4.1. Motion Capture and Analysis</b> .....	41
<b>Figure 2.4.2. Example of Frequency Analysis</b> .....	42
<b>Figure 2.4.3. Knee and Ankle Movement Waveforms</b> .....	43
<b>Figure 2.4.4. Gait Cycle Waveform</b> .....	44
<b>Figure 3.1.1. DVA Results</b> .....	49
<b>Figure 3.2.1. Waveforms of Torso Translation and Head Pitch Movement</b> .....	50
<b>Figure 3.2.2. Fourier Amplitude Spectra of Head Pitch Movement</b> .....	50
<b>Figure 3.2.3. Head Movement re Space</b> .....	52
<b>Figure 3.2.4. Head Pitch re Space Percent-Change Curves</b> .....	53
<b>Figure 3.2.5. Head Roll re Space Percent-Change Curves</b> .....	54
<b>Figure 3.2.6. Head Yaw re Space Percent-Change Curves</b> .....	55
<b>Figure 3.2.7. Vertical Torso Translation</b> .....	58
<b>Figure 3.2.8. Torso Movement re Space</b> .....	59
<b>Figure 3.2.9. Head Movement re Torso.</b> .....	60

<b>Figure 3.2.10. Head re Torso Pitch Percent-Change Curves</b> .....	61
<b>Figure 3.2.11. Head re Torso Roll Percent-Change Curves</b> .....	62
<b>Figure 3.2.12A. Head re Torso Yaw Percent-Change Curves (Increases)</b> .....	63
<b>Figure 3.2.12B. Head re Torso Percent-Change Curves (Decreases)</b> .....	64
<b>Figure 3.2.13. Head Pitch Cross Correlation Values</b> .....	65
<b>Figure 3.3.1. Total Upper Body Movements in Heel Strike Window</b> .....	67
<b>Figure 3.3.2. Head Pitch in Heel Strike Window Percent-Change Curve</b> .....	68
<b>Figure 3.3.3. Total Torso Pitch in Heel Strike Window Percent-Change Curve</b> .....	69
<b>Figure 3.3.4. Torso Translation in Heel Strike Window Percent-Change Curve</b> .....	70
<b>Figure 3.3.5. Knee Flexion Total Movement</b> .....	72
<b>Figure 3.3.6. Ankle Flexion Total Movement</b> .....	72
<b>Figure 3.3.7. Total Knee Movement Percent-Change Curves</b> .....	73
<b>Figure 3.3.8. Total Ankle Movement Percent-Change Curves</b> .....	74
<b>Figure 3.4.1. Gait Cycle Timing Changes</b> .....	76
<b>Figure 3.4.2. Stride Time Percent-Change Curves</b> .....	77
<b>Figure 3.4.3. Double Support Time Percent-Change Curves</b> .....	78
<b>Figure 3.4.4. Stance Time Percent-Change Curves</b> .....	79
<b>Figure 3.5.1. Head Pitch – Torso Pitch Linear Regression Plots</b> .....	83
<b>Figure 3.5.2. Head Pitch – Torso Vertical Translation Linear Regression Plots</b> .....	83
<b>Figure 3.5.3. Knee Movement – Stance Time Linear Regression Plots</b> .....	85
<b>Figure 3.5.4. Ankle Total Movement – Torso Translation at Heel Strike Linear Regression Plots</b> .....	86

# CHAPTER 1: INTRODUCTION

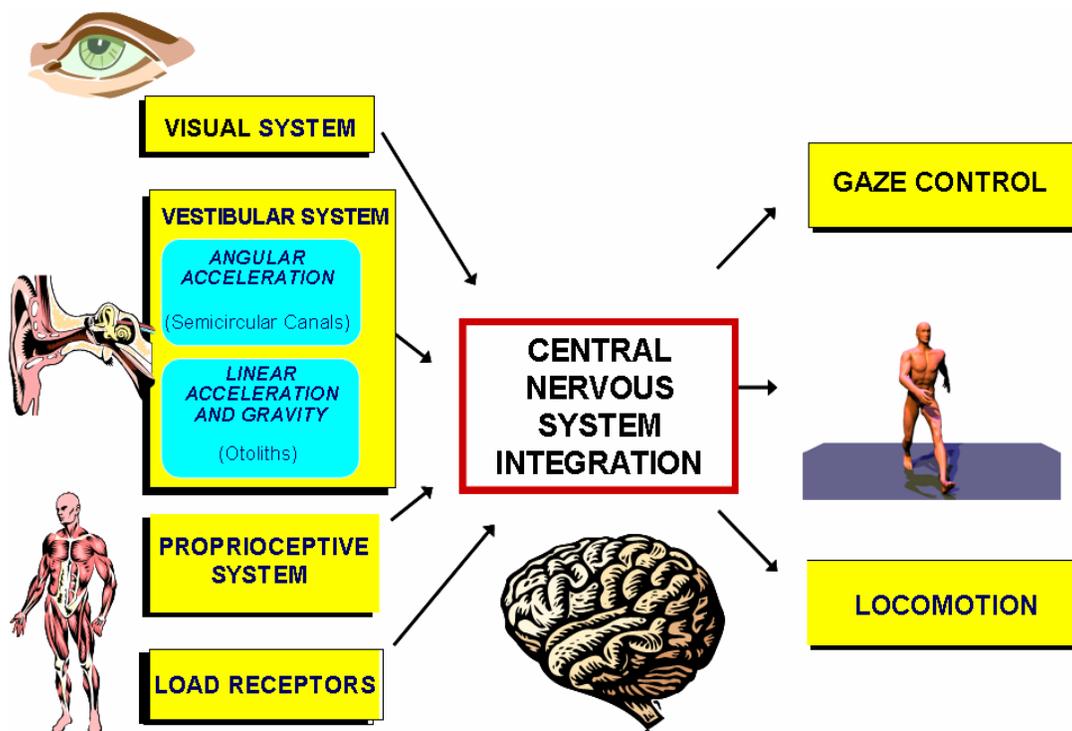
## 1.1 BACKGROUND AND SIGNIFICANCE

A particularly important somatosensory component for locomotor control is that of body load sensing. Although several studies have identified the role of body load in human locomotor control, none have investigated how body load mechanisms contribute to the control of gaze. In addition, no studies have investigated how locomotion and gaze control systems respond to *adaptive modification* in body load as an independent modulator of proprioceptive input. The purpose of this study was to determine the role of body load-regulating mechanisms in gaze control during locomotion. Results of this study will contribute to the fundamental research that seeks to elucidate the role of load-regulating mechanisms in gaze stabilization and locomotor control; the development of rehabilitation protocols that use unloading devices as retraining strategies (spinal cord injury, brain injury, stroke); and the methods used to improve astronaut post-flight health and safety, as well as an understanding of mechanisms responsible for post-flight locomotor dysfunction.

### *The Role of Load in Posture and Locomotor Control*

During locomotion, two goals must be met: maintaining stable forward translation, and maintaining gaze (McDonald et al. 1997). To achieve this goal, sensory inputs from the visual, vestibular, and proprioceptive systems are integrated within the central nervous system (CNS) (Figure 1.1.1). Load receptors that regulate and control posture and stance in locomotion have been extensively studied in both invertebrates and vertebrates (Duysens et al. 2000), and include the Golgi tendon organs and muscle

spindles at the hip, knee, and ankle joints, and the Ruffini endings and the Pacinian corpuscles in the soles of the feet (Duysens et al. 2000). The CNS receives afferent input from all these receptors (Dietz and Duysens 2000; Finch et al. 1991; Harkema et al. 1997). Previous studies have shown that electrical stimulation of the afferents from the Golgi tendon organ and muscle spindle proprioceptors extends the stance phase during walking, often delaying the initiation of the swing phase until the stimulus is terminated (Dietz and Duysens 2000). For example, during walking, when a limb is loaded, receptors that are activated include those from the foot, the stretched muscles and the joints, and the Golgi tendon organs of the extensors, which are the primary load receptors (Dietz and Duysens 2000; Duysens et al. 2000).



**Figure 1.1.1. Multiple Sensory Systems Contribute to Gaze Control and Locomotion.** Visual, vestibular, proprioceptive, and load systems interact to meet the common goals of maintaining forward locomotion and gaze stabilization.

Several techniques have been used to alter body load perception to investigate immediate changes in postural and locomotor control. These techniques include water immersion (Dietz et al. 1989; Poyhonen and Avela 2002); weight addition to the body via weight vests (Fouad et al. 2001; Stephens and Yang 1999), or removal via a suspended harness (Bastiaanse et al. 2000; Davis et al. 1996; Dietz et al. 2002; Donelan and Kram 1997; Finch et al. 1991; Harkema et al. 1997; Ivanenko et al. 2002; Stephens and Yang 1999; Threkheld et al. 2003); underwater locomotion (Newman et al. 1994); and cutaneous stimulation during microgravity exposure (Layne et al. 1998).

Particular to “online” immediate changes exhibited in postural responses related to body load-sensing mechanisms, an experiment by Roll et al. (1993) sought to investigate how muscle proprioceptive function is affected by prolonged exposure to microgravity at the levels of sensory receptors and muscle reflexes. The experiment used tendon vibrations as a means to activate propriomuscular sensor channels since mechanical vibration applied to the muscle tendons can selectively activate muscle spindle receptors. When applied in microgravity during spaceflight, the authors found that the “lift illusion” of the body in response to ankle muscle vibration resulted in an illusion of anteroposterior body tilt (the same as in 1-G) as soon as braces were used to replicate the missing axial ground pressure forces, thereby inducing an effect of increased body load. Thus, the authors concluded that the muscle proprioceptive function remains functional in microgravity, and that only the characteristics of these responses change based on the behavioral needs experienced in the microgravity environment.

Another study of postural control performed in a microgravity environment was designed to investigate whether the application of foot pressure could enhance neuromuscular activation associated with rapid arm movements (Layne et al. 1998). During spaceflight, four subjects performed unilateral arm raises with and without wearing boots designed to apply cutaneous pressure to the soles of the feet, thereby providing input to the somatosensory system alone. EMG responses were obtained from

lower limb and torso muscles. The subjects demonstrated an increase in the magnitude and duration of the activation of flexor and extensor muscles during the arm raise task while wearing the boots as compared to not wearing the boots, indicating that somatosensory information such as the increase in load perception that was provided by the boots is important in the modulation of postural muscle activity.

Dietz et al. (1989) used water immersion studies to investigate the effects of load on the postural response by stimulating receptors involved in signaling changes in the position of the body's center of mass with respect to the support surface. The water immersion technique allows the manipulation of load input perception (via changing body buoyancy) without directly altering vestibular function. Subjects were immersed in water up to their necks while standing on an underwater platform that translated forwards and backwards under the feet. The level of loading was manipulated by the addition and removal of weights around the subjects' core, effectively altering their buoyancy. The results of the study showed that the agonist EMG response via either the gastrocnemius (an extensor and antigravity muscle) or the tibialis anterior (a flexor muscle) to the platform displacements was linearly dependent upon the body weight while immersed, with greater EMG responses elicited during a 60 kg mass compared to a 10 kg mass. When the subjects were similarly loaded out of the water, any additional mass added over 10 kg failed to elicit the same linear relationship between EMG response and mass that was seen while water-immersed. The authors speculated that this response out-of-water was due to the fact that the load afferents are saturated with input at 10 kg, thus reaching their maximum influence such that addition of more mass would fail to elicit a different response.

In another study using water immersion, subjects showed a reduction in the ability to perform a maximal voluntary contraction of the gastrocnemius and soleus (antigravity extensor) muscles, accompanied by significant decreases in EMG activity and Hoffman and Achilles reflexes while immersed in water as compared to dry land (Poyhonen and

Avela 2002). The authors cited the similarities between the results in their study and those that are seen during spaceflight studies to suggest that these changes are a result of the decreased somatosensory input (load) elicited while immersed in water (Poyhonen and Avela 2002).

During locomotion, several variables decrease proportionally to unloading, including metabolic energy consumption and vertical contact forces (Davis and Cavanaugh 1993; Farley and McMahon 1992; Finch et al. 1991; Griffin et al. 1999; Ivanenko et al. 2002; Kram et al. 1997; Newman et al. 1994). In an experiment performed by Newman et al. (1994), subjects walked on an underwater treadmill while wearing a harness that was adjusted with weights as a means by which to vary the subjects' buoyancy (and thus load levels). Subjects walked at four simulated reduced gravity (G) conditions of 1/6 G, 3/8 G, 2/3 G, and 1 G. At each condition, subjects walked at three speeds: 1.8 km/hr, 5.4 km/hr, and 8.3 km/hr. Energetics were measured by oxygen uptake during locomotion and revealed that even at higher speeds, the energy expenditure exhibited was less during walking at the lower gravitational levels as compared to 1G walking. In the same study, peak vertical forces and stride frequency were significantly less at all reduced levels than those measured during 1 G walking.

With regard to locomotion, studies have shown that body loading is of particular importance as a somatosensory input because it is essential for modulation of motor control during locomotion (Dietz and Duysens 2000), particularly with regard to shaping motor output patterns during stepping (Duysens et al. 2000; Harkema et al. 1997; Kozlovskaya et al. 1981). Body load sensing is also important for controlling balance and posture during locomotion, and the termination of locomotion (Dietz 1996; Dietz et al. 2002; Harkema et al. 1997; Layne et al. 1998). A study by Harkema et al. (1997), examined the role of sensory information related to lower extremity weight bearing in modulating the efferent motor patterns of spinal cord-injured subjects during manually assisted stepping on a treadmill. During walking with various levels of body weight

support supplied by an overhead motorized lift and harness, the gastrocnemius and soleus extensor muscles were most affected by changes in subjects' body weight per step, and the EMG amplitude within each step was highly dependent on the phase of the step cycle regardless of load. Furthermore, these EMG responses were more closely associated with limb peak load, rather than stretch reflexes. Thus, the authors concluded that the level of loading on the lower limbs provides information that enables the spinal cord to modulate efferent output in a manner that may facilitate the generation of stepping.

In a study investigating the afferent sources and their contribution to the organization of stepping movements using a driven gait orthosis (DGO), Dietz et al. (2002) showed that the combination of sensory input from the hip joint and those from the load receptors contributes to the neuromuscular activation patterns seen during walking. The DGO was designed to drive locomotion, thus enabling passive, upright stepping movement for subjects, and was used during 70% and 100% unloading of subjects' body weight in groups of both paraplegic and healthy subjects. In both groups, when the DGO generated stepping leg motions while 100% unloaded, minimal muscle activity was elicited in the legs; however, when the DGO movements were coupled with a 30% increase in load, locomotor activity patterns were evident in the leg muscles.

Stephens and Yang (1999) sought to determine whether group I sensory input from extensor muscles controls the duration of the stance phase in walking in humans, similar to those studies previously done in decerebrate cats. Two load profiles were used during treadmill locomotion: (a) sustained increase or decrease in load, and (b) a sudden, unexpected increase or decrease in load. Subjects responded to the changes in body load by increasing the extensor muscle activity: the average extensor EMG response amplitude and duration significantly increased for the soleus during the stance phase, and for the quadriceps in the early part of the stance phase during (a) sustained increases in loads and (b) sudden unexpected increases in loads. Furthermore, the removal of these loads resulted in decreased EMG amplitudes. When subjects were unloaded by 30% via a

harness system, the soleus muscle EMG burst duration (but not the amplitude) was decreased. This study provides another example of how responsive the leg muscles are to changes in load perception during walking, including the effects on extensor muscles during the stance phase of gait cycle.

Bastiaanse et al. (2000) demonstrated the effects of body loading on the activity of the cutaneous reflexes in the feet during locomotion. In this study, the sural nerve, which provides sensory innervation to the lateral aspect of the foot, was electrically stimulated at different phases in the gait cycle during locomotion as a means by which to stimulate the cutaneous reflexes of the tibialis anterior (flexor muscles) and the antigravity muscles gastrocnemius and soleus (extensor muscles). During locomotion, unloading was achieved by suspending the subjects from a parachute harness connected to an overhead crane, while a counterweight was used to vary the degree of unloading. Increases in body load were achieved by wearing a vest with different lead weights. During locomotion, the gastrocnemius was the most affected by load variations, (as well as the soleus to a lesser degree) showing a significant reduction of reflexive activity with unloading and increased activity with increased body loading. Based on these results, the authors proposed that the load receptors are involved in the regulation of cutaneous reflex responses in order to adapt the locomotor pattern to practical changing environmental conditions during walking.

In studies that use pneumatically-controlled body weight support (BWS) harnesses during locomotion, gait cycle parameters and joint angle kinematics have been shown to change with increases in BWS (Davis et al. 1996; Donelan and Kram 1997; Finch et al. 1991; Ivanenko et al. 2002; Newman et al. 1994). In a study by Finch et al. (1991), subjects walked on a treadmill with 0, 30, 50, and 70% BWS and at full body weight (FBW) via a modified climbing harness at same speed levels for both FBW and BWS trials. EMG was obtained from leg muscles, footswitch signals were obtained to delineate gait cycle events, and video recordings of joint movements were collected to

determine changes in kinematic coordination. Significant differences that were found between BWS and FBW trials included decreased stance time, decreased double support time, and decreased hip and knee flexion in the swing phase during BWS. Additionally, EMG mean burst amplitudes were significantly reduced in the extensor muscles and significantly increased in the flexor muscles in their stance phase activity during BWS trials as compared to FBW trials.

Increased BWS has also been shown to decrease the angular displacements at the hip and knee joints during heel strike, foot flat, and toe-off and at the point of maximum swing (Finch et al. 1991; Ivanenko et al. 2002; Threkheld 2003). These changes in the joint angles are functionally related. For example, at the knee the significant reductions occur immediately following the heel strike because of the reduced body weight to be supported (Finch et al. 1991). In a study by Threkheld et al. (2003), subjects walked on a treadmill at 4.5 km/hr with BWS provided by a commercial pneumatic device and harness assembly at levels of “minimal”, 10, 30, 50, and 70% BWS. At levels of increased BWS the percentage of the gait cycle spent in the stance period and the double support period decreased proportionally with increased BWS. These gait cycle parameters are consistent with results in a BWS study by Finch et al. (1991). Peak knee flexion during early stance also decreased, and is consistent with other locomotion studies with BWS (Donelan and Kram 1997; Finch et al. 1991).

In a similar study by Ivanenko et al. (2002), there was a significant reduction in vertical contact forces during increased BWS provided by a pneumatic device that unloaded subjects at the waist, close to the body's center of mass. Additionally, increasing BWS between 0 and 95% resulted significantly in reduced stride length and stance time, similar to that seen by Donelan and Kram (1997), accompanied by drastic changes in lower limb activation patterns, but limited changes in inter-segmental coordination. Foot path shape and variability was not significantly altered with graded BWS conditions, but the EMG mean burst amplitudes in the gluteus maximus (hip

extensor) and lateral gastrocnemius decreased proportionally with increased BWS, consistent with their functions as antigravity muscles. The authors concluded that all of these changes during BWS indicated that the same basic kinematic control mechanisms are employed during BWS and normal body walking; however, these mechanisms can be significantly modified based on the changes in body load perception (Ivanenko et al. 2002).

To summarize, the immediate, “online” changes that occur during the gait cycle during BWS include decreased vertical reaction forces; decreased cadence; increased step length; decreased percentage in the stance period and double support period; and increased percentage in the swing period. Changes in joint kinematics include increased knee and ankle flexion during heel strike, foot-flat, and toe-off and at the point of maximum swing. In addition, muscle activity patterns of the extensors during their activity in the stance phase of the gait cycle are significantly reduced while the flexor activity is increased. No studies have been done to investigate changes in torso and head control during graded BWS. With regard to the role of body load sensing mechanisms during locomotion, these studies have reported only the *immediate strategic* changes in the subsystems contributing to locomotor control. However, no studies have been done to investigate the plastic adaptive effects on locomotor control induced by a prolonged alteration in body load-regulating mechanisms.

### ***Effects of Load Adaptation on Motor Systems***

Various techniques have been employed to investigate *motor system* responses to prolonged changes in body load-sensing mechanisms. In animal studies, rat hindlimb suspension and spaceflight studies have been classic unloading models for investigating muscle activity and reflexes (Alford et al. 1987; Kyparos et al. 2005; Recktenwald et al. 1999; Roy et al. 1988). In human studies, dry immersion (Iwase et al. 2000; Kozolvskaya

et al. 1982; Kozolvskaya et al. 1988; Nicogossian et al. 1993) and spaceflight investigations (Bloomberg and Mulavara 2003; Kozolvskaya et al. 1981; Layne et al. 1997; Layne et al. 1998; McDonald et al. 1996; Reschke et al. 1998; Roll et al. 1993) have been explored.

Several studies on hindlimb suspension in rats and exposure of primates to prolonged periods of unloading have shown changes in the levels of recruitment of motor pools during locomotion, as well as changes in muscle activity (Edgerton et al. 2001; Kyparos et al. 2005; Recktenwald et al. 1999; Roy et al. 1988). An early experiment by Alford et al. (1987) demonstrated that unloading the hindlimbs of rats by tail suspension initially results in a significant decrease in the daily amount of neuromuscular activity of the gastrocnemius and soleus. In a follow-on study, Roy et al. (1988) further analyzed the EMG signals from the soleus and gastrocnemius following 7 days of suspension and found an alteration in the normal recruitment pattern of the two muscles. Kyparos et al. (2005) demonstrated that dynamic foot stimulation can serve as a countermeasure to muscle atrophy in hindlimb-suspended rats. When hindlimb-suspended rats wore pressure boots that provided plantar contact, there was a prevention of approximately 85% of atrophy in type I myofiber cross-sectional area in the soleus, as well as prevention of 57% reduction in cross-sectional area in type I myofibers and 43% in type II myofibers in the medial gastrocnemius muscle.

Recktenwald et al. (1999) performed a study on Rhesus monkeys during post-spaceflight locomotion that investigated EMG activity patterns in soleus, gastrocnemius, tibialis anterior, and vastus lateralis muscles. Like that which was found in rat hindlimb suspension, the EMG burst amplitude was significantly reduced in the soleus and gastrocnemius muscles, and were associated with shorter stepping patterns during locomotion. Additionally, there was an increase in burst amplitude of the tibialis anterior muscle. These changes in recruitment patterns were attributed to modulations in the nervous system related to locomotor control, particularly with respect to the lack of load-

related somatosensory and proprioceptive input experienced during microgravity exposure (Recktenwald et al.1999).

Other studies have investigated the adaptive effects on the human sensorimotor systems involved in motor control after prolonged exposure to unloading alone. Kozlovskaya, et al. (1981; 1982; and 1988) evaluated different parts of the sensorimotor system in two groups of subjects exposed to real and simulated weightlessness of the microgravity environment after short and prolonged exposure periods. Dry Immersion was used to provide the unloaded environment (simulated microgravity), a technique in which the human floats on waterproof cloth that covers thermoneutral water (Iwase et al. 2000; Nicogossian et al. 1993). The results from these studies indicated that changes in independent systems induced by body unloading depend on the period of exposure, and include proprioceptive hyper-reactivity, significant decreases in the tendon reflex and Hoffman-reflex thresholds with no change in the muscle response thresholds, and a decline in the strength and stiffness of leg extensors such as the medial and lateral gastrocnemius and the soleus. Additionally, there was no change in strength, and minimal changes in stiffness, in the flexors such as the tibialis anterior. The authors further report that upon analyzing the in-flight exercise and posture control protocols used by the crewmembers of different spaceflight durations, the postural control changes were reduced when there was use of support loads used during the in-flight exercise protocols.

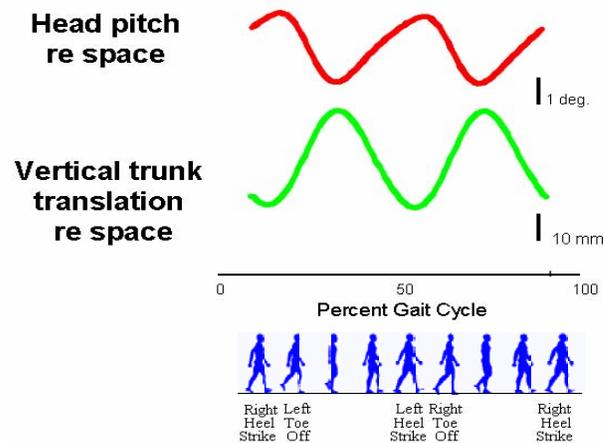
Several spaceflight studies have been performed on humans that provide insight to the effects of long-term changes in body load perception on motor systems. Exposure to microgravity during spaceflight induces adaptive modification in the sensorimotor integration process that allows astronauts to function adequately in that environment. However, upon return to 1-G, astronauts experience disturbances in spatial orientation, perception, posture, gait, and eye-head coordination (Reschke et al. 1998). The ability to maintain dynamic visual acuity is also reduced during post-flight walking (Bloomberg

and Mulavara 2003). Locomotor head-torso coordination strategies are altered and include restrictions in head pitch movement and decreased coherence between head pitch and vertical torso movements indicating a diminished coordination between the head and torso following spaceflight (Bloomberg et al. 1997). Studies of post-flight locomotor control have also shown that changes in gait are also apparent, including a wider stance, loss of postural stability when rounding corners, and inability to maintain a straight walking path (Bloomberg and Mulavara 2003; Reschke et al. 1998). Knee and ankle flexion has been shown to increase in the window from heel strike to peak knee flexion, presumably to absorb shock transmitted from the foot to head in an effort to maintain a stable head (Bloomberg and Mulavara 2003). Additionally, more reliance is placed on vision for postural and gait stability.

### ***Full-Body Contribution to Gaze Control During Locomotion***

To maintain the goal of gaze control during locomotion during daily activities, full-body coordination of movement patterns is essential for maintaining head stability. Such predominant contributions to gaze control during locomotion include head-torso coordination and knee and ankle flexion movements (Bloomberg et al. 1997; Bloomberg and Mulavara 2003; Mulavara et al. 2005). For example, head-torso coordination has been shown to aid in dynamic equilibrium control by using the head as a stabilized inertial guidance platform to provide a stable reference frame for visual and vestibular integration during complex body movements, and to maintain visual acuity during locomotion through a changing environment (Berthoz and Pozzo 1994; Bloomberg et al. 1992; Bloomberg et al. 1997; Bril and Ledebt 1998; Crane and Demer 1997; Demer and Viirre 1996; Hirasaki et al. 1999; McDonald et al. 1997; Mulavara and Bloomberg 2003; Mulavara et al. 2002; Mulavara et al. 2005; Pozzo et al. 1990). With each step, the oscillatory nature of locomotion necessarily induces vertical torso and head translations

(Cromwell et al. 2001; Grossman 1988; MacDougall and Moore 2005; Mulavara et al. 2002). This head and torso movement is reflective of the lower limb kinematics during walking. During the swing phase of walking, the torso translates upward; its greatest peak occurs during the single stance phase of the gait cycle, and its lowest point occurs during the double support phase as the initiation of the swing phase of the next leg is induced (MacDougall and Moore 2005). Additionally, there are significant linear and angular head movements: the head oscillates vertically and rotates in the pitch plane to compensate for its vertical translation in an effort to maintain a stable gaze: as the head translates up, the head pitches down (Figure 1.1.2) (Bloomberg et al. 1992, Cromwell et al. 2001; Grossman et al. 1988; Pozzo et al. 1990). In a study investigating head control and gaze stabilization during natural walking, Cromwell et al. (2004) found that differences in head and torso movement patterns while viewing head-fixed and earth-fixed targets during over-ground walking indicate that there is a reciprocal relationship in which gaze stability also facilitates horizontal head stability.



**Figure 1.1.2 Compensatory Head Pitch Movements.** Head pitch is compensatory for torso translation that occurs during each step in the gait cycle, and aids in gaze stabilization.

To determine the effects of spaceflight during locomotion, a short-duration spaceflight study (8-15 days) was performed on subjects following Space Shuttle flights (Bloomberg et al. 1997). Subjects walked on a treadmill at 6.4 km/hr while visually fixating their gaze on an earth-fixed target. At 6.4 km/hr, it has been shown that head pitch movements work to compensate for the vertical torso movements that occur with each step in the gait cycle (Bloomberg et al. 1997; Hirasaki et al. 1999; MacDougall and Moore 2005; Pozzo et al. 1990; Pozzo et al. 1995). The mean coherence between head pitch and vertical torso translations during post-flight locomotor testing was significantly reduced compared to pre-flight values, reflecting a decreased coordination between head and torso during walking. Furthermore, subjects showed a reduction in compensatory head pitch amplitude during post-flight locomotion.

Another study designed to characterize head-torso coordination during locomotion performed on astronauts following long-duration spaceflight (4-6 months) on the MIR Space Station showed a significant change in reflexive head control mechanisms (Bloomberg and Mulavara 2003). Subjects walked on a treadmill at 6.4 km/hr before and after spaceflight while visually fixating on an earth-fixed target. Head and torso pitch movements with respect to space and torso vertical translation with respect to space were transformed into the frequency domain, and the power in these signals were summed in the frequency range of 1.5 Hz -2.5 Hz, which has been shown to reflect the contributions of reflexive head control mechanisms (Keshner et al. 1995a; Keshner et al. 1995b; Keshner and Peterson 1992; Mulavara and Bloomberg 2005). Subjects showed no change in torso vertical translation or pitch; however, there was a significant decrease in head pitch movement, indicating that the head reflexive mechanisms, and not torso translation, accounted for the functional change in head movement during walking. The authors speculated that the reduction of head movement was a head-lock-to-torso strategy employed by the subjects as an effort to restrict the degrees of freedom of head movement during early motor reacquisition skills upon return to the 1-G environment of

Earth, similar to that strategy seen in patients with vestibular deficits (Mulavara and Bloomberg 2003).

Astronauts also experience significant oscillopsia and reduced visual acuity during walking following spaceflight, similar to that seen in patients with vestibular deficiency (Bloomberg and Mulavara 2003). The eyes must be stabilized in space for clear vision during head movement, and the vestibulo-ocular reflex (VOR) contributes to gaze stabilization by generating compensatory eye movements in response to head motion. However, the VOR gain is never exactly 1.0, and decreases during activities like walking and running for stabilization of images of distant targets (Demer et al 1993; Demer and Amjadi 1993; Demer and Viirre 1996). Because natural head movements have high frequency components, retinal image slip velocity can degrade visual acuity (Demer and Amjadi 1993). In a study by Bloomberg and Mulavara (2003), six astronauts walked at 6.4 km/hr on a treadmill while performing a number recognition task before and after long-duration spaceflight. This task required subjects to identify numbers of varying font sizes displayed on a laptop located 2 m in front of the eyes. Post-flight results indicated that subjects had a decreased ability to correctly identify the numbers while walking; however, subjects showed a recovery to pre-flight levels within the first week. These results indicate that gaze stabilization mechanisms were adaptively modified during spaceflight, leading to decreased visual acuity upon return to a 1-G environment. The authors speculated that additional strategies must be in use by the head-torso complex and lower limbs to maintain a stable gaze when the body is in motion.

During locomotion, the high-energy phases of the gait cycle include heel strike, weight transfer from one foot to the other, and push-off of the toe from the ground. This window from heel strike to peak knee flexion during walking appears to be critical with regard to gaze stabilization. The energy resulting from these events has been shown to propagate throughout the body to the head. Light et al. (1980) characterized the vertical

component of this “shock wave” using an accelerometer mounted to the tibia and to the head. During heel strike, the tibia exhibited 20 – 80 m/s<sup>2</sup> deceleration forces while measurements at the head showed a magnitude no greater than 10 m/s<sup>2</sup>. This attenuation was also demonstrated in a study by Wosk and Voloshin (1981) that found that the shock attenuation at the head was reduced by about 70% of that recorded at the tibia. The results of these studies support the concept that the musculoskeletal system is designed to filter out certain components of the foot-contact shock transmission, thus providing attenuation for the purpose of maintaining a stable head. Several studies have attributed the shock mitigation solely to increased knee and ankle flexion strategies; however evidence in support of a combination of factors for shock attenuation is supported by the fact that the transient force measured during heel strike lasts for about only 20 ms, but ankle flexion occupies 80 ms of heel strike while peak knee flexion occurs in the stance phase 150 ms *after* heel strike (Whittle 1999). Therefore, Whittle (1999) attributes the attenuation to slower walking velocities, knee and ankle flexion increases, and viscoelastic properties of the heel pad of the foot, the musculoskeletal arrangement of the body, and materials in footwear. A study by LaFortune et al. (1996) demonstrated that when impact forces were applied to the heel of the foot in supine subjects, impact velocities and surface softness changes appeared to modify shock measured at the head; however, the most significant contributor to attenuation of shock appeared to be increased knee flexion, which caused significant reduction in axial stiffness of the body, thus improving shock attenuation as measured at the head. The authors in the study concluded that overall, the body guarded against potentially harmful impact shock that traveled from the shank to the head by 75%, and it was delayed by 5 ms and its frequency components above 10 Hz were attenuated by 5 dB. These attenuations were attributed by the authors as being beneficial in preventing disturbance of the head, which is critical for vestibular and visual integration, and are likely a result of a combination of strategies that include increased knee flexion at ground contact, slower walking velocities, and softer

impact surfaces through footwear or flooring designs (LaFortune et al. 1996). In a separate study investigating the involvement of body segment coordination in attenuation of vibrations to the head during walking, Capozzo (1982) found that coordinated actions of the head-torso complex and torso-pelvis complex also work to minimize the disturbances reaching the head, suggesting that in addition to the passive mechanical attenuation by the muscles and joints, specific coordinated actions in body segments can contribute to the head stabilization process. Such interactions are important for maintaining head stability: if these vibrations were left unattenuated, the consequence could be a disruption the visual-vestibular sensory systems in the head, resulting in reduced visual acuity (Holt et al. 1995; McDonald et al 1997; Mulavara et al. 2002; Mulavara and Bloomberg 2003; Pozzo et al. 1990; Smeathers 1989; Voloshin 1988; Whittle 1999).

Studies of astronauts returning from short-duration spaceflight (8-9 days) have shown increased variability in knee and hip flexion, and increases in the relative amplitude of the underlying muscle activation, particularly around the heel strike and toe-off events (Layne et al. 1997; Layne et al. 1998; McDonald et al. 1996). After long duration spaceflight, astronauts showed that during treadmill walking (6.4 km/h), knee flexion during the stance phase significantly increased and then subsequently returned to normal within 6-10 days (Bloomberg and Mulavara 2003). This increase in knee flexion during locomotion results in a reduction of the axial stiffness of the lower limb complex during the critical stance phase following heel strike. After spaceflight, accelerations measured along the superior inferior axis at the head and tibia showed a significant reduction of the shock experienced at the tibia (40% average reduction) and the head (20% average reduction) segments but the mean shock experienced by the head normalized to per unit tibial shock showed a significant increase of 40% during locomotion testing one day post-flight (Mulavara et al. 2002).

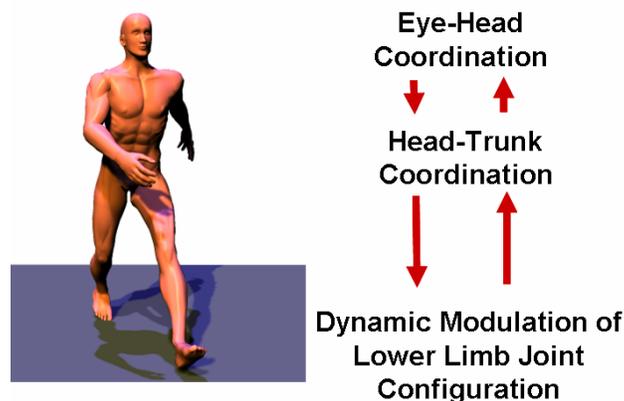
Based on the study of the literature, it is clear that postural control, gait cycle timing, muscle activation patterns, extensor and flexor reflex coordination, knee flexion during the stance phase, transmission characteristics of the shock wave at heel strike, head movement control, and dynamic visual acuity are all functionally inter-related. Consequently, appropriate attenuation of energy transmission during locomotion, achieved by the modulation of the lower limb joint configurations coupled with appropriate eye-head-torso coordination strategies, form the fundamental features of an *integrated gaze stabilization system*.

To test the hypothesis that the whole body serves as an integrated gaze stabilization system, Mulavara and Bloomberg (2003) investigated the effect of changes in gaze stabilization task constraints during locomotion. Nine subjects performed two gaze stabilization tasks while walking at 6.4 km/hr on a motorized treadmill: 1) focusing on a central point target, and 2) reading numeral characters; both stimuli presented 2m away at eye level. While reading numeral characters as compared to the central point target the compensatory head pitch movement with respect to space was on average 22% greater. The peak acceleration measured at the head was significantly reduced by an average of 13% in four of the six subjects. Also, the knee joint total movement was on average 11% greater during the period from the heel strike event to the peak knee flexion event in stance phase of the gait cycle.

Recently, Mulavara et al. (2005) further investigated how introducing a plastic adaptive modification of eye-head coordination, by modifying the VOR gain, alters eye-head-torso coordination and causes the reorganization of lower limb joint configurations to help preserve gaze stabilization during locomotion. The adaptive stimulus was a 30-minute exposure to 0.5x minifying lenses worn during self-generated sinusoidal vertical head rotations while the subject was seated facing a projected complex visual scene. Before and after VOR adaptation 14 subjects walked (6.4 km/h) on a motorized treadmill while performing a number recognition task. There was a significant decrease in the

amplitude of head movement with respect to space, and a significant increase in the amount of knee flexion during the initial stance phase of the gait cycle. These results indicate that visual-vestibular conflict induced by the minifying lenses caused alteration in full-body strategies consistent with the requirement to aid gaze stabilization during locomotion. These strategic changes returned to pre-adaptation levels within the 10 repeated trials completed immediately after the adaptation period.

In summary, the spaceflight and ground-based data confirm that the whole body can serve as an *integrated gaze stabilization system*, in which several subsystems contribute, leading to accurate visual acuity during body motion (Figure 1.1.3). These studies have demonstrated that during locomotion, changes in reflexive head stabilization mechanisms, changes in transmission characteristics of the shock wave at heel strike, and increased total knee movement during the subsequent stance phase can be adaptively modified to meet the requirements of the environment in an effort to maintain a stable gaze. Coordination of all of these components preserves head stability during locomotion; therefore, the whole body acts as a gaze stabilization system: head-torso activity and lower body movement coordinate to provide strategic locomotor control in order to maintain a stable gaze during locomotion (Bloomberg and Mulavara 2003).



**Figure 1.1.3. The Integrated Gaze Stabilization System.** The whole body can serve as an *integrated gaze stabilization system*, in which several subsystems contribute, leading to accurate visual acuity during body motion.

### ***Vestibular - Somatosensory Interactions***

In studies of postural control, it has been shown that the visual, vestibular, and somatosensory systems have pathways that converge both anatomically and physiologically in the spinal cord, vestibular nuclei, thalamus, cortex, and cerebellum to allow for multiple complex exchanges. (Aiello et al. 1983; Horak 2001; Rubin et al. 1979; Wilson 1991; Wilson et al. 1995). Studies in humans and animals have shown that interactions exist between the vestibular and somatosensory systems such that one sensory system can modulate the activity in the other to maintain posture and function when the sensory input in the other is absent or unreliable (Bles 1984; Dieringer 1984; Dieringer 1997; Inglis et al. 1995; Pfaltz 1983; Putkonen 1977). It has been well-documented that non-labyrinthine inputs influence the activity of vestibular nucleus neurons within the brainstem. Physiological experiments from early vestibular nuclei studies have found that in addition to integration of signals from the labyrinth and neck, these vestibular nuclei also receive inputs from the spinal cord, including the proprioceptive signals from the limbs, and that these signals can influence the activity of the vestibular nucleus neurons (Fredrickson et al. 1966; Smeathers 1989; Wilson et al. 1995). A recent study by Jian et al. (2002) aimed to determine the patterns of convergence of non-labyrinthine inputs from the limbs onto vestibular nucleus neurons receiving signals from the vertical semicircular canals and otoliths. A secondary goal of the study was to determine if non-labyrinthine inputs could modulate the activity of these vestibular nuclei neurons in decerebrate cats with bilateral labyrinthectomies. In this study, cellular recordings were taken from the vestibular nuclei as limb nerves were electrically stimulated, in both labyrinthine-intact and labyrinthine deficient decerebrate cats. The authors found that 72% of the vestibular nucleus neurons whose activity is modulated in the vertical planes also receive inputs from the limbs. Additionally, such stimulation of peripheral nerves affected an even higher proportion of vestibular nuclei neuronal activity in the labyrinthectomized cats than in labyrinth-intact animals. This

suggests that adaptive plasticity that occurs following peripheral vestibular lesions may enhance the effects of non-labyrinthine inputs to the vestibular nuclei as a means by which to compensate for the loss of labyrinthine inputs. Although the functional implication of this convergence is largely unknown, the authors speculate that such vestibular-somatosensory interaction can allow for more precise information about the body's position in space, thus achieving more control over the components involved in modulating motor output (Jian et al. 2002).

In human studies, the effect of galvanic vestibular stimulation on postural sway has provided substantial evidence for vestibular-somatosensory interaction, especially those studies that have shown that conflicting or absent somatosensory input results in increased reliance on vestibular input in an effort to maintain postural or head stability (Britton et al. 1993; Day et al. 1997; Fitzpatrick et al. 1994; Horak and Hlavacka 2001; Inglis et al. 1995). During bipolar galvanic vestibular stimulation, electrode leads are placed on either side of the jaw bone while a low current is passed to a cathode on one side, and an anode on the other side. This arrangement effectively induces an artificial conflict of vestibular activity as a result of relative inhibition of the eighth nerve on the side of the anode and relative excitation on the side of the cathode. The functional consequence of this activity is observed as directionally-specific postural sway toward the side of the anode, possibly as an attempt for the balance system to compensate for the "sensation" of head movement induced by the vestibular conflict (Fitzpatrick and Day 1996; Horak and Hlavacka 2001). Several studies have shown that the severity of postural sway can be modulated depending on the state of somatosensory information when the vestibular stimulus is maintained constant (Lund and Broberg 1983; Nashner and Wolfson 1974). Other studies have shown that changes in somatosensory information from the support surface can change the intensity of responses to galvanic vestibulospinal stimulation (Day et al. 1997; Fitzpatrick et al. 1994; Gurfinkel et al. 1988; Horak et al. 1994; Inglis et al. 1995). Inglis et al. (1995) demonstrated that normal subjects standing

on a translating surface showed increased postural responses to galvanic stimulation due to the conflict in somatosensory input. Day et al. (1997) and Gurfinkel et al. (1988) found that galvanic vestibular stimulation results in greater postural sway while subjects concurrently make voluntary movements that cause conflicting proprioceptive inputs. In a separate study by Fitzpatrick et al. (1994), subjects showed no muscle response in the legs to galvanic vestibular stimulation when they were seated or when their torsos were stabilized with external support; however, when subjects stood on an unstable surface, galvanic stimulation elicited a significant increase in muscle activation from the legs. Horak et al. (1994) demonstrated that even without galvanic stimulation, subjects who stood on an unstable surface displayed increased head perturbations and resultant increases in ankle muscle response in an effort to maintain a stable vestibular platform. Horak and Hlavacka (2001) demonstrated that subjects with diabetic peripheral neuropathy, and thus reduced somatosensory input, showed greater anterior postural sway in response to galvanic vestibular stimulation as compared to healthy, age-matched subjects.

With respect to quantitative load influences on vestibular information and postural control, a study performed by Marsden et al. (2003) provided evidence that body loading influences vestibular control of balance, particularly with respect to the head and torso. In this study, galvanic vestibular stimulation was used as a means by which to provide a descending vestibular signal as subjects stood symmetrically while loaded by 16%, 33%, and 55% of their body weight by varying the amount of weights attached to their torso; or, as they were unloaded by 10%, 20%, and 30% of their body weight from the legs using a whole-body harness that partially lifted the body during standing. Results showed that the head and torso behaved differently in response to load changes; the rate of head tilt increased and torso tilt decreased in space in the sagittal plane in response to increased loading and decreased loading, respectively. However, the rate of head tilt with respect to torso remained constant across all loading conditions, whereas the torso tilt

with respect to the pelvis changed with load. The authors concluded that the responses seen in this study are indicative that load-related afferent input from the lower limbs influences the processing of vestibular information for the control of balance.

Studies of sensory loss have shown that vestibular-somatosensory substitution can occur when either the vestibular or somatosensory input is lost. In several of these studies, peripheral vestibular lesions in animals resulted in an increased sensitivity in vestibular nuclei (Dieringer 1997; Dieringer et al. 1984; Pfaltz 1983; Putkonen et al. 1977). In humans, Dietz et al. (2001) showed that the amount of proprioceptive information from the legs determined the influence of vestibulospinal input on body movements. When subjects were rotated in place while suspended from a harness with no foot contact with the ground, they subsequently displayed a larger rotation effect while hopping in place with eyes closed than while walking in place, which provided more foot contact with the ground. The results of this study showed that as somatosensory input from the feet decreased, compensatory vestibulospinal dependence increased. Additionally, a study by Bles et al. (1984) demonstrated a stronger dependency on somatosensory input from the feet and neck on compensatory eye movements in space in subjects with vestibular loss.

All of these studies support the premise that vestibular input becomes increasingly critical for maintaining balance and posture control as somatosensory input becomes conflicting or absent (Mergner and Rosemeier 1998). This concept of convergence of sensory systems provides further evidence that the *whole body* integrates multiple inputs to coordinate purposeful, appropriate motor control, and is especially pertinent to the preservation of gaze as a function of postural control during locomotion. Additionally, little is known, about how the plastic changes induced by the adaptive modification of load sensing alone contribute to whole-body gait modulation in an effort to maintain a stable gaze. **The goal of this research is to determine the role of body load-regulating mechanisms in gaze control during locomotion. The general hypothesis behind the**

**proposed research is that body load-regulating mechanisms ultimately contribute to gaze stabilization, and adaptive changes in these load-regulating mechanisms will require reorganization in the full-body gaze control system so that visual acuity can be maintained during locomotion.**

## **1.2 SPECIFIC AIMS**

To support the hypothesis of this research, three specific aims were identified that were designed to characterize how the full body gaze stabilization system is reorganized following *adaptive alteration in body load-regulating mechanism as a result of prolonged unloaded locomotion*. Because the whole body contributes to gaze stabilization, functional changes following unloaded locomotion can be quantified through dynamic visual acuity assessment during post-unloaded walking. To characterize the particular strategic reorganization of the systems that contribute to these functional changes, the specific aims identified are designed to measure the plastic changes that occur in head-torso coordination, lower limb kinematics, and gait-cycle timing, all of which contribute to preserving gaze stabilization.

*Specific Aim I:* Characterize changes in head-torso coordination that occur to preserve gaze stabilization in response to adaptive alteration in body load-regulating mechanisms produced by prolonged exposure to unloaded locomotion.

Rationale: Head-torso coordination is essential for maintaining stabilized gaze during locomotion. This specific aim will investigate whether prolonged exposure to body unloading during locomotion induces adaptive effects in body load mechanisms that lead to alterations in head-torso coordination patterns that are produced to preserve gaze stabilization. Subjects walked on a motorized treadmill while performing a gaze

stabilization task before and after prolonged unloaded locomotion. Head and torso 3D kinematic data were obtained using a video-based motion analysis system before and after the unloaded locomotion adaptation session.

*Hypothesis:* Adaptive modification in body load mechanisms produced during prolonged unloaded locomotion will result in an increased restriction in head movement with respect to the torso during post-adaptation locomotion to reduce perturbations to the head, thus preserving gaze stability during locomotion.

***Specific Aim II:*** Characterize changes in lower body kinematics that occur to preserve gaze stabilization in response to adaptive alteration in body load-regulating mechanisms produced by prolonged exposure to unloaded locomotion.

*Rationale:* Increased knee and ankle flexion during walking provide a shock-absorption mechanism during the load transfer phase of walking (stance phase, following heel strike) and therefore serve to dampen disturbances to the head contributing to gaze stabilization during locomotion. This specific aim investigated whether prolonged exposure to body unloading during locomotion induces adaptive effects that alter lower limb kinematics in an effort to preserve gaze stabilization. Subjects walked on a motorized treadmill while performing a gaze stabilization task before and after prolonged unloaded locomotion. Lower limb 3D kinematic data were obtained using a video-based motion analysis system before and after the unloaded locomotion adaptation sessions.

*Hypothesis:* Adaptive modification in body load mechanisms produced during prolonged unloaded locomotion will result in an increase in lower body limb flexion

during post-adaptation locomotion to reduce perturbations to the head, thus preserving gaze stability during locomotion.

***Specific Aim III:*** Characterize changes in gait-cycle timing that occur to preserve gaze stabilization in response to adaptive alteration in body load-regulating mechanisms produced by prolonged exposure to unloaded locomotion.

*Rationale:* Alterations in gait-cycle timing (decreased stride time, increased double support time) is presumed to contribute to increased overall postural stability during locomotion. This specific aim investigated whether prolonged exposure to body unloading during locomotion induces adaptive effects that alter gait-cycle timing during walking. Subjects walked on a motorized treadmill while performing a gaze stabilization task before and after prolonged unloaded locomotion. Stride time and double support time data were collected by foot switches positioned under the heel and toe of the subjects' shoes.

*Hypothesis:* Adaptive modification in body load mechanisms produced during prolonged unloaded locomotion will result in decreased stride time and an increase in double support time during post-adaptation locomotion in an effort to increase postural stability, thus preserving gaze stability during locomotion.

## CHAPTER 2: MATERIALS AND METHODS

### 2.1 SUBJECTS

Thirteen subjects (seven females and six males) were recruited in this study. Their ages, heights, and weights respectively were, average ( $\pm$  one standard error of mean, SEM) 32 ( $\pm$  6.93) years, 1.73 ( $\pm$  0.08) meters, and 71.99( $\pm$  15.58) kilograms. Subjects had no history of neurologic, otologic, cardiovascular or significant orthopedic disorders, and gave informed consent before participation in this study. All subjects were volunteers recruited through the National Aeronautics and Space Administration Johnson Space Center (NASA-JSC) Human Test Subject Facility. The study was performed on-site in the Neuroscience Laboratories at NASA-JSC with the approval of the JSC Committee for the Protection of Human Subjects. Subjects were also given a questionnaire concerning the frequency and type of exercise program they currently, or ever have, participated in to be used only in the event that a subject's movement data was significantly different from standard parameters or the parameters of other subjects in the study.

### 2.2 TESTING CONDITIONS

#### *Integrated Treadmill Locomotion Protocol*

The Integrated Treadmill Locomotion Protocol (ITLP) consisted of two testing periods: pre-adaptation ITLP and post-adaptation ITLP. The pre-adaptation ITLP was used as a baseline data collection session. Subjects wore close-fitting cycling shorts, a sleeveless shirt, and running shoes throughout their testing (Converse, North Andover, MA). Subjects walked on a motorized instrumented treadmill, the "data collection treadmill," with surface dimensions of 51 cm x 156 cm (Model #9810S1x, Kistler Instrument Corp., Amherst, NY.) while performing a goal-directed gaze stabilization task that required subjects to identify the position of the gap in Landolt C optotypes presented

centrally on a computer screen located 4m away at eye-level. Subjects walked on the data collection treadmill without body weight support (0% BWS) at 5.8 km/hr for one trial of 3 minutes in duration during the pre-adaptation ITLP to obtain baseline, “pre” data. Immediately following the 30 min adaptation protocol, the subjects again walked on the data collection treadmill for 10 trials each of 70 seconds with an alternating one-minute rest period to obtain post-adaptation ITLP “post” data. Figure 2.2.1 (a) depicts a subject outfitted with data collection instrumentation. To prevent injury, each subject wore a full-body harness that was attached to an overhead gantry that shut the treadmill off and supported the subject if the subject fell. This harness provided no BWS and did not interfere with the natural movement of the torso or limbs during walking. The subject used this harness for all periods (pre-adaptation ITLP, adaptation, and post-adaptation ITLP) of the experimental protocol. Prior to the start of the pre-adaptation ITLP, subjects were given the opportunity to walk on the treadmill for a period not to exceed one minute to establish familiarity with the treadmill speed and locomotion.

### ***Adaptation Protocol***

A second treadmill, the “BWS treadmill,” with surface dimensions of 51 cm x 156 cm (Model #685, Kistler Instrument Corp., Amherst, NY.) was used to provide body weight support (BWS) during the 30 minute adaptation protocol. The BWS treadmill was integrated with a pneumatically-controlled BWS system (Pneumex, Inc, Standpoint, Idaho) that was used to provide BWS during the adaptation protocol as depicted in Figure 2.2.1 (b). The pneumatically-controlled harness system allows selection of a pre-calculated weight to be unloaded from the subject’s legs, up to 68.04 kg. For each subject, the harness was attached to the BWS as depicted in Figure 2.2.1 (b), and 40% of the subject’s weight was supported from the legs to provide BWS. Subjects walked on this BWS treadmill for 30 minutes at 40% BWS at 5.8km/hr while watching a movie on

a computer screen positioned at eye level 4m away, which provided a consistent gaze task during the adaptation period. No data were collected during this period. Immediately following completion of the 30-minute 40% BWS adaptation protocol, subjects were seated in a chair and were rolled over to the data collection treadmill that was located next to the BWS treadmill to begin post-adaptation ITLP data collection.

The walking speed selected for all 3 phases of this study was based on unloaded locomotion studies performed by Kram et al. (1997) that allows comfortable fast-paced walking without inducing a run. According to Kram et al., the range of preferred speeds for walking, before switching to a run, that can be used with 40% BWS is more limited than at 0% BWS (Kram et al. 1997; Minetti 2001). Subjects can maintain a walking pattern at speeds  $\leq 5.8$  km/hr from 0% to 50% BWS (Ivanenko et al. 2002). Hence, subjects were unloaded to 40% of body weight while walking at a speed 5.8 km/hr. Subjects walked at this speed during all three phases of the experiment to determine the effects of adaptation to unloading alone, thereby eliminating variation in speeds as a covariant during the adaptation and testing phases.

## **2.3 DATA COLLECTION**

### ***Dynamic Visual Acuity (DVA)***

Research has shown that posture control during quiet standing is dependent upon the motion of a virtual moving target and can be modulated as a function of distance to these targets (Lee and Lishman 1975; Dijkstra et al. 1994; Stoffregen et al. 1999; Stoffregen et al. 2000). Stoffregen et al. (2000) performed an experiment where the visual performance tasks included an inspection task of fixating on a blank target and a search task wherein subjects were asked to count the frequency of a given letter. Postural sway results showed that head fore-aft sway amplitude can be modulated adaptively as a result of the performance of these visual tasks. Mulavara and Bloomberg (2003) further

demonstrated that during locomotion, such goal-directed responses of head movements are not dependent solely on passive inertial and viscoelastic properties of the head-neck system, but may be actively modulated to respond to changes in gaze control requirements. Hence, to provide a consistent goal-directed task for the subjects during locomotion, a dynamic visual acuity assessment (DVA) was performed during the pre-adaptation and post-adaptation ITLP data collection periods.

The DVA test displayed a sequence of Landolt C optotypes on a screen in one of four orientations: gap up, gap down, gap left, gap right as depicted in Figure 2.3.1 (Peters and Bloomberg 2005). The subject was asked to verbally identify the open position for each optotype centrally displayed for a period of 500 ms on a laptop positioned at the subject's eye-level, 4m away while walking. The orientation of each optotype was presented randomly, but the gap size changed progressively, depending on the subject's ability to correctly identify the successive gap openings. Subjects' answers were entered into the computer by the test administrator using a metric keypad (Peters and Bloomberg 2005).

The methodology and details of this DVA test have been reported previously and are described here in brief (Peters and Bloomberg 2005). A Matlab (The Mathworks Inc., Natick, MA) program was used to create Landolt C optotypes. The program created Bitmap images of black-on-white optotypes in 15 sizes, ranging from 1.0 to -0.4 logMAR. Using the logMAR scale, 1.0 and 0.0 are equivalent to the Snellen ratios of 20/200 and 20/20, respectively. The 0.1 logMAR step change between optotype sizes is equivalent to a 20% size increase from one size to the next larger size. The size of the Landolt C's and their gap positions during subject presentation was controlled using a custom-written program using National Instruments software (National Instruments, Austin, TX) and was modeled after the Freiburg Visual Acuity Test to determine the subjects' visual acuity threshold (Peters and Bloomberg 2005). The Best PEST (i.e. parameter estimation by sequential testing) psychophysical threshold detection algorithm

was used to determine the visual acuity threshold for each condition as reported previously (Peters and Bloomberg 2005).

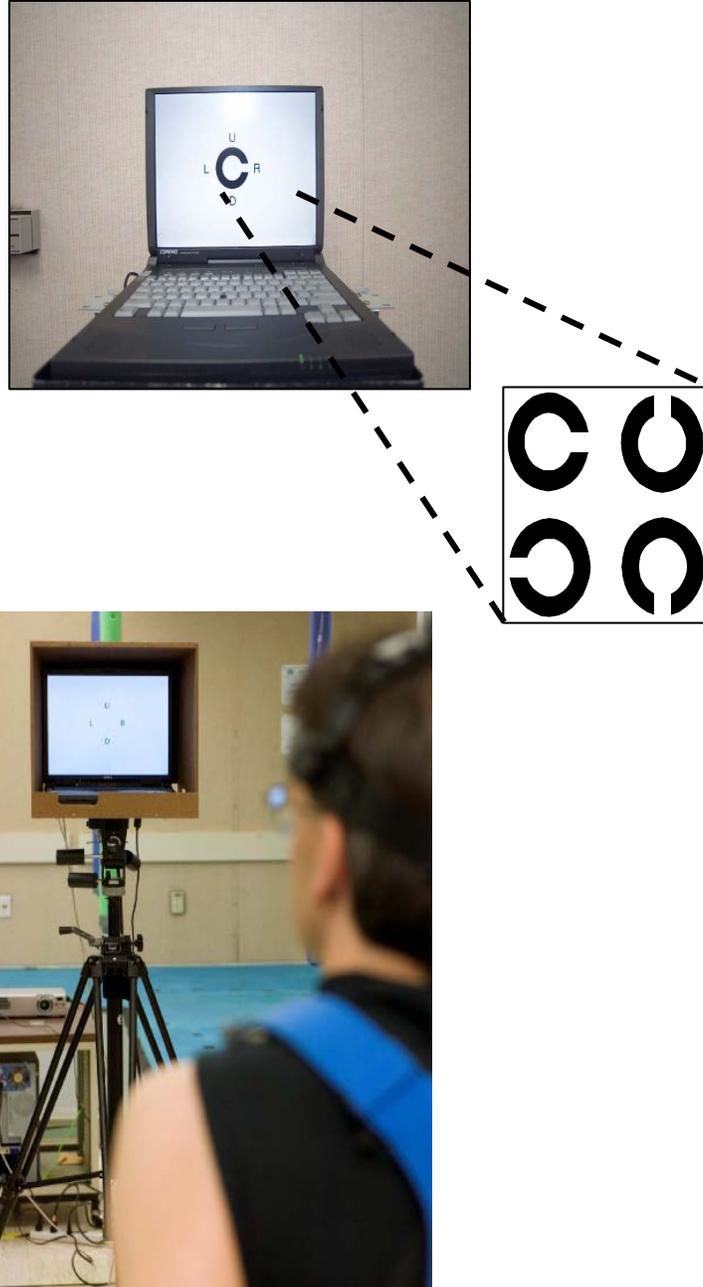
**A)**



**B)**



**Figure 2.2.1. Laboratory Treadmill Configurations.** **A)** Configuration of the data collection treadmill and kinematic equipment used for pre- and post-adaptation ITLP data collection, (harness not depicted). **B)** Configuration of the BWS treadmill with integrated Pneumex, Inc. PneuLift unloading harness system to provide body weight support during the 30 min BWS adaptive protocol (the pictured harness was used in all three protocols).



**Figure 2.3.1. Dynamic Visual Acuity Assessment (DVA) display.** The DVA program displayed a sequence of Landolt C optotypes on a screen in one of four orientations: gap up, gap down, gap left, gap right.

## ***Kinematics***

To investigate the changes in reflexive head control due to prolonged BWS, motion data was collected for head movement, torso movement and torso vertical translation motion with respect to space, as well as head movements with respect to torso in the reflexive head control frequency ranges. To investigate pre- and post-BWS adaptation changes in lower body kinematics, ankle and knee movement data were collected. The movements of different body segments were measured using a video-based motion measurement system (Motion Analysis Corp., Santa Rosa, CA). The methodology and accuracy of measurements have been reported previously (McDonald et al. 1996, Miller et al. 2002, Mulavara et al. 2002). Six time-synchronized cameras, sampling at 60 Hz, were used to obtain the three dimensional positions of light weight retro-reflective markers placed on the various body segments, according to Figure 2.3.2 and Table 2.3.1 below. The subjects walked in the +X direction (forward) and the belt moved in the -X direction (backward); the vertical axis orthogonal to the surface of the treadmill was +Z (up), and the +Y axis was orthogonal to the X-Z plane (+Y to the subject's left). Three cameras fitted with 8mm lenses were aimed to capture upper body motion data while the remaining three cameras fitted with 6mm lenses were aimed to capture the lower limb motion. Each camera in this “two split-body” measurement setup was positioned between 1.8 and 2.5 meters from the center of the calibration volume, in a distribution that covered from “two o'clock” to “seven o'clock” in the xy-plane (with 12 o'clock being in the direction of forward locomotion, “+X”).

A four-marker calibration device in the shape of an “L” was used to define the X, Y, and Z axes in the camera calibration volume for the 3 cameras used for upper body data collection. This “calibration seed” was placed at the origin of the treadmill such that the long side of the “L” was positioned along the path of the treadbelt to identify the greatest points of +X, -X during data collection, and the short side of the “L” was positioned along the width of the treadbelt for +Y, -Y data collection. Any items that

could induce a reflection and thus mis-calibration of the cameras were identified and removed from the view of the cameras. A three-marker “calibration wand” was used for establishing camera linearization parameters for motion capture. This wand was used during a 60-second calibration procedure during which it was waved in the air vertically and horizontally in the calibration volume to be used during data collection (each three-camera setup views a calibration volume of 0.75 X 0.50 X 0.98 meters). Following calibration with the seed and the wand, the calibration was extended to the remaining three cameras via the calibration software. A previous study performed by this lab using a similar calibration configuration showed that the resolution and repeatability were computed to 0.1mm, and accuracy ranged from 0.05-0.16 mm (Miller et al. 2002; Mulavara et al. 2002; Richards et al. 2004).

Six degree of freedom motions of the head, torso, pelvis, thigh, shank and foot were calculated using the three dimensional trajectories of a minimum of three markers placed on each of the segments. The trajectories of these markers were measured with respect to an inertial laboratory fixed coordinate system, coincident to the surface of the treadmill. All motions of individual segments were referenced with respect to their anatomical axes orientations determined during seated and quiet standing calibration trials.

### ***Gait Cycle Timing***

Foot-switches with force sensing resistors (Figure 2.3.3) were attached to the subjects’ shoes on the plantar surface at the heel and toe to enable the determination of heel strike and toe off events for each gait cycle (Motion Lab Systems, Baton Rouge, La). The foot-switch data were acquired at a sampling rate of 1000 Hz using the Gaitway™ Gait Analysis System and Software (Model #9810S1X, Kistler Instrument Corp., Amherst, NY). The foot-switches were used to identify heel strike and toe-off events of



<b>Body Segment Measured</b>	<b>Marker Name</b>	<b>Anatomical Location</b>	<b>Movement Measured</b>
<b>Head</b>	Ant	Antennae attached to helmet above vertex	Head pitch, roll, yaw, translation
	Rear	Antennae attached to helmet lateral to vertex	Head pitch, roll, yaw, translation
	Vertex	Vertex of head/helmet	Head pitch, roll, yaw, translation
	Rmets	Right trigion	Used for defining head anatomical axes
	Lmets	Left trigion	Used for defining head anatomical axes
	Orbit	Right infra orbitale	Used for defining head anatomical axes
<b>Torso</b>	Ntorso	Tip of spinous process of 7 <sup>th</sup> cervical vertebrae	Torso pitch, roll, yaw, translation
	Ltorso	Left of midline at the level of 10 <sup>th</sup> thoracic vertebrae	Torso pitch, roll, yaw, translation
	Rtorso	Right of midline at the level of 10 <sup>th</sup> thoracic vertebrae	Torso pitch, roll, yaw, translation
<b>Pelvis</b>	Rpsis	Right posterior superior iliac spine	Pelvis pitch, roll, yaw, translation
	Lpsis	Left posterior superior iliac spine	Pelvis pitch, roll, yaw, translation
	Sacr	Sacrum	Pelvis pitch, roll, yaw, translation
<b>Thigh</b>	Rhip	Greater trochanter	Thigh pitch, roll, yaw, translation
	Rthigh	Approximate midpoint of the line that joins the right anterior superior Iliac spine and the superior point of the right knee cap	Thigh pitch, roll, yaw, translation
	Rknee	Lateral femoral condyle	Thigh pitch, roll, yaw, translation
<b>Shank</b>	Fib_head	Fibular head	Shank pitch, roll, yaw, translation
	Rtib	Below Tibial tuberosity on tibial crest	Shank pitch, roll, yaw, translation
	Rtib2	Tibial crest below Rtib	Used for defining shank anatomical axes
	Rmal	Lateral Malleolus	Shank pitch, roll, yaw, translation
<b>Foot</b>	Rmt5	5 <sup>th</sup> metatarsal	Foot pitch, roll, yaw, translation
	Rheel	Posterior Calcaneous	Used for defining foot anatomical axes
	Rnav	Above Navicular	Foot pitch, roll, yaw, translation
	Rcalc	Lateral Calcaneous	Foot pitch, roll, yaw, translation
	Rtoe2	Distal 2 <sup>nd</sup> toe	Used for defining foot anatomical axes

**Table 2.3.1. Kinematic Markers and Locations.** Placements determined calculations in all axes.



**Figure 2.3.3. Foot-switch.** One foot-switch was placed on the heel and toe of the shoe sole of each foot.

## 2.4 DATA ANALYSIS

### *Dynamic Visual Acuity (DVA)*

Data regarding the sizes of the displayed optotypes and the subject responses were analyzed using a similar probability calculation used to determine the size of the displayed optotypes during the test. During pre-adaptation and post-adaptation ITLP, the subject's visual acuity threshold was assumed to be the point of the maximum probability (Peters and Bloomberg 2005). Post-adaptation ITLP logMAR values were averaged ( $\pm$  95% CI) across subjects and compared to the pre-adaptation ITLP logMAR averages ( $\pm$  95% CI) across subjects to determine significant changes.

## ***Kinematics***

Three-dimensional position information of each marker relative to a coordinate frame coincident with the surface of the treadmill was processed using the Motion Analysis System's analysis software as depicted in Figure 2.4.1 (Motion Analysis Corp., Santa Rosa, CA). The marker trajectories were filtered using a fourth order low-pass, zero phase response, Butterworth filter with its cut-off frequency at 6 Hz. A segmental axis system was defined using a right-hand orthogonal system based on bony landmarks obtained during the quiet standing trial and was used to provide a consistent frame of reference independent of body segment position (McConville et al. 1980). The rotational motion of a body in 3-D space or relative to another body may be defined using a transformation matrix between the laboratory inertial axes and a set of body fixed axes or between the two sets of body fixed axes. An eularian angle convention referred to as the gyroscopic system was used to calculate the angular motion about the three axes for the segment axes defined using the quiet standing trial (zero reference angle) (Chao 1980 Mulavara et al. 2002; Mulavara and Bloomberg 2003). The vertical (z-axis) torso translation was determined from the marker placed coincident with the tip of the C7 spinous process.

## **Measuring Head Reflexive Control Mechanisms**

To investigate the changes in reflexive head control due to prolonged BWS, we measured head movement, torso movement and torso vertical translation motion with respect to space, as well as head movements with respect to torso in the reflexive head control frequency ranges. Each variable was binned into 10-second periods for each trial and was subjected to Fourier analysis with a frequency resolution of 0.1Hz as depicted in Figure 2.4.2. The amplitude of the signals in the frequency range of 1.5–2.5Hz was summed to estimate the predominant contributions of vestibular reflexive mechanisms to head pitch movement control, and 0.5 – 1.5 Hz for roll and yaw movement control

(Keshner et al. 1995a; Keshner et al. 1995b; Keshner and Peterson 1992,; Mulavara and Bloomberg 2003; Mulavara and Bloomberg 2005). It has been shown that during driven locomotion, head pitch frequency matches the frequency of stepping, and reflexive control mechanisms are most dominant in the bandwidth of 0.8 – 1.9 Hz. Reflexive head control contributions were found for head yaw to be between 0.8 – 1.6 Hz bandwidths, and for head roll between 1.0 – 1.6 Hz (Keshner and Peterson 1992). The coordination between the head and torso was measured using the cross correlation function between the head and torso pitch with respect to space as well as that between the head pitch and torso vertical translation with respect to space. The temporal variations of the head pitch angular position, torso pitch angular position and vertical torso translation with respect to space for each trial were time normalized over the gait cycle - heel strike (0%) to the following heel strike (100%) of the right foot - at one percent gait cycle intervals. These time-normalized waveforms were used to determine the cross correlation functions between the head pitch and torso pitch orientations (HPTP) and the head pitch and torso vertical translations (HPTV). The maximum and minimum values closest to the zero phase lag were quantified as the estimate of coordination between the head and torso pitch orientations and the head pitch and vertical torso translations, respectively. Trials in which HPTP values exceeded 20% gait cycle intervals from zero phase lag and which HPTV values exceeded 10% gait cycle intervals from zero phase lag were not included in the analysis.

### **Measuring Total Movement At Heel Strike**

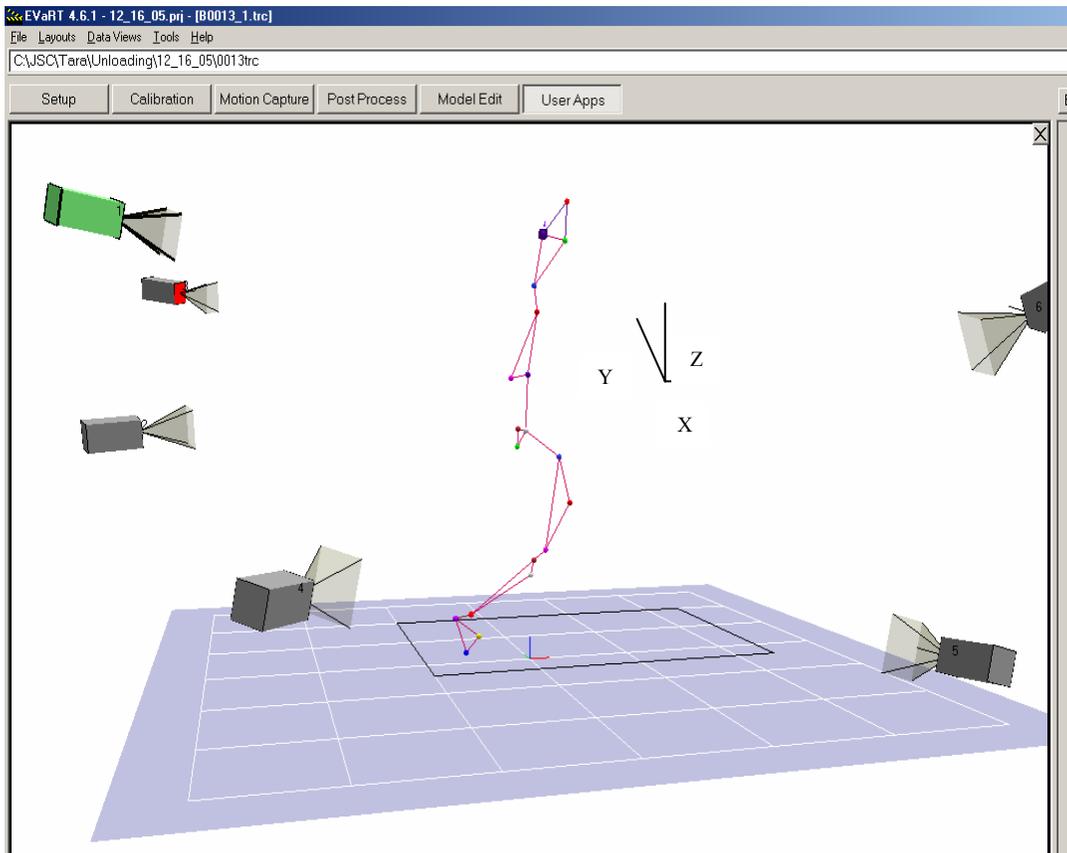
The high-energy transfer phases of the gait cycle occur during the double support phase of locomotion when the foot contacts the ground (heel strike), weight transfers from one foot to the other, and the toe pushes off from the ground (initial peak knee flexion) as depicted in Figure 2.4.3 (a), (b). Following the heel strike event, both legs are

on the support surface (double support phase). During this period, one leg moves into flexion while the other leg gets ready to push off from the support surface. The event of the push-off marks the completion of weight transfer from the trailing leg to the leading right leg (Mulavara and Bloomberg 2003). McDonald et al. (1996) and Layne et al. (1997) reported that the threat to gaze stabilization comes not only from the heel strike event of the gait cycle, but also the toe push-off events during walking. Therefore, to determine the joint responses that help reduce disturbances to the head from the high-energy transfer events during locomotion following 40% BWS adaptation, the total movement angles of the ankle, knee, torso, and head in the sagittal plane were normalized with respect to their quiet standing trials and calculated in the time interval from heel strike to initial peak flexion (Bloomberg and Mulavara 2003, McDonald et al. 1996, Mulavara and Bloomberg 1999, Mulavara et al 2005).

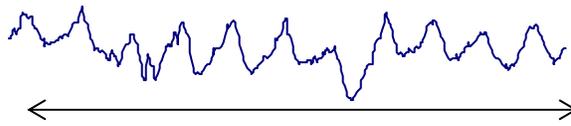
### ***Gait Cycle Timing***

One gait cycle was defined as the time when the heel foot-switch was turned on by the foot touching the ground to the following heel strike of the same foot. Heel strike and toe-off information from both feet were used to calculate the following parameter for the pre and post adaptation ITLP testing periods as depicted in Figure 2.4.4:

- Stride time (gait cycle time): Heel strike of the right foot to heel strike of the same foot;
- Stance time: Heel strike of the right foot to the following toe-off of the same foot; and,
- Double support time: Heel strike of the right foot to the toe off of the left foot.



**Figure 2.4.1. Motion Capture and Analysis.** Depiction of the three-dimensional position information of each marker relative to a coordinate frame coincident with the surface of the treadmill that was processed using the Motion Analysis System's analysis software.

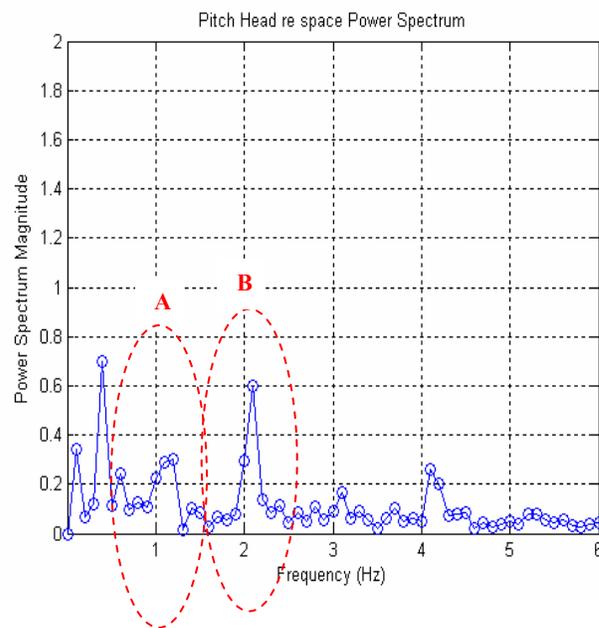


**Raw Movement Data**

**10 seconds**



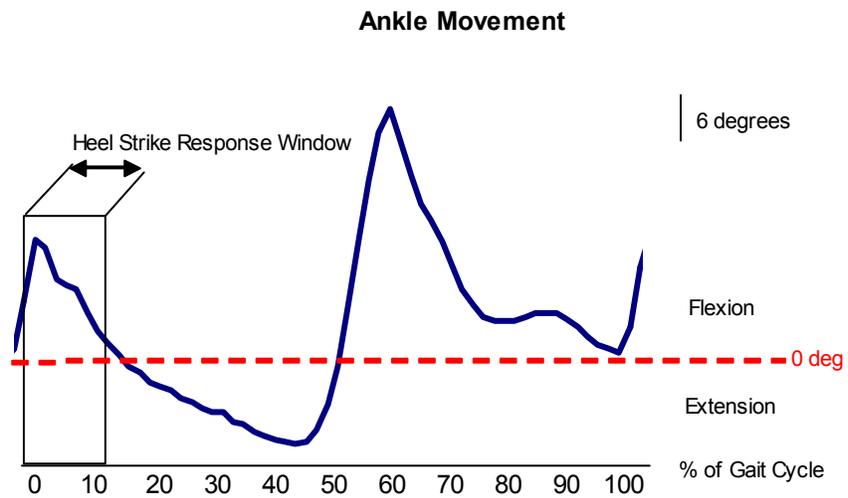
**Fourier Analysis**



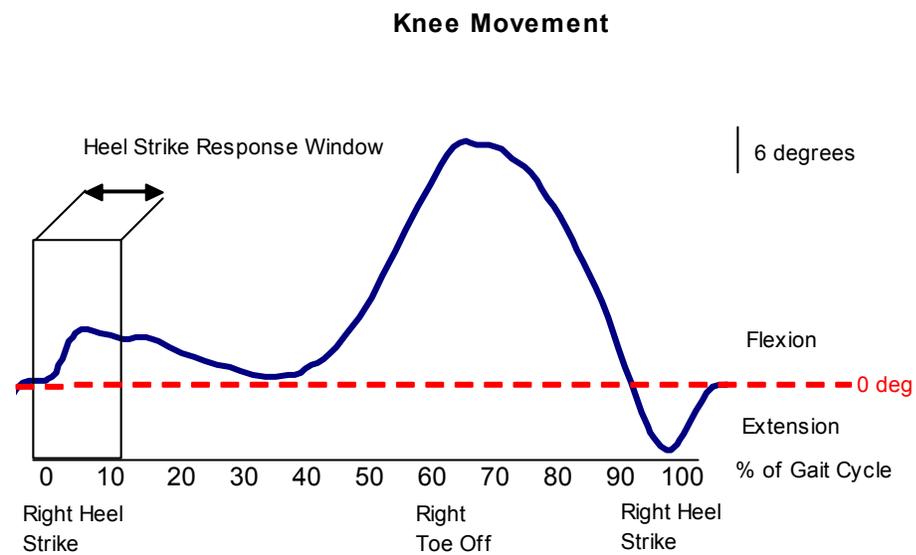
**Power Spectrum**

**Figure 2.4.2. Example of Frequency Analysis.** Raw movement data is placed into 10-second bins and processed by Fourier Analysis. A) Peak frequency of reflexive head movement control in the 0.5 – 1.5 Hz bandwidth for roll and yaw B) Peak frequency of reflexive head movement control in the 1.5 – 2.5Hz bandwidth for head pitch.

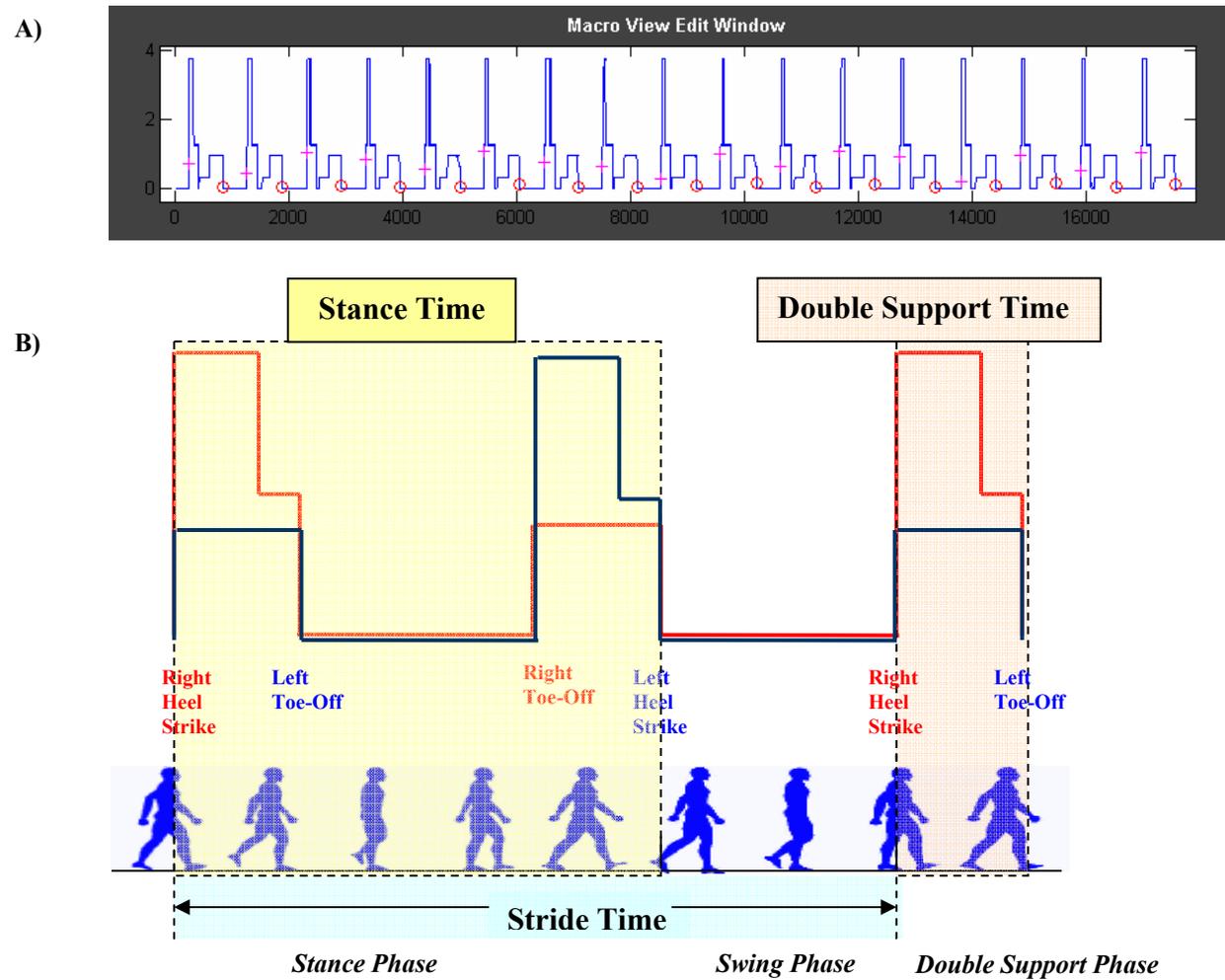
A)



B)



**Figure 2.4.3. Knee and Ankle Movement Waveforms.** Sample waveform of a typical subject depicting the ankle movement (A), and knee movement (B) through the entire gait cycle (0 to 100%). The red shaded area indicates the knee and ankle flexion in the time interval from heel strike to initial peak knee flexion, which is the variable of interest for this study.



**Figure 2.4.4. Gait Cycle Waveform.** A) Sample waveform of a subject depicting the gait cycle data from the right foot through 17 gait cycles. The red “+” indicates a heel strike event, and the red “o” indicates a toe-off event. B) Representation of the right (blue) and left (red) gait cycle event.

## 2.5 STATISTICAL ANALYSES

### *Sample Size*

All calculations for sample size were done using the statistical software GPOWER (Buchner et al. 1997, Cohen 1988). The sample size calculation was based on head pitch movement with respect to space data from a study by Mulavara and Bloomberg (2003) that identified full body contributions to gaze stabilization during locomotion. Using the factorial analysis of variance (ANOVA) design, assumptions for this calculation were an average head pitch movement with respect to space of  $2.96 \pm 0.34$  degrees (mean  $\pm$  standard deviation) with a change of  $\leq 23\%$  in the treatment group giving an effect size of  $\geq 0.25$ . This change in head pitch movement with respect to space would be detected in an F-test with probability (power) of  $\geq 0.80$  and a significance level of  $\leq 0.05$ , when the sample size is 12 subjects. Accommodating a 10% drop out of subjects recruited, the experiment required 13 subjects.

### *Data Analysis*

Previous studies have shown that sensorimotor integration tasks following an adaptive exposure are associated with a wide range of adaptive behavioral responses (Bloomberg et al. 1997, Davids et al. 2003, Layne et al. 1997, Mulavara et al. 2005). Therefore, each subject's movement patterns were examined individually and the predominant responses for the group were described in order to characterize the emergent strategies elicited among head and torso movement patterns during locomotion after the adaptive period. This method of data analysis has been accepted previously (Bloomberg et al. 1997, Davids et al. 2003, Mulavara et al. 2005). Individual subjects' post-adaptation performance was compared with the corresponding parameters prior to the BWS adaptive period for each of the variables: head pitch, roll, and yaw with respect to space, torso vertical translation with respect to space, torso roll, pitch, and yaw with

respect to space, head pitch, roll, and yaw with respect to torso in the bandwidth for head reflexive control; total ankle movement, total knee movement, total head movement, total vertical torso translation, and total torso pitch in the window from heel strike to peak knee flexion; stance time, stride time, and double support time. Due to data processing complications, of the 13 subjects obtained for this study, 10 were used for head and torso movement analysis, 12 were used for total ankle and knee movement analysis as well as stance time and stride time analysis, and 10 were used for double support time analysis.

For each variable that was obtained for analysis in the head reflexive frequency bandwidth, values from each 10-second bin were used across the last 60-second pre-adaptation ITLP trial, yielding 6 data points per subject. These 6 data points were then averaged ( $\pm 95\%CI$ ) and used as the “Pre” value. A preliminary analysis of the 10 post-adaptation ITLP trials performed indicated that greatest predominant changes occurred during the first post-adaptation ITLP walking trial immediately following the 30-minute 40% BWS adaptation protocol. Therefore, only the first trial (out of the entire 10 trials) was analyzed during the post-adaptation ITLP testing (“Post”) to determine whether there was a significant difference between pre- and post-values. For this post-ITLP trial, values from each 10-second bin were used across the first 60 seconds of the 70 second trial, yielding 6 data points per subject. These six data points were then averaged ( $\pm 95\% CI$ ) and used as the “Post” value. The same method of analysis was used for the data obtained for the variables of total movement within the window from heel strike to peak knee flexion; however, instead of processing as 10-second bins, the average of every 10 gait cycles was used. Subjects’ responses for each variable considered for analysis were classified into three groups based on the overlap of the Pre and Post confidence limits: Group A- Significantly increased (A), Group B – no change (B), and Group C – significantly decreased (C), relative to pre-adaptation values.

To determine the extent of adaptive change for the subjects who showed predominant changes for each variable, the percent-change was calculated for each

variable. For each subject, the percent-change was calculated between the average of the last 6 10-second bins (or gait cycles) of the pre-trial (“Pre” value) and each 10-second bin (or gait cycle) value in the first post-trial (“Post” value) as depicted by  $R_i$  (intra-trial) below. Calculation of  $R_i$  allows inspection of the immediate predominant changes that occur within the first post-trial by each 10-second bin, in an effort to detect any transient changes that may otherwise be missed if the 10-second bin values were averaged together to form one.  $R_a$  (across-trials) below depicts the percent-change between the average of the last 6 10-second bins (or gait cycles) of the pre-trial (“Pre” value) and the average of the first 6 10-second bins (or gait cycles) for each of the 10 post-trials (“Post” value for each post-trial) as follows:

$$(R_i)_k = \frac{(\text{Post Value})_k - \overline{\text{“Pre” Value}}}{\overline{\text{“Pre” Value}}} \times 100 \quad \text{Where } k = 1 \dots 6$$

10 sec. Bins (or  
gait cycles) of

$$(R_a)_j = \frac{(\text{Post Value})_j - \overline{\text{“Pre” Value}}}{\overline{\text{“Pre” Value}}} \times 100 \quad \text{Where } j = 1 \dots 10$$

post trials

After the individual subjects’  $R_i$  and  $R_a$  percent-change values were calculated, the values were averaged ( $\pm$  95% CI) across all of the subjects showing the predominant change for each variable and plotted to determine the extent of the change, and whether there was a trend towards recovery over time.

To identify relationships between all variables measured, a Pearson’s correlation analysis was performed on the  $R_i$  between pairs of variables. Only the  $R_i$  values were used in the Pearson’s analysis because, as mentioned previously, the greatest predominant changes in movements occurred within the first Post trial, immediately following the 30-minute 40% BWS adaptive period. Data were analyzed at a significance level of 0.05 using a standard statistical software packaged (SPSS v 10.0, Chicago, IL).

## **CHAPTER 3: RESULTS**

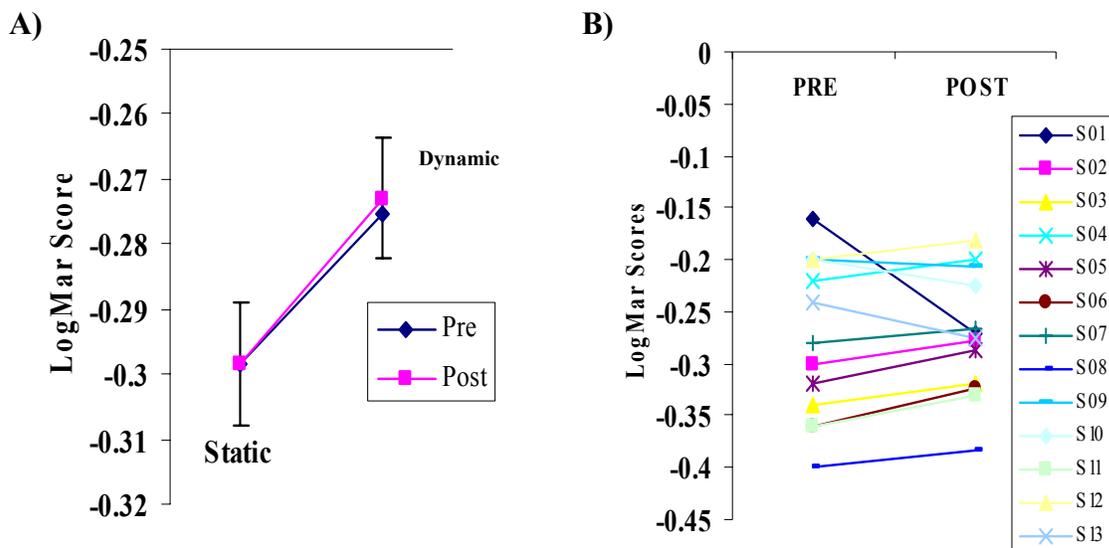
### **3.1 DYNAMIC VISUAL ACUITY**

The average DVA scores ( $\pm$  95% CI) across subjects (a) and within subjects (b) for static and pre- and post-adaptation ITLP scores are depicted in Figure 3.1.1. Figure 3.1.1 (a) shows the significant decrease in visual acuity between static and walking conditions, which is consistent with other studies investigating visual acuity changes during locomotion (Peters and Bloomberg 2005; Hillman et al. 1999). The overlapping confidence intervals between pre- and post-adaptation dynamic ITLP scores indicate that there was no significant change in the subjects' ability to maintain visual acuity following the BWS adaptation period. Figure 3.1.1 (b) shows that all subjects but one showed less than one line change decrement during the post-adaptation ITLP as compared to pre-adaptation ITLP DVA scores, indicating that there was no functional change in the subjects' ability to maintain the gaze stability task following adaptation (Peters and Bloomberg 2005).

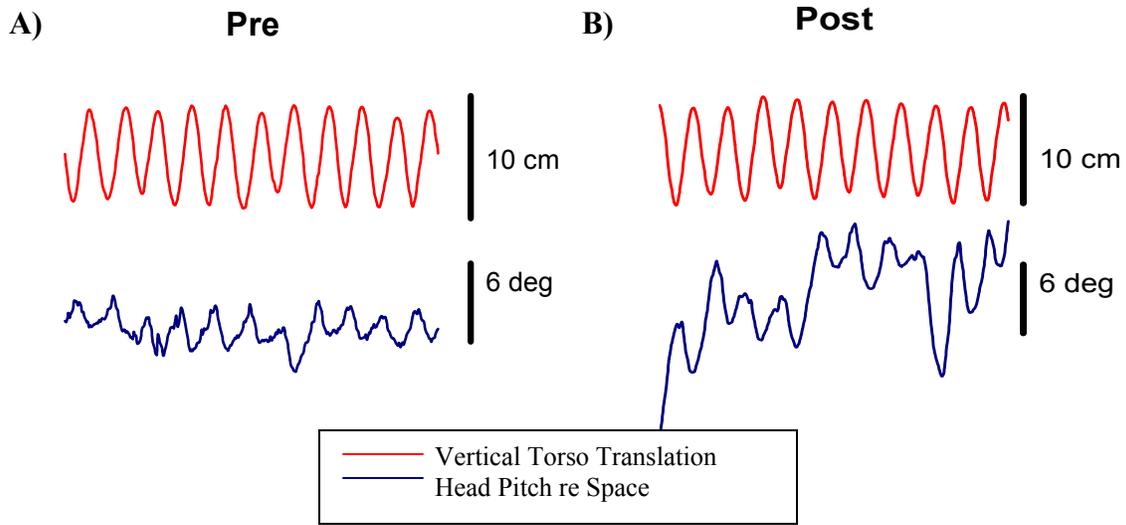
### **3.2 CHANGES IN THE HEAD REFLEXIVE CONTROL BANDWIDTHS**

Figure 3.2.1 shows an example from one subject of the relationship between vertical torso translation that occurs during each step of the gait cycle and the corresponding pitch angular head movement during the pre-adaptation period (a) and the post-adaptation period (b). During the pre- and post-adaptation ITLP testing, pitch head movements act in a compensatory manner to oppose the vertical torso translation while walking, thereby assisting in maintaining a stable vestibular platform. Following the 30-minute 40% BWS adaptation period, it is clear that this subject showed no change in

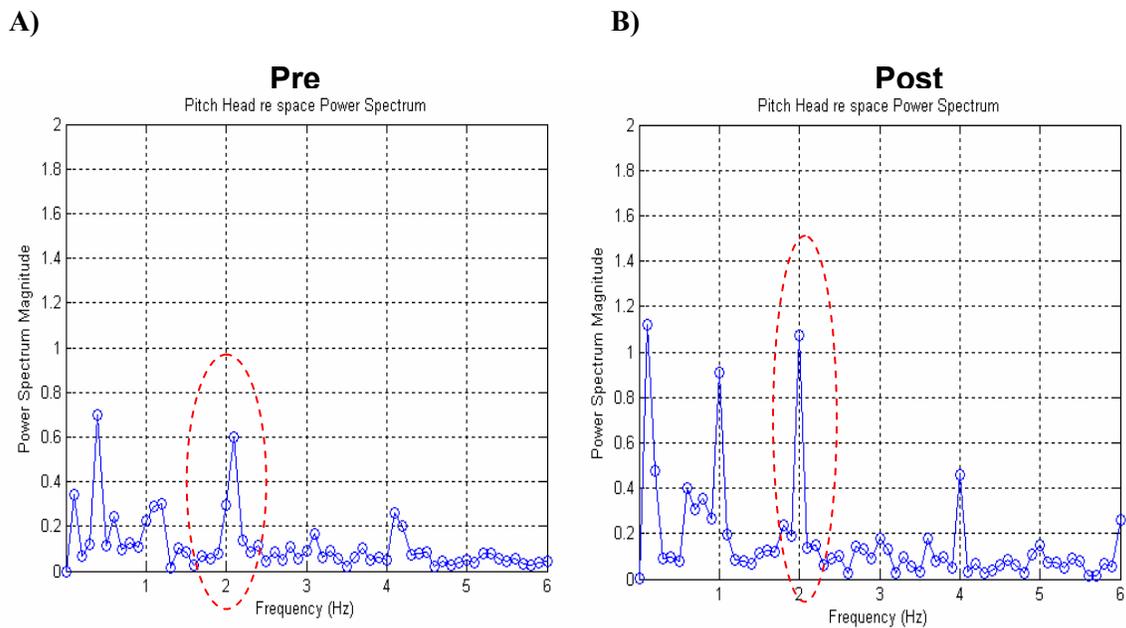
variation in vertical torso translation during locomotion; however, there appears to be a significant increase in the pitch angular head movements. Figure 3.2.2 depicts a pre-adaptation and post-adaptation example from one subject of a Fourier amplitude spectra of pitch angular head movement during locomotion. There is an apparent increase in the amplitude of the predominant frequency component at 2 Hz in the post-adaptation spectrum.



**Figure 3.1.1. DVA Results.** There was no significant change in DVA scores following BWS locomotion. **A).** The significant decrease in DVA values is typical during walking (dynamic) versus standing (static). There was no change in pre- and post-adaptation ITLP scores during walking. **B).** All but one subject showed less than one line change in DVA following BWS adaptation.



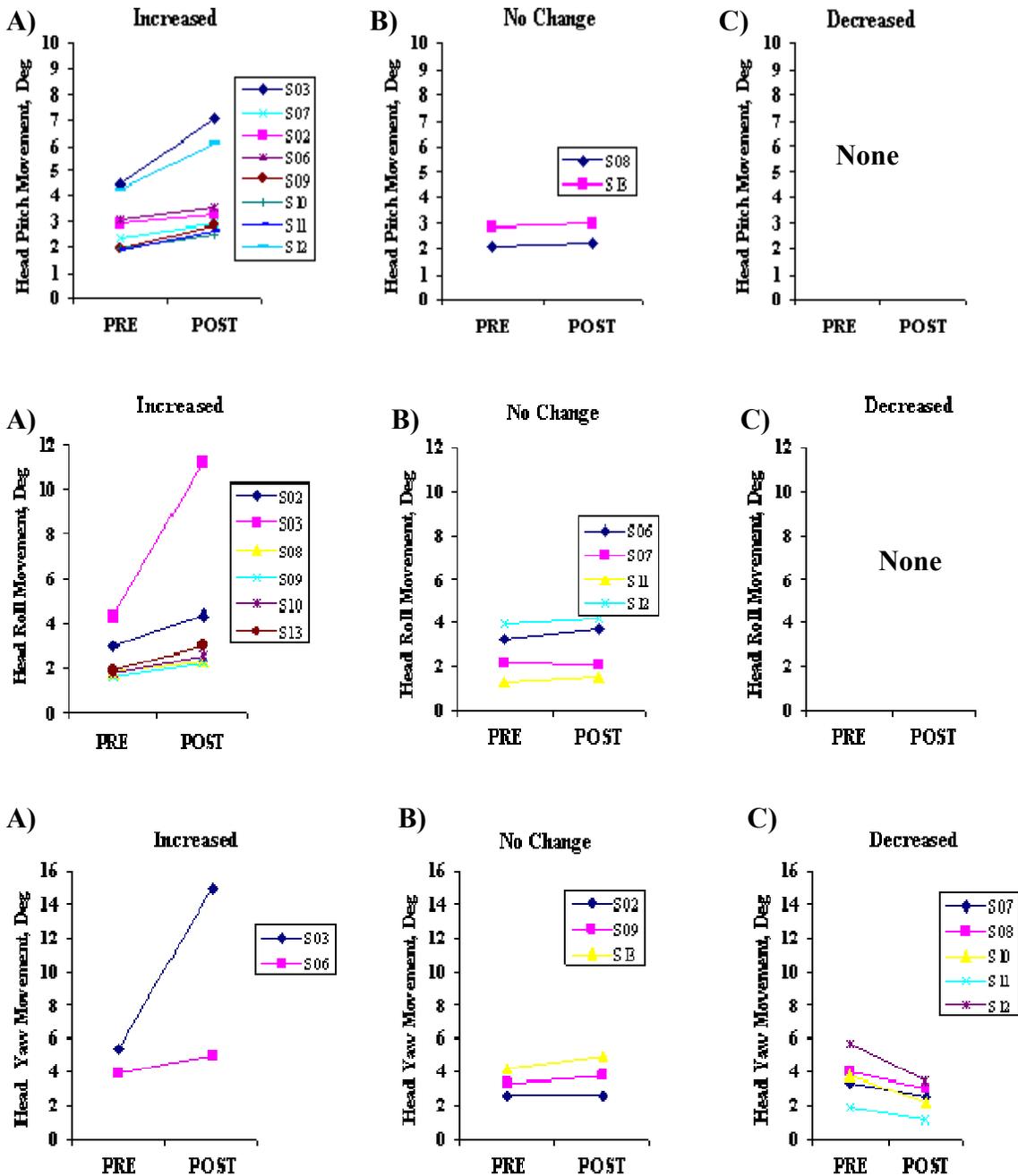
**Figure 3.2.1. Waveforms of Torso Translation and Head Pitch Movement.** Exemplar waveform of a typical subject depicting the relationship between vertical translation of the torso and corresponding pitch angular head movement while walking on the data collection treadmill. Note the increased amplitude in head pitch re space during the post-adaptation ITLP data collection (B) as compared to pre-adaptation ITLP data (A), while vertical torso translation remains unchanged.



**Figure 3.2.2. Fourier Amplitude Spectra of Head Pitch Movement.** Exemplar Fourier amplitude spectra of pitch head angular displacement for one subject during treadmill locomotion. Note the increase in the amplitude of the predominant frequency component at 2 Hz for the post-adaptation ITLP (B) as compared to the pre-adaptation ITLP component (A).

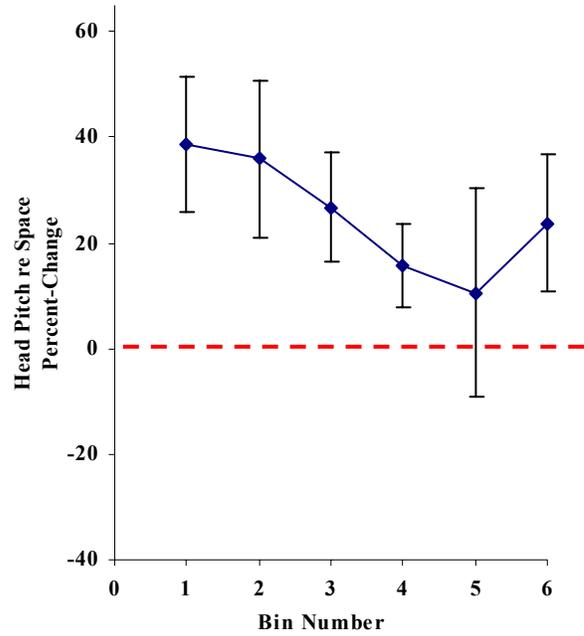
The Pre and Post average for each subject of the sum of the magnitude under the spectral curve in the 1.5 – 2.5Hz bandwidth for the angular head pitch movement, and 0.5-1.5 Hz bandwidth for the angular head roll and yaw movement with respect to space is depicted in Figure 3.2.3 (top row: head pitch movement, degrees), angular head roll with respect to space (middle row: head roll movement, deg), and angular head yaw with respect to space (bottom row: head yaw movement, deg). After 40% BWS adaptation, 8/10 subjects (80%) showed a significant increase in head pitch movement magnitudes, while the remaining 2/10 subjects (20%) showed no significant change. Six subjects (60%) showed a significant increase in head roll magnitudes, while the remaining 4/10 subjects (40%) showed no change. No subjects showed a significant decrease in magnitudes for head pitch and roll movements. Two subjects (20%) showed a significant increase in head yaw movement magnitudes, while 3/10 subjects (30%) showed no significant change and the remaining 5/10 subjects (50%) showed a significant decrease in head yaw movement magnitudes. Thus, such significant changes seen in the majority of the subjects in this study indicates a modification in the reflexive head control mechanisms.

Figures 3.2.4, 3.2.5, and 3.2.6 show the average percent-changes for the subjects who showed significant changes in head pitch with respect to space, head roll movement re space, and head yaw movement re space, respectively. The average ( $\pm$  95% CI) percent-change, “ $R_i$ ” across subjects between pre- and post-adaptation ITLP values for each 10-second bin during the last 60 seconds was determined and depicted as (A). The average ( $\pm$  95% CI) percent-change, “ $R_a$ ” across subjects between the pre- and post-adaptation ITLP values for each 10-second bin during the first 60 seconds of each of the 10 post-adaptation ITLP trials was determined and depicted as (B). Confidence intervals that cross the red line at zero indicate a significant return to pre-adaptation values. Subjects showed a clear significant return to pre-adaptation values after the fourth post-adaptation ITLP trial.

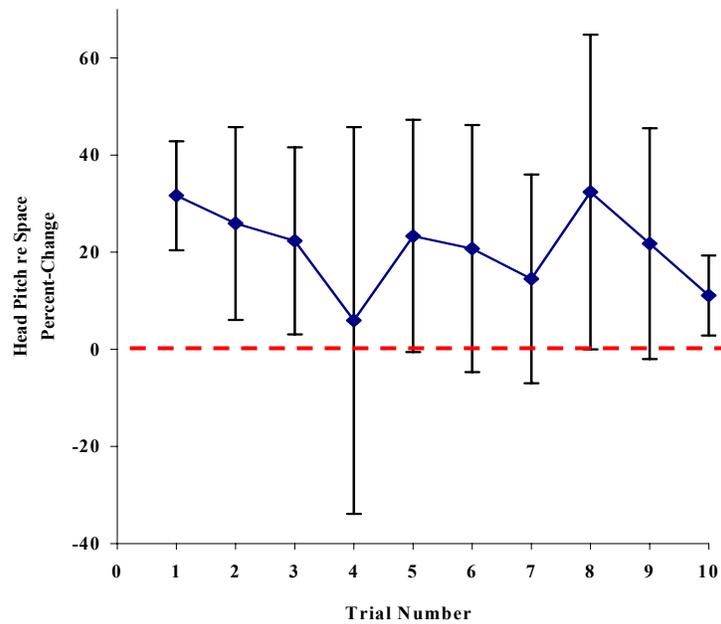


**Figure 3.2.3. Head Movement re Space.** Pre and Post average for each subject of the sum of the magnitude under the spectral curve in the reflexive bandwidths for the head angular pitch motion with respect to space (top row: head pitch movement, deg), the head roll motion with respect to space (second row: head roll movement, deg), and the head yaw motion with respect to space (bottom row: head yaw movement, deg). **A)** significantly increased, **B)** no change, and **C)** significantly decreased, relative to pre-adaptation trials.

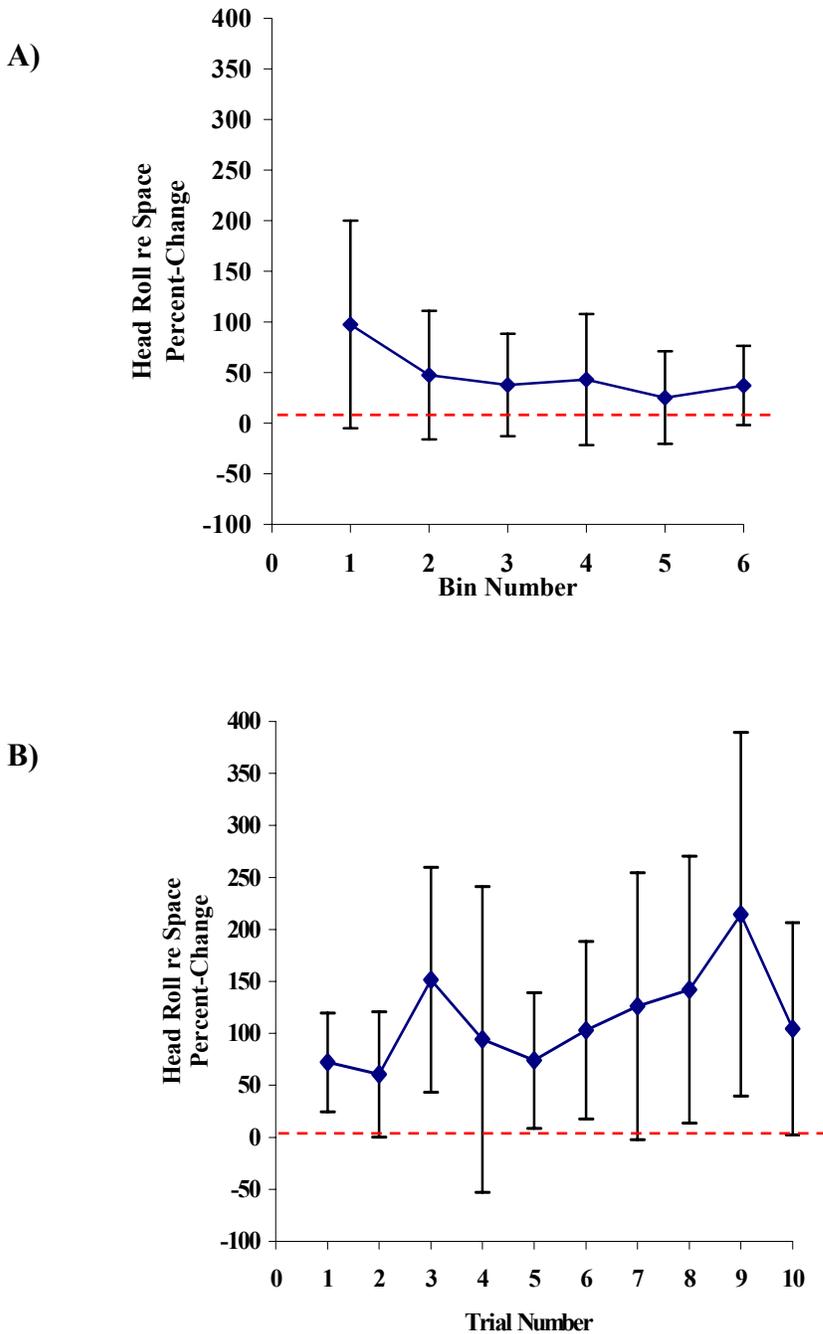
A)



B)

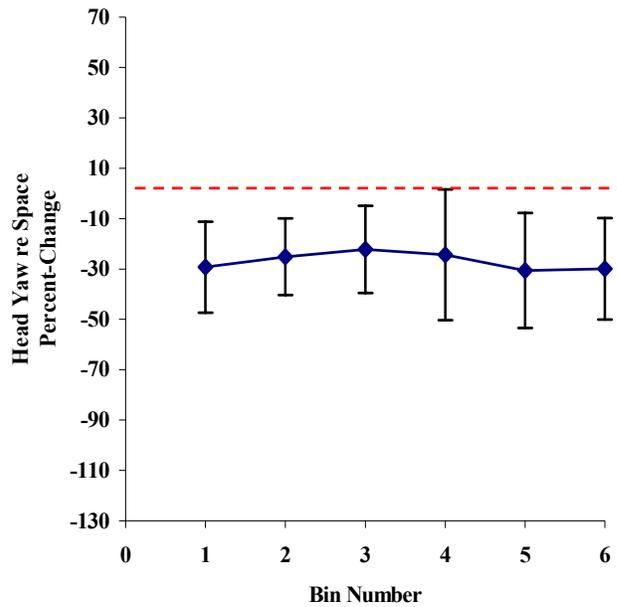


**Figure 3.2.4. Head Pitch re Space Percent-Change Curves.** A percent-change curve was established for head pitch movement re space in the 1.5-2.5 Hz reflexive control bandwidth to determine if the 8/10 subjects who showed a significant increase subsequently showed a return to pre-adaptation values. Values that cross the red line indicate return to pre-adaptation values. **A)** The average ( $\pm 95\%$  CI) percent-change ( $R_i$ ) across subjects between pre- and post-adaptation ITLP values for each 10-second bin during the first 60 sec of the first post-ITLP trial and **B)** The average ( $\pm 95\%$  CI) percent-change across subjects between pre- and post-adaptation ITLP values for the first 60 sec of each of the 10 post-adaptation trials ( $R_a$ ).

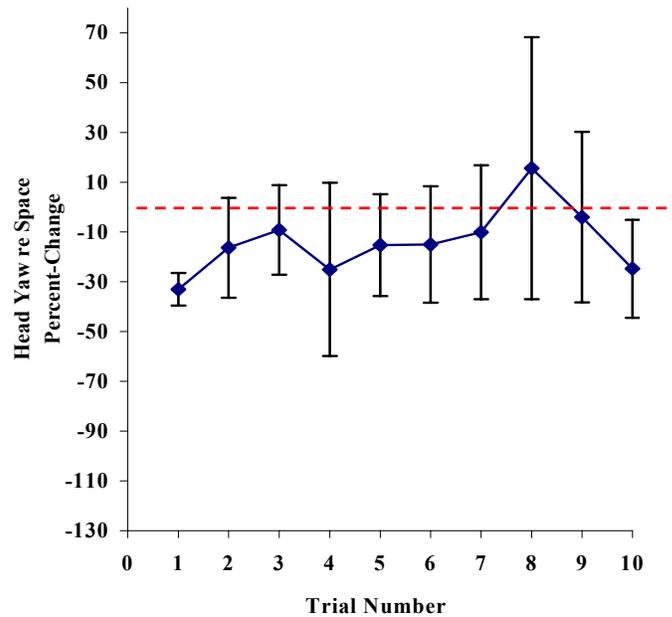


**Figure 3.2.5. Head Roll re Space Percent-Change Curves.** A percent-change curve was established for head roll movement re space in the 0.5 – 1.5 Hz bandwidth to determine if the 6/10 subjects who showed a significant increase subsequently showed a return to pre-adaptation values. Values that cross the red line indicate return to pre-adaptation values. **A)** The average ( $\pm 95\%$  CI) percent-change ( $R_i$ ) across subjects between pre- and post-adaptation ITLP values for each 10-second bin during the first 60 sec of the first post-ITLP trial and **B)** The average ( $\pm 95\%$  CI) percent-change across subjects between pre- and post-adaptation ITLP values for the first 60 sec of each of the 10 post-adaptation trials ( $R_a$ ).

A)



B)



**Figure 3.2.6. Head Yaw re Space Percent-Change Curves.** A percent-change curve was established for head yaw movement re space in the 0.5 – 1.5 Hz bandwidth to determine if the 5/10 subjects who showed a significant decrease subsequently showed a return to pre-adaptation values. Values that cross the red line indicate return to pre-adaptation values. **A)** The average (+95% CI) percent-change ( $R_i$ ) across subjects between pre- and post-adaptation ITLP values for each 10-second bin during the first 60 sec of the first post-ITLP trial and **B)** The average (+95% CI) percent-change across subjects between pre- and post-adaptation ITLP values for the first 60 sec of each of the 10 post-adaptation trials ( $R_a$ ).

The Pre and Post average for each subject of the sum of the magnitude under the spectral curve in the 1.5-2.5 Hz bandwidth for the vertical torso translation with respect to space is shown in Figure 3.2.7 (torso translation, mm). After 40% BWS adaptation, 1/10 subject (10%) showed a significant increase in torso translation, while 8/10 subjects (80%) showed no significant change, and 1/10 subjects (10%) showed a significant decrease. These results clearly indicate that torso vertical translation during post-adaptive locomotion was not affected by the increased BWS adaptive protocol.

The Pre and Post average for each subject of the sum of the magnitude under the spectral curve in the 1.5 – 2.5 Hz bandwidth for the torso pitch movement, and 0.5- 1.5 Hz bandwidth for the torso yaw and roll movement with respect to space is depicted in Figure 3.2.8 (top row: torso pitch movement, deg), torso roll movement magnitude (second row: torso roll movement, deg), and torso yaw movement magnitude (third row: torso yaw movement, deg). Four subjects (40%) showed a significant increase in torso pitch movement with respect to space, while 5/10 subjects (50%) showed no significant change, and only 1/10 subject (10%) showed a significant decrease in movement. Four subjects (40%) showed a significant increase in torso roll magnitude, 4/10 subjects (40%) showed no significant change, and only 2/10 subjects (20%) showed a significant decrease in torso roll magnitude. For torso yaw movement, 6/10 (60%) showed no significant change in magnitude, while only 2/10 (20%) showed each an increase and a decrease. Thus, to some extent, torso angular movement was modified following the BWS adaptive protocol in the majority of subjects.

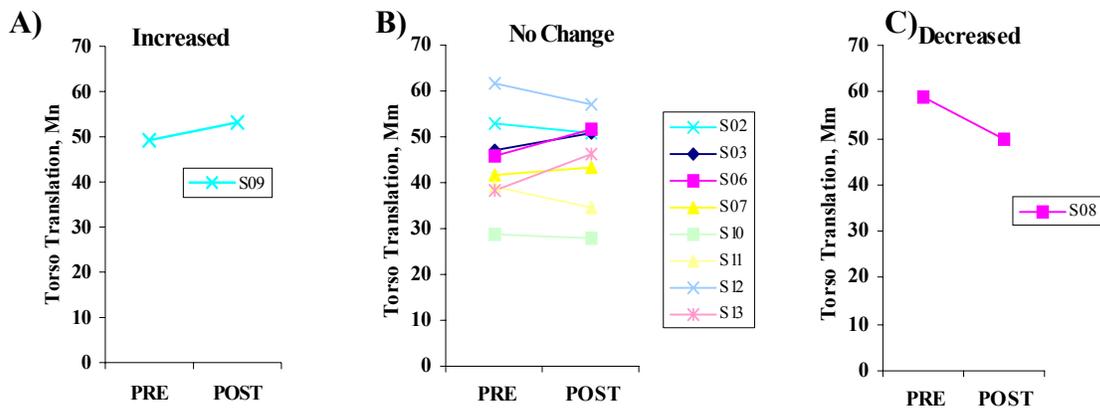
The Pre and Post average for each subject of the sum of the magnitude under the spectral curve in the 1.5 – 2.5 Hz bandwidth for the angular head pitch movement, and the 0.5-1.5 Hz bandwidth for the angular head roll and yaw movement with respect to torso is depicted in Figure 3.2.9 (top row: head pitch re torso movement, deg), head roll angular movement magnitude with respect to torso (middle row: head roll re torso movement, deg), and head yaw angular movement magnitude with respect to torso

(bottom row: head yaw re torso movement, deg). Six subjects (60%) showed a significant increase in head pitch movement with respect to torso, while 4/10 (40%) subjects showed no significant change, and no subjects showed a significant decrease. Four subjects (40%) showed a significant increase in head roll magnitude with respect to torso movement, 3/10 (30%) subjects showed no significant change and 3/10 (30%) subjects showed a significant decrease in head roll magnitude with respect to torso movement. For head yaw movement, 3/10 (30%) subjects showed an increase in magnitude with respect to torso movement, while 4/10 (40%) subjects showed no change and 3/10 (30%) showed a significant decrease. These results are in agreement with the changes in head re space that were found following the BWS adaptive protocol.

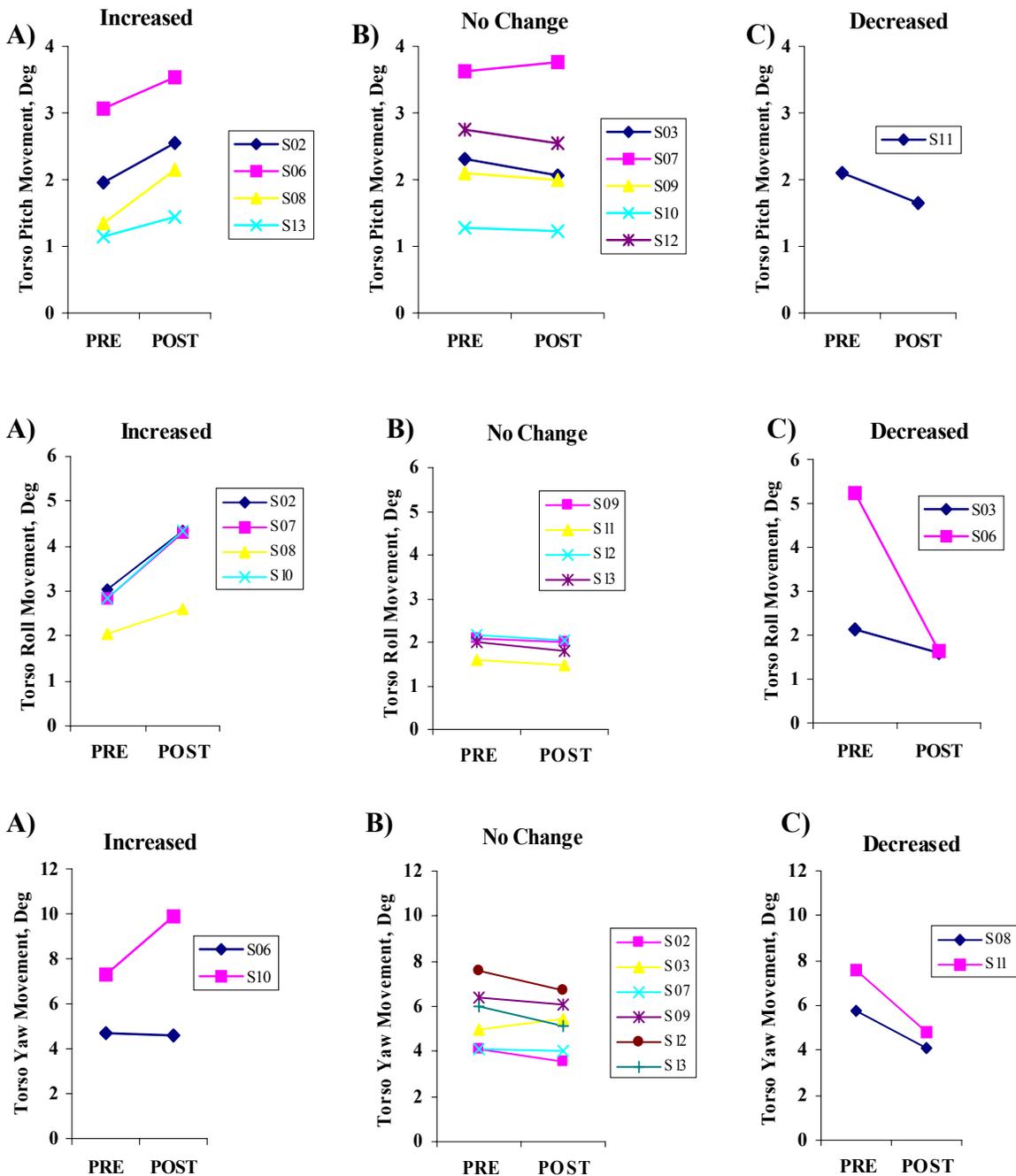
Figures 3.2.10, 3.2.11, and 3.2.12 show the percent-changes for the subjects who showed significant changes in head pitch movement with respect to torso, head roll movement re torso, and head yaw movement re torso, respectively. The average ( $\pm$  95% CI) percent-change, “ $R_i$ ” across subjects between pre- and post-adaptation ITLP values for each 10-second bin during the last 60 seconds was determined and depicted as (A). The average ( $\pm$  95% CI) percent-change, “ $R_a$ ” across subjects between the pre- and post-adaptation ITLP values for each 10-second bin during the first 60 seconds of each of the 10 post-adaptation ITLP trials was determined and depicted as (B). Confidence intervals that cross the red line at zero indicate a significant return to pre-adaptation values. Values remained elevated throughout all trials, and despite an apparent trend towards recovery within the first 60 seconds, there was no significant return to baseline values over all 10 post-trials, indicating a sustained change in response to the proprioceptive changes induced by 30 min of 40% BWS.

Cross-correlation analysis showed no significant change in coordination between the head pitch movement with respect to space and torso pitch movements with respect to space for 9/10 subjects (90%) for the post-adaptation period as compared to the pre-adaptation period, as depicted in Figure 3.2.13. Additionally, no significant changes were

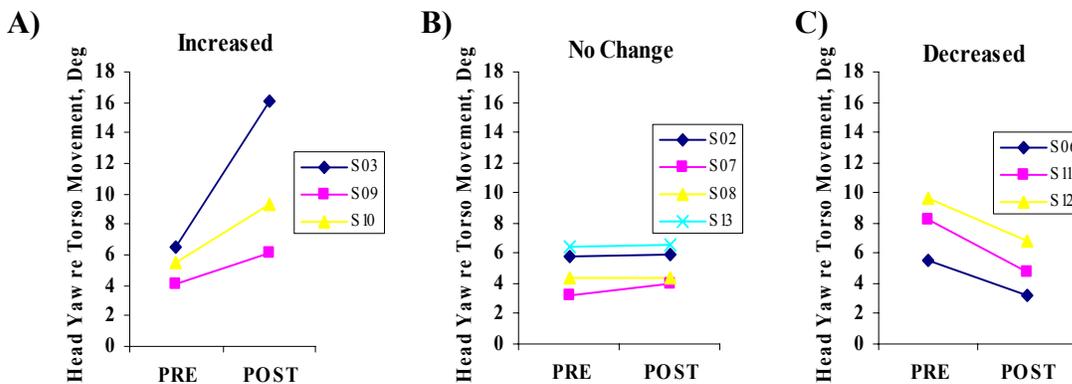
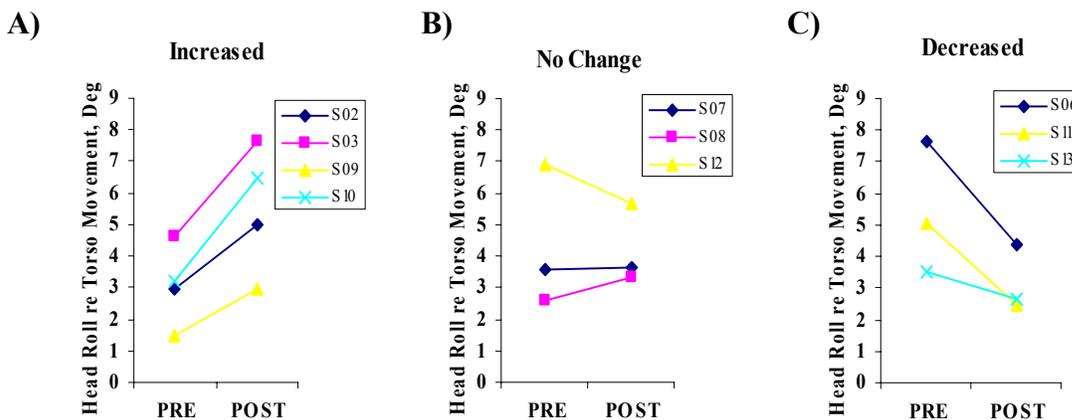
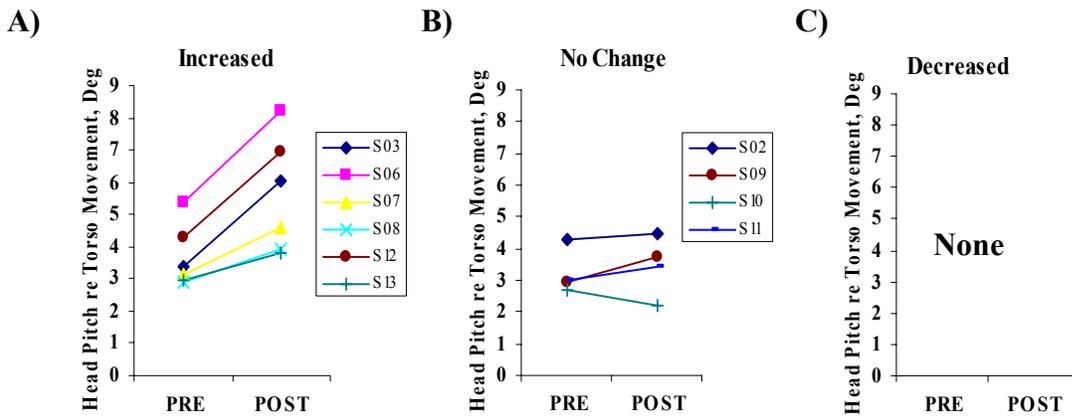
found for all subjects for a change in coordination between the head pitch with respect to space and torso vertical translation with respect to space. Thus, these results indicate that the patterns of coordination between head and torso movement were not significantly affected following the adaptive BWS period.



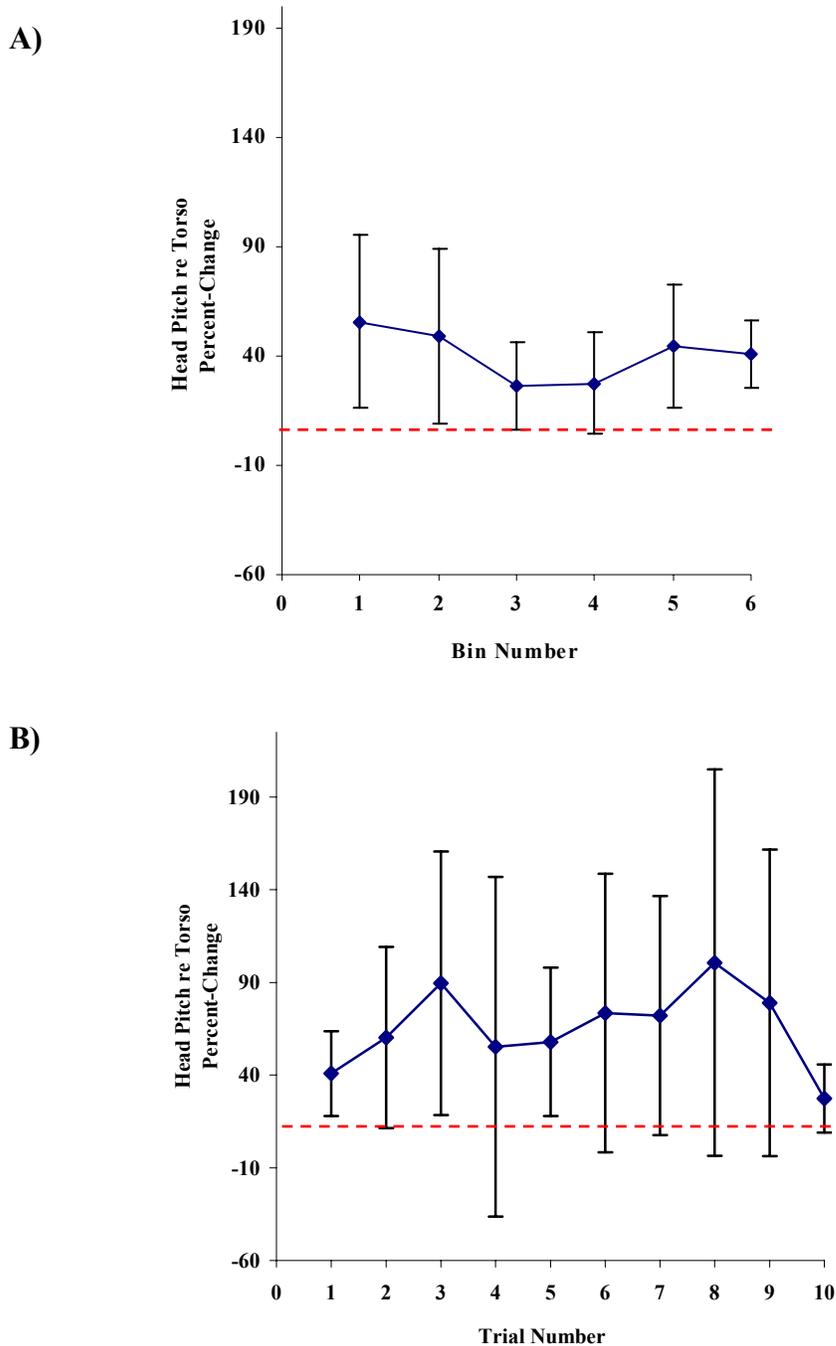
**Figure 3.2.7. Vertical Torso Translation.** Pre and Post average for each subject of the sum of the magnitude under the spectral curve in the 1.5-2.5 Hz bandwidth for the vertical torso translation. **A)** significantly increased, **B)** no change, and **C)** significantly decreased, relative to pre-adaptation trials



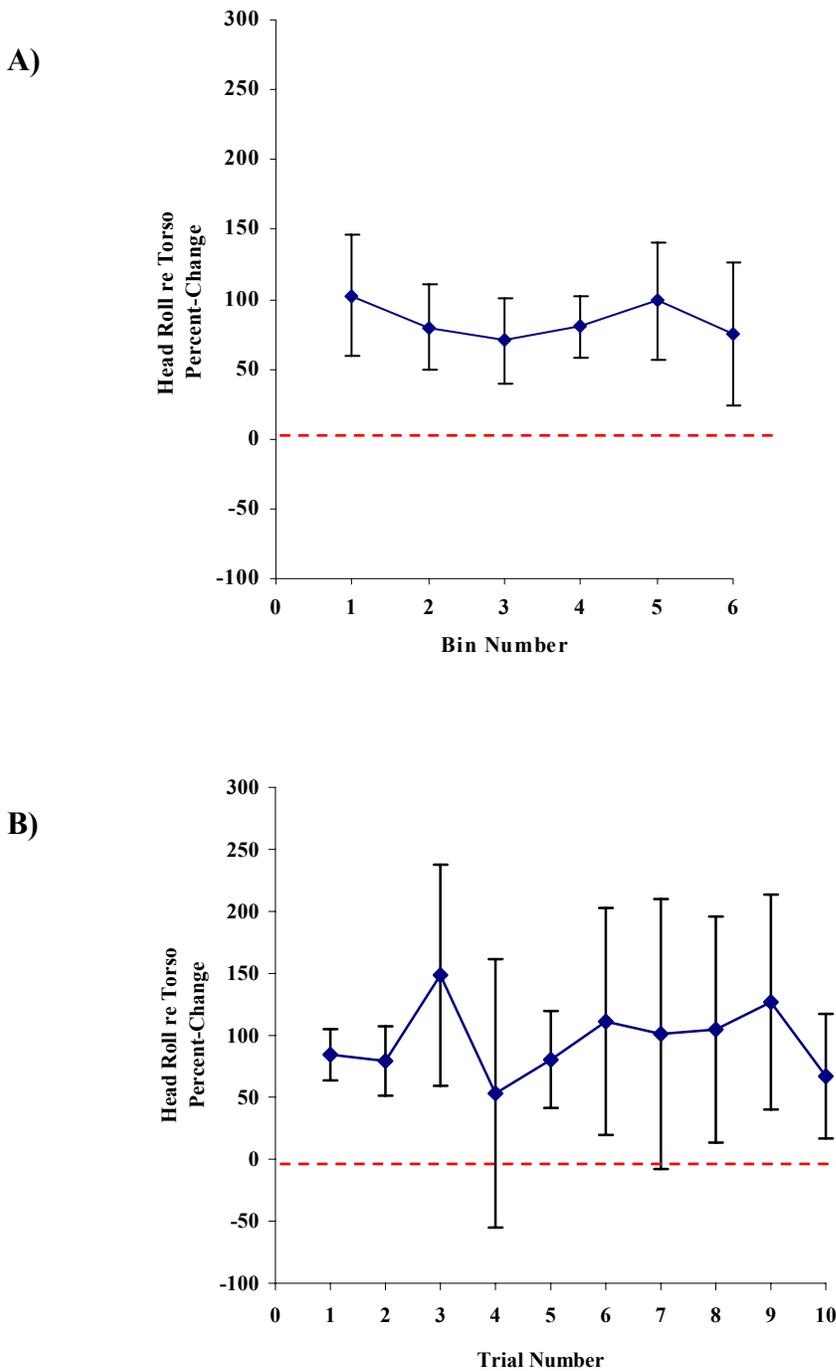
**Figure 3.2.8. Torso Movement re Space.** Pre and Post average for each subject of the sum of the magnitude under the spectral curve in the head reflexive control bandwidth for the torso angular pitch motion with respect to space (top row: torso pitch movement, deg), the torso roll motion with respect to space (second row: torso roll movement, deg), and the torso yaw motion with respect to space (bottom row: torso yaw movement, deg). **A)** significantly increased, **B)** no change, and **C)** significantly decreased, relative to pre-adaptation trials.



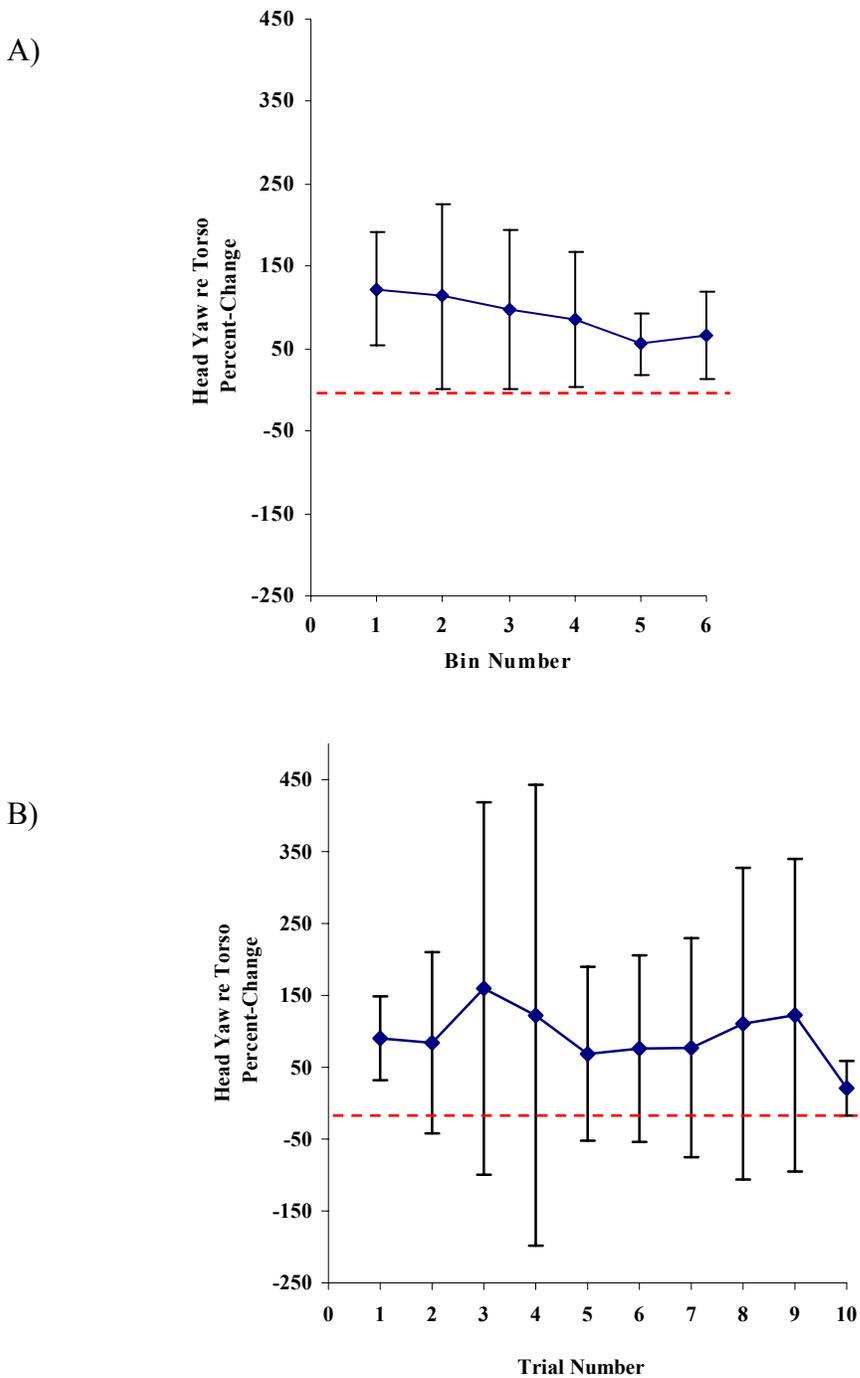
**Figure 3.2.9. Head Movement re Torso.** Pre and Post average for each subject of the sum of the magnitude under the spectral curve in the head reflexive control bandwidth for the head angular pitch motion with respect to torso (top row: head pitch re torso movement, deg), head angular roll motion with respect to torso (second row: head roll re torso movement, deg), and the head angular yaw motion with respect to torso (bottom row: head yaw re torso movement, deg). **A)** significantly increased, **B)** no change, and **C)** significantly decreased, relative to pre-adaptation trials.



**Figure 3.2.10. Head re Torso Pitch Percent-Change Curves.** A percent-change curve was established for head movement re torso pitch in the 1.5 – 2.5 Hz head reflexive control bandwidth to determine if the 6/10 subjects who showed a significant change (increase) subsequently showed a return to pre-adaptation values. Values that cross the red line indicate return to pre-adaptation values. **A)** The average ( $\pm 95\%$  CI) percent-change ( $R_i$ ) across subjects between pre- and post-adaptation ITLP values for each 10-second bin during the first 60 sec of the first post-ITLP trial and **B)** The average ( $\pm 95\%$  CI) percent-change across subjects between pre- and post-adaptation ITLP values for the first 60 sec of each of the 10 post-adaptation trials ( $R_a$ ).

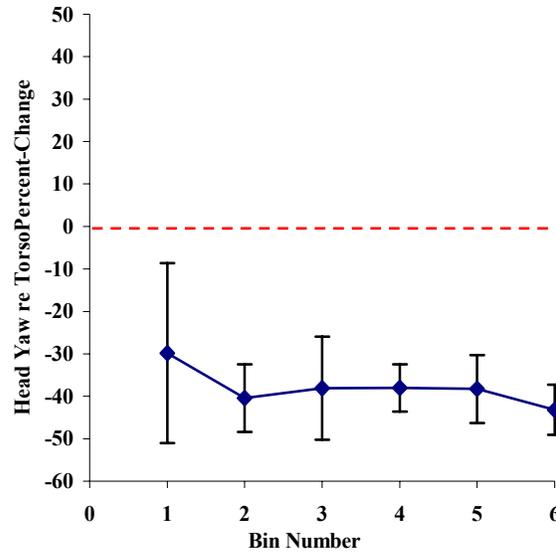


**Figure 3.2.11. Head re Torso Roll Percent-Change Curves.** A percent-change curve was established for head movement re torso roll in the 0.5 – 1.5 Hz head reflexive control bandwidth to determine if the 4/10 subjects who showed a significant increase subsequently showed a return to pre-adaptation values. Values that cross the red line indicate return to pre-adaptation values. **A)** The average ( $\pm 95\%$  CI) percent-change ( $R_i$ ) across subjects between pre- and post-adaptation ITLP values for each 10-second bin during the first 60 sec of the first post-ITLP trial and **B)** The average ( $\pm 95\%$  CI) percent-change across subjects between pre- and post-adaptation ITLP values for the first 60 sec of each of the 10 post-adaptation trials ( $R_a$ ).

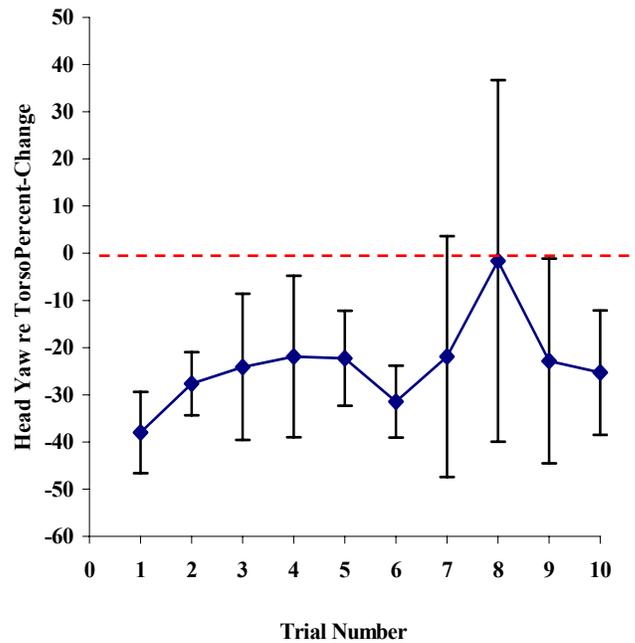


**Figure 3.2.12A. Head re Torso Yaw Percent-Change Curves (Increases).** A percent-change curve was established for head movement re torso yaw in the 0.5 – 1.5 Hz bandwidth to determine if the 3/10 subjects who showed a significant increase subsequently showed a return to pre-adaptation values. Values that cross the red line indicate return to pre-adaptation values. **A)** The average ( $\pm 95\%$  CI) percent-change ( $R_i$ ) across subjects between pre- and post-adaptation ITLP values for each 10-second bin during the first 60 sec of the first post-ITLP trial and **B)** The average ( $\pm 95\%$  CI) percent-change across subjects between pre- and post-adaptation ITLP values for the first 60 sec of each of the 10 post-adaptation trials ( $R_a$ ).

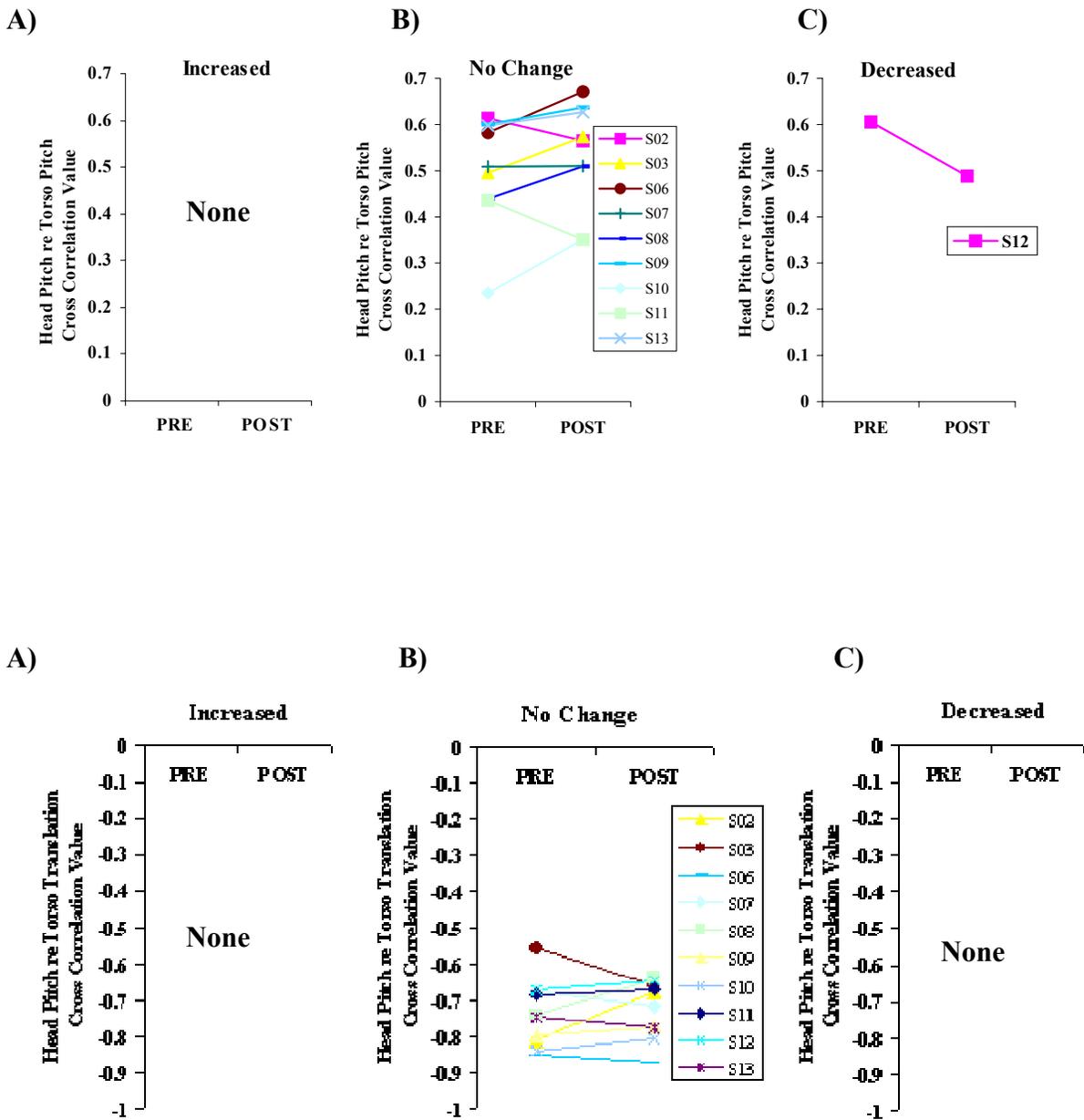
A)



B)



**Figure 3.2.12B. Head Yaw re Torso Percent-Change Curves (Decreases).** A percent-change curve was established for head movement re torso yaw in the 0.5 – 1.5 Hz bandwidth to determine if the 3/10 subjects who showed a significant decrease subsequently showed a return to pre-adaptation values. Values that cross the red line indicate return to pre-adaptation values. **A)** The average ( $\pm 95\%$  CI) percent-change ( $R_i$ ) across subjects between pre- and post-adaptation ITLP values for each 10-second bin during the first 60 sec of the first post-ITLP trial and **B)** The average ( $\pm 95\%$  CI) percent-change across subjects between pre- and post-adaptation ITLP values for the first 60 sec of each of the 10 post-adaptation trials ( $R_a$ ).



**Figure 3.2.13. Head Pitch Cross Correlation Values.** Pre and Post average for each subject of the cross correlation values for the head angular pitch motion with respect to torso pitch (top row: head pitch re torso pitch cross correlation values) and head angular pitch motion with respect to vertical torso translation in the 1.5-2.5 Hz head reflexive control bandwidth (bottom row: head pitch re vertical torso translation. **A)** significantly increased, **B)** no change, and **C)** significantly decreased, relative to pre-adaptation trials.

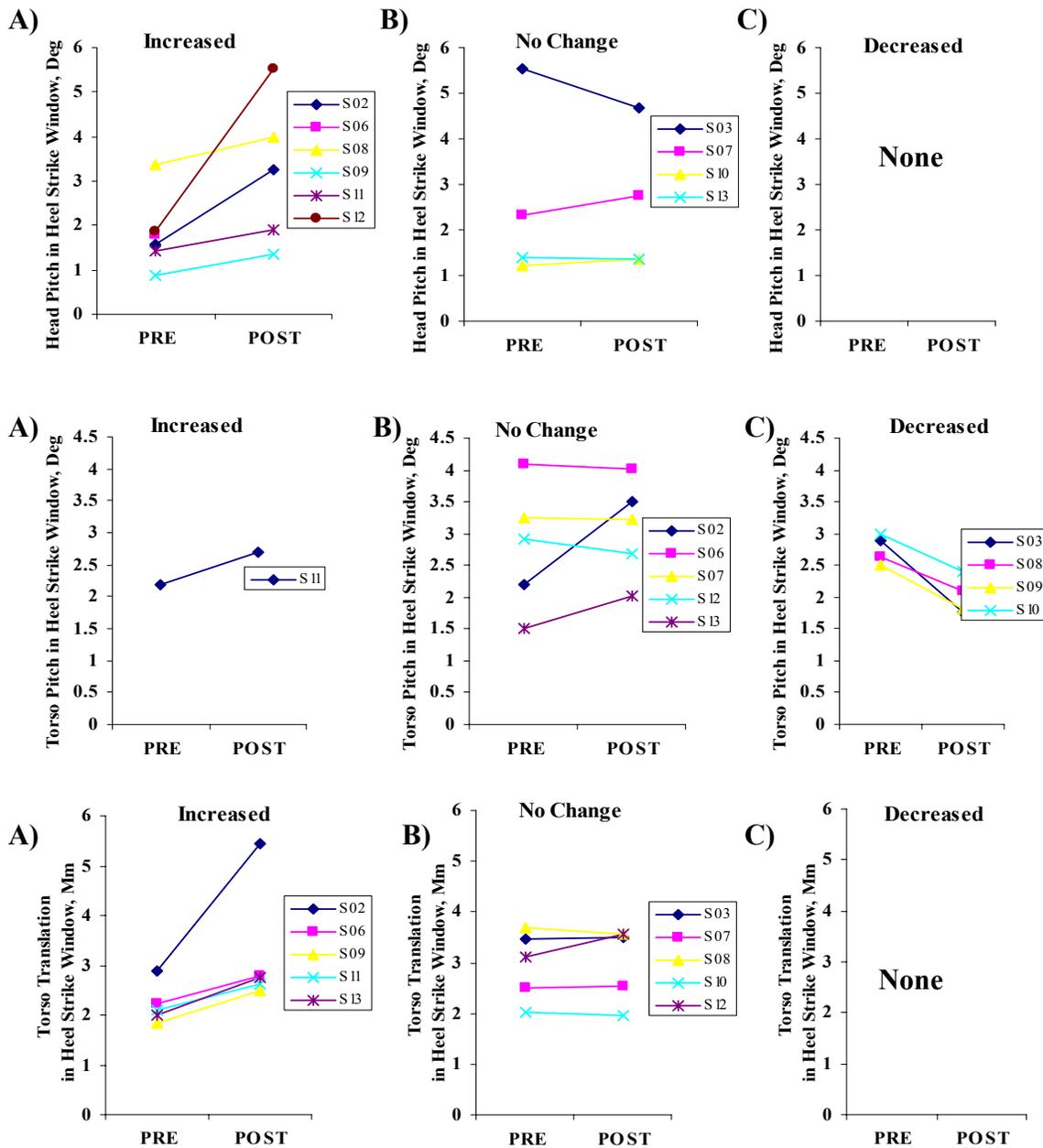
### 3.3 TOTAL MOVEMENT CHANGES IN THE HEEL STRIKE WINDOW

#### *Upper Body Changes*

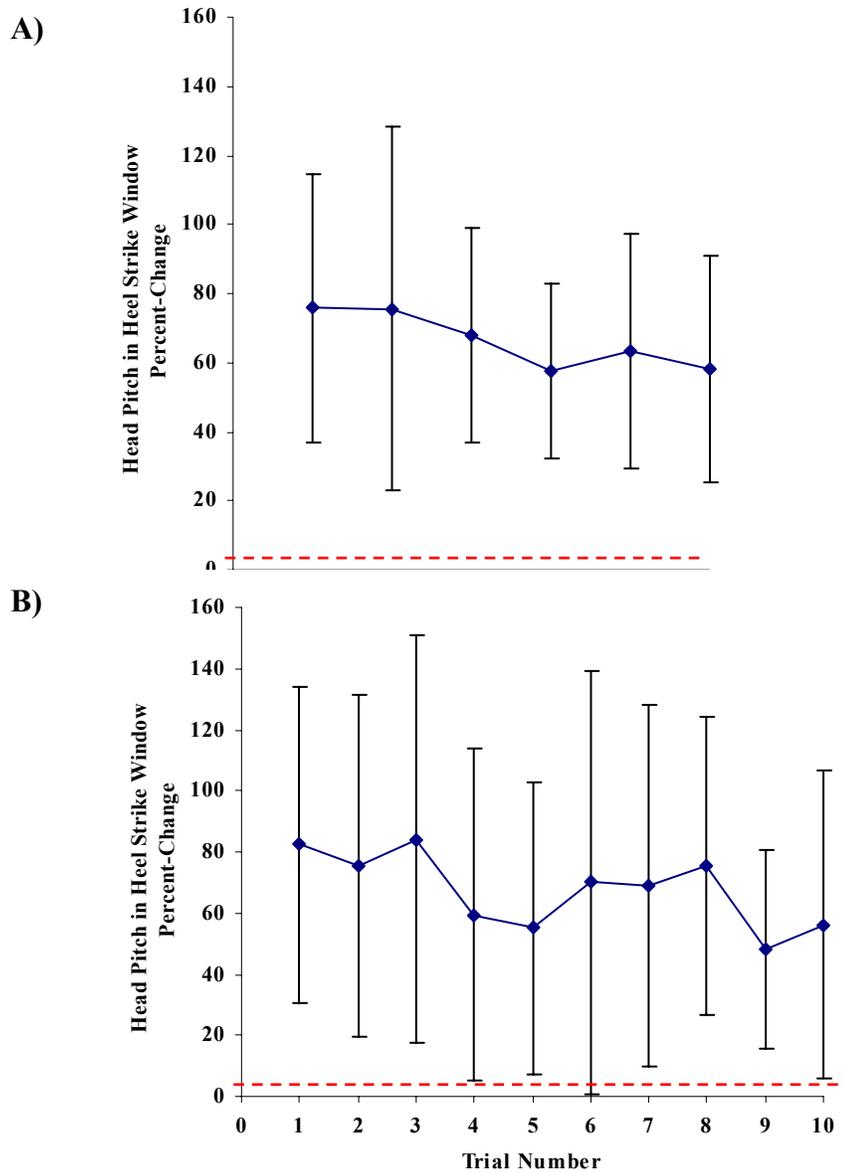
The Pre and Post average for each subject for the total movement within the window from heel strike to peak knee flexion is shown in Figure 3.3.1 for the head pitch movement with respect to space (top row: head pitch movement, degrees), torso pitch movement with respect to space (middle row: torso pitch movement, deg), and vertical torso translation (bottom row: vertical torso translation, deg). After BWS adaptation, 6/10 subjects (60%) showed a significant increase in head pitch movement magnitudes, while the remaining 4/10 subjects (40%) showed no significant change. One subject (10%) showed a significant increase in torso pitch magnitude, while 4/10 subjects (40%) showed a significant decrease, and 5/10 subjects (50%) showed no change. Five subjects (50%) showed a significant increase in vertical torso translation, while the remaining 5/10 (50%) showed no significant change. Thus, based on these results, it appears that significant adaptive changes occur in upper body segmental movements within the high-impact phase of the gait cycle of heel strike to peak knee flexion immediately following 30 minutes of exposure to 40% BWS.

Figures 3.3.2, 3.3.3, and 3.3.4 show the average percent-changes for the subjects who showed significant changes in the total head pitch movement with respect to space, total torso pitch movement with respect to space, and torso vertical translation with respect to space, respectively, within the heel strike window. The average ( $\pm$  95% CI) percent-change, “ $R_i$ ” across subjects between pre- and post-adaptation ITLP values for each 10-gait cycle bin during the last 60 seconds was determined and depicted as (A). The average ( $\pm$  95% CI) percent-change, “ $R_a$ ” across subjects between the pre- and post-adaptation ITLP values for each 10-gait cycle bin during the first 60 seconds of each of the 10 post-adaptation ITLP trials was determined and depicted as (B). Confidence intervals that cross the red line at zero indicate a significant return to pre-adaptation values. Subjects showed no return to pre-adaptation values over all 10 post-trials,

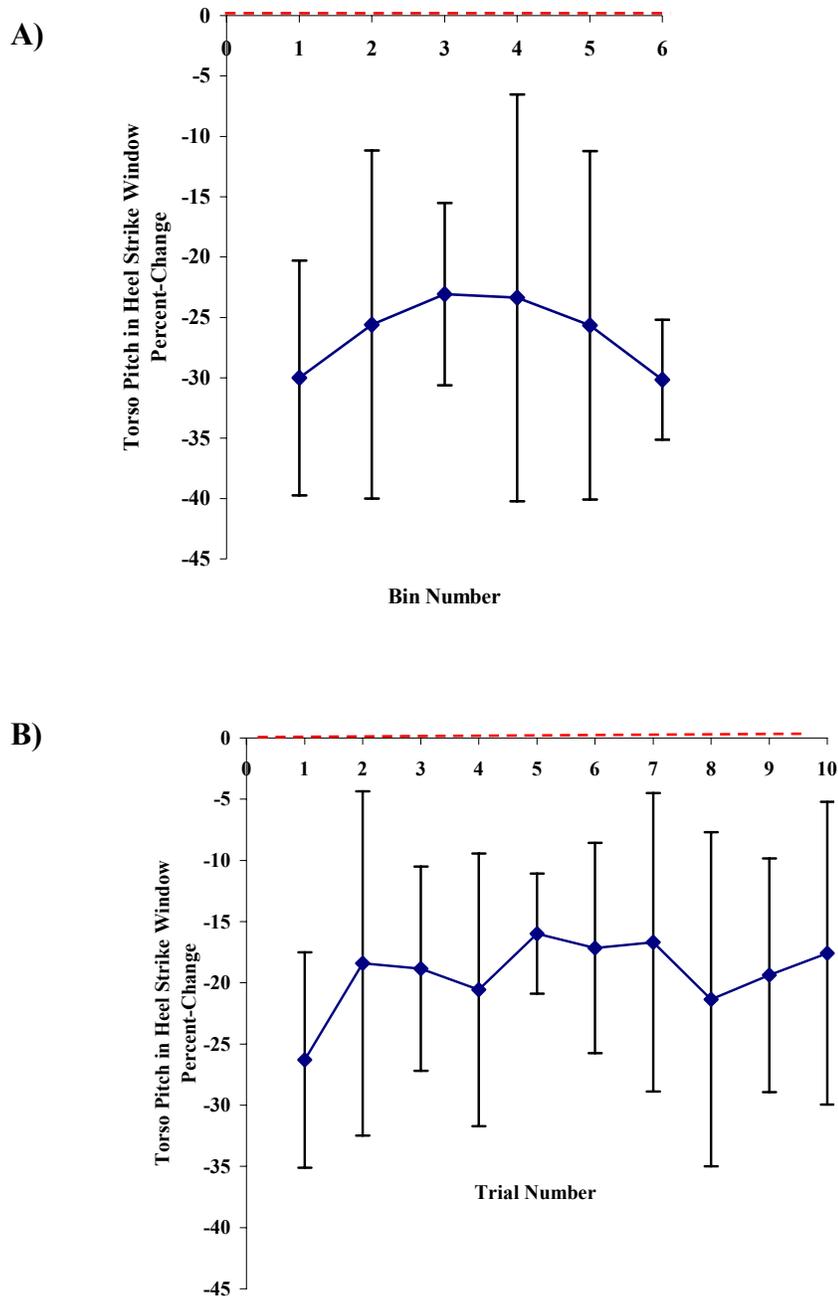
indicating a sustained change in response to the proprioceptive changes induced by 30 min of 40% BWS.



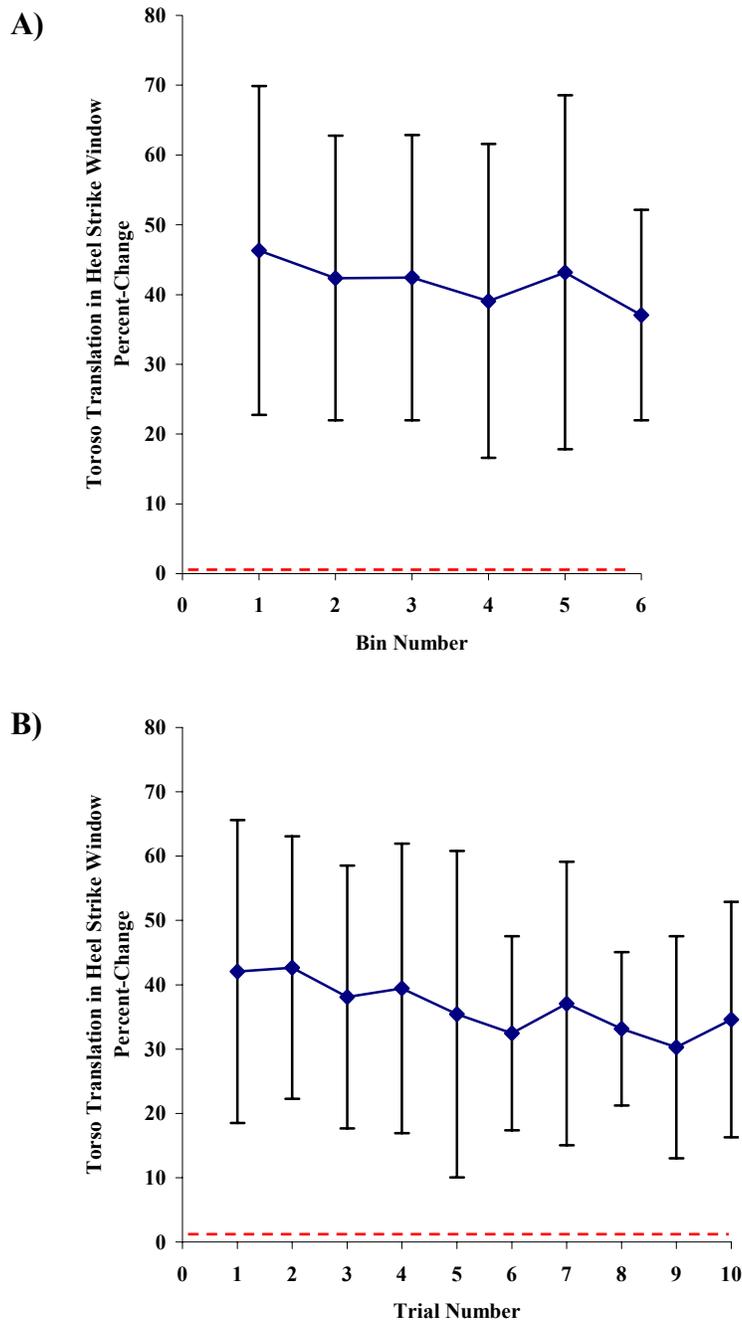
**Figure 3.3.1. Total Upper Body Movements in Heel Strike Window.** Pre and Post average for each subject in the window from heel strike to peak knee flexion for the total head pitch movement with respect to space (top row: head pitch in heel strike window, deg), total torso pitch movement with respect to space (second row: torso pitch in heel strike window, deg), and the total vertical torso translation with respect to space (bottom row: torso translation in heel strike window, mm). **A)** significantly increased, **B)** no change, and **C)** significantly decreased, relative to pre-adaptation trials.



**Figure 3.3.2. Head Pitch in Heel Strike Window Percent-Change Curve.** A percent-change curve was established for head pitch movement re space in the window from heel strike to peak knee flexion to determine if the 6/10 subjects who showed a significant increase subsequently showed a return to pre-adaptation values. Values that cross the red line indicate return to pre-adaptation values. **A)** The average ( $\pm 95\%$  CI) percent-change ( $R_i$ ) across subjects between pre- and post-adaptation ITLP values for each 10-gait cycle bin during the first 60 sec of the first post-ITLP trial and **B)** The average ( $\pm 95\%$  CI) percent-change across subjects between pre- and post-adaptation ITLP values for the first 60 gait cycles of each of the 10 post-adaptation trials ( $R_a$ ).



**Figure 3.3.3. Total Torso Pitch in Heel Strike Window Percent-Change Curve.** A percent-change curve was established for total torso pitch movement re space in the window from heel strike to peak knee flexion to determine if the 4/10 subjects who showed a significant decrease subsequently showed a return to pre-adaptation values. Values that cross the red line indicate return to pre-adaptation values. **A)** The average ( $\pm 95\%$  CI) percent-change ( $R_i$ ) across subjects between pre- and post-adaptation ITLP values for each 10-gait cycle bin during the first 60 sec of the first post-ITLP trial and **B)** The average ( $\pm 95\%$  CI) percent-change across subjects between pre- and post-adaptation ITLP values for the first 60 gait cycles of each of the 10 post-adaptation trials ( $R_a$ ).



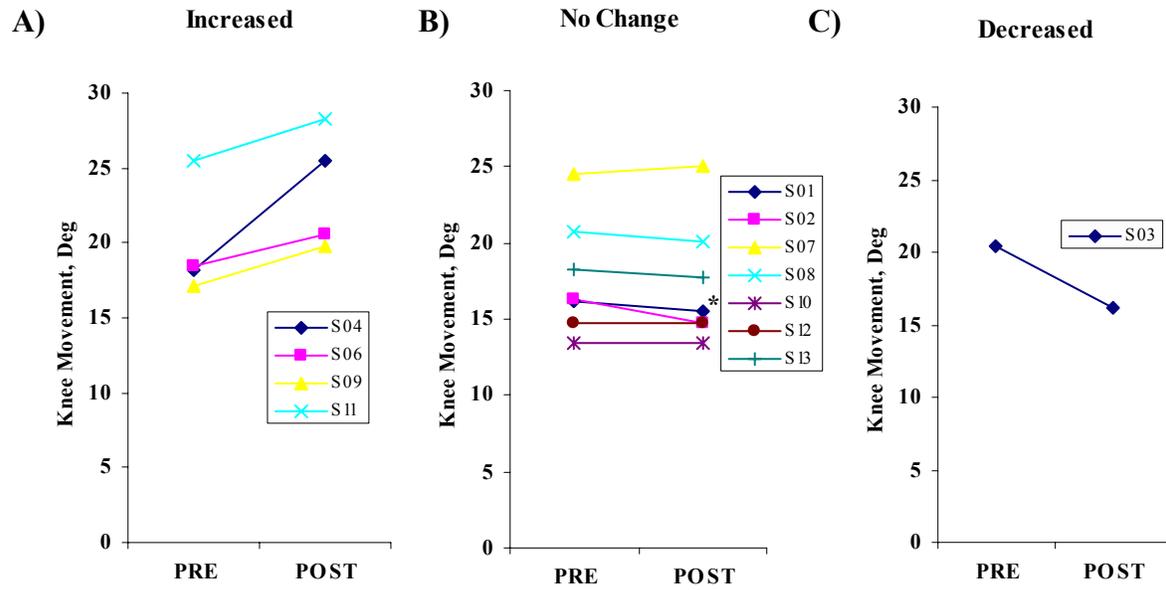
**Figure 3.3.4. Torso Translation in Heel Strike Window Percent-Change Curve.** A percent-change curve was established for vertical torso translation re space in the window of heel strike to peak knee flexion to determine if the 5/10 subjects who showed a significant increase subsequently showed a return to pre-adaptation values. Values that cross the red line indicate return to pre-adaptation values. **A)** The average ( $\pm 95\%$  CI) percent-change ( $R_i$ ) across subjects between pre- and post-adaptation ITLP values for each 10-gait cycle bin during the first 60 sec of the first post-ITLP trial and **B)** The average ( $\pm 95\%$  CI) percent-change across subjects between pre- and post-adaptation ITLP values for the first 60 gait cycles of each of the 10 post-adaptation trials ( $R_a$ ).

### ***Lower Body Changes***

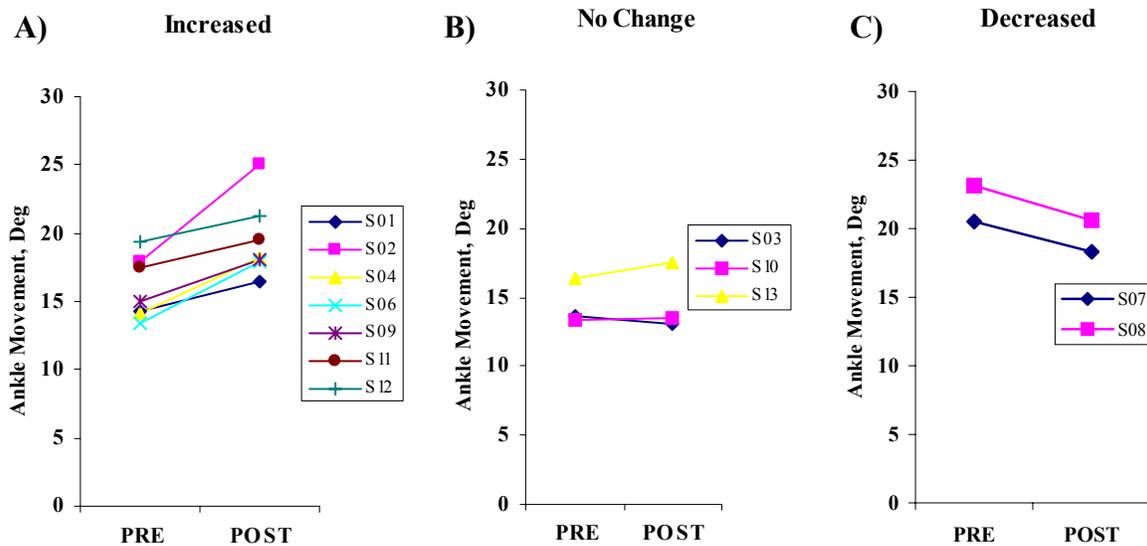
The Pre and Post average for each subject for the total movement calculated in the time frame from right heel strike to peak flexion of the knee during stance phase is shown in Figure 3.3.5 for the knee joint angular movements. After BWS adaptation, 4/12 (33%) showed a significant increase in knee flexion, while 7/12 (58%) showed no change and 1/12 (9%) showed a significant decrease.

The Pre and Post average for each subject for the total movement calculated in the time frame from right heel strike to peak flexion of the knee during stance phase is shown in Figure 3.3.6 for the ankle joint angular movements. After BWS adaptation, 7/12 (58%) subjects had a significant increase in ankle flexion, 3/12 (25%) showed no change, and 2/12 (17%) showed a significant decrease.

Figures 3.3.7 and 3.3.8 show the average percent-changes for the subjects who showed significant changes in the total knee movement and total ankle movement, respectively, within the heel strike window. The average ( $\pm$  95% CI) percent-change, “ $R_i$ ” across subjects between pre- and post-adaptation ITLP values for each 10-gait cycle bin during the last 60 seconds was determined and depicted as (A). The average ( $\pm$  95% CI) percent-change, “ $R_a$ ” across subjects between the pre- and post-adaptation ITLP values for each 10-gait cycle bin during the first 60 seconds of each of the 10 post-adaptation ITLP trials was determined and depicted as (B). Confidence intervals that cross the red line at zero indicate a significant return to pre-adaptation values. Subjects showed no return to pre-adaptation values over all 10 post-trials, indicating a sustained change in response to the proprioceptive changes induced by 30 min of 40% BWS.

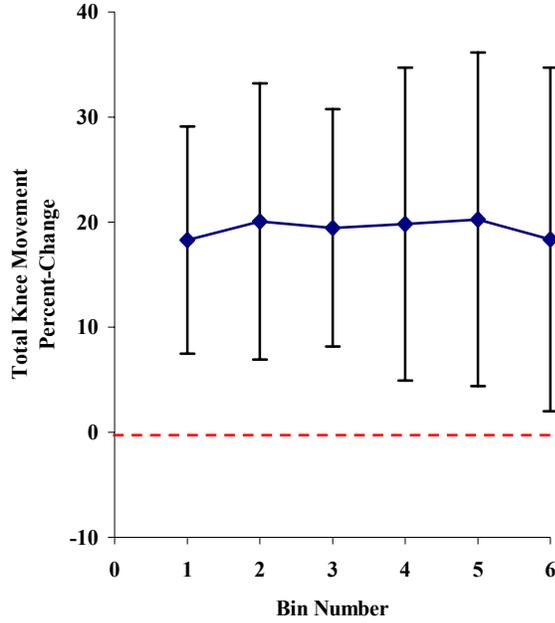


**Figure 3.3.5. Knee Flexion Total Movement.** Pre and Post average for each subject of the total movement calculated in the time frame from right heel strike to peak flexion of the knee during the stance phase for the knee joint. Individual subject responses for each variable were classified into three groups: **A)** significantly increased, **B)** no change, and **C)** significantly decreased, relative to pre-adaptation trials.

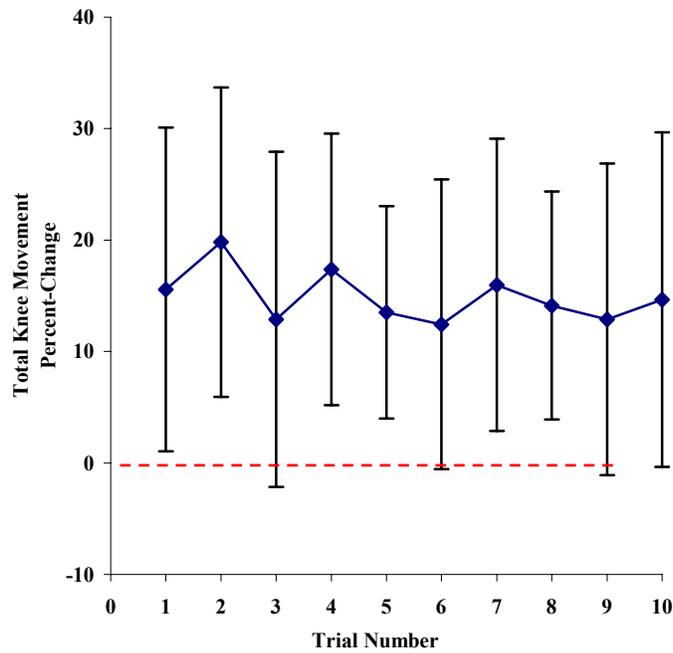


**Figure 3.3.6. Ankle Flexion Total Movement.** Pre and Post average for each subject of the total movement calculated in the time frame from right heel strike to peak flexion of the knee during the stance phase for the ankle joint. Individual subject responses for each variable were classified into three groups: **A)** significantly increased, **B)** no change, and **C)** significantly decreased, relative to pre-adaptation trials.

A)

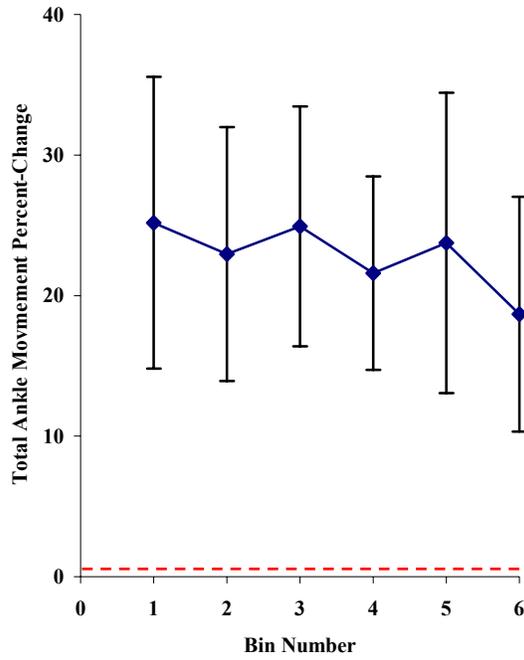


B)

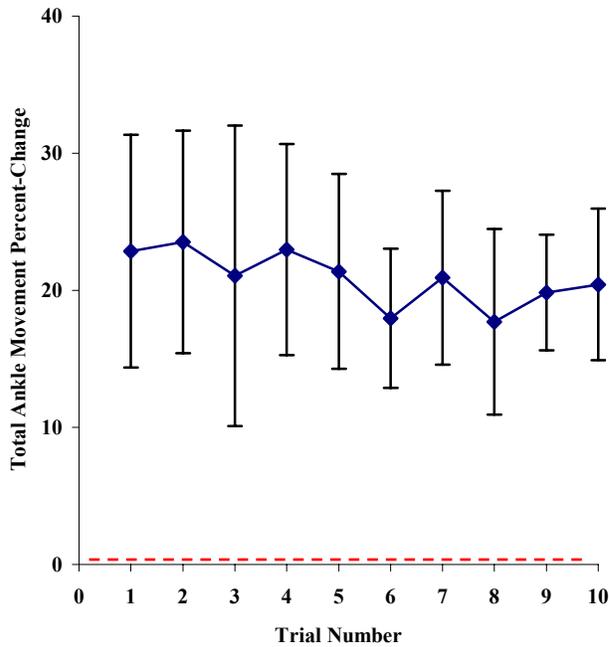


**Figure 3.3.7. Total Knee Movement Percent-Change Curves.** A percent-change curve was established for knee total movement to determine if the 4/10 subjects who showed a significant change increase subsequently showed a return to pre-adaptation values. Values that cross the red line indicate return to pre-adaptation values. **A)** The average ( $\pm 95\%$  CI) percent-change ( $R_i$ ) across subjects between pre- and post-adaptation ITLP values for each 10-gait cycle bin during the first 60 sec of the first post-ITLP trial and **B)** The average ( $\pm 95\%$  CI) percent-change across subjects between pre- and post-adaptation ITLP values for the first 60 gait cycles of each of the 10 post-adaptation trials ( $R_a$ ).

A)



B)

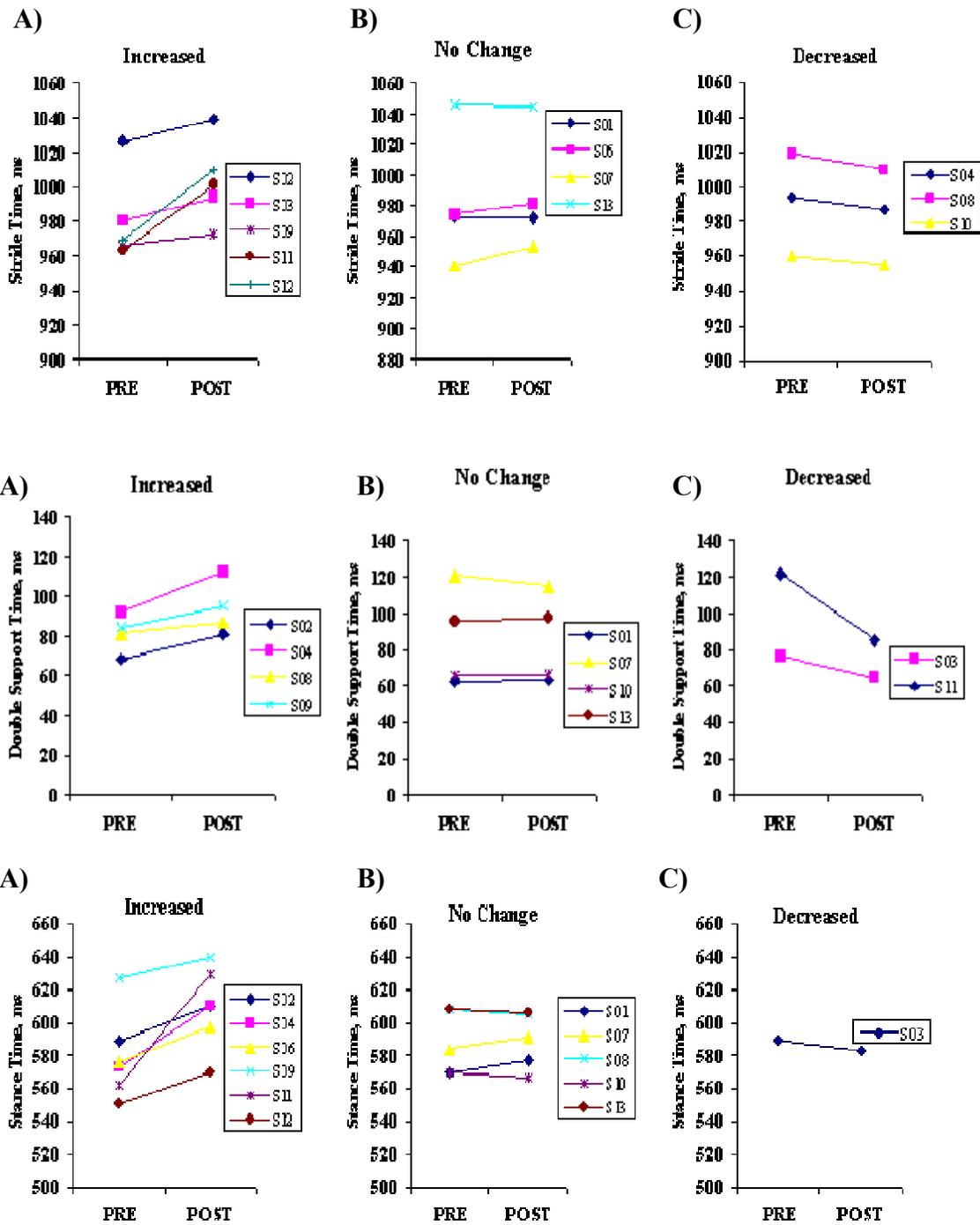


**Figure 3.3.8. Total Ankle Movement Percent-Change Curves.** A percent-change curve was established for ankle total movement to determine if the 7/12 subjects who showed a significant increase subsequently showed a return to pre-adaptation values. Values that cross the red line indicate return to pre-adaptation values. **A)** The average ( $\pm 95\%$  CI) percent-change ( $R_i$ ) across subjects between pre- and post-adaptation ITLP values for each 10-gait cycle bin during the first 60 sec of the first post-ITLP trial and **B)** The average ( $\pm 95\%$  CI) percent-change across subjects between pre- and post-adaptation ITLP values for the first 60 gait cycles of each of the 10 post-adaptation trials ( $R_a$ ).

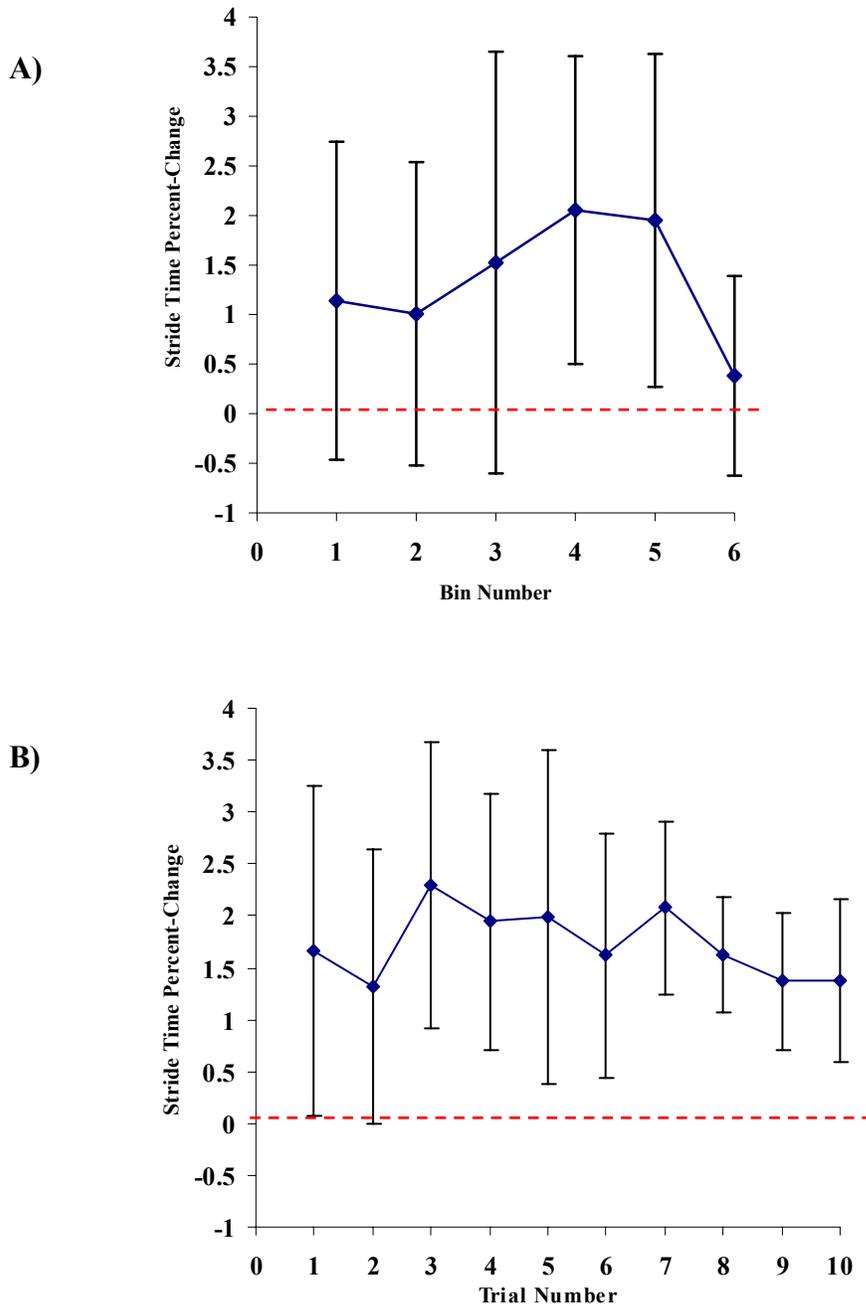
### 3.4 CHANGES IN GAIT CYCLE TIMING

The Pre and Post average for each subject for changes in gait cycle timing is shown in Figure 3.4.1. Stride time results were calculated based on the amount of time from heel strike to heel strike of the same foot. Following the BWS adaptation period, 5/12 (42%) subjects showed a significant increase in stride time, while 4/12 (33%) showed no change and 3/12 (25%) showed a significant decrease in stride time in the Post values as compared to Pre values. For double support time, which was calculated as the average amount of time between the heel strike of the right foot to the toe off of the left foot, 4/10 (40%) subjects showed each a significant increase or no change, while 2/10 (20%) subjects showed a significant decrease in double support time. Stance time (heel strike to toe-off of the right foot), was also significantly increased in 5/12 (42%) subjects, while there was no change in 6/12 (50%) and a significant decrease in 1/12 (8%) subjects.

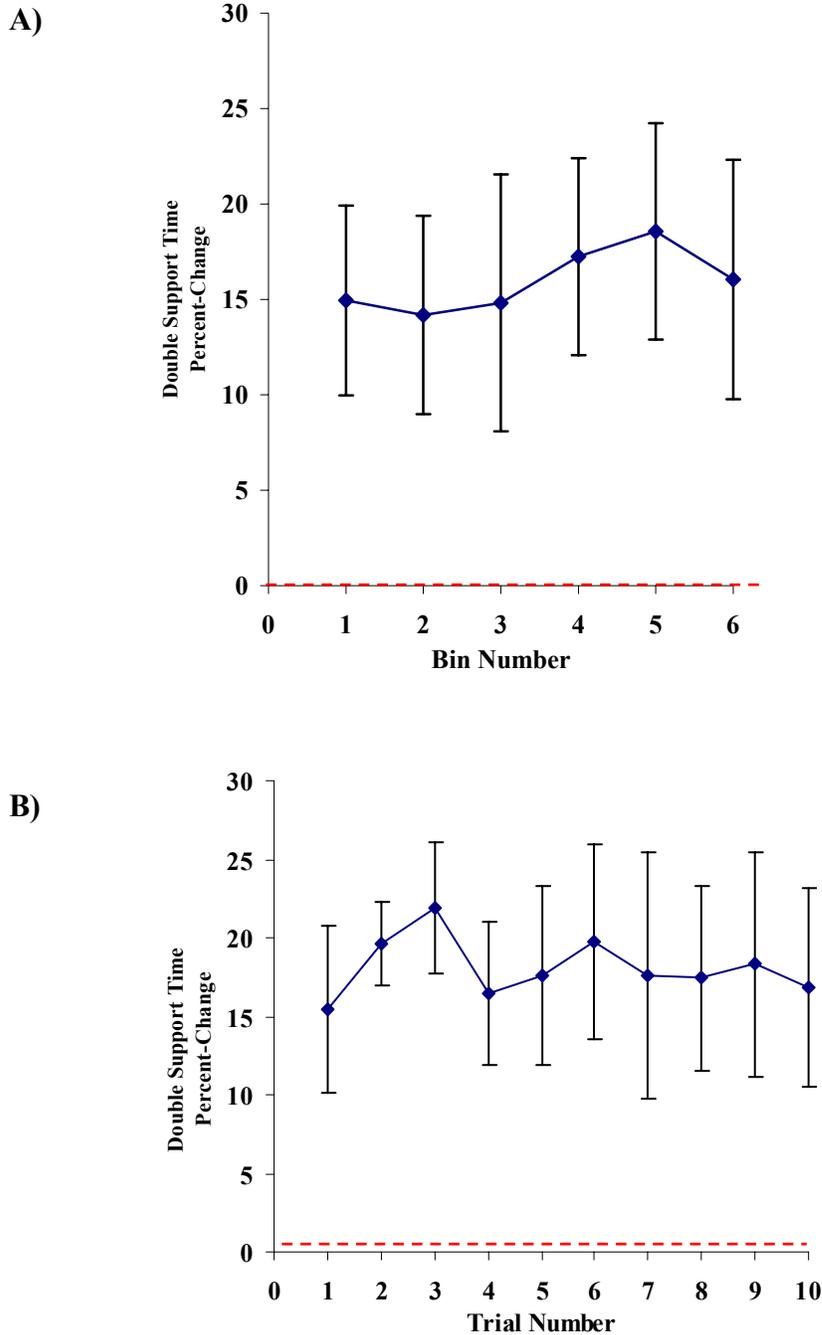
Figures 3.4.2, 3.4.3, and 3.4.4 show the average percent-changes for the subjects who showed significant changes in gait cycle timing. The average ( $\pm$  95% CI) percent-change, “ $R_i$ ” across subjects between pre- and post-adaptation ITLP values for each 10-gait cycle bin during the last 60 seconds was determined and depicted as (A). The average ( $\pm$  95% CI) percent-change, “ $R_a$ ” across subjects between the pre- and post-adaptation ITLP values for each 10-gait cycle bin during the first 60 seconds of each of the 10 post-adaptation ITLP trials was determined and depicted as (B). Confidence intervals that cross the red line at zero indicate a significant return to pre-adaptation values. Subjects showed no return to pre-adaptation values over all 10 post-trials, indicating a sustained change in response to the proprioceptive changes induced by 30 min of 40% BWS.



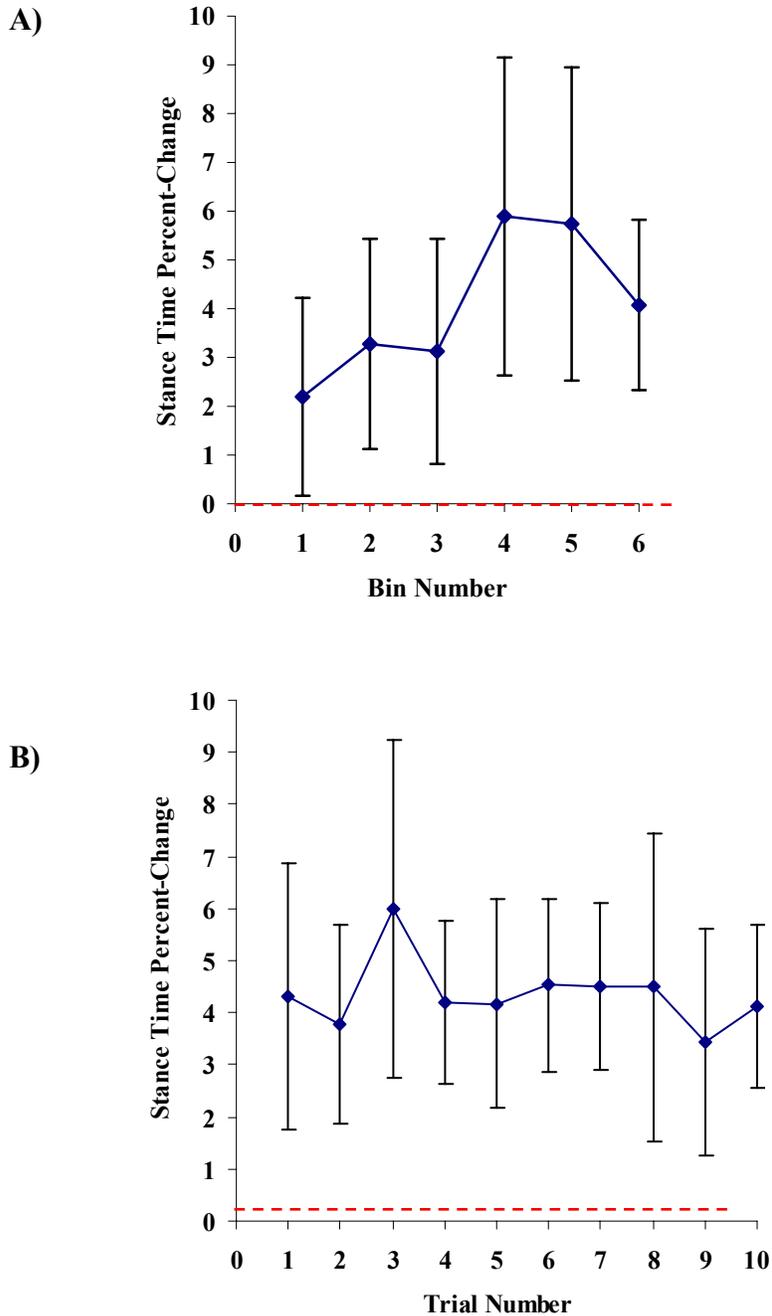
**Figure 3.4.1. Gait Cycle Timing Changes.** Pre and Post average for each subject for the timing in the different phases of the gait cycle, including stride time (top row: stride time, ms), double support time (middle row: double support time, ms), and stance time (bottom row: stance time, ms). Individual subject responses for each variable were classified into three groups: **A)** significantly increased, **B)** no change, and **C)** significantly decreased, relative to pre-adaptation trials.



**Figure 3.4.2. Stride Time Percent-Change Curves.** A percent-change curve was established for stride time to determine if the 5/12 subjects who showed a significant increase subsequently showed a return to pre-adaptation values. Values that cross the red line indicate return to pre-adaptation values. **A)** The average ( $\pm 95\%$  CI) percent-change ( $R_i$ ) across subjects between pre- and post-adaptation ITLP values for each 10-gait cycle bin during the first 60 sec of the first post-ITLP trial and **B)** The average ( $\pm 95\%$  CI) percent-change across subjects between pre- and post-adaptation ITLP values for the first 60 gait cycles of each of the 10 post-adaptation trials ( $R_a$ ).



**Figure 3.4.3. Double Support Time Percent-Change Curves.** A percent-change curve was established for double support time to determine if the 4/12 subjects who showed a significant increase subsequently showed a return to pre-adaptation values. Values that cross the red line indicate return to pre-adaptation values. **A)** The average ( $\pm 95\%$  CI) percent-change ( $R_i$ ) across subjects between pre- and post-adaptation ITLP values for each 10-gait cycle bin during the first 60 sec of the first post-ITLP trial and **B)** The average ( $\pm 95\%$  CI) percent-change across subjects between pre- and post-adaptation ITLP values for the first 60 gait cycles of each of the 10 post-adaptation trials ( $R_a$ ).



**Figure 3.4.4. Stance Time Percent-Change Curves.** A percent-change curve was established for stance time to determine if the 6/12 subjects who showed a significant increase subsequently showed a return to pre-adaptation values. Values that cross the red line indicate return to pre-adaptation values. **A)** The average ( $\pm 95\%$  CI) percent-change ( $R_i$ ) across subjects between pre- and post-adaptation ITLP values for each 10-gait cycle bin during the first 60 sec of the first post-ITLP trial and **B)** The average ( $\pm 95\%$  CI) percent-change across subjects between pre- and post-adaptation ITLP values for the first 60 gait cycles of each of the 10 post-adaptation trials ( $R_a$ ).

### 3.5 VARIABLE RELATIONSHIPS

Table 3.5.1 depicts the results of the correlation analysis, Pearson coefficient with p-values, performed between the percentage-change values of all pairs of the body segment variables considered for analysis within the head reflexive control bandwidths across subjects. Following the BWS adaptation period, there was a significant negative correlation between torso pitch and head pitch percent changes at a value of -0.809 ( $p < .01$ ). Thus, after prolonged 40% BWS adaptation, the percent changes in head pitch - torso pitch with respect to space describe a negative relationship, indicating as the torso pitch decreases, head pitch increases with respect to space. A linear regression analysis was performed for the relationship between percent changes head pitch and torso pitch to determine the strength of the relationship as depicted in Figure 3.5.1. The resulting linear regression  $R^2$  value of 0.6559 confirms the strongly-correlated Pearson values, reflecting a negative relationship between head pitch and torso pitch.

Since torso vertical translation is typically highly correlated with head pitch movement in a compensatory manner during normal locomotion, a linear regression analysis was also performed to confirm the Pearson correlation result that indicated that there is no significant relationship in head pitch movement and torso translation immediately following the 40% BWS adaptive period. With the linear regression confirmation depicted in Figure 3.5.2, it is clear that the increased head pitch motion seen in 80% of the subjects is not correlated with torso vertical translation following BWS adaptation, indicating that the increased head pitch movement observed after exposure to BWS adaptation cannot be due to increased vertical translation, and therefore must be related to some other factor or events that occur in the post-adaptation locomotion phase.

Table 3.5.2 depicts the results of the Pearson coefficient analysis with p-values performed between the percent-change values of all pairs of the body segments and gait cycle events for all subjects. After the BWS adaptation period, there was a significant

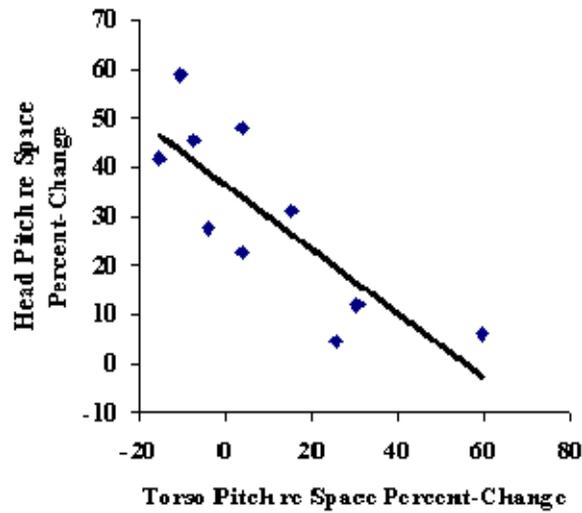
correlation between stance time changes and knee total movement changes of 0.781 ( $p < .01$ ). Thus, after 30 minutes of 40% BWS adaptation, the percent changes in stance time and percent changes of total knee movement at heel strike describe a positive relationship, indicating as the stance time increases, knee total movement at heel strike increases. A linear regression analysis was performed for the relationship between the percentage change of knee total movement and the percentage change in stance time to determine the strength of the relationship as depicted in Figure 3.5.3. The resulting linear regression  $R^2$  value of 0.6097 confirms the Pearson correlation value that indicates that the positively-associated relationship between knee movement and stance time is relatively strong.

Table 3.5.3 depicts the results of the Pearson coefficient analysis with p-values performed between the percent-change values of all pairs of the body segments in the heel strike window for all subjects. A significant positive correlation was found between ankle total movement changes and torso translation changes. A linear regression analysis was performed to determine the strength of the relationship of these variables as depicted in Figure 3.5.4. The  $R^2$  value of 0.5827 confirms the Pearson correlation value that indicates that the relationship between ankle movement and torso translation is relatively strong.

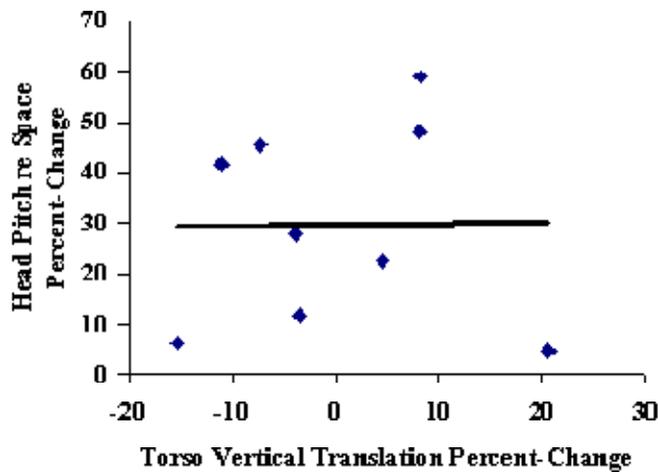
Segment Variables for the Head Reflexive Control Bandwidth	Pearson correlation	P-value
Head pitch - Torso vertical translation	0.012	0.977
Head pitch - Knee total movement	0.065	0.869
Head pitch - Ankle total movement	0.02	0.96
Head pitch - Head roll	0.336	0.343
Head pitch- Head yaw	0.439	0.205
Head pitch - Torso roll	-0.424	0.222
Head pitch - Torso yaw	0.241	0.502
Head roll - Torso roll	-0.201	0.578
Head roll - Torso pitch	-0.132	0.716
Head roll - Torso yaw	0.307	0.388
Head yaw - Torso roll	-0.475	0.166
Head yaw - Torso pitch	-0.161	0.658
Head yaw - Torso yaw	0.231	0.521
Vertical torso translation - Head pitch re torso	0.110	0.778
Vertical torso translation - Head roll re torso	0.086	0.826
Vertical torso translation - Head yaw re torso	0.408	0.276
Vertical torso translation - Knee total movement	0.228	0.500
Vertical torso translation - Ankle total movement	0.104	0.761
Vertical torso translation - Head roll	0.405	0.279
Vertical torso translation - Head yaw	0.485	0.186
Vertical torso translation - Torso roll	-0.344	0.331
Vertical torso translation - Torso yaw	0.394	0.260
Torso pitch - Head pitch	-0.809(*)	0.005
Torso pitch - Knee movement	-0.153	0.653
Torso pitch - Ankle movement	0.052	0.880
Torso pitch - Torso translation	-0.210	0.560
Torso pitch - Head roll	-0.132	0.716
Torso pitch - Head yaw	-0.161	0.658
Torso pitch - Torso roll	0.184	0.610
Torso pitch - Torso yaw	-0.356	0.313
Knee total movement - Ankle total movement	0.408	0.188
Knee total movement - Head roll	-.353	0.351
Knee total movement - Head yaw	-0.574	0.083
Knee total movement - Torso roll	-0.166	0.625
Knee total movement - Torso yaw	0.176	0.604
Knee total movement - Head pitch re torso	-0.329	0.353
Knee total movement - Head roll re torso	-0.287	0.421
Knee total movement - Head yaw re torso	-0.574	0.083
Ankle total movement - Head roll	-0.149	0.682
Ankle total movement - Head yaw	-0.048	0.895
Ankle total movement - Torso roll	-0.347	0.296
Ankle total movement - Torso yaw	0.027	0.937
Ankle total movement - Head pitch re torso	-0.463	0.178
Ankle total movement - Head roll re torso	-0.035	0.924
Ankle total movement - Head yaw re torso	-0.401	0.251

\* Significant to  $p < .01$

**Table 3.5.1. Pearson Correlations Between Movements.** Pearson Correlation values and P-values were calculated to determine whether a relationship exists between segmental movements.



**Figure 3.5.1. Head Pitch – Torso Pitch Linear Regression Plots.** To examine the strength of the relationship between head pitch and torso pitch, linear regression was performed. There is a significant negative correlation between percent-changes in head pitch and torso pitch percent changes.

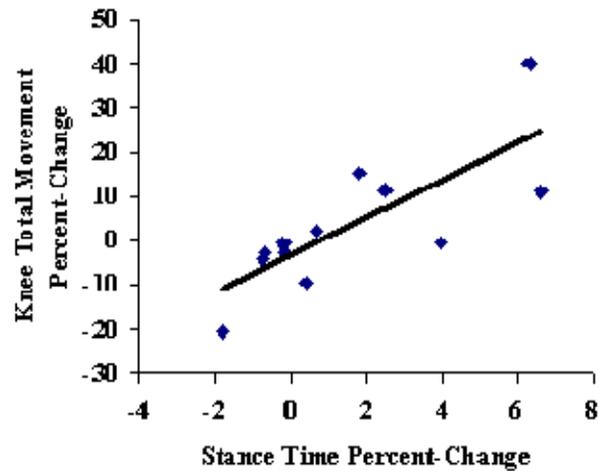


**Figure 3.5.2. Head Pitch – Torso Vertical Translation Linear Regression Plots.** To examine the strength of the relationship between head pitch and torso translation, linear regression was performed. There is no significant relationship between percent-changes in head pitch and torso translation, confirming that the significant changes in head pitch are not related to changes in torso vertical translation.

<b>Segment Variables for the Head Reflexive Control</b>		
<b>Bandwidth and Gait Cycle Timing</b>	<b>Pearson correlation</b>	<b>P-value</b>
Stance Time - Head pitch	0.317	0.373
Stance Time - Vertical torso translation	-0.016	0.962
Stance Time - Knee total movement	0.781(*)	0.003
Stance Time - Ankle total movement	0.406	0.190
Stance Time - Torso pitch	-0.475	0.140
Stance Time - Head roll	-0.588	0.074
Stance Time - Head yaw	-0.487	0.153
Stance Time - Torso roll	-0.258	0.444
Stance Time - Torso yaw	-0.158	0.643
Stance Time - Head pitch re Torso	-0.343	0.332
Stance Time - Head roll re torso	-0.578	0.080
Stance Time - Head yaw re torso	-0.482	0.227
Stride Time - Head pitch	0.498	0.173
Stride Time - Vertical torso translation	0.119	0.744
Stride Time - Knee total movement	0.584	0.076
Stride Time - Ankle total movement	0.621	0.055
Stride Time - Torso pitch	0.627	0.071
Stride Time - Head roll	-0.394	0.335
Stride Time - Head yaw	-0.436	0.280
Stride Time - Torso roll	0.236	0.541
Stride Time - Torso yaw	0.145	0.709
Stride Time - Head pitch re torso	-0.211	0.558
Stride Time - Head roll re torso	-0.443	0.200
Stride Time - Head yaw re torso	-0.334	0.346
Double Support Time - Head pitch	0.483	0.157
Double Support Time - Vertical torso translation	-0.258	0.444
Double Support Time - Knee total movement	-0.188	0.559
Double Support Time - Ankle total movement	-0.005	0.988
Double Support Time - Torso pitch	0.645	0.084
Double Support Time - Head roll	-0.228	0.527
Double Support Time - Head yaw	-0.180	0.619
Double Support Time - Torso roll	-0.083	0.807
Double Support Time - Torso yaw	-0.493	0.123
Double Support Time - Head pitch re torso	-0.526	0.181
Double Support Time - Head roll re torso	0.440	0.276
Double Support Time - Head yaw re torso	-0.316	0.446

\* Significant to  $p < .01$

**Table 3.5.2. Pearson Correlations Between Movements and Gait Cycle Timing.** Pearson Correlation values and P-values were calculated to determine whether a relationship exists between segmental movements and gait cycle timing.

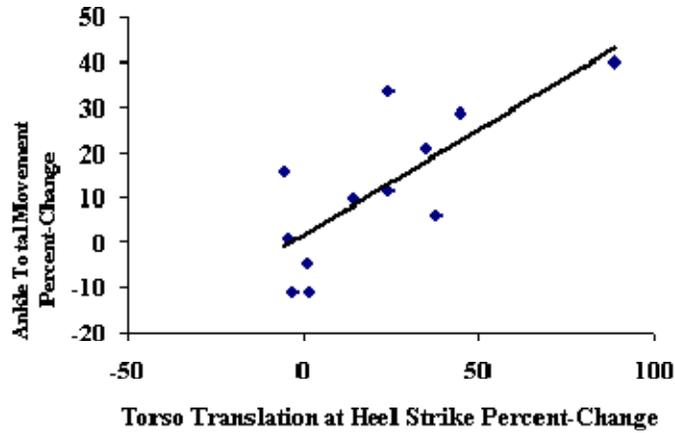


**Figure 3.5.3. Knee Movement – Stance Time Linear Regression Plots.** To examine strength of the relationship between knee movement and stance time, linear regression was performed. There is a significant relationship between percent-changes in knee total movement and stance time percent-changes.

Segment Variables from Heel Strike to Peak Knee Flexion	Pearson correlation	P-value
Head pitch - Torso vertical translation	0.358	0.310
Head pitch - Knee total movement	0.193	0.592
Head pitch - Ankle total movement	0.532	0.113
Head pitch - Torso Pitch	0.225	0.531
Torso pitch - Knee movement	-0.056	0.862
Torso pitch - Ankle movement	0.442	0.150
Torso pitch - Torso vertical translation	0.353	0.261
Torso vertical translation - Ankle total movement	0.766*	0.004
Torso vertical translation - Knee total movement	0.236	0.461
Double Support Time - Head pitch	0.601	0.513
Double Support Time - Torso pitch	0.151	0.676
Double Support Time - Torso vertical translation	0.558	0.094
Stride Time - Head pitch	0.448	0.194
Stride Time - Torso pitch	0.068	0.833
Stride Time - Torso vertical translation	0.089	0.783
Stance Time - Head pitch	0.489	0.151
Stance Time - Torso pitch	0.008	0.979
Stance Time - Torso vertical translation	0.304	0.336

\* Significant to  $p < .01$

**Table 3.5.3. Pearson Correlations Between Movements in Heel Strike Window.** Pearson Correlation values and P-values were calculated to determine whether a relationship exists between segmental movements in the window from heel strike to peak knee flexion.



**Figure 3.5.4. Ankle Total Movement – Torso Translation at Heel Strike Linear Regression Plots.** To examine the strength of the relationship between ankle movement and torso translation in the window from heel strike to peak knee flexion, linear regression was performed. There is a significant positive relationship between percent-changes in ankle total movement and torso translation percent-changes.

### 3.6 SUMMARY OF RESULTS

Overall, subjects showed no significant changes in DVA scores following the 40% BWS adaptation period; however, significant changes were found in head and torso movement control, as well as lower body kinematics and gait cycle timing. Table 3.6.1 summarizes the data that reflect the predominant changes that occurred during this study as a result of 30 minutes of walking with 40% BWS.

Movement	Predominant Change	Number of Subjects	Average Percent Change in First "Post" Trial
<b>In Head Reflexive Control Bandwidth</b>			
Head Pitch re Space	Increased	8/10	25.21
Head Roll re Space	Increased	6/10	48.05
Head Yaw re Space	Decreased	5/10	-26.93
Torso Pitch re Space	Increased	4/10	32.66
Torso Roll re Space	Increased	4/10	43.41
Torso Yaw re Space	2/10 Decreased 2/10 Increased	2/10	-32.56 16.65
Head Pitch re Torso	Increased	6/10	40.84
Head Roll re Torso	Increased	4/10	84.35
Head Yaw re Torso	3/10 Decreased 3/10 Increased	3/10	-37.99      90.25
Vertical Torso Translation	No change	8/10	-
<b>In Window from Heel Strike to Peak Knee Flexion</b>			
Total Ankle Movement	Increased	7/12	22.85
Total Knee Movement	Increased	4/12	19.37
Total Head Pitch	Increased	6/10	66.45
Total Torso Pitch	No change	9/10	-
Vertical Torso Translation	Increased	5/10	41.74
<b>Gait Cycle Timing</b>			
Stride Time	Increased	5/12	4.05
Stance Time	Increased	6/12	1.34
Double Support Time	Increased	4/10	15.97

**Table 3.6.1. Summary of Changes following 30 min of 40% BWS.**

## CHAPTER 4: DISCUSSION

The purpose of this study was to determine if a prolonged exposure to 40% BWS during locomotion caused adaptive modifications in the full-body gaze stabilization mechanisms: head-torso coordination, lower limb coordination, and gait cycle timing. Results of the study demonstrate that following 30 minutes of treadmill walking at 40% BWS subjects exhibited adaptive changes in head and torso movement, knee and ankle flexion total movement, and gait cycle timing while maintaining visual acuity.

Within the bandwidth for reflexive head control with respect to space, the predominant change expressed in 80% of the subjects was increased head pitch, while 60% of the subjects showed increased head roll, and 50% of the subjects showed decreased head yaw. Within the bandwidth for reflexive head control with respect to torso, the predominant change observed in 60% of the subjects was increased head pitch, while 40% showed increased head roll and 30% showed equally increased head yaw and decreased head yaw. Increased torso pitch and roll with respect to space each were the predominant changes observed in 40% of the subjects, while 60% showed no significant change in torso yaw movement with respect to space. No change in torso translation was observed in 80% of subjects. Based on the cross-correlation analysis, there was also no change observed in head-torso coordination.

In the window from heel strike to peak knee flexion, the predominant changes observed included increased head pitch in 60% of the subjects, no change in torso pitch in 90% of the subjects, and increased torso translation in 50% of the subjects. The predominant change in total ankle movement in 58% of the subjects was an increase in flexion. Although 58% of the subjects showed no change in knee total movement, 33% of subjects did show increased knee flexion. Gait cycle timing parameters were also

changed in that 42% of subjects showed increased stride time, 50% of subjects showed increased stance time, and 40% of subjects showed increased double support time. Thus, it is clear that body load-regulating mechanisms can be adaptively modified, and such adaptation is reflected functionally as changes in the full-body gaze stabilization system.

While this study has shown that the full-body gaze control system can be reorganized in response to adaptive modification of sensory systems following prolonged changes in body load perception, the question remains as to how the vestibular and somatosensory systems functionally interact to induce these changes. Anatomic studies have shown that motor efferent pathways leave the central vestibular nuclei and descend in the spinal cord, where they terminate on the neurons that activate neck, torso, and limb muscles. There is evidence that vestibular signals contribute in a variety of ways to the selection of appropriate postural strategies for the environmental conditions, including head and torso movement coordination, tonic activation of antigravity (extensor) muscles, and triggering of postural responses (Horak et al. 1994). There is further evidence that one sensory system can compensate for loss of another with regard to somatosensory and vestibular postural control and balance strategies (Dietz et al. 2001; Horak et al. 1994; Mergner and Rosemeir 1998).

Vestibular information becomes critical for postural and equilibrium control in the event that somatosensory information becomes unreliable or unstable (Horak et al. 1994, Horak and Hlavacka 2001; Mergner and Rosemeir 1998). Mergner's model proposes that the CNS normally compares "bottom-up" control information from the somatosensory system with "top-down" control information from the vestibular system (Mergner and Rosemeir 1998). If the comparison between the two systems suggests that the surface is unstable, vestibular influence becomes predominant. Studies to support this model have shown that somatosensory information becomes inappropriate for postural

control and balance when healthy subjects stand on a spring-loaded surface (Fitzpatrick and McCloskey 1994), on compliant foam (Shumway-Cook and Horak 1986), in water (Dietz et al. 1989), in microgravity (Clement et al. 1985; Massion et al. 1998; Reschke et al. 1998), or when the body is not in constant contact with surfaces, such as when jumping or running (Berthoz and Pozzo 1988).

The effects of vestibular-somatosensory interactions have been documented in several spaceflight studies. During spaceflight, the vestibular system is adapted to the loss of gravity reference in microgravity, and upon sudden reintroduction of gravity on Earth, the CNS must readapt to the novel environment, resulting in sensory discordance during a period of adaptive flux during which postural instabilities and changes in movement patterns are observed (Paloski et al. 1993). In a study by Paloski et al. (1993), astronauts returning from long-duration spaceflight showed a significant modification in otolith-mediated sensorimotor interactions required for postural control caused by a CNS recalibration of the vestibular otoliths that occurred during their prolonged stay in microgravity. Additionally, Reschke et al. (1984) found that otolith-mediated Hoffman reflexes were heightened after adaptation to microgravity, resulting in increased ataxia and increased movements at the hips to maintain control of upright posture. Watt et al. (1989) described the adaptive changes induced in posture and locomotor control systems following microgravity exposure as being a result of the degradation of postural reflexes within otolith-spinal pathways in microgravity because postural control “is meaningless” in microgravity. These studies support the idea that the CNS is capable of recalibration of vestibular-somatosensory interactions in an effort to provide postural and balance control based on conflicting inputs from the environment, and that such changes may occur “...in partial compensation for the degraded performance” of the other feedback systems (Black et al. 1995; Reschke et al. 1998).

Thus, the results of this study provide evidence that altered somatosensory input can induce adaptive modifications in the body load sensing mechanisms which ultimately renders the vestibular system the primary source of information for postural control. As a result of these vestibular-somatosensory interactions, reorganization of control strategies emerge in the subsystems that contribute to gaze stabilization. With particular regard to spaceflight, these results are especially critical in demonstrating that body load plays a central role in the regulation of post-flight locomotor and postural dysfunction.

#### **4.1 SPECIFIC AIM I: PROLONGED BWS LOCOMOTION CAUSES ADAPTIVE MODIFICATION OF BODY LOAD SENSING MECHANISMS THAT ALTER HEAD REFLEXIVE CONTROL AND TORSO MOVEMENT**

The goal of Specific Aim I was to characterize changes in head-torso coordination that occur to preserve gaze stabilization in response to adaptive alteration in body load-regulating mechanisms produced by prolonged exposure to unloaded locomotion. The hypothesis was that adaptive modification in body load mechanisms produced during prolonged unloaded locomotion would result in an increased restriction in head movement with respect to the torso during post-adaptation locomotion to reduce perturbations to the head, thus preserving gaze stability during locomotion.

##### ***Prolonged BWS Locomotion Results in Hyperresponsive Vestibular Activity***

The vestibulocollic reflexes (VCRs) are a set of automatic responses of the neck to activation of the receptors (otoliths and semi-circular canals) of the vestibular labyrinth. Although they are different from voluntary head movements, the VCRs may be modified by voluntary processes and by the context in which the vestibular input occurs (Peterson and Boyle 2004). For instance, during voluntary head movements,

vestibular inputs to vestibulospinal neurons involved in the VCR are typically suppressed. The VCRs must work to stabilize the head while the torso and lower body move underneath during locomotion.

After prolonged BWS, almost all of the subjects in this study showed a significant increase in power in the frequency bandwidth of 1.5 – 2.5 Hz that represents the VCR control mechanisms for head pitch in space and with respect to torso. In the 0.5-1.5 Hz VCR bandwidth, the predominant change for head roll was a significant increase, and the predominant change for head yaw was a significant decrease. Similar to other studies that have shown that the sensory systems that contribute to locomotor control can be adaptively modified after prolonged exposure to an adaptive stimulus, the changes in head movement control in this study can be attributed to an adaptive modification of the VCR gain that occurred during the 30-minute 40% BWS period. For example, it has been demonstrated that head movements increase during locomotion after the VOR gain is modified during a 30-minute protocol of voluntary head pitch movements while wearing 0.5X minifying lenses (Mulavara et al. 2005), and prolonged exposure to variations in optic flow stimuli have shown to affect the trajectory of locomotion (Richards et al. 2006). Additionally, in another study, an adaptive effect termed “podokinetic after-rotation” was observed in subjects following prolonged stepping in place on a rotating disk with head and torso aligned in the forward direction (Weber et al. 1998). Following exposure to the stimulus, subjects showed a curved trajectory opposite in direction to the stimulus during stepping on a stationary surface, indicating an adaptive remodeling of the somatosensory signals due to conflicts in torso movement with respect to space and with respect to the feet.

Horak et al. (1994) suggests that the vestibular system is capable of becoming hyperresponsive when sensory input is altered over a period of time, and reasons that the

hyperresponsive vestibular system may overestimate the velocity of head motion signals during body sway, and so the CNS may respond to small perturbations as though they were much bigger. As a result, inappropriate postural instabilities arise and result in destabilization. This link between a hyperresponsive vestibular system and altered postural control is demonstrated in the literature. A study by Horak and Hlavacka (2001) demonstrated that subjects with diabetic peripheral neuropathy, and thus reduced somatosensory input leading to impaired capability, showed increased sensitivity to galvanic vestibular stimulation as compared to healthy, age-matched subjects. In addition, utricular afferents have been found to be hypersensitive in toadfish following 5 days of exposure to microgravity during spaceflight when load information is absent (Boyle et al. 2001). Indeed, the data in our study support the concept that the altered somatosensory input during the 30-minute adaptation period of 40% BWS locomotion likely induced recalibration of the vestibular system, rendering it hyperresponsive, and this was observed functionally as increased head pitch and roll in the reflexive head control bandwidth during post-adaptation locomotion.

The majority of the subjects in this study also displayed increased head pitch with respect to torso movements, and the Pearson correlation analysis shows a significant negative correlation between change in torso pitch and change in head pitch movement magnitudes. These results lend further support to the concept that the head pitch movements occur as a result of a modified vestibular system, independent of torso movements, and is consistent with a modified VCR-induced strategy for head stability in an effort to preserve gaze.

With respect to torso translation during normal locomotion, head movements are attributed to being compensatory for torso translation in an effort to maintain a stable head, and thus stable vision by means of the VOR (Bloomberg et al. 1992; Bloomberg et

al. 1997; Demer and Viirre 1996; Hirasaki et al. 1999; Moore et al. 1999; Pozzo et al. 1990; Pozzo et al. 1991). In the current study, the results of head movement in the VCR frequency bandwidth do not appear to be simply a biomechanical response to torso translation. For example, if the head movement changes were to be attributed solely to changes in torso vertical translations, we would have expected torso translation results to also be significantly increased in these bandwidths, and we would further expect a positive significant relationship between change in torso vertical translation and change in head movement magnitude with respect to space in the Pearson's correlation analysis. However, the individual subject data show that there were indeed no significant changes in torso translation in the reflexive head control bandwidths, and the Pearson's correlation further confirms a lack of significance between torso vertical translation and head movement with respect to space and with respect to torso. These data provide further evidence that the head changes in this study can be attributed to a plane-specific modified VCR system, similar to what is observed in previous spaceflight studies (Bloomberg et al. 1997; Bloomberg and Mulavara 2003).

Previous studies have shown that head yaw movements within the 0.5 – 1.5 Hz frequency range that we used in this study can contain both voluntary and reflexive head control components. For example, the VCR contribution to reflexive head control in the yaw plane has been identified in the bandwidth of 0.8 – 1.6 Hz during driven locomotion (Keshner and Peterson 1992), but during seated rotation in a horizontal plane, head control movements have been shown to be dominated by voluntary mechanisms at low frequencies, while frequencies between 1 -2 Hz were dominated by reflexive head control mechanisms (Keshner et al. 1995a). Therefore, it is possible that the significantly decreased head yaw movements that occurred in the majority of the subjects in this study may represent a reduction in the contribution of reflexive head control mechanisms and

an increase in voluntary control mechanisms in the horizontal plane designed to aid in gaze stabilization when the system is introduced to the novel post-adaptive locomotor environment. These reduced head movements are not unlike what is exhibited in subjects during the early learning stages of new motor skills and astronauts returning from long-duration spaceflight. This “head-lock-to-torso” strategy for head movement control presumably reduces the degrees of freedom in an attempt to simplify the control problem until “practice” allows a return to natural movements (Bloomberg and Mulavara 2003; Mulavara et al. 2005; Nashner 1985; Vereijken et al. 1992). This reduction of angular head movement during locomotion may reduce potential canal-otolith discord during a period of sensorimotor conflict in a novel environment, and may thus serve to better coordinate head-torso movements in an effort to allow an easier determination of head in space. However, Bloomberg and Mulavara (2003) suggest that such a strategy is not necessarily optimal for gaze stabilization, since it results in a disruption in the consistent compensatory nature of head movements required during locomotion that may actually aid in gaze stabilization. Indeed, this strategy is associated with decreased visual acuity during locomotion in astronauts returning from long duration spaceflight (Bloomberg and Mulavara 2003). However, in this study, the restricted head yaw movements did not alone adversely affect the subjects’ post-adaptive DVA scores and may therefore be attributed only to a voluntary control mechanism that simplifies movement in the post-stimulus environment.

The head movement strategies elicited by the majority of the subjects in this study reflect the adaptive modification of the VCR system, which was rendered hyperresponsive as a result of the extended somatosensory conflict during 30 minutes of BWS locomotion. Such interactions between body load sensing and vestibular activity

offers insight into the convergence of sensory systems employed in an effort to maintain a stable head, and thus a stable gaze during locomotion.

### ***Torso Movement Changes are Indicative of Altered Vestibular Activity***

The increased torso pitch and roll each in 40% of the subjects in this study may also reflect recalibrated vestibular activity that occurred as a result of adaptive modification of body load sensing mechanisms. It has been suggested that the vestibular system primarily controls the orientation of torso in space rather than the whole body system of mass in an effort to maintain postural stability (Mergner and Rosemeir 1998). A previous study by Horak et al. (1990) showed that vestibular information is the most critical input for torso control in space for maintenance of postural stability. Subjects with somatosensory deficits have been shown to use a “hip strategy” to maintain postural stability against conflicting somatosensory input from a translating platform because the vestibular system becomes the primary source for reliable input when the support surface becomes unstable. Such a strategy allows for movement of only the torso to maintain postural stability (Horak et al. 1990; Mergner and Rosemeir 1998). Horak et al. (1994) described this “hip strategy” for postural control as the preferred strategy for use on narrow (beamlike) or compliant surfaces, or when the body’s center of mass position needs to be adjusted quickly and consists of rapid body motions about the hip joints that transmit horizontal forces to the support surface. Thus, the changes in torso movement exhibited by some of the subjects in this study following 40% BWS locomotion are consistent with the “hip strategy” of postural control in response to a hyperresponsive VCR system that was adaptively modified during the 30-minute BWS adaptation phase when somatosensory information was interpreted by the CNS as unreliable or absent.

Torso pitch and torso translations cause perturbations to the head; however, as mentioned previously, during normal walking, head pitch compensates for torso vertical translation, and head pitch motion is in phase with the torso pitch. In this study, this is reflected in the cross correlation functions of Head Pitch-Torso Pitch (HPTP) and Head Pitch-Vertical Torso Translation (HPTT) values that were calculated to quantify the coordination between the head and the torso. The maximum and minimum values of these functions showed that the temporal relationship between the head and torso was not altered following the 30-minute adaptation phase. Therefore, head-torso coordination was not affected by 30 minutes of 40% BWS locomotion.

In summary, Specific Aim I demonstrated that adaptive modification in body load mechanisms produced during prolonged unloaded locomotion resulted in predominant changes of increased head pitch and roll movement, and decreased head yaw movement with respect to space and with respect to the torso. The increased head movements were plane-specific for the sagittal and transverse planes and can be attributed to an adaptation of the VCR reflexes induced during the BWS period when the vestibular system became hyperresponsive as a result of prolonged altered somatosensory input exhibited during increased BWS. The decreased head yaw movements can be attributed to a combination of an adapted VCR system and the use of a voluntary head-lock-to-torso strategy that helps reduce the degrees of freedom of head movement during a period of adaptive flux after the BWS period. Additionally, increased torso angular movements were also plane-specific for sagittal and transverse planes, and can also be attributed to the changes in vestibular sensitivity. Thus, we have inferred that the changes in head and torso movements are representative of adaptive modifications in body load sensing mechanisms, leading to modification of vestibular-mediated head and postural responses.

#### **4.2 SPECIFIC AIM II: PROLONGED BWS LOCOMOTION CAUSES ADAPTIVE MODIFICATION OF BODY LOAD SENSING MECHANISMS THAT ALTER LOWER BODY KINEMATICS**

The goal of Specific Aim II was to characterize changes in lower body kinematics that occur to preserve gaze stabilization in response to adaptive alteration in body load-regulating mechanisms produced by prolonged exposure to unloaded locomotion. The hypothesis was that adaptive modification in body load mechanisms produced during prolonged unloaded locomotion would result in an increase in lower body limb flexion during post-adaptation locomotion to reduce perturbations to the head, thus preserving gaze stability during locomotion.

##### ***Adaptive Modification of Body Load Sensing Mechanisms Causes Changes in Lower Limb Coordination that may Aid in Gaze Stabilization***

During the BWS locomotion period, the need to support full body load is reduced, resulting in prolonged decreased input to the body load sensors in the feet, hips, and lower limb joints, and decreased ankle and knee total movements. As a result, the body load sensing mechanisms are recalibrated within the CNS, resulting in a system that is hyperresponsive to increased loads. The effects of this hypersensitivity are exhibited as increases in knee and ankle total movement in the subjects in this study immediately following BWS locomotion as compared to pre-adaptation values. Similar lower limb coordination patterns are also observed following long-duration spaceflight and following VOR adaptation (Bloomberg and Mulavara 2003; Mulavara and Bloomberg 2005). For example, the ankle proprioceptive feedback loop has been shown to change in some astronauts, and is attributed to CNS adaptation to decreased postural loading or new movement strategies experienced in microgravity (Reschke 1998). Upon return to Earth, subjects enter a period of readaptive flux during which these changes ultimately return to pre-flight movement patterns after several days or weeks.

Appropriate attenuation of the forces experienced throughout body segments during locomotion minimizes the disturbance of the visual and vestibular systems, and preserves head stability. During walking, the increase in knee flexion during the stance phase after heel strike has been associated with the rapid transfer of weight during the double support phase, thus helping to dampen out any disturbing forces to the head (Gard and Childress 1999; McMahon et al. 1987; Sutherland et al. 1994). In our study, subjects displayed increased head pitch movements but no change in torso pitch movements in this window. While the majority of the subjects in this study showed no significant changes in knee flexion, it appears that the 1/3 of the subjects who did show significantly increased knee flexion likely used a shock-absorption strategy to help dampen the disturbances that could potentially cause perturbations in the head immediately following the BWS adaptive period. The same strategy can be used to explain the predominant changes in the majority of the subjects in this study who showed increased ankle flexion in the heel strike window.

In the window of heel strike to peak knee flexion, half of the subjects showed increased torso vertical translation; however, the Pearson's correlation analysis showed that torso translation was not significantly related to the changes in total knee movement during the stance phase. There was also no significant correlation between magnitude of knee flexion and magnitude of head movement. This is consistent with other studies in the literature that show that the stance phase knee flexion was not found to significantly reduce the amplitude of torso vertical displacement during walking (Gard and Childress 1999; Mulavara and Bloomberg 2005). However, the Pearson analysis did show a positive significant relationship between ankle movement and torso translation in the heel strike window, suggesting that these components of the gaze system converge to affect both the upper and lower body movements for the common goal of stabilizing vision

during locomotion. This result is similar to that found in Mulavara and Bloomberg's VOR adaptation study (2005), and also suggests the potential role that the ankle joint may be linked functionally, though indirectly, to head movements (Mulavara and Bloomberg 2005).

In summary, Specific Aim II demonstrated that adaptive modification in body load mechanisms produced during prolonged unloaded locomotion resulted in increased knee and ankle flexion during post-adaptation locomotion. These changes appear to be indicative of a hyperresponsive body load sensing system as a result of prolonged direct unloading, and additionally, these changes may have served to help mitigate head disturbance during the high-impact phases of the gait cycle, thus preserving gaze stability during locomotion.

#### **4.3 SPECIFIC AIM III: PROLONGED BWS LOCOMOTION CAUSES ADAPTIVE MODIFICATION OF BODY LOAD SENSING MECHANISMS THAT ALTER GAIT CYCLE TIMING**

The goal of Specific Aim III was to characterize changes in gait cycle timing that occur to preserve gaze stabilization in response to adaptive alteration in body load-regulating mechanisms produced by prolonged exposure to unloaded locomotion. The hypothesis was that adaptive modification in body load mechanisms produced during prolonged unloaded locomotion would result in decreased stride time and an increase in double support time during post-adaptation locomotion in an effort to increase postural stability, thus preserving gaze stability during locomotion.

### ***Adaptation of Body Load Sensors During BWS Locomotion Induces Changes in Stability Requirements***

During the 40% BWS adaptive phase, the decreased load and increased vertical displacement of the body's center of mass induced "online" strategic changes in gait cycle timing such as decreased stance time and double support time. During the 30 minutes of exposure to the 40% BWS adaptive stimulus, it is likely that these persistent changes in somatosensory and proprioceptive inputs induced an adaptive modification of body load-regulating mechanisms. This adaptive modification was consequently observed in most subjects as increases in double support time and stance time immediately following the BWS adaptation period.

The increased double support time and stance time that were observed in most subjects immediately following the 30-minute adaptive phase are classic indicators of the need for increased postural stability and balance control, and can be attributed to the somatosensory adaptation caused by the induced prolonged changes in body load sensing and joint angle position during the prolonged exposure to 40% BWS; and a subsequent hypersensitive response to the subsequent immediate reintroduction to load in the post-adaptive period, representative of a novel sensory environment. These gait cycle strategies used in an effort to maintain postural stability and balance are similar to those used by astronauts returning from long-duration spaceflight (Bloomberg and Mulavara 2003; Bloomberg et al. 1997; McDonald et al. 1996), elderly populations (Cromwell and Newton 2004; Keshner 2000), and vestibular-deficient patients (Horak et al. 1994; Keshner 2000). The increased stance and double support time may also be the result of an attempt to gain more reliable and stable somatosensory information by increasing foot contact with the ground, thus allowing the CNS to default to this preference of input for postural stability when hyperresponsive vestibular information is present. Additionally, the positive significant correlation between stance time and total knee movement

suggests that, when considered with the observation that stride time is also increased and encompasses the stance phase of the gait cycle, a greater time is spent in knee flexion during the stance phase, allowing for more control over disturbances following heel strike in an attempt to mitigate head perturbations. This provides further evidence that the need for increased postural stability stems from head stabilization requirements.

In summary, Specific Aim III demonstrated that adaptive modification in body load mechanisms produced during prolonged unloaded locomotion resulted in increased stance time, double support time, and stride time during post-adaptation locomotion in an effort to increase postural stability, thus preserving gaze stability during locomotion. These changes are typical control strategies used to maintain greater foot contact with the ground, thus creating a more stable environment that works to mitigate risks of falls and maintaining a stable gaze during forward locomotion following an adaptive change.

#### **4.4 ADAPTIVE RECOVERY**

Astronauts returning from long-duration spaceflight have demonstrated adaptive changes in dynamic visual acuity, head-torso coordination and lower limb movement strategies that permit them to walk during a recovery period that trends towards preflight levels over a period of days or weeks (Bloomberg and Mulavara 2003). This period represents a time of sensorimotor “adaptive flux” that allows astronauts to reorganize their motor responses to patterns that are more appropriate for function in Earth’s gravity environment (Bloomberg and Mulavara 2003). In the current study, the percent-change curves reflect this period of recovery that is observed in head movement control, which trends towards to pre-adaptation values within the first four ITLP post-adaptation trials, but interestingly, no recovery is observed in lower limbs and gait cycle timing as the adaptation persists throughout the entire 10 post-adaptive ITLP trials.

The VCR adaptation that occurred during the 40% BWS adaptation period in all planes was observed as a brief period of adaptive flux in the reflexive head control mechanisms that are employed upon re-introduction to the post-adaptive sensory environment of normal body load. This quick recovery of head movement control may demonstrate the role that the DVA gaze task plays in providing feedback that allows subtle head control corrections that reinforce the recovery of a highly-sensitive VCR system in an effort to control the critical visual and vestibular information necessary for head stability during locomotion. Additionally, because the head itself was not directly unloaded as was the torso and lower limbs during the 40% BWS locomotion period, this quick recovery of head control may reflect an indirect adaptive response in response to the prolonged increased BWS.

Unlike the VCR system, which was indirectly adaptively modified by the reduced load during BWS, the lower limbs and feet were directly unloaded by the BWS device, resulting in prolonged pronounced changes in knee and ankle movement patterns and decreased input at the load receptors. This direct unloading of the limbs likely induced a hypersensitivity in the body load sensors that resulted in persistent changes in lower limb and gait cycle timing parameters that did not show a recovery to pre-adaptation values throughout all post-adaptation ITLP trials. In addition to this hypersensitivity, the lack of a correctional-control feedback mechanism similar to that which the DVA gaze task provided in head movement recovery may have contributed to this prolonged adaptive response in lower limbs and gait cycle timing. Hence, it is reasonable to conclude that such a hyperresponsive lower limb strategy would remain in place until the CNS accurately reinterpreted the post-adaptive somatosensory information from the body load sensors as reliable and stable.

Thus, the rapid recovery observed in the critical VCR system, combined with the persistency of the changes in lower limb movement and gait cycle timing are reflective of adaptive control mechanisms that are implemented in an effort to maintain posture and head stability in a post-stimulus sensory environment.

#### **4.5 VESTIBULAR – SOMATOSENSORY CONVERGENCE**

In the current study, the changes in head and torso movement, lower limb coordination, and gait cycle timing observed immediately following the 40% BWS adaptive period suggest that the reduced body load during BWS locomotion was interpreted by the CNS as a conflicting or unstable somatosensory input, resulting in a modulatory influence on the vestibular system that induced hyperresponsive vestibular activity. The effects of this vestibular-somatosensory interaction were observed in the subjects as reorganization of the full-body gaze stabilization system.

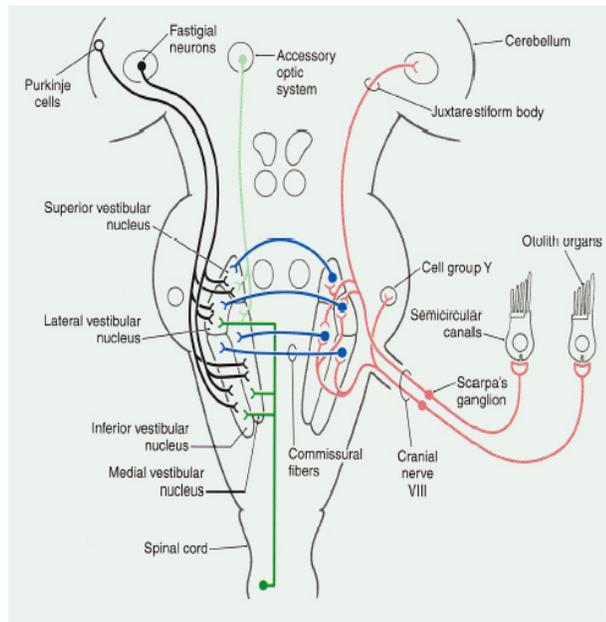
Vestibular-somatosensory interactions with respect to body load for posture and locomotor control have been demonstrated previously. Marsden et al. (2003) provided evidence for the convergence of vestibular and somatosensory input when they found that vestibular control of head and torso movements was altered with different levels of increased and decreased body load. In another study, Dietz et al. (2001) showed that the removal of foot pressure decreased the amount of somatosensory information from the feet, resulting in greater compensation from the vestibular system for postural control via the vestibulospinal pathway. When subjects were rotated in place while suspended from a harness with no foot contact with the ground, they subsequently displayed a larger rotational effect while hopping in place with eyes closed than while walking in place, which provided more foot contact, and thus somatosensory feedback, with the ground. Thus, the authors concluded that proprioceptive input that likely arises from load

receptors and stretch reflexes during leg movements influences vestibulospinal activity (Dietz et al 2001).

The findings can be substantiated anatomically. For example, during typical CNS integration of somatosensory and vestibular signals for postural control, the descending lateral vestibulospinal tract (LVST) controls posture by projecting excitatory input received primarily from neurons in the inferior and lateral vestibular nuclei that integrate information from the vestibular receptors, the vestibulocerebellum, the fastigial nucleus, and the spinal cord, to all levels of the ipsilateral spinal cord and out to extensor muscle motor neurons (Figure 4.5.1). In parallel, the ascending spinal cord pathways provide proprioceptive modulation to the vestibular nuclei that in turn drive vestibulospinal activity. The ascending spinovestibular tract has been shown to arise from all levels of the spinal cord, and relays proprioceptive information primarily to the medial and lateral vestibular nuclei in the brain stem (Wilson et al. 1966). Additionally, the dorsal columns (fasciculus gracilis and fasciculus cuneatus) carry information about proprioception, fine touch, and vibration originating from pressure receptors, muscle spindles and golgi tendon organs.

Experimentally, evidence of vestibular-somatosensory convergence was demonstrated when extracellular recordings of single lateral vestibular neurons that receive input from the lumbar spinal cord in cerebellectomized cats increased in activity upon stimulation of the leg nerves and the spinal cord at both the lumbar and cervical levels (Wilson et al. 1966). Another study by Jian et al. showed that peripheral electrical stimulation of the limbs in decerebrate cats resulted in activation of vestibular nuclei following peripheral vestibular lesions, and may enhance the effects of non-labyrinthine inputs to the vestibular nuclei as a means by which to compensate for the loss of labyrinthine inputs (Jian et al. 2002). With regard to descending locomotor control,

Zangemeister et al. (1991) demonstrated that during normal locomotion, when subjects walked with their head in a retroflexed (head down) position, altered lower limb muscle coordination patterns consequently followed. The authors suggested a functional linkage between otolith activity at various head positions and the muscle activity patterns produced in the lower limbs during walking. This functional linkage provides behavior evidence for integration of vestibular and somatosensory information critical for locomotor control.

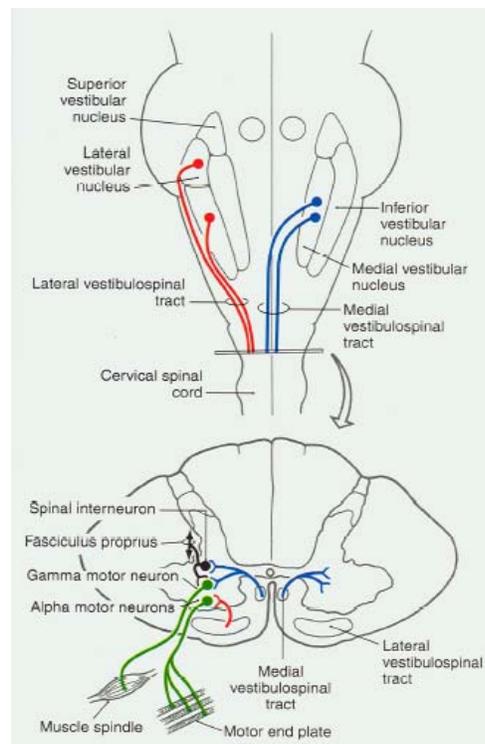


**Figure 4.5.1. Afferent Projections to the Vestibular Nuclei.** Ascending spinal cord projections carrying proprioceptive input to the vestibular nuclei can regulate vestibulospinal activity for posture and head control. Open cell bodies represent inhibitory projections. Figure used with permission from David Dickman, Ph.D. (Dickman 2006).

This convergent relationship can be demonstrated behaviorally in Dietz et al.'s study when subjects walked in place at 1 Hz, which provided the most foot contact with the ground, subjects displayed no significant rotational effect. The pronounced rotational effects imposed on the subjects in Dietz's study when the feet had less contact with the ground demonstrates the significant contribution of proprioceptive input in modulating vestibulospinal influence through the convergence of pathways. Although the authors do not identify which particular ascending spinal cord pathway(s) participate in this convergence, anatomical and experimental evidence suggests that the spino-vestibular ascending tract may be a primary contributor (Dickman 2006; Wilson et al. 1966). Dietz's study effectively demonstrates that the removal of load input at the feet may consequently reduce the excitatory input from ascending somatosensory projections, resulting in a disinhibition of the vestibular nuclei that in turn modulate vestibular activity on head and posture control. The result of this vestibular-somatosensory interchange is increased reliance on vestibular activity for postural and balance control.

The results of our study further demonstrate that prolonged reduced somatosensory input via the body's load sensors in the feet, knee, and hip joints consequently results in disinhibition of vestibular nuclei activity, which is reflected functionally as an increase in vestibular dependence for motor control in an effort to maintain a stable gaze. In particular, the vestibular system became hyperresponsive during the BWS locomotion adaptation period, reflected as modification in the VCR system. Anatomically, the VCR reflex is regulated via the descending medial vestibulospinal tract (MVST), which originates predominantly from the medial vestibular nucleus that receives input from vestibular receptors, the cerebellum, and spinal cord, and terminates at the cervical levels of the spinal cord (Figure 4.5.2). These MVST fibers carry both inhibitory and excitatory signals, and they terminate on neck flexor and

extensor motor neurons, and on propriospinal neurons. The MVST neurons process this information and transmit excitatory signals to the neck flexor muscles, while inhibitory signals are concurrently sent to the neck extensor muscles. The net effect of this activity is neck movement that occurs in a manner appropriate to maintaining head stability. MVST activity must be regulated to appropriately perform its VCR function, and this may be attributed to proprioceptive information provided by the ascending spinovestibular tract and dorsal columns, similar to LVST regulation. This demonstration of anatomical convergence of proprioceptive and vestibular pathways lends support to the observed changes in VCR function in this study that are attributed to the altered somatosensory input that occurred during prolonged BWS locomotion.



**Figure 4.5.2. Efferent Projections From the Vestibular Nuclei.** Descending spinal cord projections carrying vestibular information to muscle spindles and motor end plates can regulate proprioceptive activity for posture and head control. Figure used with permission from David Dickman, Ph.D. (Dickman 2006).

Do the results of this study reflect an increased gain of vestibulospinal pathways in the CNS as a result of somatosensory-induced vestibular nuclei disinhibition, or could they be attributed solely to a decreased somatosensory loop gain due to the increased BWS? Horak et al. (2001) posed this very question in a study that used galvanic vestibular stimulation to investigate vestibular-somatosensory substitution in postural control on patients with decreased somatosensory capability from the feet. In the study, the authors collected data from a group of patients and healthy subjects and created a control model of vestibular and somatosensory information for body orientation in space based on vestibular and somatosensory loops. In the model, galvanic vestibular stimulation represented changes in vestibular feedback, and compliant foam represented somatosensory feedback. Data collected from both of the subject populations was inputted into the model to reveal that the strategy of postural control was a result of both a central vestibular gain increase as well as a peripheral somatosensory gain decrease, together resulting in an overall gain change of the vestibulospinal system. Hence, this model provides further evidence for vestibulospinal disinhibition at the motor neuronal level as a result of modulation of somatosensory input. The authors attributed the functional importance of such adaptive vestibulospinal gain change as a daily life necessity as we attempt to orient our posture for a wide variety of surface conditions, as well as a compensatory mechanism for periodic loss of somatosensory information. They also suggested that this type of sensory substitution mechanism may be similar to the adaptive increase in somatosensory loop gain seen in patients with chronic loss of the vestibular system (Bles et al. 1984; Horak et al. 2001; Strupp et al. 1999).

Thus, when combined with previous anatomical and experimental evidence of vestibular-somatosensory integration, the results of our study provide further evidence that vestibular-somatosensory interactions do occur for the maintenance of posture and

head control, and can be appropriately modified to provide compensation when one system becomes unstable or absent. The neural basis for this modulation appears to be due to the anatomical arrangement and functional interactions between the ascending spinal tracts, the vestibular nuclei, and the descending spinal tracts for the control of posture and balance during locomotion.

#### **4.6 CAVEATS AND FUTURE WORK**

Could the changes observed in the locomotion parameters in this study be a consequence of walking-induced fatigue? Subjects walked for 3 minutes in the pre-adaptation ITLP period, 30 minutes during the BWS adaptation period, and for 10 trials of 70 seconds each with an alternating one minute rest period in the post-adaptation ITLP period. Effects of fatigue during locomotion have been documented previously as contribution to changes in gait cycle timing and lower limb coordination (Mizrahi et al. 2000). In a study of subjects during treadmill running for 30 minutes, Mizrahi et al. (2000) found that the average stride rate was significantly decreased, while average knee flexion resulting from heel strike decreased. These results are contrary to the results of predominant changes obtained from our subjects who performed the 30 minutes of 40% BWS locomotion. In a separate study where subjects walked for 3 hours at a preferred pace, Yoshino et al. (2004) found increased variability of gait rhythm proportional to the amount of time spent walking. This increased variability was not observed in our BWS subjects, as each subject maintained consistent gait rhythm as evidenced by their lack of significant differences in stride time, stance time, and double support time between each of the 10 post-adaptive ITLP trials. Additionally, the effect of fatigue is mitigated further when taken into consideration that our subjects walked at 40% BWS for 30 minutes of the study, and previous metabolic studies indicate that BWS walking requires less energy

than locomotion with normal BWS (Farley and McMahon 1992; Newman et al. 1994; Wortz and Prescott 1966). Therefore, the results observed in the BWS were not likely due to walking fatigue.

The effects of the torso harness on kinematic dynamics can also be directly addressed in this study. Subjects wore the same harness in all 3 phases of this experiment, thus eliminating effects of various harnesses on kinematic changes. However, all techniques for providing BWS involve challenges, including balancing subject comfort with the appropriate BWS stimulus to induce an effect. Our method of BWS used a commercially-available device that is employed regularly in locomotor rehabilitation protocols for cases like stroke and brain injury. The device applied vertical forces directly to the torso, and as a result, the limbs may have ultimately experienced less BWS during the adaptation period. Nevertheless, the goal of this study was to investigate how the full body reorganizes during adaptation to changes in load, which includes the load receptors in the hips, knee, ankles, and soles of the feet, all of which received some level of BWS as evidenced by the kinematic changes that are seen in studies with use of similar BWS devices as in this study (Bastiaanse et al. 2000; Davis et al. 1996; Dietz et al. 2002; Donelan and Kram 1997; Finch et al. 1991; Harkema et al. 1997; Ivanenko et al. 2002; Stephens and Yang 1999; Threkheld et al. 2003). Furthermore, the BWS technique used in this study was sufficient to induce significant adaptive changes in kinematics and gait cycle timing in the post-adaptation ITLP period, thus validating the intent of the study.

The use of a treadmill was preferred over over-ground walking in this study because it allowed a controlled condition in which to simultaneously evaluate all of the full-body strategies used in locomotor control during a gaze stabilization task. For example, Nelson et al. (1972) observed less vertical and horizontal velocity variability in

treadmill running than in over-ground running, and Woolley and Winter (1979) found that the stride-to-stride variability of locomotion was significantly greater over ground, suggesting that the treadmill induces greater constraints on walking. Thus, in this study, the use of the treadmill allows introduction of only BWS as our experimental variable, under controlled conditions that provided for a consistent measure of performance between subjects, thus minimizing the effects of parameters such as inconsistent speed and direction that would otherwise be observed in over-ground walking.

Due to the novel nature of this study, future investigations with respect to adaptive modifications to body loading mechanisms are warranted. For example, analyzing head movement dynamics during the BWS adaptation period and the forces imparted at the feet, tibia, and head during the high-impact phases of the gait cycle during and immediately following the BWS adaptive period would be useful in understanding the extent of head perturbation that is induced during the BWS adaptive period, providing additional information concerning otolith recalibration and integration with the somatosensory system. Measuring otolith-mediated Hoffman reflexes would provide additional information concerning vestibulospinal sensitivity, and measuring muscle activation latencies in lower limbs, torso, head, and neck muscles could provide information concerning feedback loops between body segments, providing insight to the mechanisms responsible for anticipatory and reactive integration of the muscles and joints involved in control of head stabilization following adaptation of body load perception.

Additionally, the results of this study warrant further investigation with regard to post-flight locomotor disturbances demonstrated by astronauts returning from long-duration spaceflight. Because our results suggest that body load input alone plays a central role in mediating vestibular activity and locomotor control, investigations should

be performed to determine the appropriate amount of body load exposure required to potentially mitigate post-flight locomotor disturbances. For example, because our results show that body load sensors can be adaptively modified, and the resulting locomotor control patterns can be unique to the individual's neural adaptation capability, there may be some benefit in pre-flight training of astronauts in an effort to create more robust, predictable vestibular-somatosensory activity unique to each astronaut. Additionally, individual in-flight treadmill exercise protocols may be enhanced when appropriate amount of load is integrated in a manner that may facilitate quicker recovery to terrestrial locomotion. Thus, future studies are warranted to determine appropriate load levels for the development of protocols that can enhance safety of performance during such scenarios as emergency egress upon return to Earth, or exploration of the moon and Mars.

#### **4.7 CONCLUSIONS**

Based on the results of the three specific aims investigated in this study, it is evident that even just 30 minutes of 40% BWS during locomotion was enough sensory conflict to induce adaptive modifications in the sensory systems that contribute locomotion and gaze stabilization. Immediately following the BWS adaptation period, subjects were able to satisfy the two goals of locomotion: maintaining a stable forward translation and stabilizing gaze, both of which require the integration of multiple sensory systems. The data clearly demonstrate individual variations in strategies of locomotor control after being exposed to vestibular-somatosensory conflict for 30 minutes, and were depicted by the classification of the subjects' individual gaze stabilization subsystem responses as observed predominant changes. Therefore, the changes observed in function of these various subsystems after body load adaptation represent an *adaptive*

*reorganization* of motor behavior in response to altered vestibular-sensorimotor input as a strategy in aiding gaze stabilization during locomotion.

In conclusion, following adaptation of the body load-sensing system, the predominant changes during locomotion that subjects displayed were: increased head pitch and roll movements and decreased head yaw movements in the head reflexive bandwidth; increased torso pitch and roll in the head reflexive bandwidth, increase in knee and ankle flexion and increased torso vertical translation following heel strike; and increased stride, double support, and stance time. Thus, the results of this study support the general hypothesis **that body load-regulating mechanisms ultimately contribute to gaze stabilization, and adaptive changes in these load-regulating mechanisms require reorganization in the full-body gaze control system so that visual acuity can be maintained during locomotion.** Such adaptive modifications are indicative of significant vestibular-somatosensory interactions that can be altered with prolonged exposure to the novel BWS stimulus, and serve as the basis for facilitating gait adaptation to new environments. Furthermore, somatosensory input has a central role in this process and thus in locomotor adaptability training in general. These findings will contribute new knowledge to the fundamental research that seeks to elucidate the role of load-regulating mechanisms in gaze stabilization and locomotor control; the development of rehabilitation protocols that use unloading devices as retraining strategies (spinal cord injury, brain injury, stroke); and the methods used to improve astronaut post-flight health and safety, as well as an understanding of mechanisms responsible for post-flight locomotor dysfunction

## REFERENCES

- Aeillo I, Rosati G, Serra G, Tugnoli V, Manica M. Static vestibulospinal influences in relation to different body tilts in man. *Exp Neurol* 1983; 79:18-26.
- Alford E, Roy R, Hodgson J, Edgerton V. Electromyography of rat soleus, medial gastrocnemius, and tibialis anterior during hind limb suspension. *Exp Neurol*. 1987; 96:635-649.
- Allum J, Gresty M, Keshner E, Shupert C. The control of head movements during human balance corrections. *J Vestib Res* 1997; 7(2-3): 189-218.
- Aoki M, Matsunami K, Han X, Tamada H, Muto T, Ito Y. Neck muscle responses to abrupt vertical acceleration in the seated human. *Exp Brain Res* 2001; 140(1): 20-24.
- Bastiannse C, Duysens J, Dietz V. Modulation of cutaneous reflexes by load receptor input during human walking. *Exp Brain Res* 2000; 135:189-198.
- Berthoz A and Pozzo T. Head and Body coordination during locomotion and complex movements. In: Swinnen SP, Massion J, Heuer H, Casaer P, ed. *Interlimb Coordination: Neural, Dynamical, and Cognitive Constraints*. Boston, MA: Academic Press; 1994:147-165.
- Berthoz A and Pozzo T. Intermittent head stabilization during postural and locomotory tasks in humans. In: Amblard B, Berthoz A, Clarac F (Eds). *Posture and Gait: Development, Adaptation and Modulation*. Elsevier: Amsterdam. 1988, pp189-198.
- Black F, Paloski W, Doxey-Gasway D, Reschke M. Vestibular plasticity following orbital spaceflight: recovery from postflight postural instability. *Acta Otolaryng (Stockholm)* 1995; 520:450-454.
- Bles W, Vianney De Jong JMB, and De Wit G. Somatosensory compensation for loss in labyrinthine function. *Acta Otolaryngol* 1984; 97:213-221.
- Bloomberg J, Reschke M, Huebner W, Peters B. The effects of target distance on eye and head movement during locomotion. *Ann NY Acad Sci* 1992; 656:699-707.
- Bloomberg J, Peters B, Huebner W, Smith S, Reschke M. Locomotor head-trunk coordination strategies following space flight. *J Vestib Res* 1997; 7(2-3):161-177.

- Bloomberg J, Mulavara A. Changes in walking strategies after spaceflight. *IEEE Engineering in Medicine and Biology Magazine*, 2003; 22(2): 58-62.
- Boyle R, Messinger A, Yoshida K, Usui S, Intravaia A, Tricas T, Highstein S. Neural readaptation to Earth's gravity following return from space. *J Neurophys* 2001; 86: 2118-2122.
- Bril B and Ledebt A. Head coordination as a means to assist sensory integration in learning to walk. *Neurosci Biobehav Rev* 1998; 22(4):555-63.
- Britton T, Day B, Brown P, Rothwell J, Thompson P, Marsden C. Postural electromyographic responses in the arm and leg following galvanic vestibular stimulation in man. *Exp Brain Res*. 1993; 94:143-151.
- Buchner A, Erdfelder E, Faul, F. (1997). How to Use G\*Power [WWW document]. URL <http://www.psych.uni-duesseldorf.de/aap/projects/gpower>.
- Capozzo A. Low frequency self-generated vibration during ambulation in normal men. *J Biomech* 1982; 15(8):599-609.
- Chao E. Justification of triaxial goniometer for the measurement of joint rotation. *J Biomech* 1980; 13:989-1006.
- Clement G, Gurfinkel V, Lestienne F, Lipshits M, Popov K. Changes of posture during transient perturbations in microgravity. *Aviat Space Environ Med* 1985; 56:666-671.
- Cohen, J. *Statistical power analysis for the behavioral sciences* (2nd edition). Hillsdale, NJ: Erlbaum (1988).
- Crane B, Delmer J. Human gaze stabilization during natural activities: Translation, rotation, magnification and target distance effects. *J Neurophys* 1997; 78: 2129-2144.
- Cromwell R, Newton R, Carlton L. Horizontal plane head stabilization during locomotor tasks. *J Motor Behav*. 2001; 33(1): 49-58.
- Cromwell R., Pidcoe P, Griffin L, Sotillo T, Ganninger D, Feagin M. Adaptations in horizontal head stabilization in response to altered vision and gaze during natural walking. *J Vest Res* 2004; 14:367-373.
- Cromwell R. and Newton R. Relationship between balance and gait stability in healthy older adults. *J Aging Phys Activ* 2004; 12(1):90-100.

- Davids K, Glazier P, Arujo D, and Bartlett R. Movement systems as dynamical systems: the functional role of variability and its implications for sports medicine. *Sports Med* 2003; 33:245-260.
- Davis B, Cavanagh P. Simulating reduced gravity: A review of biomechanical issues pertaining to human locomotion. *Aviat Space Environ Med*, 1993; 64:557-566.
- Davis, B, Cavanagh P, Sommer, H 3rd, Wu G. Ground reaction forces during locomotion in simulated microgravity. *Aviat Space Environ Med* 1996; 67(3): 235-242.
- Day B, Severac C, Bartolomei L, Pastor M, Lyon I. Human body-segment tilts induced by galvanic stimulation: a vestibularly-driven balance protection mechanism. *J Physiol (Lond)* 1997; 500:661-672.
- Demer J and Amjadi F. Dynamic visual acuity of normal subjects during vertical optotype and head motion. *Invest Ophthalmol Vis Sci* 1993; 34(6):1894-1906.
- Demer J, Viirre E. Visual-vestibular interaction during standing, walking and running. *J Vestib Res* 1996; 6:295-313.
- Dickman, D. The Vestibular System. In: D. Haines (ed), *Fundamental Neuroscience*, Williams and Wilkins, New York, 2006.
- Dieringer N, Kunzle H, Precht W. Increased projection of ascending dorsal root fibers to vestibular nuclei after hemilabyrinthectomy in the frog. *Exp Brain Res* 1984; 55: 574-578.
- Dieringer N. Vestibular compensation: neural plasticity and its relations to functional recovery after labyrinthine lesions in frogs and other vertebrates. *Prog Neurobiol* 1997; 46:97-129.
- Dietz V, Muller R, Colombo G. Locomotor activity in spinal man: significance of afferent input from joint and load receptors. *Brain* 2002; 125(Pt 12):2626-2634.
- Dietz V, Baaken B, Colombo G. Proprioceptive input overrides vestibulo-spinal drive during human locomotion. *Neuroreport* 2001; 12(12):2743-6.
- Dietz V, Duysens J. Significance of load receptor input during locomotion: a review. *Gait Posture*. 2000 Apr; 11(2):102-10.
- Dietz V. Interaction between central programs and afferent input in the control of posture and locomotion. *J Biomech* 1996; 29(7):841-4.

- Dietz V, Horstmann G, Trippel M, Gollhofer A. Human postural reflexes and gravity- an underwater simulation. *Neurosci Lett* 1989; 106:350-355.
- Dijkstra T, Schoner G, Gielen C. Temporal stability of the action-perception cycle for postural control in a moving visual environment. *Exp Brain Res.* 1994; 97:447-486.
- Donelan J, Kram R. The effect of reduced gravity on the kinematics of human walking: a test of the dynamic similarity hypothesis for locomotion. *J Exp Biol* 1997; 200(24):3193-201.
- Duysens J, Pearson K. Inhibition of flexor burst generation by loading ankle extensor muscles in walking cats. *Brain Res* 1980; 187(2):321-32.
- Duysens J, Clarac F, Cruse H. Load-regulating mechanisms in gait and posture: comparative aspects. *Physiol Rev* 2000; 80(1):83-133.
- Edgerton V, McCall G, Hodgson J, Gotto J, Goulet C, Fleischmann K, Roy R. Sensorimotor adaptations to microgravity in humans. *J Exp Biol.* 2001 Sep; 204(18):3217-24.
- Farley C, McMahon T. Energetics of walking and running: insights from simulated-reduced gravity experiments. *J Appl Physiol* 1992; 73(6): 2709-12.
- Finch L, Barbeau H, Arsenault B. Influence of body weight support on normal human gait: Development of a gait retraining strategy. *Phys Ther* 1991; 71:842-855.
- Fitzpatrick R and McCloskey D. Proprioceptive, visual and vestibular thresholds for the perception of sway during standing in humans. *J Physiol (Lond)* 1994; 478:173-186.
- Flynn T, Canavan P, Cavanaugh P, and Chiang, J. Plantar pressure reduction in an incremental weight-bearing system. *Phys Ther* 1997; 77(4): 410-417.
- Fouad K, Bastiaanse C, Dietz V. Reflex adaptations during treadmill walking with increased body load. *Exp Brain Res* 2001; 137:133-140.
- Fredrickson J, Schwarz D, Kornhuber H. Convergence and interaction of vestibular and deep somatic afferents upon neurons in the vestibular nuclei of the cat. *Acta Otol.* 1966; 61:168-188.
- Gard S and Childress D. The influence of stance-phase knee flexion on the vertical displacement of the trunk during normal walking. *Arch Phys Med Rehabil* 1999; 80(1):26-32.

- Griffin T, Tolani N, Kram R. Walking in simulated reduced gravity: mechanical energy fluctuations and exchange. *J Appl Physiol* 1999; 86(1):383-90.
- Grossman G, Leigh R, Abel L, Lanska D, Thurston S. Frequency and velocity of rotational head perturbations during locomotion. *Exp Brain Res* 1988; 70:470-476.
- Gurfinkel V, Levik Y, Popov K, Smetanin B, Shlikov V. Body scheme in the control of postural activity. In: *Stance and Motion: Facts and Theories*, edited by Gurfinkel V, Yoffe M, Massion J, Roll J. New York: Plenum, 1988, p. 185-193.
- Harkema S, Hurley S, Patel U, Requejo P, Dobkin B, Edgerton V. Human lumbosacral spinal cord interprets loading during stepping. *J Neurophysiol* 1997; 77(2):797-811.
- Hess B. Vestibular signals in self-orientation and eye movement control. *News Physiol Sci* 2001; 16: 234-238.
- Hillman E, Bloomberg J, McDonald P, Cohen H. Dynamic visual acuity while walking in normals and labyrinthine deficient patients. *J Vest Res.* 1999; 9:49-57.
- Hirasaki E, Moore S, Raphan T, Cohen B. Effects of walking velocity on vertical head and body movements during locomotion. *Exp Brain Res* 1999; 127(2):117-130.
- Holt K, Jeng S, Ratcliffe R, Hamill J. Energetic cost and stability during human walking at the preferred stride frequency. *J Motor Beh* 1995; 27:164-178.
- Horak F, Schupert C, Dietz V, Horstmann G. Vestibular and somatosensory contributions to responses to head and body displacements in stance. In: *Vestibular Rehabilitation*, edited by Herdman SJ. Philadelphia: Davis, 1994, p. 22-46.
- Horak F, Nashner L, and Diener H. Postural strategies associated with somatosensory and vestibular loss. *Exp Brain Res* 1990; 82:167-177.
- Horak F and Hlavacka F. Somatosensory loss increases vestibulospinal sensitivity. *J Neurophys* 2001; 86:575-585.
- Imai T, Moore S, Raphan T, and Cohen B. Interaction of the body, head and eyes during walking and turning. *Exp Brain Res* 2001; 136: 1-18.
- Inglis J, Shupert C, Hlavacka F, and Horak F. The effect of galvanic vestibular stimulation on human postural responses during support surface translations. *J Neurophysiol* 1995; 73: 896-901.

- Ito Y, Corna S, von Brever M, Bronstein A, Rothwell J, Gresty M. Neck muscle responses to abrupt freefall of the head: comparison of normal with labyrinthine-defective human subjects. *J Physiol* 1995; 489:911-916.
- Ivanenko Y, Grasso R, Macellari V, Lacquaniti F. Control of foot trajectory in human locomotion: role of ground contact forces in simulated reduced gravity. *J Neurophysiol* 2002; 87(6):3070-3089.
- Iwase S, Sugiyama Y, Miwa C, Kamiya A, Mano T, Ohira Y, Shenkman B, Egorov A, Kozlovskaya I. Effects of three days of dry immersion on muscle sympathetic nerve activity and arterial blood pressure in humans. *J Auto Nerv Sys.* 2000; 79:156-164.
- Jian, B, Shintani T, Emanuel B, Yates B. Convergence of limb, visceral, and vertical semicircular canal or otolith inputs onto vestibular nucleus neurons. *Exp Brain Res* 2002; 144:247-257.
- Keshner, E and Peterson, B. Multiple control mechanisms contribute to functional behaviors of the head and neck. In: Berthoz A, Vidal P, Graf W (Eds). *The Head-Neck Sensorimotor System*. Oxford University Press: New York. 1992, Chapter 58, 381-386.
- Keshner E, Cromwell RL Peterson B. Mechanisms controlling human head stabilization. II. Head-neck characteristics during random rotations in the vertical plane. *J Neurophysiol.*, 1995a; 73:2302-2312.
- Keshner E and Peterson B. Mechanisms controlling human head stabilization. I. Head-neck dynamics during random rotations in the horizontal plane. *J Neurophysiol.*, 1995b; 73:2293-2301.
- Keshner E. Postural abnormalities in vestibular disorders. In: Herdman SJ (Ed). *Vestibular Rehabilitation, Second Edition*. FA Davis Company: Philadelphia. 2000, Chapter 3, 52-76.
- Kram R, Domingo A, Ferris D. Effect of reduced gravity on the preferred walk-run transition speed. *J Exp Biol* 1997; 200:821-826.
- Kozlovskaya I, Dmitrieva I, Grigorieva L, Kirenskaya A, Kreydich Y. Gravitational mechanisms in the motor system. Studies in real and simulated weightlessness. In: *Stance and Motion.*, 1988, Eds. VS Gurfinkel, MY Ioffe, J Massion. Plenum, NY, p. 37-48.
- Kozlovskaya I, Aslanova I, Grigorieva, L, Kreydich Y. Experimental analysis of motor effects of weightlessness. *Physiologist*. 1982; 25(6S): S49-S52.

- Kozlovskaya I, Kreidich Y, Rakhmanov A. Mechanics of the effects of weightlessness on the motor system of man. *Physiologist* 1981; 24(6S): S59-S64.
- Kyparos A, Feedback D, Layne C, Martinez D, Clarke M. Mechanical stimulation of the plantar foot surface attenuates soleus muscle atrophy induced by hindlimb unloading in rats. *J Appl Phys* 2005; 99:739-746.
- Layne C, McDonald P, Bloomberg J. Neuromuscular activation patterns during locomotion after spaceflight. *Exp Brain Res*. 1997; 113:104-116.
- Layne C, Lange G, Pruett C, McDonald P, Merkle L, Smith S, Kozlovskaya I, Bloomberg J. Adaptation of neuromuscular activation patterns during locomotion after long-duration space flight. *Acta Astro* 1998; 43:107-119.
- Lee D and Lishman J. Visual proprioceptive control of stance. *J Human Move Studies* 1975; 1:87-95.
- Light L, McLellan G, Klenherman L. Skeletal transients on heel strike in normal walking with different footwear. *J Biomech* 1980; 13:477-480.
- Lund S and Broberg C. Effects of different head positions on postural sway in man induced by a reproducible vestibular error signal. *Acta Physiol Scand* 1983; 117:307-309.
- MacDougall H, Moore S. Marching to the beat of the same drummer: the spontaneous tempo of human locomotion. *J Appl Physiol* 2005; 99:1164-1173.
- Massion J, Amblard B, Assiante C, Mouchnino L, Vernazza S. Body orientation and control of coordinated movements in microgravity. *Bain Res Rev* 1998; 28:83-91.
- Marsden J, Blakey G, Day B. Modulation of human vestibular-evoked postural responses by alterations in load. *J Physiol*. 2003 May 1; 548(3):949-53.
- McConville J, Churchill T, Kaleps I, Clauser C, and Cuzzi J. Anthropometric relationships of body and body segments of inertia. AFAMRL-TR-80-119, 1980; Dayton, OH. Wright-Patterson AFB.
- McDonald P, Basdogan C, Bloomberg J, Layne C. Lower limb kinematics during treadmill walking after space flight: Implications for gaze stabilization. *Exp Brain Res* 1996; 112:325-334.

- McDonald P, Bloomberg J, Layne C. A review of adaptive change in musculoskeletal impedance during space flight and associated implications for postflight head movement control. *J Vestib Res* 1997; 7:239-250.
- McMahon T, Valiant G, Frederick E. Groucho running. *J Appl Physiol.* 1987; 62:2326-2337.
- Mergner T and Rosemeier T. Interaction of vestibular, somatosensory and visual signals for postural control and motion perception under the terrestrial and microgravity conditions- a conceptual model. *Brain Res Rev* 1998; 28:118-135.
- Miller C, Mulavara A, Bloomberg J. A quasi-static method for determining the characteristics of a motion capture camera system in a split-volume configuration. *Gait Posture* 2002; 16(3): 283-287.
- Minetti A. Walking on other planets. *Nature*, 2001; 409(25): 467-469.
- Mizrahi J, Verbitsky O, Isakov E, Daily D. Effect of fatigue on leg kinematics and impact acceleration in long distance running. *Hum Move Sci* 2000; 19:139-151.
- Mulavara A, Verstraete M, Bloomberg J. Modulation of head movement control during walking. *Gait Posture* 2002; 16(3):271-282.
- Mulavara A, Bloomberg J. Identifying head-trunk and lower limb contributions to gaze stabilization during locomotion. *J Vestib Res* 2003; 12: 255-269.
- Mulavara A, Houser J, Peters B, Miller C, Richards, J. Full-body gaze control mechanisms elicited during locomotion: Effects of VOR adaptation. *J Vestib Res* 2005; 15(5-6):279-289.
- Murray M, Drought A, Kory R. Walking patterns of normal men. *J Bone Joint Surg* 1964; 46(A):335-360.
- Nashner L. Strategies for organization of human posture. In: Igarashi M and Black O (Eds). *Vestibular and Visual Control on Posture and Locomotor Equilibrium*. Karger: New York, NY. 1985, pp. 1-8.
- Nashner L and Wolfson P. Influence of head position and proprioceptive cues on short latency postural reflexes evoked by galvanic stimulation of the human labyrinth. *Brain Res* 1974; 67:225-268.
- Nelson R, Dillman C, Lagasse P, Bickett P. Biomechanics of overground versus treadmill running. *Med Sci Sports Exerc* 1972; 4:233-240.

- Newman D, Alexander H, Webbon B. Energetics and mechanics for partial gravity locomotion. *Aviat Space Environ Med*, 1994; 65:815-823.
- Nicogossian A. Microgravity simulations and analogues. In: Nicogossian AE, Huntoon CL, Pool SL (Eds.). *Space Physiology and Medicine*. Lea & Febiger: Philadelphia. 1993, Chapter 20, 363-371.
- Paloski W, Black O, Reschke M, Calkins D, Shupert C. Vestibular ataxia following shuttle flights: effects of microgravity on otolith-mediated sensorimotor control of posture. *Am J Otolaryngol* 1993; 14(1):9-17.
- Peters B, Bloomberg J. Dynamic visual acuity using “far” and “near” targets. *Acta Otolaryngol* 2005; 125(4):353-357.
- Peterson B, Boyle R. Vestibulocollic Reflexes. In: Highstein S, Fay R, Popper A (Eds). *The Vestibular System*. Springer. New York. 2004, Chapter 8, 343-374.
- Pfaltz C. Central compensation of vestibular dysfunction. I. Peripheral lesions. *Adv Otorhinolaryngol* 1983; 30: 335-348.
- Poyhonen T. and Avela J. Effect of head-out water immersion on neuromuscular function of the plantarflexor muscles. *Av Space Env Med* 2002 73(12):1215-8.
- Pozzo T, Berthoz A, Lefort L. Head stabilization during various locomotor tasks in humans I. Normal Subjects. *Exp Brain Res* 1990; 82:97-106.
- Pozzo T, Berthoz A, Lefort L, Vitte E. Head stabilization during various locomotor tasks in humans II. Patients with bilateral peripheral vestibular deficits. *Exp Brain Res* 1991; 85:208-217.
- Pozzo T, Levik Y, Berthoz A. Head and trunk movements in the frontal plane during complex dynamic equilibrium tasks in humans. *Exp Brain Res* 1995; 106(2):327-38.
- Putkonen P, Courjon J, and Jeannerod M. Compensation of postural effects of hemilabyrinthectomy in the cat. A sensory substitution process? *Exp Brain Res* 1977; 28: 249-257.
- Raphan T, Imai T, Moore S, and Cohen B. Vestibular compensation and orientation during locomotion. *Ann NY Acad Sci* 2001; 942:128-139.
- Recktenwald M, Hodgson J, Roy R, Riazanski S, McCall G, Kozlovskaya I, Washburn D, Fanton J, Edgerton V. Effects of spaceflight on rhesus quadrupedal locomotion after return to 1G. *J Neurophysiol*. 1999; 81(5):2451-2463.

- Reschke M, Bloomberg J, Harm D, Paloski W, Layne C, McDonald P. Posture, locomotion, spatial orientation, and motion sickness as a function of space flight. *Brain Res Rev* 1998; 28:102-117.
- Reschke M, Anderson D, Homick J. Vestibulospinal reflexes as a function of microgravity. *Science* 1984; 225:212-214.
- Richards J, Mulavara A, Bloomberg J. The interplay between strategic and adaptive control mechanisms in plastic recalibration of locomotor function. *Exp Brain Res* In Press.
- Rieser J, Pick H Jr, Asmead D, Garing A. Calibration of human locomotion and models of perceptual-motor organization. *J Exp Psychol Hum Percept Perform* 1995; 21:480-497.
- Roll J, Popov K, Gurfinkel V, Lipshits M, Deshayes A, Gilhodes J, Quoniam C. Sensorimotor and perceptual function of muscle proprioception in microgravity. *J Vestib Res.* 1993; 3:259-273.
- Roy R, Hutchinson D, Hodgson J, Edgerton V. EMG amplitude patterns in rat soleus and medial gastrocnemius following seven days of hindlimb suspension. *ISSS Eng Med Bio.* 10<sup>th</sup> Annual International Conference. 1988; 1710-1711.
- Rubin A, Liedgren S, Odkvist L, Larsby B, Aschan G. Limb input to the cat vestibular nuclei. *Acta Otol* 1979; 87:113-122.
- Shumway-Cook A and Horak F. Assessing the influence of sensory interaction on balance: suggestions from the field. *Phys Ther* 1986; 66:1548-1550.
- Smeathers J. Transient vibrations caused by heel strike. *Eng Med* 1989; 203:181-186.
- Stephens M, Yang J. Loading during the stance phase of walking in humans increases the extensor EMG amplitude but does not change the duration of the step cycle. *Exp Brain Res* 1999; 124:363-370.
- Stoffregen T, Smart L, Bardy B, Pagulayan R, Postural stabilization of looking. *J Exp Psychol Hum Percept Perform* 1999; 25:1641-1658.
- Stoffregen T, Pagulayan R, Bardy B, Hettinger L. Modulating postural control to facilitate visual performance. *Hum Move Sci* 2000; 19:203-220.
- Strupp M, Arbusow V, Pereira C, Dieterich M, Brandt T. Subjective straight-ahead during neck muscle vibration: effect of aging. *Neuroreport* 1999; 10:3191-3194.

- Sutherland D, Kauffman K, Moitza J. Kinematics of normal human walking. In: J Rose and E Gamble (Eds). *Human Walking*, 2<sup>nd</sup> ed. Williams and Wilkins: Baltimore, MD. 1994, p23-44.
- Threlkeld A, Cooper L, Monger B, Craven A, Haupt H. Temporalspatial and kinematic gait alterations during treadmill walking with body weight suspension. *Gait Posture* 2003; 17:235-245.
- Vereijken B, VanEmmerik R, Whiting H, Newell K. Freezing the degrees of freedom in skill acquisition. *J Motor Behav.* 1992; 24:133-142.
- Voloshin A. Shock absorption during running and walking. *J Am Pod Med Assoc.* 1988; 78(6): 295-299.
- Watt D, Money K, Tomi L. MIT/Canadian vestibular experiments of the Spacelab-1 mission: 3. Effects of prolonged weightlessness on a human otolith-spinal reflex. *Exp Brain Res* 1986; 64:308-315.
- Weber K, Fletcher W, Gordon C, Melville Jones G, Block E. Motor learning in the podokinetic system and its role in spatial orientation during locomotion. *Exp Brain Res.* 1998; 120:377-385.
- Whittle M. Generation and attenuation of transient impulsive forces beneath the foot: a review. *Gait Posture* 1999; 10:264-275.
- Wilson V, Kato M, Thomas R, Peterson B. Excitation of lateral vestibular neurons by peripheral afferent fibers. *J Neurophysiol* 1966; 29:508-529.
- Wilson V. Vestibulospinal and neck reflexes: interaction in the vestibular nuclei. *Arch Ital Biol* 1991; 129:43-52.
- Wilson V, Boyle R, Fukushima K, Rose P, Shinoda Y, Sugiuchi Y, Uchino Y. The vestibulocollic reflex. *J Vestib Res* 1995; 5(3):147-170.
- Woolley S and Winter D. Mechanical energies in overground and treadmill walking. 3<sup>rd</sup> Annual conference of the American Society of Biomechanics; University Park PA, 1979.
- Wortz E and Prescott E. The effects of subgravity traction simulation on the energy costs of walking. *Aerosp Med* 1966; 37:1217-1222.
- Wosk J and Voloshin A. Wave attenuation in skeletons of young healthy persons. *J Biomech* 1981; 14(4): 261-267.

Yoshino K, Motoshige T, Araki T, Matsuika K. Effect of prolonged free-walking fatigue on gait and physiological rhythm. *J Biomech* 2004; 1271-1280.

Zangemeister W, Bulgheroni M, Pedotti A. Normal gait is differentially influenced by the otoliths. *J Biomed Eng* 1991; 13: 451-58.

## VITA

Tara Ruttley was born on September 23, 1975 to David and Debra Ruttley. She is married to her high school sweetheart, Paul Colosky Jr. Tara enrolled in the Neuroscience Graduate Program at the University of Texas Medical Branch in 2002. She has concurrently held a position with NASA Johnson Space Center as the lead engineer for the Health Maintenance System for the International Space Station throughout her graduate studies at UTMB. While at UTMB, Tara was awarded a GSBS Associates Award, a NASA patent award, and a membership with Who's Who Among Students in American Colleges and Universities. She also co-authored and published two peer-reviewed papers while at UTMB. Tara can be contacted through the Graduate School of Biomedical Sciences at UTMB.

### Education

B.S. Biology, 1998, Colorado State University, Ft Collins, Colorado  
M.S. Mechanical Engineering, 2000, Colorado State University, Ft. Collins, Colorado

### Publications

Mulavara A.P., Richards J.T., Ruttley T. M., Marshburn A., Nomura Y., Bloomberg J.J. Exposure to a rotating virtual environment during treadmill locomotion causes adaptation in heading direction. *Experimental Brain Research*. 166(2):210-9, 2005.

Kaufman, G., Weng, T., Ruttley, T. A rodent model for artificial gravity: VOR adaptation and Fos expression. *Journal of Vestibular Research*. 15(3):131-47, 2005.

Ruttley, TM, Colosky PE Jr., James, SP. A gravity-independent constant force resistive exercise unit. *Biomedical Sciences. Instrumentation*. 37:87-93, 2001.

### Abstracts

Kaufman, G., Ruttley, T., Weng, T. Fos Expression and Video-oculography during Cross-coupling Training in the Gerbil. Association for Research in Otolaryngology 2004 Mid-Winter Research Meeting, Abstract #270.

### Patents

United States Patent: Paul Colosky, Jr. and Tara Ruttley. *Constant Force Resistive Exercise Unit*, s/n: 09/931,142 (issued Feb. 2004).