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Stefan I. Madansingh
December 2016

LEVERAGING SENSORIMOTOR ADAPTIVE GENERALIZABILITY TO
MINIMIZE DYNAMIC FALL RISK

A Dissertation

Presented to

The Faculty of the Department
of Health & Human Performance
University of Houston

In Partial Fulfillment

of the Requirements of the Degree:

Doctor of Philosophy

in Kinesiology

By

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ABSTRACT

Post-flight balance control disturbances have long been a focus for the human spaceflight program and recently an effort to identify predictors of sensorimotor adaptation to microgravity has been proposed to customize and enhance the efficacy of space flight countermeasures. Balance related changes due to sensorimotor adaptation in the microgravity environment are of particular interest due to increased locomotor dysfunction and risk of falls – real risks for astronauts returning home or embarking on discovery missions.

Unfortunately, there is no single technique or countermeasure to address these issues, and their severity is highly individualized. This dissertation explored within-individual sensorimotor adaptation performance during manual and locomotor control tasks, as well as recovery responses to whole-body gait perturbations, such as slips and trips. It was hypothesized that individuals adept at achieving motor adaptation during manual control would show improved adaptation performance during a locomotor adaptation task, as a result of effective forward model updating in the cerebellum. By better understanding motor adaptation performance within individuals, it was further hypothesized that whole-body postural recovery to locomotor challenges would be related to this performance, predicting trip and slip recovery step reaction time, recovery step force and time to recover to normal gait. Finally, this dissertation assessed the effectiveness of a novel split-belt treadmill slip and trip perturbation system to produce challenging and unpredictable locomotor stressors, for which practice and training of opposing tasks would show minimal transfer effects. A population of 58 healthy, college-aged participants (30 female) performed two sensorimotor adaptation tasks: a rotated-input joystick matching task and a 3:1 split-belt walking protocol, and navigated a block-randomized set of 10 trip and 10 slip perturbations to characterize

postural recovery during locomotion. A pair of exponential curve fits were used to estimate adaptation performance in the two sensorimotor tasks. Whole-body motion capture and treadmill force-plates captured postural recovery kinematics and kinetics. The results of this dissertation identified a strong relationship among manual and locomotor adaptation performance ($r = 0.799$), suggesting adaptation performance may be centrally mediated by a common mechanism, likely located within the cerebellum. Individual split-belt adaptation performance was also observed to be predictive of slip recovery time after a bout of training ($r = 0.338$), as well as trip ($r = 0.427$) and slip ($r = 0.312$) recovery time improvement (% change) after a bout of 10 perturbations. This suggests a level of strategic motor adaptation related to plastic adaptation performance, within-individuals, in a set of very challenging discrete motor tasks. Finally, all participants were observed to improve significantly in recovery step force and time to recover after repeated slip or trip perturbations, but there were no meaningful transfer effects of a bout of trip training (10 perturbations) upon a novel slip, nor a bout of slip training (10 perturbations) upon a novel trip. Taken together, these results are the first to show a strong individualized link among manual and locomotor adaptation tasks, and significant correlations between adaptation performance and whole-body postural recovery during slips and trips. It is suggested that these relationships represent a deeper, generalizable connection among short-term strategic adaptation and traditional plastic adaptation observed during a simple motor adaptation task, bridging a previously unobserved gap between discrete and continuous motor control tasks.

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I. Introduction

Losing one's balance – or more specifically, experiencing a fall – is an almost universal human experience. As children and adolescents, falls typically result in insignificant injuries at best, and minor fractures, at worst. Although the potential for danger exists, for young, healthy individuals these injuries are typically more nuisance than danger, owing to stronger, more flexible bodies and healthier recovery systems. As we age, the systems we rely on to protect us from falling, as well as those which help us recover when we become injured, begin to slow and become less effective. Even in otherwise healthy elderly individuals capable of independent living (typically considered to be 65yrs+), approximately one in three older people will experience a fall each year (Tromp et al., 2001). The adoption of increasingly sedentary lifestyles, resulting in decreased bone (risk for osteoporosis) and muscle mass (risk for sarcopenia) (Grimby, 1986; Janssen, Heymsfield, & Ross, 2002; M. Nelson et al., 2007), as well as many common comorbidities, such as diabetes (Meneilly & Tessier, 2001; Ott et al., 1996; Selvin, Coresh, & Brancati, 2006), Parkinson's (de Rijk et al., 1995; Fall, Saleh, Fredrickson, Olsson, & Granéus, 2003; B. H. Wood, Bilclough, Bowron, & Walker, 2002), and dementia (Allan, Ballard, Rowan, & Kenny, 2009; Buchanan & Horak, 2001; Camicioli, Panzer, & Kaye, 1997; Härlein, Dassen, Halfens, & Heinze, 2009), are well known factors which increase the risk of falling in elderly individuals.

Fall risk, however, is not defined solely by physiological changes as a result of injury, aging or an associated pathology—these are simply examples of intrinsic fall risk factors. Other examples of intrinsic fall risk factors are cardiovascular issues which may result in a

pre/syncope state (Kenny, Bhangu, & King-Kallimanis, 2013; Rubenstein & Josephson, 2002) and disorders of the vestibular system, such as vertigo, BPPV (benign paroxysmal positional vertigo) or Meniere's disease. Attentional distraction, executive function capability and a simple increase in fear of falling also directly affect balance performance and have been observed to influence fall risk (Maki, 1997; D. Winter, 1995; M. Woollacott & Shumway-Cook, 2002; Yogev-Seligmann, Hausdorff, & Giladi, 2008). Postural stability, or the ability to maintain one's upright stance, is a multisensory goal, requiring integration of various physiological systems, as well as psychological and cognitive faculties. Any changes, intrinsic or extrinsic in nature, which impede the interaction or proper performance of these systems, however, limit one's ability to overcome postural stressors encountered on a daily basis— in the worst case, resulting in a fall (Bell et al., 2008, 2013; Tzeng & Yin, 2008). Environmental stressors, such as unstable surfaces or physical obstacles, represent perturbations to our postural stability system that may result in trips, slips and other unbalancing events. Environmental hazards, such as slippery floors and misplaced items, can be minimized to reduce fall risk (Amandus, Bell, Tiesman, & Biddle, 2012), however discrete perturbations to balance are improbable to completely avoid and impossible to predict. As a result, we develop individualized movement strategies to deal with extrinsic postural challenges within the context of the performance and limitations of our internal systems.

In organizing our responses to these environmental stressors, our sensorimotor system, central nervous system and autonomous reflex systems are responsible for acquiring sensory information and responding with appropriate motor outputs. The sensorimotor system is primarily composed of the visual, somatosensory (including proprioception) and

vestibular sensory systems, as well as the internal central processing and effector generating systems (CNS and spinal cord mediated motor signaling) which drive outputs to the musculoskeletal system. Deterioration of any of these systems, as a result of aging, age-related comorbidities, or other systemic pathology can increase fall risk, especially when exposed to environmental stressors, as a result of the plastic adaptive changes adopted to maintain performance. Rapid changes to these systems, on the other hand, require rapid adaptation of movement and control strategies to maintain performance, that is to say, maintain upright postural stability when exposed to day-to-day environmental stressors. This challenge is exacerbated by attentional refocusing and cognitive demands, commonly observed as a dual-task scenario, and represents a significant increase in fall risk (K. L. Martin et al., 2013; Mirelman et al., 2012; Taylor & Thoroughman, 2008). Observing multisensory impairments, and the resultant sensorimotor adaptation, is challenging in aging individuals or those with pathological conditions, such as Parkinsonian's, due to performance degeneration over time. The extended time course of changes among these populations prompt minor performance errors which require plastic adaptation, producing only subtle changes in strategy. Individuals exposed to spaceflight for extended periods of time, however, are forced to experience a very rapid set of systemic adaptations to the removal one of humanity's evolutionary constants – gravity.

Although the systemic changes among astronauts and aging individuals vary in both source and time scale, these astronauts and cosmonauts – individuals who experience prolonged exposure to microgravity – represent a new model for observing the effects physiological changes across multiple sensory systems (Vernikos & Schneider, 2010; E. Wang, 1999). Research and development in the field of space life sciences has focused on

the gross physiological changes caused by microgravity exposure, including cardiovascular deconditioning (Convertino, 2005), muscular atrophy (G. R. Adams, Caiozzo, & Baldwin, 2003; Edgerton et al., 1995), depletion of bone density (Lang et al., 2004) and a loss of fine balance control (Bruce, 2003) – all important for functional performance and effective responses to extrinsic environmental challenges. In this way, exposure to microgravity can act as an analog for the study of multiple intrinsic affectors of postural stability, such as: aging (musculoskeletal degeneration) (T. Trappe, 2009; Vernikos & Schneider, 2010; E. Wang, 1999); vestibular adaptation and pathology, such as ataxia (Paloski, 1998; Paloski, Black, Reschke, Calkins, & Shupert, 1993; Reschke et al., 2009); proprioceptive and somatosensory adaptation, requiring a change in movement control strategy (Clément & Ngo-Anh, 2013; Glasauer et al., 1995; Kornilova et al., 2004; Mulavara et al., 2012; Peters et al., 2013); and cardiovascular deconditioning, resulting in orthostatic intolerance (Convertino, 2005; Hughson & Shoemaker, 2004; Moore, Lee, Charles, Greenisen, & Schneider, 2001; Yates & Kerman, 1998), for example. Both extended spaceflight and the time course of aging are characterized by insufficient mechano-transduction, better known as unloading, necessary for the maintenance of sensorimotor performance. Astronauts experiencing microgravity become deconditioned due to gravity deprivation (G. R. Adams et al., 2003), while aging individuals typically experience withdrawal from gravity loading as they adopt an increasingly sedentary lifestyle (D. W. Brown et al., 2003; Ferrucci et al., 2000; Vernikos & Schneider, 2010). As both populations adapt to their unloaded environments over time, adopting a new set of motor strategies, aged and astronaut populations similarly lose the ability to respond effectively to environmental stressors unfamiliar to their current sensory calibration. When challenged by an unexpected

environment, or reintroduced to gravity, both populations exhibit levels of locomotor dysfunction, increasing their risk of injury, and in the case of the astronauts, overall mission success.

In order to ensure crew safety and maintain mission performance, microgravity countermeasures have been developed over the decades of human space travel to counteract some of the deleterious effects of gravitational unloading. Microgravity countermeasures are primarily exercise focused (combinations of aerobic and resistive training), coupled with nutritional and pharmacological therapeutics to maintain musculoskeletal and cardiovascular function (Cavanagh, Licata, & Rice, 2007; Convertino, 2005; S. M. Smith et al., 2012). To date, however, there is no single countermeasure for the physiological consequences of body weight unloading or vestibular adaptation during spaceflight, and astronauts performing long-duration missions still experience the negative effects described above. In recent years, through a greater control of nutrition and the availability of the Advanced Resistive Exercise Device (ARED), Smith et al. (2014) have observed minimal bone mineral density loss in astronauts, regardless of gender. Unfortunately, due to the inability to reproduce the gravitational forces necessary for whole-body loading and terrestrial vestibular function, changes to balance and locomotor strategies as a result of microgravity adaptation remain largely unaddressed by countermeasures (Bloomberg & Mulavara, 2003; Bloomberg, Peters, Cohen, & Mulavara, 2015; Bloomberg, Peters, Smith, Huebner, & Reschke, 1997; Lowrey et al., 2014; Mulavara et al., 2012; Paloski et al., 2008; Reschke et al., 1998; S. J. Wood, Loehr, & Guilliams, 2011). It is these changes, reminiscent of those observed in aged individuals and pathological populations, which suggest an increased risk of falling, and fall-related

injuries, for our astronauts upon return to a gravity-rich environment, such as return to Earth, or exploration-class missions to Mars.

The transitory period of return-to-gravity represents the greatest operational risk to astronauts performing mission-critical maneuvers, such as safely navigating an off-nominal or challenging vehicular egress, especially in future-planned Orion water landings (Bloomberg et al., 2015). Rapid sensorimotor adaptation is required to navigate the reintroduction of vestibular and proprioceptive information, updating movement strategies to account for gravity while overcoming the challenges of re-entry and landing. It is during this adaptation period where perceptual and motor risk is greatest, including the risk of loss-of-stability and fall related injuries – risks exacerbated by a dangerous egress procedure or operational environment. Locomotor dysfunction and falling are not the only risks attributed to the transitory period of adaptation, however, Peters et al. (2013) have shown that reaction time and the metabolic cost of physical activity are both detrimentally effected during sensorimotor adaptation. This can be taken to suggest that astronauts experiencing sensorimotor adaptation to gravity will be less proficient at sudden perturbations, which may be a risk for slip and trip hazards (Pater, Rosenblatt, & Grabiner, 2015), as well as more susceptible to fatigue due to a higher energy expenditure experienced during periods of locomotor instability (Peters et al., 2013). These are both safety and operational risks during space exploration, and may have mission-critical implications upon extra-vehicular activity (EVA) and exploration activities (Carr & Newman, 2007), especially in emergency situations. Unless the adaptive effects of microgravity upon the sensorimotor systems can be negated – perhaps through the introduction of artificial gravity during spaceflight – the time-

course of risk associated with sensorimotor dysfunction during these transitory periods are directly related to the amount of time spent adapting to this ‘new’ environment.

To further complicate the issue of return-to-gravity adaptation, the time constant upon which adaptation takes place, or the rate of adaptation, is largely individualized among the astronaut population (Mulavara et al., 2012), during their novel experiences to-and-from the microgravity environment. Repeat flyers have shown improved performance adapting to microgravity, with reduced incidences of space motion sickness (Reschke et al., 1998), as well as improved static postural equilibrium recovery after return to Earth (Paloski, Reschke, Black, Doxey, & Harm, 1992), suggesting this adaptation performance is transferred among repeated exposures to the challenging environmental transitions associated with spaceflight. This notion of adaptation transfer is supported by the motor learning theory of adaptive generalizability (Seidler, 2004, 2010; Welch, Bridgeman, Anand, & Browman, 1993) which suggests that individuals have the capacity to interpolate new motor solutions to environmental changes, based upon previous experiences with similar requirements, such that they can solve a class of problems, instead of a specific challenge (Batson et al., 2011). Prediction of first-time flyer performance and the impacts of sensorimotor adaptation upon motor and perceptual dysfunction is a major research focus at this time.

Current work in the development of balance and fall risk countermeasures have focused on identifying predictors of this adaptability, for the purposes of individualizing training to minimize the risk to space explorers during gravitational re-adaptation. To identify predictors, researchers at NASA’s Neurosciences Laboratory have focused on observing the relationship between individual sensory biases, such as locomotor visual dependency (Brady et al., 2012; Brady, Peters, & Bloomberg, 2009), as well as individual

motor learning strategies, such as the relationship between short-term strategic versus long term plastic-adaptive responses (Mulavara et al., 2005; Nomura, Mulavara, Richards, Brady, & Bloomberg, 2005), in order to predict sensorimotor adaptability. A greater understanding of the adaptation, and re-adaptation, process is important for minimizing fall risk in novel environments due to the fact that during these re-adaptations, astronauts experience disturbances in perception, spatial orientation, posture and gait (Glasauer et al., 1995; Reschke et al., 1998), as well as modified lower limb kinematics (Bloomberg & Mulavara, 2003), and reduced mobility during an obstacle course (Mulavara et al., 2010). Furthermore, adaptation to a novel environment has been observed to increase cognitive load (Batson et al., 2011; Peters et al., 2013), and act as a significant attentional distraction (Bedard & Song, 2013; Laura A. Malone & Bastian, 2010; Redding, Rader, & Lucas, 1992; Taylor & Thoroughman, 2007, 2008; Torres-Oviedo, Vasudevan, Malone, & Bastian, 2011), where attentional deficits and distracted executive function have been identified as intrinsic factors contributing to an increased risk of falling (Mirelman et al., 2012; M. Woollacott & Shumway-Cook, 2002; Yogev-Seligmann et al., 2008). These findings suggest that individuals who can adapt more quickly to a novel environment, utilizing their adaptive generalizability to maximize adaptation performance, will minimize this exposure to distraction and reduced executive function, thereby reducing fall risk. It is currently unknown, however, the extent to which adaptation performance itself is predictive of an individual's ability to respond to stressors of postural stability, such as a sudden shift in the floor during quiet standing, or slip and trip perturbations during locomotion.

Recent evidence that sensorimotor adaptation can be improved in one domain through the exposure, or training, of adaptation in another domain (Batson et al., 2011; Bhatt, Wang,

Yang, & Pai, 2013; Seidler, 2006; Yang, Bhatt, & Pai, 2013) offers great opportunities for the creation of nontraditional and individualized training and rehabilitation programs for fall prevention. While it has been shown that an individual can generalize sensorimotor adaptation across tasks (Cunningham & Welch, 1994; Seidler, 2004), and that adaptive generalizability occurs in both upper extremity manual (Seidler, 2004; Shadmehr & Moussavi, 2000) and lower extremity locomotor (Batson et al., 2011; L. A. Malone, Vasudevan, & Bastian, 2011) movement tasks, it is not clear whether this motor performance occurs as a result of a learning or an adaptive mechanism which is shared across different motor control tasks. The discovery of a link between manual and locomotor task adaptability, as well as the relationship between motor adaptability and postural recovery during slips and trips, could be used to improve training and rehabilitation outcomes in motor deficient and at-risk populations, such as the elderly, or astronauts during environmental transitions which overwhelm the sensory systems.

We hypothesize that a common central mechanism is employed for all sensorimotor adaptive systems. Thus, adaptive generalizability within an individual will produce similar adaptation performance across upper and lower extremity tasks, that is, individuals who exhibit rapid adaptation during a manual control task will also exhibit rapid adaptation during a locomotor task (and vice versa). Furthermore, we hypothesize that those more adept at motor adaptation will produce more effective strategic adaptations to dynamic and whole-body sensorimotor challenges, such as slips or trips. In this way, better plastic adaptors will better exhibit improved strategic adaptation over the course of a series of locomotor perturbations. To test these hypotheses, we explored the within-individual capacity for sensorimotor adaptation across upper extremity manual control, lower extremity locomotor

control and relate these findings to whole-body postural recovery during challenging split-belt treadmill induced gait perturbations. A third hypothesis emerged during the completion of this dissertation, questioning the ability to transfer postural recovery performance among opposing perturbations, such that a bout of trip training would improve novel slip performance, and vice versa. As mentioned, Bhatt et al. (2013) and their team have observed performance transfer among over-ground trip perturbations and postural recovery during over-ground slip perturbations, however we hypothesized that the difficulty and unpredictable nature of the treadmill induced perturbations designed for this dissertation would minimize these transfer effects.

The experiments performed during this dissertation estimated adaptation performance in two motor adaptation tasks, as well as characterized individual motor responses to treadmill induced trips and slips. The three motor control tasks were randomized for each subject and included: a manual control target matching task, estimating the rate-of-adaptation to a rotated joystick input, a lower extremity locomotor adaptation task, during which the adaptation split-belt walking was observed and rate-of-adaptation was estimated, and postural recovery to slip and trip perturbations, in the form of whole-body kinetics and kinematics. The slip and trip perturbations were block-randomized among participants, allowing for a comparison among novel and trained responses. A custom split-belt treadmill control system was developed as part of this dissertation to produce ambulatory perturbations in the form of slips and trips, allowing for greater experimental control and repeatability. We expect that those individuals more adept at manual control adaptation will show comparable adaptation performance during split-belt walking, and will exhibit improved postural recovery, in the form of decreased recovery step kinetics, recovery step reaction time and perturbation

recovery time. These studies will lead to new insights into the breadth of applicability of adaptive generalizability across manual, locomotive and postural stability tasks. Applications of these insights include: the enhancement of training paradigms to improve dynamic balance performance during stressful environments, the ability to estimate or predict adaptation performance across multiple sensorimotor and postural stability tasks, and the ability to further study dynamic postural recovery through the development of a novel set of split-belt slip and trip perturbations. A secondary goal of this dissertation is the evaluation of the split-belt treadmill slip and trip gait perturbation system developed in our laboratory. Ensuring minimal postural recovery performance transfer among opposing perturbations supports the use of opposing perturbations in the same experimental framework without introducing training bias. These results will inform the future use of this device for experimental design, as well as identify areas of improvement for future development.

As mentioned briefly, the challenge of maintaining postural stability exists all throughout life and falls occur across the spectrum of age and health related demographics (Talbot, Musiol, Witham, & Metter, 2005). In young and middle-aged healthy individuals, the outcomes of falls and the risks associated with falling are much less traumatic, however the source of these falls – 37% and 30% of all falls in young and middle aged individuals, respectfully – are attributed to environmental factors. Better understanding how an individual, young, aged or astronaut, adapts to a novel environment can have impacts in both understanding the risks imposed by that environment, such as those to postural stability, as well as identify areas for improvement to minimize those risks. These comparisons will inform the future of individualized training, providing greater care to protect from fall risk during unfamiliar or stressful situations. Due to the novelty of this experimental framework,

and the inherent risk of gait perturbations, this dissertation was limited to the observation of healthy individuals to lay the groundwork for future studies. Generalizing this understanding of adaptive performance and environmental adaptation across multiple populations is supported by work in the elderly showing retention of the ability to adapt to sensorimotor challenges, regardless of age (Bock, 2005; Bock & Schneider, 2002; Buch, Young, & Contreras-Vidal, 2003; Cressman, Salomonczyk, & Henriques, 2010; Seidler, 2007).

I.I Specific Aims and Hypotheses

Sensorimotor adaptation is imperative for the maintenance of movement performance and avoidance of injury during sudden changes to one's environment. Adaptive generalizability, or the ability to 'learn to learn,' is a motor learning theory which suggests sensorimotor adaptation can be improved in one domain through the exposure, or training, of adaptation in another domain. This supposition suggests a common mechanism is employed during adaptation to novel sensorimotor environments, which can be primed or enhanced through repeated or simulated exposure. Adaptive generalizability has been exhibited in studies of exclusively upper extremity manual (Seidler, 2004; Shadmehr & Moussavi, 2000; Wu, Miyamoto, Gonzalez Castro, Ölveczky, & Smith, 2014) or lower extremity locomotor (Batson et al., 2011; L. A. Malone et al., 2011) movement tasks, but no attempt has been made to estimate the degree to which adaptability in a manual control task relates to adaptability in a lower extremity locomotor task (or vice versa). Among the many neural structures thought to be involved, the cerebellum has been identified as a key contributor to the sensorimotor adaptation process for both the upper (Imamizu et al., 2000; Seidler, 2004) and lower (Horak & Diener, 1994; Morton, 2006) extremities, supporting a hypothesis of commonality between manual and locomotor adaptation processes.

The primary objective of this study is to examine the link between manual and locomotor sensorimotor adaptation by exploring the strength of the relationship within individual sensorimotor adaptation performance and its generalizability to strategic adaptation during postural recovery. To that end, the following hypotheses were tested:

Hypothesis 1: A common central mechanism is employed for all sensorimotor adaptive systems; thus, individuals who are more effective at sensorimotor adaptation for a manual (upper extremity) task will also be more effective at sensorimotor adaptation for a locomotor (lower extremity) task.

Hypothesis 2: A relationship exists between plastic adaptation performance during sensorimotor adaptation tasks which will predict strategic adaptation, or motor learning, performance during sensorimotor responses to a postural recovery task; that is, individuals who exhibit greater sensorimotor adaptability will demonstrate improved performance after repeated exposures to whole-body sensorimotor challenges.

These hypotheses were tested in young, healthy adults of both sexes by fulfilling the following aims:

Aim 1: The first hypothesis was tested by comparing the individual performances of all subjects on a challenging, computer-based manual (upper extremity) control task with those on a challenging split-belt treadmill based locomotor adaptation task. Individuals better adept at altering movement strategies to optimize performance while completing the focal/primary motor task will exhibit a decreased time-to-adapt, or adaptation coefficient. The hypothesis is supported if a significant positive correlation ($r > 0.3$) (Mukaka, 2012; Wu et

al., 2014)) of sensorimotor adaptation performance between manual and locomotor control systems occurs.

Aim 2: The second hypothesis was tested by comparing individual sensorimotor adaptive capability in manual and locomotor control tasks performed in Specific Aim 1 with individual postural recovery performance after exposure to unexpected postural perturbations. The hypothesis is supported if individuals who exhibit greater sensorimotor adaptability in manual and/or locomotor control are shown to respond more effectively to slip and trip perturbations during locomotion; that is, exhibit decreased recovery response times, decreased recovery step kinetics or decreased recovery time after a bout of slip or trip perturbation exposures, and supported by a significant correlation ($r > 0.3$ (Mukaka, 2012; Wu et al., 2014)).

During the completion of this dissertation, a third Specific Aim was realized, questioning the novelty of the first exposure to a simulated slip or trip perturbation after exposure to and practice of a block of the opposite perturbation, i.e. experiencing a ‘training’ set of trips before experiencing a novel slip, or vice versa. To ensure unbiased sampling of the within-subjects responses to gait perturbations, the order in which participants received the perturbations were randomly assigned, however the impact of skill transfer, often referred to as generalized motor learning (Schmidt, 1976; Schmidt & Lee, 2011, p. 482) between slip and trip whole-body dynamic perturbations to treadmill walking is unknown. This dissertation provided the opportunity to measure if the difficulty of the slip and trip perturbations, respectively, were tuned to minimize skill transfer and generalization among one another. Within this motor learning and transfer framework, a third hypothesis emerged:

Hypothesis 3: If sufficiently challenging, repeated exposure to treadmill induced slip or trip perturbations will not improve postural recovery responses to a novel opposing perturbation, i.e. treadmill trip training will not impact postural recovery during a novel slip perturbation, and vice versa.

Aim 3: The third hypothesis was tested by stratifying the population of participants into two groups who received either a training set of 10 trip perturbations prior to a novel and unexpected slip perturbation, or a set of 10 slip perturbations prior to a novel and unexpected trip perturbation. The hypothesis is supported if there is no statistically significant difference between the mean performance of the two groups in measures of reaction time, recovery force production and recovery time.

II.II Expected Significance

This dissertation will add to the literature by quantifying adaptation performance across multiple sensorimotor systems within an individual, including upper extremity manual control, lower extremity locomotor control, as well as strategic adaptation to repeated whole-body postural stability challenges. Consistent classifications of adaptation performance within an individual will further support the theory that sensorimotor adaptation generalizes as a result of a common set of central and neuromuscular mechanisms. As a result, this study explores the link between sensorimotor adaptation within an individual, and its relationship to an individual's propensity for strategic adaptation to minimize fall risk due to sudden changes in their postural environment. The discovery of a link between manual and locomotor adaptive control, as well as postural recovery may lead to new techniques in rehabilitation, such as manual control adaptation training prior to ambulatory rehabilitation after surgery or locomotor adaptability training in microgravity prior to returning to Earth. In

this way, countermeasures and rehabilitation treatments may be customized to an individual's predisposition towards sensorimotor adaptation, serving to prepare or enhance performance prior to novel challenges, or improve performance after injury or a loss of function due to disease. Further potential applications include the development of better instrumentation for stressing and testing dynamic postural stability, such as treadmill induced slip and trip training, useful for the future of fall prevention.

II. Literature Review

This literature review highlights the current body of knowledge regarding adaptation performance to extrinsic stressors across multiple sensorimotor systems and the ability for individuals to apply this information to novel environments. Special focus is presented to those stressors that pose a risk to static or dynamic postural stability. The current body of knowledge has only recently begun identifying relationships between an individual's ability to 'learn to learn' through adaptation to novel environmental stimulus and the application of this strategy to minimize fall risk. Additionally, it is unknown the extent to which adaptation performance is related within an individual, across their sensorimotor systems or anthropomorphic motor sites, such as the upper and lower extremities. A deeper understanding of these two sets of relationships can lead to improved and more highly focused training and rehabilitation techniques (Bhatt et al., 2013; T.-Y. Wang, Bhatt, Yang, & Pai, 2011; Yang et al., 2013) for populations at risk of falling, such as individuals with pathologies, the elderly and astronauts re-entering a gravity rich environment, such as Earth or Mars.

This review begins with a background on fall risk, including the implications of falls in society, pathologies and other factors which influence fall risk and the current state of fall

risk assessment. Spaceflight as a model of common factors in fall risk, including musculoskeletal and sensorimotor aging (T. Trappe, 2009; Vernikos & Schneider, 2010), is discussed within the context of physiological changes and motor adaptation. Adaptation as a form of learning, adaptive generalizability, as a framework for the tolerance and maintenance of performance in a novel environment and the body of knowledge surrounding its understanding and observation are discussed. Finally, a description of training and rehabilitation techniques which may benefit from a deeper understanding of these relationships will be introduced.

II.I Fall Risk Demographics and Societal Impacts

Traumatic falls in the elderly population represent a growing epidemic in terms of both mortality and burden upon the health care system. Approximately one third of older adults, above the age of 65, will fall at least once a year (Tromp et al., 2001). These falls are the leading cause of non-fatal injury and injury-related death in the United States among older adults (Centers for Disease Control and Prevention, 2003). Adjusting for inflation, the direct cost of these medical treatments exceed \$35 billion (Stevens, Corso, Finkelstein, & Miller, 2006) in 2015, and with our consistently increasing elderly population, it is expected that these numbers will only increase (Roudsari, Ebel, Corso, Molinari, & Koepsell, 2005). Typically, a fall later in life results in both physical and psychological injury, resulting in a loss in quality of life (Rodrigues, Lima, & de Azevedo Barros, 2013; Scheffer, Schuurmans, Dijk, Hooft, & Rooij, 2008; Mizue Suzuki, Ohyama, Yamada, & Kanamori, 2002). 90% of all elderly hip fractures result from a fall (Cummings, Kelsey, Nevitt, & O'Dowd, 1985; Hayes et al., 1993), while injury or fracture to the vertebrae, wrist and legs are also observed to be common (Luukinen et al., 2000; Parkkari et al., 1999). Individuals who experience a fall not only sustain

injury and a lengthy recovery, but typically develop an increased fear of falling. This fear of falling causes elderly individuals to adopt increasingly sedentary lifestyles in order to avoid situations where another fall can occur (Maki 1997). This change in behavior has been linked directly with an increase in fall risk and a decrease in quality of life (Friedman, Munoz, West, Rubin, & Fried, 2002; Maki, 1997; Scheffer et al., 2008), as a result of a loss of mobility and strength. Epidemiological studies of fractures in different elderly populations have been successful in strengthening the link between fall related injuries and fall risk factors, including those related to balance and locomotion (Berry & Miller, 2008; Cho, Scarpace, & Alexander, 2004; Cummings et al., 1985; Rubenstein, 2006; Schwartz, Nevitt, Brown, & Kelsey, 2005; Stel, Smit, Pluijm, & Lips, 2003) This fall risk is increased dramatically with the presence of comorbidities which, themselves, result in changes to the physiological systems necessary to maintain postural stability. Rubenstein 2006 provides a comprehensive review of the sources of falls in older individuals, citing estimates of the increased relative risk with respect to various fall risk factors. These findings are adapted in Table 1 and Table 12, below.

Table 1 and Table 2: Comprehensive lists of the cause cited for falls in elderly individuals over the age of 65, and the average increase in relative fall risk (or odds ratio) with respect to a set of fall risk factors. Adapted from (Rubenstein, 2006).

Table 1. Causes of falls in elderly adults: summary of 12 studies^a that carefully evaluated elderly persons after a fall and specified a ‘most likely’ cause

Cause	Mean percentage ^b (%)	Range ^c (%)
‘Accident’/environment-related	31	1–53
Gait/balance disorders or weakness	17	4–39
Dizziness/vertigo	13	0–30
Drop attack	9	0–52
Confusion	5	0–14
Postural hypotension	3	0–24
Visual disorder	2	0–5
Syncope	0.3	0–3
Other specified causes ^d	15	2–39
Unknown	5	0–21

^aAdapted from [15].

^bMean percentage calculated from the 3,628 falls in the 12 studies.

^cRanges indicate the percentage reported in each of the 12 studies.

^dThis category includes arthritis, acute illness, drugs, alcohol, pain, epilepsy and falling from bed.

Table 2. Important individual risk factors for falls: summary of 16 controlled studies^a

Risk factor	Significant/ Total ^b	Mean RR–OR ^c	Range
Weakness	11/11	4.9 (8) ^d	1.9–10.3
Balance deficit	9/9	3.2 (5)	1.6–5.4
Gait deficit	8/9	3.0 (5)	1.7–4.8
Visual deficit	5/9	2.8 (9)	1.1–7.4
Mobility limitation	9/9	2.5 (8)	1.0–5.3
Cognitive impairment	4/8	2.4 (5)	2.0–4.7
Impaired functional status	5/6	2.0 (4)	1.0–3.1
Postural hypotension	2/7	1.9 (5)	1.0–3.4

^aAdapted from [15].

^bNumber of studies with significant association/total number of studies looking at each factor.

^cRelative risks (prospective studies) and odds ratios (retrospective studies).

^dNumber in parenthesis indicated the number of studies that reported relative risks or odds ratios.

II.II Physiology of Balance and Postural Stability

Postural stability is a multi-system challenge, requiring integration of both sensory inputs and musculoskeletal outputs to maintain upright stance. The visual, vestibular and somatosensory systems, including proprioception, make up the primary feedback sources utilized to influence motor outputs during the maintenance of upright stance and balance (Horak, Henry, & Shumway-Cook, 1997, p. 199; L. M. Nashner, 1976). Each sensory center provides complementary information which is integrated primarily by the central nervous system in order to command the appropriate adjustments and responses necessary to avoid a fall or maintain balance.

The visual system provides information regarding orientation, based on the polarization of our environment, as well as feedback describing self- or external- motion, through perception of optical flow. Classically, visual affordance theory describes our ability to observe the environment and identify the actions which can be taken upon them—specifically, the value these properties provide the individual or user (Gibson, 1979). The polarization of our environment with respect to gravity, where structures and walls are built ‘up’ (opposing gravity), the ground is ‘down,’ and we travel (typically) perpendicular to gravity (parallel with the horizon).

The affordances of these environmental characteristics passively provide us with information about our relationship with the world, and quickly highlight discrepancies between our orientation and that of our environment’s (D. N. Lee, 1980; Nomura et al., 2005). Through self- or external- motion, these visual affordances change, providing optic or visual flow. This optic flow influences our perception of position and produces sensations (vection) which is counteracted unconsciously. This phenomenon was classically observed in small children

(David N. Lee & Aronson, 1974), where the movement of an unfixed wall caused dramatic perturbations to the stance of children, causing forward leaning or backward falls. In adults, these observations are observed similarly, though decreased in magnitude (Forsberg & Nashner, 1982). This work laid the foundation for future work understanding the contributions of vision on static balance and postural control (L. Nashner & Berthoz, 1978; L. M. Nashner, 1976; L. M. Nashner, Black, & Wall, 1982) which would ultimately influence the design of the NeuroCom BalanceMaster device, currently the Gold Standard for balance and postural stability measurement. By providing erroneous or discordant visual feedback, through modified visual flow, the vision system can be tricked into perceiving self-motion. This is commonly experienced when stopped at a light and the vehicle next to you moves forward, giving you the sensation that you are moving backwards.

The importance of visual input is not limited to static balance, however. Self-motion during ambulation yields optic flow which provides information regarding the speed and direction of locomotion, directly related to the rate of optic flow feedback (Pailhous, Ferrandez, Flückiger, & Baumberger, 1990; Aftab E. Patla, 1997; Warren, Kay, & Yilmaz, 1996). In this way, we take cues from our surrounding environment and can apply them to over-ground movement strategies, such as online steering (A. E. Patla, Adkin, & Ballard, 1999), whole body coordination (Assaiante, McKinley, & Amblard, 1997), obstacle avoidance (Stergiou, Jensen, Bates, Scholten, & Tzetzis, 2001; Vallis & McFadyen, 2003) and movement control (Nomura et al., 2005; Prokop, Schubert, & Berger, 1997; Stoffregen, Schmuckler, & Gibson, 1987). This online processing of optic feedback is necessary for navigation of our environments, and becomes especially important in situations where the environment, or its properties, is unfamiliar (Batson et al., 2011; H. S. Cohen, Bloomberg, & Mulavara, 2005; Peters et al.,

2014). Two forms of optical flow exist, central and peripheral optic flow, which represent the feedback received by the central field of view of the retina in the eye (typically related to attentional focus (Bedard & Song, 2013; Pailhous et al., 1990), and feedback received by the optic organs on the peripheral portions of the retina, outside the region of focused attention, respectively. Despite demanding little attentional focus, modification to peripheral optic flow results in distinct and unintentional perturbations to locomotion parameters, such as stride length and stride frequency (Batson et al., 2011; François, Morice, Bootsma, & Montagne, 2011; Kim & Krebs, 2012; Pailhous et al., 1990), suggesting a strong role in self-orientation and motor perception. Perturbations of this nature which cause changes to normal gait, pose a risk to balance and posture, especially in novel environments (Batson et al., 2011). Misinterpretation of this peripheral optic flow may result in inappropriate responses to visual affordances, impacting one's ability to respond to challenges which would normally be taken for granted, such as stepping over an obstacle or navigating an unstable terrain. In situations where this visual information is limited, such as dark or occluded environments, or when vision is permanently unavailable, such as congenital or acquired blindness, the other sensorimotor systems, such as the vestibular and proprioceptive systems, must be employed to maintain balance. This sensorimotor reintegration is often successful in maintaining upright balance, but leaves them with little ability to withstand further dynamic stressors, such as dynamic postural perturbations (Ozdemir, Pourmoghaddam, & Paloski, 2013).

The vestibular system, which exists within each of the inner ears, provide information about whole body orientation with respect to gravity, as well as sensory feedback about the movement of the head. The otolith organs, two sets of perpendicular structures called the saccule and utricle, are designed to sense linear accelerations via deflection of hair cells.

Otoconia, a series of calcium carbonate structures, have mass within the endolymph membrane of each organ and cause deflection proportional to movement, signaling any linear accelerations experienced by the head. These are the primary gravity sensing organs in the body, which provide immediate feedback during changes of head-and-whole-body orientation, with respect to gravity (Minor, 1998), providing the ability to sense tilt and postural deviations, such as sway (L. M. Nashner, 1972, 1976).

Contributing to this position sense and system of perceptual orientation are the second set of organs in the vestibular system, the semicircular canals. Comprised of three orthogonal fluid-filled half-circles, the semicircular canals provide information regarding rate of rotational movement within the three major planes of the body: frontal, sagittal and horizontal. Operating similarly to the otoliths, during rotational movements, fluid within the canals deflect hair cells proportionally with the magnitude of change (Minor, 1998). Unlike the otoliths, however, gravity plays no significant role in the (normal) function of these organs. This is particularly important, as the semicircular canals not only provide information about current orientation and movement state, but are also fundamental for proper eye movement and gaze stabilization, as they are primary inputs to the vestibular-ocular reflex (VOR) (Barnes, 1979, p. 19; Paige & Sargent, 1991). Beyond the VOR, the vestibular system directly supports cervical and spinal reflexes via the vestibulo-spinal and vestibulo-colic reflex pathways, both of which are necessary for the maintenance of vertical head position and the determination of postural orientation. These reflexes are responsible for triggering rapid musculoskeletal outputs in the upper body to maintain balance and stabilize the head (Angelaki & Cullen, 2008). In terms of static and dynamic balance, accurate estimation of whole body orientation is necessary for the production of appropriate responses to postural

challenges, such as obstacle avoidance or navigating unstable terrain. The vestibular system provides this constant, real-time, feedback regarding whole body orientation with respect to gravity, and is responsible for producing gaze stabilization during ambulation, necessary for optimal control of steering and whole-body coordination (Hollands, Ziaavra, & Bronstein, 2004, p. 200; Honegger, Hubertus, & Allum, 2013; Mergner & Rosemeier, 1998).

The somatosensory system is comprised of a series of organs which are used together to determine position sense, also known as proprioception. Much like the case of visual and vestibular inputs for balance control, proprioception provides feedback regarding the current orientation of constituent parts of the body through the use of muscle, joint and cutaneous sensors. In the muscles, two sensory receptors exist providing information about the current state of the muscle, the muscle spindles and the Golgi tendon organs (GTOs). In their primary functions, the muscle spindles become active when a muscle is stretched, providing information about muscle length and the rate of change during muscle activity. Changes to the length of the muscle spindles result in changes to the equatorial region of the intrafusal fibers within the spindle, proportional with the muscle activation and movement taking place. This feedback provides an estimation of joint and limb position. The GTOs are situated at the interface between the whole muscle and tendon in a serial configuration, and are responsible to measuring the force generated by muscle tension upon the bone to which it attaches. This afferent feedback is generated during all force productions, in dynamic and static muscle tensioning situations, providing useful information to respond to rapid changes in required force output, as well as minimize the risk of over-contraction which can result in muscle or tendon rupturing. The ambiguity of feedback during static and dynamic situations, however, make GTO feedback alone insufficient to identify joint position, because it is not possible to

differentiate the source of muscle contraction producing GTO excitation. The GTO's provide reciprocal inhibitory signaling to the spinal cord during muscle activation to ensure proper muscle activity sequencing (e.g. to stop bicep and triceps from firing simultaneously during a bicep curl) (Purves et al., 2001). While this provides some low-threshold proprioceptive feedback, the majority of proprioceptive information is generated from the muscle spindles. The joint receptors are a class of receptor cells located within the joint capsule, and provide feedback at varying intervals throughout the range of motion of a joint. Classical studies in cats have shown inconsistent feedback signaling throughout joints, suggesting that absolute determination of joint position from these receptors is likely not possible, necessitating more information available from other sensory systems (Freeman & Wyke, 1967; Skoglund, 1956, 1973). Proske et al. (1988) have suggested that joint receptors are concerned more with identifying passive or active movement of a joint, not specifically the position of the joint itself. The cutaneous sensors provide feedback on a variety of external factors. Most notably of interest are the mechanoreceptors which exist to sense touch and pressure, known as the Pacinian corpuscles, Meissner corpuscles, Merkel's discs, Ruffini's corpuscles and free nerve endings. These cutaneous sensors are located all over the body in different densities, increasing in areas where higher sensitivity is advantages, such as the fingertips and the soles of the feet (Kavounoudias, Roll, & Roll, 1998; S. Zhang & Li, 2013). By sensing gravitational loads on the soles of the feet, this sensory feedback is able to provide an aspect of orientation contiguous with feedback from other sensory systems. A holistic estimate of the contribution of somatosensory feedback was attempted by Simoneau et al. (1995) who observed differences in static posture between healthy and diabetic populations experiencing peripheral neuropathy. In this study, they attempted to quantify the individual contributions of visual, vestibular and

somatosensory feedback on whole center-of-pressure (COP) sway, observing a significant difference in performance between diabetics with neuropathy and healthy individuals in all conditions. Vestibular contributions were minimized by placing the head in a tilted-back position, while vision was removed traditionally by closing the eyes. The results of this study showed the consequences of somatosensory loss in diabetic patients, especially in situations where vision was limited, causing COP sway to increase 150% when compared to their healthy counterparts. This study provides a model which suggests a strong relationship between somatosensory input and static balance postural stability when somatosensory information is unreliable. These results are mirrored in populations where somatosensory information is observed to degrade over time, such as the elderly (Manchester, Woollacott, Zederbauer-Hylton, & Marin, 1989; Shumway-Cook & Horak, 1986), and is suggested to play a key role in sensorimotor re-integration (Horak, 2006; Peterka, 2002) necessary to maintain posture.

When addressing the challenge of balance in static and dynamic conditions, no single source of afferent feedback in the proprioceptive system is capable of producing an estimate of whole body orientation. However, a combination of feedback describing current muscle stretch state and any changes in muscle stretch, loading at the tendons of the anti-gravity muscles, pressure at the soles of the feet and joint position estimates at the ankles, knees and hips provide an ensemble representation of the current state of the body. Through integration of these factors, as well as vestibular and visually mediated estimations of orientation and perceptual cues from the environment, individuals are equipped with a varied and redundant system designed to withstand perturbations and minimize or avoid loss of balance equilibrium. Unfortunately, when these systems become impaired, or the ability to integrate these resources itself is diminished, the maintenance of postural equilibrium and balance in a static state, as

well as our ability to preserve dynamic equilibrium during ambulation, becomes flawed. In these situations, an individual's risk of falling is increased due to the loss of our ability to sense, react or respond to balance challenges in the environment.

II.III Sensorimotor integration and balance control

The sensorimotor system, specifically the visual, vestibular and somatosensory systems, provides afferent information necessary to drive motor outputs required for balance. The processing of this sensory information and the resulting motor outputs, however, is hardly a simple task and is the primary focus of the field of motor control. Sensory information is processed in the central nervous system (CNS), a complex system comprised of the brain, including the cerebrum, cerebellum and brain stem, as well as the spinal cord. For the visual and vestibular systems, located adjacent to the primary components of the CNS, afferent feedback transmission is readily available and enters the CNS through the cranial nerves, in as little as 135ms (Carlton, 1981). Somatosensory feedback, however, is sourced from all over the body and relies on the peripheral nervous system, which carries feedback from nerves and ganglia to the spinal cord. The spinal cord, itself, is a very complex structure comprised of multiple vertebrae housing both gray and white matter. Within the gray matter, the spinal nerves branch into two roots, specifically the ventral (strictly motor neurons) and dorsal (strictly sensory neurons) roots. Within the central gray matter, the neurons are afforded three destinations: 1) the ability to synapse with another neuron, sharing their excitation to trigger a motor output, for example; and 2) move higher in the spinal cord, towards the brain for further processing, or 3) lower to other effector neurons in the ventral column (Purves 2001). Unlike the sensory organs interfacing directly at the cranial nerves, however, afferent signals from the peripheral nervous system, including all

somatosensory and proprioceptive feedback, must travel along the spinal cord if they are to be processed in the brain. In some situations, such as reflex control, peripheral afferent feedback will synapse with motor neurons and produce unconscious lower spinal control in a myotatic, or monosynaptic, (very quickly, approximately 30-50ms) or long-loop (quick response, approximately 50-80ms). Long-loop reflexes have been observed to be configurable with prior information or learning, suggesting this reflex can be modulated by higher processing centers (Evarts 1973), however not completely controlled.

This poses a challenging question for the understanding of motor control, specifically related to the timing of available feedback versus motor outputs. For example, in situations where movements are slow and continuous, afferent feedback is available from all three described sensorimotor systems in order to make corrections in a real time fashion to achieve the current movement goal. This movement strategy is referred to as close-loop control, postulated most strongly by Adams (J. A. Adams, 1971), who suggested that during movements, the current state of the body is compared a known, or estimated, reference state related to the goal of the movement. This reference state, classically suggested by von Holst (von Holst, 1954) and Sperry (Sperry, 1950) as an efference copy (Evarts, 1973; Schmidt, 1976), provided a “copy” of the efferent signals to the brain for evaluation. During each comparison between the efference copy and the returning feedback, error is detected and a corrective action is initiated, if necessary. In the closed-loop theory of motor control, these computations are continually occurring in order to minimize movement error and achieve the movement goal identified by the correct set of reference states. In control systems theory, this is referred to as a feedback system, where the results of an input are compared to the goal and any deviation or error is returned to the input to make adjustments. In classical laboratory

experiments observing manual tracking of a target, delays of approximately 180-250ms are observed between the appearance of an error and the corrective response (Bizzi, Accornero, Chapple, & Hogan, 1984; Flash & Hogan, 1985; Horak et al., 1997; Kelso, Southard, & Goodman, 1979; Newell, Carlton, Kim, & Chung, 1993). In terms of balance, a closed-loop feedback system describes the strategy being used during the long term balance tasks, such as maintaining a controlled posture during a simple standing task or locomotion through a simple environment (Collins & De Luca, 1993, 1995). However, in the face of perturbations or rapid challenges to our balance, responses are observed to occur faster than 180ms (Horak et al., 1997), suggesting either reflexes, which are rapid responses to a stimuli (such as a monosynaptic stretch reflex or a long-loop functional stretch reflex) (L. M. Nashner, 1976), or an open-loop, feedforward strategy, requiring no feedback processing.

Open-loop control, unlike closed-loop control, does not involve online feedback and therefore has no online error compensation during the course of action. This describes a scenario where the instructions for movement are preplanned and executed without regard for the environment. Classically, this hypothesis has been explored using models of de-afferentation in animals, such as de-cerebrate cats (Shik & Orlovsky, 1976; Shik, Severin, & Orlovskii, 1966). In these preparations, the peripheral sensory system of the animal is surgically detached, allowing no somatosensory feedback to be transmitted to the brain for integration and feedback control. When placed on a treadmill, at first the limbs of the animal would drag, then suddenly they would initiate stepping and produce an appropriate pattern of walking, similar to that of a healthy cat. In fact, changes to the speed of the treadmill would result in changes to stepping strategy, including trotting, suggesting that, although the afferent feedback is not reaching the brain, there is enough activity to cause lower spinal

motor control to take place and initiate a pattered motor output. Shik et al. (1966) also observed this phenomenon through electrical stimulation of the midbrain in the same decerebrate cat, which was capable of initiating walking similar to previously described. These responses are theorized to be possible due to the existence of central pattern generators (CPGs) (Duysens & Van de Crommert, 1998; Kiehn & Butt, 2003; Shik & Orlovsky, 1976), which are made up of a set of synapsing neurons within the spinal cord, providing coordination between a set of sensory and motor neurons. In human locomotion, lower limb spinal control is thought to be driven by oscillatory CPG activity as a result of sensory inputs or feedforward descending motor commands, supported simply by the fact that gait is primarily an unconscious activity, requiring little attention. In coordinated, skilled movement, feedforward open-loop models are commonly interpreted as being derived from generalized motor programs (GMPs), which outline a particular class of actions which have been previously learned and can be adapted. GMPs provide the fundamental characteristics of a planned movement, related to the order, timing and magnitude of output needed to achieve the desired goal (Schmidt, 1976), however minimize the number of estimated variables needed to perform the task, streamlining application.

Wolpert et al. (1998) describe these open- and closed-loop control modules as predictive (based on previous sensory experience) and inverse (based on current feedback), suggesting these strategies co-exist and are switched between one another depending on the context of movement. This model is influenced greatly by both the environment and the goal of the motor task, where predicted outcomes of these goals may not yet be available. These novel environmental stressors require a generalized approach to ensure performance, which can then be applied to further, similar, challenges (Wolpert & Flanagan, 2001). In this way,

open- and closed-loop models become particularly important to understand during observations of postural perturbations, such as a sudden translation in a static situation (Horak et al., 1997), or a more dramatic slip or trip during locomotion (Eng, Winter, & Patla, 1994; Jo, 2007), where responses take on many forms and strategies.

II.IV Static Balance Control and the Inverse Pendulum Model

In the maintenance of upright static posture, when confronted with extrinsic perturbations, three strategies for avoiding a fall are typically discussed: the ankle strategy, the hip strategy and the stepping/reaching strategy (Horak, 1987, 2006; Horak et al., 1997). Static postural stability has been studied for many years under the influence of the inverse (inverted) pendulum model (D. Winter, 1995), where the body is modeled as a point mass (located at the center-of-mass (CoM)) capable of rotating in the forward and backward (anterior/posterior) directions. In this way, the upright body is in a state of near instability, with limits based upon the placement of the feet, defining the current base of support area. As the CoM approaches the limits of the base of support, postural stability decreases. In the A/P direction, that is, rotation about the ankle joints, a typical healthy adult has an approximate sway envelope of 8° of forward and 4° backwards before reaching their limits of stability (L. M. Nashner et al., 1982). To avoid breaching the limits of stability in the anterior or posterior direction, especially in response to a sudden perturbation, rapid corrective actions must be taken. The ankle strategy described co-contraction of muscles in the calf causing plantar- or dorsi-flexion to produce counter-rotations at the ankle joint. This brings the CoM forward or backwards as necessary to realign with the center-of-gravity (CoG) and maintain within the base of support. This strategy is typically observed in healthy individuals with the appropriate musculature. It is also the least dynamic response to a perturbation, minimizing over-corrections. The hip strategy produces a

more rapid shift in the CoM, activating musculature in the trunk to drive the pelvis forward or backward, with the same goal of maintaining CoM/CoG alignment, see Figure 1. This strategy is typically observed in elderly individuals, and those suffering from pathological conditions which impair balance or sensorimotor function (Allum, Honegger, & Schicks, 1993; Massion, 1994), as well as the astronaut population upon return from spaceflight (Paloski et al., 1992; Speers, Paloski, & Kuo, 1998). The hip movement strategy, although very effective, is a more dynamic response to perturbations, resulting in the risk of over-correction and continued instability. The hip strategy is also associated with open-loop control of postural stability, suggesting limited reliance or integration of feedback (Collins & De Luca, 1993, p. 199). When perturbations to static balance push or pull the CoM outside the base of support, the final strategy to avoid a loss of balance is to rapidly increase the size of the base of support by taking a step, increasing the base of support around the CoM, instead of returning the CoM to the center-of-gravity. The limitation to this strategy is the challenge of a rapid response to the feedforward control system, as well as the musculoskeletal system. The neuromuscular system must be capable of identifying the balance risk (reaction time) and acting upon it (response time) in an appropriate fashion, which is limited

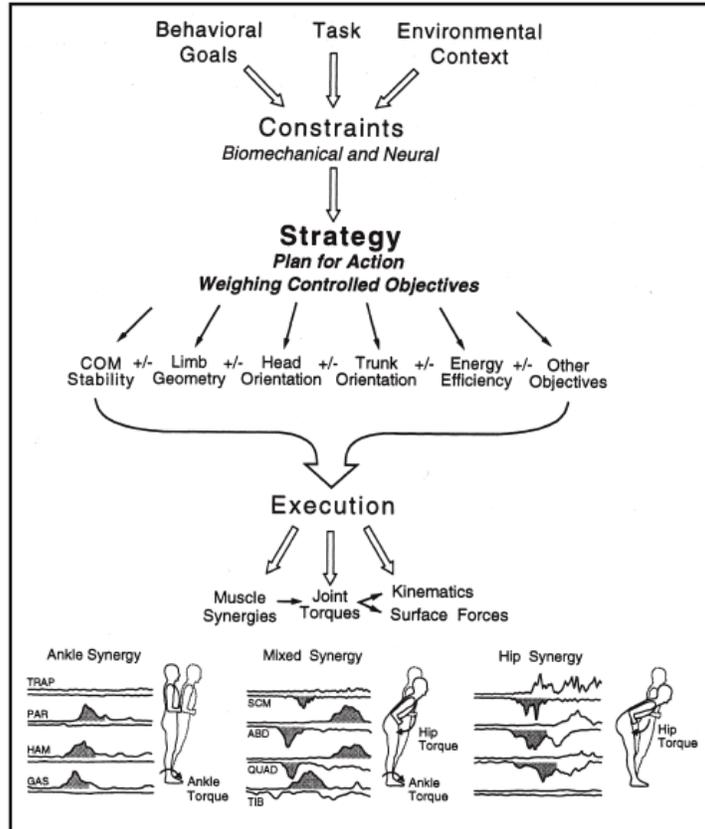


Figure 1: A conceptual framework for the maintenance of static postural stability, highlighting various sources of information and goals, the strategies employed and the musculature involved in maintaining upright stance. Adapted from (Horak et al., 1997).

by any impairment of the sensorimotor system. A combined ankle and hip strategy is also possible, where the magnitude of each response is scaled to the severity of the perturbation, more effectively returning the CoM within the boundary of stability, while minimizing over-correction and the resultant instability. This strategy is observed primarily in very healthy individuals, with highly responsive sensorimotor systems. Computerized dynamic posturography devices, such as the Neurocom EquiTest (Natus, USA) are used to quantify these CoM, COP and base of support relationships under static and perturbed situations, and represent the gold standard for balance testing in the clinical setting. In the evaluation of balance performance, these devices are able to control for the three major sensorimotor inputs

by modifying vision, optic flow and ankle proprioception using eyes open/eyes closed conditions, movement of a visual surround or sway-referenced rotation of the balance support structure.

II.V Dynamic Control of Balance during Locomotion

Human locomotion is a complex and dynamic balance task which can be understood as a goal oriented state of constant static balance instability. Although performed without difficulty in most healthy individuals, locomotion represents a state of continuous multi-limb coordination, subject to both internal and external stressors, and requiring integration from multiple sensory systems in real-time. Unlike static postural stability, where the goal is to maintain the CoM within the base of support, locomotion exists specifically within the goal of moving the CoM outside the base of support while preventing falling. In steady state gait, the CoM is predominantly outside the base of support, necessitating movement trajectories throughout the multiple phases of a step to be coordinated in such a way that balance is maintained. During ambulation, the phases of a single step cycle includes initiation, toe-off, single-support swing phase, heel strike, dual-support phase followed by a mirrored order of operations on the opposite leg (Aftab E. Patla, 2003; D. Winter, 1995). In order to maintain dynamic stability, safe placement of the swing foot is necessary to avoid a fall during every step. The resultant point of force application, described by COP shifts from left to right foot continuously throughout steady state locomotion, redefines an interim base of support, through which the CoM will travel before the next step (Lugade, Lin, & Chou, 2011; D. Winter, 1995). Patla et al. (2003) describe three strategies employed to maintain dynamic stability during gait, including reactive, predictive and anticipatory strategies. Reactive control refers to the ability to detect and respond to unexpected perturbations generated in the environment, such as

rapidly lifting a leg to avoid an obstacle and the subsequent generation of a set of recovery steps. Predictive control refers to the ability to estimate potential perturbations which are self-generated, such as current or ongoing movements, which pose a threat to maintaining control of the CoM within the periodically changing base of support. This control is based primarily on prior experience, which provides estimates of expected deviations to CoM trajectory during locomotion as a result of ongoing movements, such as waving to an acquaintance while walking. Anticipatory control describes the ongoing identification of environmental threats to dynamic postural stability, where preemptive motor strategies can be employed, such as changing stride length to avoid a tripping hazard. This feedback is primarily attained from visual information of one's surrounding, and past experience where reactive control was necessary.

Using these strategies, as long as the sensorimotor system can process and execute the necessary COP transition and CoG redirection to maintain upright posture, there is a minimal risk of experiencing a fall. Unfortunately, when stressors are placed upon the locomotion system, either internally due to changes within the sensorimotor system, or externally from the environment, such obstacles or unsecure surfaces, the ability to perform the correct balance-maintaining trajectory is diminished. Any internal degradation of the visual, vestibular or somatosensory systems decreases an individual's ability to maintain upright posture when faced with a perturbing challenge during the phases of gait where the base of support is smallest (e.g. single leg stance phase) (Aftab E. Patla, 2003). External perturbations to locomotion typically occur in the form of a trip, where an obstacle is unintentionally interacted with during the swing phase of gait (Eng et al., 1994; Aftab E. Patla, 2003; Schillings, van Wezel, Mulder, & Duysens, 2000, p. 200), or slips (Brady, Pavol, Owings, & Grabiner, 2000; Marigold &

Patla, 2002; You, Chou, Lin, & Su, 2001), where one of the feet experience an unexpected displacement due to a loss of friction control during gait, typically the forward foot when the heel makes contact with the ground (heel strike). Responding to these perturbations requires rapid and dynamic changes in the current postural state, often combining multiple strategies, such as shifting of the CoM to maintain within the base of support (Eng et al., 1994; Pai, Wening, Runtz, Iqbal, & Pavol, 2003), flexion or extension of the lower limb musculature to rapidly perform a recovery step (Marigold & Patla, 2002; Schillings et al., 2000) and/or online changes to timing between gait cycle events, such as increasing the time spent in the dual-support phase of gait during a slip (Brady et al., 2000; You et al., 2001).

II.VI Studying the Kinematics and Kinetics of Ambulatory Recovery during Trips and Slips

Recovery strategies during trips and slips have become of particular interest in the last decade, as the identification of this public risk factor continues to grow, especially in populations such as the elderly. Observing this discrete phenomenon in a laboratory setting is challenging, however, due to both the inherent risks to injury during a dynamic loss of balance, as well as the fact that trips and slips are typically unpredictable. In fact, prior knowledge of an impending balance risk has been shown to cause changes to postural stability control, often referred to as anticipatory strategies or anticipatory postural adjustments (Cham & Redfern, 2001, 2002; Marigold & Patla, 2002; Pater et al., 2015). To combat this, researchers attempt to randomize the perturbation, attempt to blind the participant to the location or timing of the perturbation, or observe only the early perturbations, in order to observe an uncorrupted or novel recovery response, depending on the purpose of the study. Across all methodologies, however, researchers attempt to make the

perturbations as consistent and comparable as possible, in order to improve their chances of observing a repeatable response.

Different strategies for stressing the dynamic postural stability system have been used to observe trips and slips across multiple populations. A trip is observed to occur when there is a rapid deceleration of the foot/leg currently in the swing phase of gait, causing an anterior acceleration of the CoM. In over-ground locomotion, this typically occurs when the foot/leg currently in the swing phase of gait interacts with an obstacle, necessitating a response either to rapidly raise the leg over the obstacle, or step down before the obstacle and cease forward locomotion (Cordero, Koopman, & van der Helm, 2004; Eng et al., 1994; Forner Cordero, Koopman, & van der Helm, 2003; Jo, 2007; Schillings et al., 2000). These are referred to as the “elevating strategy” and the “lowering strategy” (Cordero et al., 2004; Forner Cordero et al., 2003). In a laboratory setting, these perturbations are have been performed in a variety of ways, including: dropping a physical object onto a treadmill at an undisclosed time during treadmill walking (Schillings et al., 2000), a series of similar setups where a triggered metal plate is activated to produce a 90° obstacle during randomized over-ground locomotion trials (Eng et al., 1994; A. E. Patla, Prentice, Robinson, & Neufeld, 1991; T.-Y. Wang, Bhatt, Yang, & Pai, 2012), instantaneous acceleration of a treadmill from static balance (Owings, Pavol, & Grabiner, 2001) and a setup where cables are attached to the feet such that they can be pulled during a specified phase of gait (Cordero et al., 2004; Forner Cordero et al., 2003). In all experimental setups, participants are harnessed for safety, and are blinded to the timing of the perturbation, in order to minimize anticipation. When these perturbations are repeated, however, learning and adaptation is typically observed.

Treadmill perturbation configurations, as opposed to obstacle deployment in over-ground trip protocols, allow for greater control of the experimental setup and also allow for less predictability, as the perturbation can occur after any number of steps. This perturbation flexibility results in the tradeoff that treadmill walking, especially in a laboratory setting, is often criticized when generalizing results to real-world, over-ground, locomotion (Alton, Baldey, Caplan, & Morrissey, 1998; Riley, Paolini, Della Croce, Paylo, & Kerrigan, 2007; Sessoms et al., 2014). In over-ground setups, although the perturbation does not occur during every trial, the location where the perturbation occurs is fixed, therefore it is possible to anticipate the perturbation and plan a response (Pater et al., 2015), based on visual feedback. Recent work using split-belt treadmills have shown the ability to produce practically unpredictable treadmill trip-like perturbations, without the use of external obstacles, which are repeatable and offer greater control to the experimenter (Sessoms et al., 2014). In this study, a novel acceleration profile was used to rapidly decelerate one leg/foot upon completion of the swing phase of gait, observed via force-plate measured heel strike. Although this deceleration did not occur during the swing phase of gait, this perturbation protocol shows a recovery strategy similar to that of the “lowering strategy,” including a rapid forward shift in CoM, forward trunk flexion and stumbling recovery step on the unperturbed leg.

To generate repeatable slip perturbations in the laboratory, researchers have traditionally employed more dramatic stressors, resulting in dynamic participant responses. While this is important for understanding the effective strategies used to avoid and recover from slips, it makes production of repeatable, yet unpredictable, perturbations very challenging. Redfern et al. (2001) provides a very thorough review of the biomechanics of

slips, describing in detail the physics related to locomotion and frictional forces during the stance phase of gait, as well as a classification of different kinds of slips, with respect to magnitude and response. A full slip is described, in this way, by a displacement of 3 cm on the perturbed foot (Cham & Redfern, 2001), also referred to as a ‘macroslip.’ When a macroslip is experienced, but does not cause a fall, a slip-stick response is said to be observed. On the other hand, a slip is considered to be a fall when participants are unable to control the position of the perturbed heel, due to loss of friction, and/or they are forced to load their safety harness for support (considered a traumatic fall). During a slip-stick response, the slipping heel maintains contact with the decreased-friction surface in order to maintain an increased base-of-support, while simultaneously attempting to anteriorly shift the CoM to establish its location within the base-of-support and redefine the normal/shear force relationship between the slipping foot and the surface upon which it is acting. By moving the CoM towards the slipping heel, the shear forces overcoming friction can be minimized, in favor of normal forces perpendicular to the surface, which serves to decrease the change of slipping (Brady et al., 2000; Cham & Redfern, 2001; You et al., 2001). Anecdotally, this makes sense, as the typical experience of locomotion on a slippery surface, such as ice, results in people taking smaller steps, attempting to maximize their exerted normal force and minimize any slip inducing shear.

In the laboratory, numerous strategies have been used to produce macroslips. Most notably, experimental setups include sliding platforms, which are free to move in the anterior/posterior direction (Bhatt, Wening, & Pai, 2006; Kajrolkar, Yang, Pai, & Bhatt, 2014; Pai & Bhatt, 2007; Pai, Bhatt, Wang, Espy, & Pavol, 2010; Patel & Bhatt, 2015; Pavol & Pai, 2002; T.-Y. Wang et al., 2011; Yang, Bhatt, & Pai, 2009), walkways made of steel

rollers (Marigold, Bethune, & Patla, 2003; Marigold & Patla, 2002), and artificial ice, made primarily of vinyl sheeting and different oil or soap concoctions (Brady et al., 2000; Cham & Redfern, 2001; Lockhart, Smith, & Woldstad, 2005; Moyer, Chambers, Redfern, & Cham, 2006; Troy & Grabiner, 2006; You et al., 2001). More recently, a new treadmill induced slipping protocol has been developed where a sudden forward acceleration of a treadmill belt, during controlled locomotion, simulates a slip-like event during the single-leg stance phase of gait (Yang et al., 2013), and has shown similar kinematic responses to large magnitude slips, dependent on the configuration of the treadmill. In single-belt treadmills, this slip perturbation is limited only to the single-leg stance phase of one foot/leg during gait, constraining the possible foot/heel displacement possible. This results in a different large-perturbation macroslip than traditional slipping techniques, however affords the ability to dramatically increase the randomization of the perturbation and minimize prediction and anticipation. Much like the tripping protocols described above, prior knowledge of the perturbation results in anticipatory changes to gait strategies (Cham & Redfern, 2002), therefore some attempt must be made to blind subjects to the upcoming postural stressor. In the case sliding platforms, the location of these platforms were fixed, however the release of the platform, and subsequent slip perturbation, was computer controlled and could therefore be randomized to minimize prediction. A similar control scheme was available for the steel roller configurations, where a slip perturbation could be produced on demand, in an experimentally randomized fashion. Artificial ice has been produced in a number of similar ways, typically employing a smooth, predictable surface, such as vinyl flooring, which has been contaminated with an oily substance including motor oil (Cham & Redfern, 2001; Lockhart et al., 2005), mineral oil (Brady et al., 2000, p. 200) and/or soap (You et al., 2001).

To blind participants to the application of these contaminants, they are often placed in a low visibility environment (or blindfolded completely (Brady et al., 2000, p. 200)) or distracted during the application of the contaminant (Bhatt & Pai, 2009; Lockhart et al., 2005). With the exception of the treadmill induced slips, these protocols have been designed to mimic over-ground locomotion as accurately as possible, within the constraints of a safe laboratory environment. This dissertation proposes a novel treadmill slip protocol using a split-belt treadmill, previously unexplored in the literature. Although this configuration retains the typical limitations cited when comparing over-ground and treadmill locomotion (Sessoms et al., 2014; Yang et al., 2013), it allows for the ability to effectively limit anticipation, as well as allow for a larger displacement of the slipped heel/foot during perturbation, separate from the contralateral leg.

II.VII Pathologies which influence balance and increase fall risk

When pathologies impair the sensory afferent, motor effector or central processing systems of the body, our ability to integrate inputs and outputs in order to withstand the challenge of postural stability becomes severely limited. In the balance literature, neurological pathologies are frequently studied as models which parse specific losses in functionality to better understand the overarching control system. These pathologies include Parkinson's disease (Duncan et al., 2012, 2015; Herdman, Schubert, & Tusa, 2001; Konczak et al., 2009; Nemanich et al., 2013; Stolze et al., 2004), Type-I and Type-II diabetes (Jernigan, Pohl, Mahnken, & Kluding, 2012; Roman de Mettelinge, Cambier, Calders, Van Den Noortgate, & Delbaere, 2013), multiple sclerosis (Huisinga, Yentes, Filipi, & Stergiou, 2012), hemi-parietic stroke (Friedman et al., 2002; Kajrolkar et al., 2014), cerebellar dysfunction (Bastian, 2006; Diener, Dichgans, Bacher, & Gompf, 1984; Morton, 2006;

Morton & Bastian, 2007; Morton, Tseng, Zackowski, Daline, & Bastian, 2010; Serrao et al., 2012), and various vestibular disorders, such as benign paroxysmal positional vertigo (BPPV), vestibular migraines, Meniere's disease and vestibular neuritis (Agrawal, Carey, Della Santina, Schubert, & Minor, 2009; Agrawal, Ward, & Minor, 2013; Lacour et al., 1997, p. 20; L. M. Nashner, 1972; Yardley et al., 2001; Yoo, Kim, & Shin, 2015).

Parkinsonians suffer from the inability to properly initiate gait and exhibit kinematic changes to normal locomotion, such as decreased step length and a shuffling gait. Decreased step length has been associated with poor locomotor stability, as it decreases the available base-of-support, limiting the ability for Parkinsonian individuals to withstand any perturbations to their dynamic balance. Furthermore, postural tremors, such as essential tremor or neuropathic tremor, reduce the ability to accurately maintain postural stability during quiet stance, dramatically increasing COP sway during quiet stance, and can be viewed as an unpredictable perturbation during locomotion, for which rapid adjustments are limited (Halliday, Winter, Frank, Patla, & Prince, 1998; Shen & Mak, 2014). Limited research has been done on the effects of multiple sclerosis (MS) upon balance and postural stability, however early results have shown distinct increases in the variability, and the pattern of the variability using non-linear approaches, in the sway patterns of MS patients during quiet stance (Huisinga et al., 2012). In individuals who have experienced hemi-paretic strokes, compensatory strategies are adopted to maintain movement performance. During slip perturbations, stroke survivors adopted a strategy of favoring the non-paretic leg, performing a compensatory stepping response to maintain stability (Kajrolkar et al., 2014). Although performance was decreased compared to healthy individuals, in this study, stroke survivors were capable of maintaining dynamic postural stability, especially after practicing or training

on a sliding platform slip-perturbation system. Diabetic individuals experiencing either Type-I or Type-II diabetes, are prone to experiencing a loss of fine afferent feedback from the peripheral extents of the limbs, specifically the hands and feet. For the motor control of balance, especially static balance, losses in the proprioceptive and somatosensory feedback of the lower extremities results in a decrease in postural stability(Fulk, Robinson, Mondal, Storey, & Hollister, 2010; Simoneau et al., 1995), especially in situations where visual cues are limited. These are often best observed as increases to postural sway in the AP and ML directions (Fulk et al., 2010). Cerebellar dysfunction, typically characterized as cerebellar ataxia, results in abnormal and seemingly uncontrolled gait and posture (Morton & Bastian, 2007). These dysfunctions show not only increased AP sway, suggestive of postural instability in comparison with healthy controls (Diener et al., 1984), but also limits the ability to maintain consistency in timing, length and direction of steps during gait (Morton, 2006; Morton & Bastian, 2007). Beyond the direct issues associated with static and dynamic balance stability, individuals with cerebellar dysfunction as a result of stroke, atrophy or lesion, show decreased motor adaptive capability during movement tasks, such arm movements (Izawa, Criscimagna-Hemminger, & Shadmehr, 2012) and the maintenance of upright posture (Bastian, 2006; Ioffe, Chernikova, & Ustinova, 2007; Morton, 2006; Morton & Bastian, 2007; Reisman, Wityk, Silver, & Bastian, 2007). Disorders of the vestibular system, of which there are many, share a similar ailment, specifically the sensation of dizziness (Agrawal et al., 2009). Bilateral (BVL) and unilateral vestibular loss (UVL) refer to the loss of function in one or both sets of the vestibular organs, resulting in impaired feedback and sensations of dizziness and vertigo. Older patients with vestibular deficits, on average, fall more regularly than healthy individuals of similar age where greater than 50%

of patients between the ages of 65 and 74 who suffer from BVL will fall (Herdman et al., 2001). BPPV occurs when the otoconia within the otoliths become dislodged and end up in the semi-circular canals, causing erroneous or unexpected rotational signaling, resulting in sensations of vertigo and dizziness. BPPV is the most commonly reported vestibular disorder, making up approximately 30% of all clinical diagnoses (Agrawal et al., 2013). Vestibular migraines, or migraine associated vertigo, occurs during the duress of a migraine episode, where vestibular dysfunction is observed. In this case, patients exhibit signs of balance instability and are often unable to walk in a straight line. Meniere's disease is caused by a buildup of inner ear fluid within the semicircular canals which produces an incorrect set of hair cell stimulation during rotation of the head, resulting in symptoms of dizziness and vertigo. Finally, vestibular neuritis occurs outside the labyrinths and is a disorder of the vestibulocochlear nerve, typically resulting in inflammation. This inflammation causes issues with the conduction of vestibular afferent feedback, resulting in sensorimotor discordance during head movements, and subsequently, symptoms of vertigo and dizziness. Agrawal et al. (2009) reported that between 2001 and 2004, individuals diagnosed with vestibular disorders had a 12 fold increase in the odds of falling.

II.VIII Effects of Aging and Spaceflight on Postural Stability

Specific pathologies are not the only source of sensory and motor degradation, however. As the human body ages naturally, functionality of both the afferent and effector systems, as well as the ability to integrate multiple sensory inputs and execute appropriate motor outputs, becomes limited, deteriorating from approximately the age of 50 onwards (Mancini & Horak, 2010; Prieto, Myklebust, Hoffmann, Lovett, & Myklebust, 1996). These limitations hinder the ability to perform optimal static and dynamic postural control, and are

often cited as the major contributing factor to falls in aging population (Maki, 1997; Shaffer & Harrison, 2007; M. H. Woollacott, Shumway-Cook, & Nashner, 1986). Sturnieks et al. (2008) provides a comprehensive review of the factors associated with aging and postural stability risk, describing the intrinsic changes to sensory processing as well as the depreciation of motor effector systems to produce corrective adjustments when challenged. This combination of slowly changing, or adapting, sensory biases (re-weighting), in the peripheral somatosensory systems and vestibular systems, as well as a loss of motor function due to bone and muscle weakness (disuse), are the similarities between normal aging and exposure to microgravity. In both situations, changes within the sensorimotor systems have been observed, including vision, vestibular and proprioceptive sensory integration and their resultant motor outputs, in terms of strength, coordination and timing (Sturnieks et al., 2008; T. Trappe, 2009; Vernikos & Schneider, 2010; E. Wang, 1999). In terms of clinical balance assessment, and subsequent increase in fall risk as a result of poor balance stability, astronaut populations have been observed to score below clinical thresholds during objective measures of posturography (Paloski et al., 1992; Speers et al., 1998). Immediately after return to Earth, they are observed to adopt hip-strategies to maintain static balance, similar elderly participants when recovering from extrinsic perturbations (Paloski et al., 1992, p. 199), and express increased COP sway during quiet stance (Speers et al., 1998) similar to those experiencing pathology which influence balance, such as those with peripheral neuropathy (Fulk et al., 2010) or vestibular disorders (Lacour et al., 1997; Mancini & Horak, 2010; Paloski et al., 1993).

Vision plays a significant role in the navigation of one's environment, and as described previously, is paramount for obstacle avoidance during locomotion and the

maintenance of postural stability during static balance. Aging results in three primary changes to vision: broadly defined visual diseases (i.e. age-related macular degeneration (AMD), glaucoma), ability to resolve visual contrast (specifically decreased acuity under low-light situations) and processing of visual information (visual reaction time) (Gittings & Fozard, 1986; Lord & Dayhew, 2001; Owsley, 2011). Recently, astronauts exposed to long-duration spaceflight have begun to exhibit signs of visual changes, namely quantified by changes in acuity (E. S. Nelson, Mulugeta, & Myers, 2014; L.-F. Zhang & Hargens, 2014) requiring short-term use of increased-strength glasses or other vision correction, which has been termed the visual impairment due to increased intracranial pressure (VIIP) syndrome. Between aged individuals and astronauts, the mechanisms resulting in vision changes are not thought to be comparable (degeneration versus deformation), however both reduce the effective visual cues necessary for balance and postural stability. As a result of the microgravity adaption of vestibular and proprioception systems, vision is thought to become the primary sensor of feedback (Bloomberg & Mulavara, 2003; Glasauer et al., 1995; Paloski et al., 1992) as it continues to provide veridical information. Based on the importance of vision to balance, as observed during tests of static postural stability (Forssberg & Nashner, 1982), any changes become compelling risks to stability (Clément, Gurfinkel, Lestienne, Lipshits, & Popov, 1984; Paloski et al., 1993; Reschke et al., 1998), decreasing measures of balance performance.

The vestibular system is of particular interest after adaptation to the space flight environment, due to its reliance upon gravity to function correctly (Minor, 1998). Without gravity, the otoliths are unable to reliably differentiate linear and rotational acceleration, often resulting in illusions referred to as the otolith tilt-translation reinterpretation, where

otolith stimulation during tilt upon return to Earth is sensed as forward or reverse translation due to sensory integration mismatching (Parker, Reschke, Arrott, Homick, & Lichtenberg, 1985; Reschke et al., 1998). Vestibular adaptation through gravity transitions occur more quickly than other motor or sensory adaptations, but can be very compelling, resulting in motion sickness (space motion sickness) (Reschke et al., 1998) and have been hypothesized to influence changes to movement strategies, during static balance (Minor, 1998; Paloski, 1998; Paloski et al., 1993, 1992; Speers et al., 1998) or locomotion (Bloomberg & Mulavara, 2003; Madansingh & Bloomberg, 2015; Miller et al., 2010; Mulavara et al., 2010, 2012), upon return to Earth. Aging, on the other hand, does not provide a direct analog to spaceflight in this sensory system, as microgravity exposure is highly uncommon in elderly individuals, however it is not devoid of parallels. A recent review by Iwasaki et al. (2015) highlighted age-related declines in the vestibular system, such as reduced performance during vestibular evoked myogenic potentials (VEMPs) tests and tests of the vestibulo-ocular reflex (VOR). This review describes findings which suggest a reduction in vestibular hair cells and vestibular ganglion neurons with respect to age, upwards of 12-25% decrease between 80 and 90 year olds, compared to a group of younger, healthy participants (ages 42-67). From a balance and stability point of view, in both situations, dizziness and instability result from vestibular impairment, which pose a risk to static and dynamic fall risk (Bloomberg & Mulavara, 2003; Paloski et al., 1993; Sturnieks et al., 2008) and require systemic adaptations to maintain performance.

The effects of aging upon the musculoskeletal and somatosensory systems are among the most profound contributor to fall risk for elderly individuals, as their ability to both sense and respond to postural perturbations becomes limited (Shaffer & Harrison, 2007).

Proprioception, based on input from its multiple somatosensory organs, becomes particularly important when vision or vestibular inputs have become limited (L. M. Nashner, 1972), especially with respect to static postural stability. Proprioception, including the somatosensory information derived from foot sensitivity, has been observed to decline with age (Kaplan, Nixon, Reitz, Rindfleish, & Tucker, 1985; Robbins, Waked, & McClaran, 1995), leading to decrements in movement performance and changes to postural sway (Hsu, Chou, & Woollacott, 2013). In fact, a large sample of postural balance of subjects 30 to 80+ years of age showed changes in balance performance even at middle-aged groups (Era et al., 2006), as measured by the variability of their COP velocity. Aging reduces the functionality of the somatosensory organs, limiting the afferent feedback available to make corrective actions and maintain postural stability (Herter, Scott, & Dukelow, 2014; Shaffer & Harrison, 2007; Sturnieks et al., 2008). Muscle and bone strength are commonly observed to decrease with age. Muscle cross-sectional area has been observed to decrease by up to 40% between the ages of 20 and 60 years (Doherty, 2003) across genders, while bone loss tends to be more gender specific. Starting from approximately 30 years old, women lose between 35-50% of their cortical and trabecular bone, while men lose approximately 20-35%, across their lifetimes (Hunter & Sambrook, 2000). The sum of these musculoskeletal changes are thought to limit the strength and speed of motor outputs (Doherty, 2003), decreasing the ability to withstand challenges to static (Camicioli et al., 1997; Era et al., 2006; Fernie, Gryfe, Holliday, & Llewellyn, 1982; Forth, Metter, & Paloski, 2007, p. 200; Lord, Clark, & Webster, 1991; Manchester et al., 1989) or dynamic postural stability (Janssen et al., 2002; Lockhart et al., 2005; Maki, 1997; Swash & Fox, 1972; M. H. Woollacott et al., 1986). On top of this, reaction time and attentional capacity have been observed to change with age,

resulting in slower responses and difficulty successfully navigating novel or complex environments (Sturnieks et al., 2008; Teasdale & Simoneau, 2001). During long duration exposure to spaceflight, similar changes to the musculoskeletal system are observed, primarily as a result of disuse and unloading of the lower limb bones and muscles (S. M. Smith et al., 2012; T. Trappe, 2009; E. Wang, 1999). These changes place the astronauts at risk for fall related injuries as they experience an upwards loss of 1.5% bone mineral density (in the hip) per month (Lang et al., 2004). In the muscles of the lower limbs, necessary for postural stability, losses of up to 13% have been observed in the calf and 10% in the gastrocnemius (S. Trappe et al., 2009) after 6 months of exposure aboard the International Space Station. Functional performance of the astronauts are expected to reduce as muscle and strength loss occurs during unloading (Ryder et al., 2013), limiting their operational performance and reducing their ability to withstand static and dynamic postural challenges, similar to aged individuals.

Current exercise, pharmaceutical and nutritional countermeasures have shown improvements in bone mineral density retention, focusing on macronutrients involved in the one-carbon metabolism (vitamin D) and the inclusion of the advanced resistive exercise device (ARED), capable of higher body loading levels (S. M. Smith et al., 2012).

Unfortunately, these results do not comment on the type or quality of bone, which therefore may not be representative of a decrease in fall related fracture, as increased bone density does not relate directly with increased bone strength. Coincident with these results, muscular atrophy has been decreased during long-duration exposure to microgravity through the use of the ARED device. In this way, under strict adherence to an exercise program, the astronauts are capable of maintaining their physical strength and therefore, theoretically, functional

performance (S. M. Smith et al., 2014). Unfortunately, the current battery of countermeasures are unable to control any changes to the vestibular and somatosensory systems, which require an expected gravitational constant, or protect against the recently discovered vision issues, thought to result from a head-ward shift of fluid. These systemic losses of feedback continue impact astronaut health and safety as fall risk factors, impair balance and locomotion upon return to Earth. Current unpublished results showing the impact of eyes-closed locomotion during a tandem walk highlight this instability, as recently returned astronauts struggle to maintain upright posture during this task (Miller et al., 2015). Furthermore, it is theorized that the vestibular system plays a role in the integration of somatosensory information, known as vestibular-somatosensory convergence (Madansingh & Bloomberg, 2015; Mulavara et al., 2012), whereby vestibular sensory information is modulated by somatosensory inputs, both of which are altered during microgravity and must be reintroduced and reintegrated between gravity/microgravity environments. During the transitory periods between gravity and microgravity, the sensorimotor systems require rapid adaptation to maintain performance and minimize risk in order to complete mission critical objectives (Batson et al., 2011; Peters et al., 2013).

Facilitating a comparison between astronaut and aged populations from a sensorimotor point of view requires focusing on the relative changes to performance, as opposed to a collection of acute changes due to a variety of very different mechanisms. In both elderly populations and those exposed to long duration microgravity, bone and muscle loss are observed, due primarily to disuse and insufficient loading. These deficiencies manifest themselves in performance decrements over different time scales, resulting in the need for both long term (elderly) and very short term (astronaut) adaptation. Exercise and

physical activity are the primary countermeasures for these changes in both population groups, with strength training, balance and tai chi programs showing significant improvements to fall risk factors in elderly care (Ambrose, Cruz, & Paul, 2015; Blankevoort et al., 2010; Gillespie et al., 2012; Wolf et al., 2003; Wolfson et al., 1996). The other major sensorimotor systems – vision, vestibular and somatosensory – express degraded performance among both populations, requiring sensorimotor adaptation to either reintegrate changing feedback or change motor outputs to match decreased control in order to cope with environmental stressors, such as those to balance. A better understanding of the sensorimotor adaptation process and its relationship with motor (re)learning provides a vehicle for streamlining this coping mechanism and maintaining safe balance and postural stability.

II.IX Sensorimotor adaptation and motor learning

Adaptation is the process of change by which an organism or species becomes better suited to their current environment. It occurs on multiple time scales, from short term (minutes, hours and days) to long term adaptation (weeks, months and years to adapt) and within all domains of biological science, from the cellular to psychological (Huether & McCance, 2013; Platek, 2007). The goal of systemic adaptation is to maintain levels of homeostasis within the body, such that appropriate functionality and performance are maintained in humans and animals for survival (Wohlwill, 1974). Physiological adaptation takes many forms in response to a change in habitat or environment, such as the tanning of the skin during increased exposure to sun and ultraviolet light, or changes to musculoskeletal definition after the adoption of a more active lifestyle. The sensorimotor system, specifically, provides afferent, or sensory, information to the central nervous system (CNS) in order to maintain fine and precise control of motor function. These sensing systems include vision,

auditory perception, somatosensory sensation (including proprioception) and vestibular afference, providing us with the information necessary to perform everyday motor tasks, such as maintaining upright balance and performing steady ambulation, safely and effectively.

When confronted by environmental stressors, the sensorimotor system demonstrates motor adaptation to maintain safe and effective movement performance (Shadmehr, Smith, & Krakauer, 2010). Traditional examples of environmental stressors include changes in visibility (i.e. light/dark/occlusion), changes in temperature (i.e. hot/cold climates) or changes to support surfaces (i.e. uneven/unstable ground). Sensorimotor adaptations are not limited to environmental stressors, however. Pathological diseases such as Parkinson's (Konczak et al., 2009), as well as aging (Krampe, 2002), result in changes to the sensorimotor system itself, necessitating adaptation to maintain motor performance and safety. A recent addition to the list of environmental stressors which require adaptation, due to its challenge to the basic evolutionary constant of Earth gravity, is weightless experienced during spaceflight.

In the literature, various methods of providing systematic and consistent perturbations have been used to observe and quantify motor output adaptation to novel sensory inputs. Motor adaptation is considered a short-term learning process (Reisman, Bastian, & Morton, 2010) and typically, these tasks are designed to minimize motor variability and observe a specific output. For example, manual tasks in the upper extremities, such as the movement of an object through a specific trajectory in the face of position-disturbing force fields (Shadmehr et al., 2010; M. A. Smith, Ghazizadeh, & Shadmehr, 2006), the matching of a cursor to a target using a rotated input joystick device (Seidler, 2004, 2006) or throwing an object to meet a target under the influence of vision shifted goggles (Roller, Cohen, Kimball,

& Bloomberg, 2001, 2002) are commonly used. Motor adaptation paradigms are not limited to the upper extremities, however, visuomotor and proprioceptive adaptation protocols, such as gait perturbations via discordant visual feedback (Batson et al., 2011; Prokop et al., 1997) or split-belt treadmill walking, where the individual treadmill belts are set to independent movement speeds (L. A. Malone et al., 2011; Laura A. Malone & Bastian, 2010; Prokop, Berger, Zijlstra, & Dietz, 1995; Reisman, 2005; Reisman et al., 2010) are also used commonly. In the world of postural stability, the classical tests of Nashner et al. (1976; 1982) employing sliding and rotating support surfaces to stress static postural stability, as well as more modern strategies of slip and trip perturbations to locomotion, have been used to observe motor adaptation performance (Bhatt et al., 2013; Patel & Bhatt, 2015; T.-Y. Wang et al., 2012; Yang et al., 2013).

Imaging studies have shown distinct differences in neuronal activation between upper and lower limb movements (Luft et al., 2002; Miyai et al., 2001), suggesting a limit to the relationship between the activation patterns and motor strategies employed during movement and task adaptation. Neuronal activation during upper extremity adaptation tasks have primarily localized in the lateral and posterior cerebellar cortices in tasks similar to joystick-controlled position matching (Doyon & Benali, 2005; Imamizu, Kuroda, Miyauchi, Yoshioka, & Kawato, 2003). In a recent review, Reisman et al. (2010) describes CNS involvement in split-belt locomotor adaptation, citing no obvious adaptive difficulties in adults with chronic cerebral stroke and hemiparesis (Reisman et al., 2007), although in models exhibiting cerebellum damage, significant impairments to motor adaptation during locomotion is observed. This suggests that locomotor adaptation occurs primarily in the cerebellum and that the motor cortex, located in the cerebrum, plays little role. From a motor

strategy point of view, this corresponds with classical notions of rhythmic motor control based on spinal excitability and central pattern generators (Duysens & Van de Crommert, 1998). Unfortunately, traditional high resolution imaging techniques, such as fMRI (functional magnetic resonance imaging) and PET (positron emission tomography), are challenging during locomotion and to date no functional near-infrared spectroscopy (fNIRS) or electroencephalography (EEG) studies have focused on cortical activity during lower-limb motor adaptation paradigms. Although upper-and-lower extremity movement appear to have different mechanisms for motor control (Seidler, 2004), there have been no attempts to compare their performance from a sensorimotor adaptation point of view.

Adaptation performance in motor tasks can also be classified by motor strategy, not simply motor site, as open-loop (feedforward) or closed-loop (feedback) systems. In the rotated-input joystick matching tasks and the discordant visual flow locomotion task, closed-loop feedback systems are considered to be used for online corrections to any errors produced by the task challenges (Finley, Statton, & Bastian, 2014; Seidler, 2004).

Performance is observed to improve through the use of this feedback, until a steady state is achieved, signaling that motor learning has taken place. Richards et al. (2007) describe the early stages of this learning as strategic learning, which occurs very rapidly, in response to a novel environmental perturbation. Extended exposure to this perturbation results in retained movement strategies to reduce error and improve performance, termed plastic recalibration, or simply, motor adaptation. This adaptation is best recognized in situations where motor performance is observed to decrease (typically in the opposite direction of adaptation) when the perturbations are removed and the environment returns to baseline, termed ‘after-effects’ (Reisman et al., 2010). Feedforward, open-loop, control is considered to be the primary

strategy for modifying motor commands during adaptation in split-belt walking (Pavol & Pai, 2002), where belt speeds are not congruent and ballistic target matching tasks (Roller et al., 2001, 2002), where vision is shifted through the use of prisms. No online corrections are possible during these tasks, and updates to the upcoming movement (either ball throw or next step), or motor program, can only take place after the conclusion of the previous output.

In each motor task, although the goals of each are dramatically different – achieve a target, maintain normal walking as best as possible – the resultant performance over time shares similarities. In healthy individuals, regardless of age (Buch et al., 2003; Seidler, 2007), motor performance is observed to improve towards baseline levels, and, although performance may never achieve baseline, due usually to the difficulty of the task or limitations in the system, the expected response is that of improvement towards a steady-state of performance. This suggests the possibility of an underlying mechanism for learning, or ‘learning to learn,’ which has been referred to as the theory of adaptive generalizability (Seidler, 2004; Welch et al., 1993).

II.X Adaptive generalizability and fall risk factors in the astronaut population

As previously described, balance control in astronauts has been studied since the early days of the manned spaceflight program, due to the direct effects of microgravity on the gravito-sensitive sensors of the vestibular (Reschke et al., 2009) and somatosensory systems (Madansingh & Bloomberg, 2015; Mulavara et al., 2012). These sensorimotor changes manifest themselves as locomotor and balance dysfunction, increasing instability and the risk of falls (S. J. Wood et al., 2011), especially upon return to Earth. To date, no known microgravity countermeasure has been effective at mitigating the effects of vestibular dysfunction due to spaceflight. This results in provocative adaptations periods during

transitions to and from gravity environments, associated with nausea, motion sickness (Lackner & DiZio, 2000) and a decrease in postural stability. These responses are not constant, however, across all astronauts, and seem to be modulated by experience or repeat exposure, although even this is not consistent in all cases (Reschke et al., 1998). This pattern of individualization is observed commonly in the astronaut population, especially during sensorimotor tests pre- and post- microgravity adaptation, immediately after return to Earth (Bloomberg & Mulavara, 2003; Clément & Ngo-Anh, 2013; Glasauer et al., 1995; Madansingh & Bloomberg, 2015; Mulavara et al., 2012; Peters et al., 2013).

Understanding the relationship between adaptation performance and resilience to postural instability is critical to future efforts to minimize fall risk in the astronaut population, as well as other clinical populations at an increased risk of falls and fall related injuries. Previous work understanding the implications of spaceflight upon the sensorimotor system have observed significant inter-subject variation (Mulavara et al., 2012), making generalized interventions and training protocols ineffective. Current work in spaceflight countermeasures, summarized by Seidler et al. (2015) and Bloomberg et al. (2015) have focused on the study of adaptation generalization and predictors of adaptation using various techniques. Of note, a system employing discordant visual information and treadmill induced gait perturbations, accomplished by placing the treadmill atop a moving platform, has shown significant success improving adaptation performance through variability training where a component of adaptation is required. It has been suggested that adaptation performance may be predictive of responses to other novel stimuli through the theory of adaptive generalizability (Seidler, 2004; Welch et al., 1993), where the CNS is capable of applying motor strategies developed in one situation to a similar class of problems. Currently, no

direct mapping of adaptation performance to measures of fall risk, specifically responses to static and dynamic postural perturbations, has been attempted.

Within the framework of adaptive generalizability, it is possible that the systems responsible for generation, retention and application of these adaptive strategies are common across motor activities and may allow for the development of training prescriptions to exploit an individual's unique sensory biases and adaptive capabilities. Furthermore, a better understanding of adaptation performance across different motor tasks, such as those requiring feedforward or feedback strategies, or across different motor sites, such as upper extremity or lower extremity, will provide the opportunity to estimate the effect of adaptation performance upon static and dynamic postural stability. This is of particular interest because, with respect to adaptation performance between motor tasks and motor sites, distinct differences exist in the handling of afferent sensory information and motor effector signals, both from a strategic point of view (closed-loop feedback versus open-loop motor programs) or a control point of view (lower spinal versus higher level processing). How this relates to the closed-loop strategies of static balance control (L. M. Nashner, 1972) or open-loop strategies of locomotion (Pavol & Pai, 2002), is currently unknown.

II.XI Rehabilitation, fall prevention and motor control

For populations at risk of falls, such as the elderly and those experiencing pathologies which impair their sensorimotor systems, adaptation training or 'learning to learn' may represent a novel therapy for fall risk prevention, or rehabilitation after a fall. Currently, fall prevention in these populations takes the form of environmental advice, such as reducing potential trip or slip hazards, avoiding low-light and unfamiliar areas, as well as maintaining physical activity (Gillespie et al., 2012). Only one of these solutions represents real changes

for at-risk populations, such as the elderly, and the goal of maintaining physical activity is more easily said than done. This approach is considered the current standard of care for patients identified as at-risk for falling, often receiving prescriptions for physical therapy with an emphasis on balance exercise and training. In the elderly populations, balance training and Tai Chi have been observed to improve scores on clinical tests of posture, reducing COP sway and improving strength measures (Ambrose et al., 2015; Blankevoort et al., 2010; Ledin et al., 1990; Wolf et al., 2003; Wolfson et al., 1996). In elderly women with osteoporosis, as a subset of the elderly population, balance training paradigms have been successful in improving functional balance performance (Madureira et al., 2007). In Parkinsonian populations, balance and strength training are commonly prescribed if fall risk is suspected and have been observed to provide significant improvements to static postural stability (Hirsch, Toole, Maitland, & Rider, 2003; Toole, Hirsch, Forkink, Lehman, & Maitland, 2000, p. 200). Diabetics suffering for peripheral neuropathy who experience balance issues are similarly prescribed physical therapy and balance training, showing improvements in measures of static COP sway (Allet et al., 2010; Morrison, Colberg, Mariano, Parson, & Vinik, 2010; Salsabili, Bahrpeyma, Forogh, & Rajabali, 2011) and gait dynamics (Allet et al., 2010), including walking speed.

In many situations, individuals deemed to be at risk of falling are provided assistive walking devices, such as canes or walkers, in order to provide postural stability. These devices operate by widening an individual's available base of support, while limiting postural sway and COP/COG movement. These devices build reliance and have actually been observed to increase prospective fall risk (odds ratio, 3.98), showing decreased gait performance in walking speed and smaller step lengths (Roman de Mettelinge & Cambier,

2015). Unfortunately, as described previously, the fear of falling, especially in those adults who have experienced a fall or fall related injury in the past, limit the adoption of an active lifestyle through exercise programs or Tai Chi, for example (Scheffer et al., 2008).

Across the board, these balance training paradigms exploit closed-loop motor control strategies to explore the limits of an individual's base of support, producing sensory feedback. By stressing the limits of an individual's postural stability through this training, the sensorimotor system can compute errors with respect to their current model of postural stability. This redefines the model of their available base of support, while encouraging muscle strengthening and improving balance responsiveness. Open-loop training of balance, that is, balance training that does not employ real-time feedback in the production of postural responses, is typically dynamic in nature and uncommon in elderly and pathological populations.

Recently, some rehabilitation experts have begun exploring the possibility of training the actual fall perturbation response in an open-loop fashion, through controlled slip and trip protocols (Bhatt et al., 2013; Kajrolkar et al., 2014; Pai et al., 2010, 2003; Pavol, Owings, Foley, & Grabiner, 1999; T.-Y. Wang et al., 2011; Yang et al., 2013) where participants adapt to dynamic postural stressors. Pai et al. (2010) exposed healthy elderly adults to over-ground slips through the use of sliding plates, and showed that the ability to acquire and utilize fall-resistance skills after repeated perturbations was intact, comparable with young healthy participants. Follow-on work by Yang et al. (2013) has shown that adaptation to treadmill induced slips produces a generalizable fall-resistance skill, which can be applied successfully to unexpected over-ground slip perturbations using sliding platforms in healthy participants. A recent study observed adaptive changes in reactive balance control associated

with treadmill slips (Patel & Bhatt, 2015), based upon the previous work of Yang et al. (2013), both of which showing a strong relationship between motor adaptation and changes in fall susceptibility. Wang et al. (2011) discusses briefly the propensity for individuals to rapidly react and adapt to stressors of postural stability while observing adaptation similarities between two very different tasks: sit-to-stand-to-slip perturbation and over-ground slip perturbations.

Further support for the notion of adaptation performance training in rehabilitation comes from studies observing the minimal effects of aging on sensorimotor adaptation (Bock, 2005; Bock & Schneider, 2002; Buch et al., 2003; Cressman et al., 2010, p. 210; Seidler, 2007). In these studies, elderly participants, when compared to young healthy controls, are able to adapt to novel sensorimotor tasks and often exhibit improved after-effect retention in the form of decreased error when the novel environment is removed. Overall performance in the task, such as adapted accuracy or response time, is typically reduced with age, and is cited as the consequence of decreased cognitive capacity during dual-and-multi-task situations (Bock, 2005; Mirelman et al., 2012; Stelmach, Zelaznik, & Lowe, 1990; Verrel, Lövdén, Schellenbach, Schaefer, & Lindenberger, 2009). Regardless of overall performance, adaptive generalizability has been observed in aged populations (Buccello-Stout et al., 2008; Seidler, 2007), and provides further support for the future of this strategy in fall prevention.

Unfortunately, these dynamic training paradigms involve a level of risk to participants which may not be appropriate for all at-risk individuals, especially those with comorbidities such as osteoporosis or neurological disorders which impair motor function. That being said, these results provide strong evidence that not only does training the required

skills for fall-resistance improve performance and serve to decrease the risk of falling, but also that these skills can be developed in a surrogate fashion, consistent with the framework of adaptive generalization. If adaptation is truly generalizable, and it is possible to acquire skills rapidly applicable to novel environments which pose a risk to postural stability, a new paradigm of fall prevention training becomes available. In this way, it is possible to train proficiency in surrogate tasks of varying levels of similarity in either motor site (upper or lower extremity) or motor strategy (open- or closed-loop), to those which cause perturbations to static and dynamic postural stability. This framework would minimize the risks associated with training real slips and trips in a clinical or laboratory setting and provide a new paradigm for balance health and safety.

III. Experimental Methods

The protocol was approved by the University of Houston Committee for Protection of Human Subjects and conducted according to the university standards for ethical conduct of research with human subjects. The informed consent document is provided in Appendix D. All participants provided written informed consent before beginning experimental procedures. The experiments took place at the University of Houston Center for Neuromotor and Biomechanics Research in the Texas Medical Center. All testing was performed during one visit to the laboratory, lasting approximately 2.5 hours.

III.I Participants

65 healthy adults, ages 18-40 years, were recruited to participate in the Experiment, however only 58 (28 male, 30 female) completed successfully. Four subjects were excluded during data collection: two who requested to leave the study part way through data collection

due to scheduling issues or discomfort, and two others were asked to leave due to being physically unwell. Three participants were excluded after data collection for individual reasons including: admitting to ‘not trying’ and participating only for the incentives (extra credit in a University of Houston class); admitting to prior knowledge and experience with the testing apparatus, which was not disclosed during participant screening; and finally one participant who exhibited clinically significant balance issues during static posture. All participants completed two sensorimotor adaptation protocols, including split-belt treadmill adaptation and rotated-input joystick target matching, see Figure 2, as well as the dynamic balance measures in the form of postural recovery during perturbed treadmill locomotion.

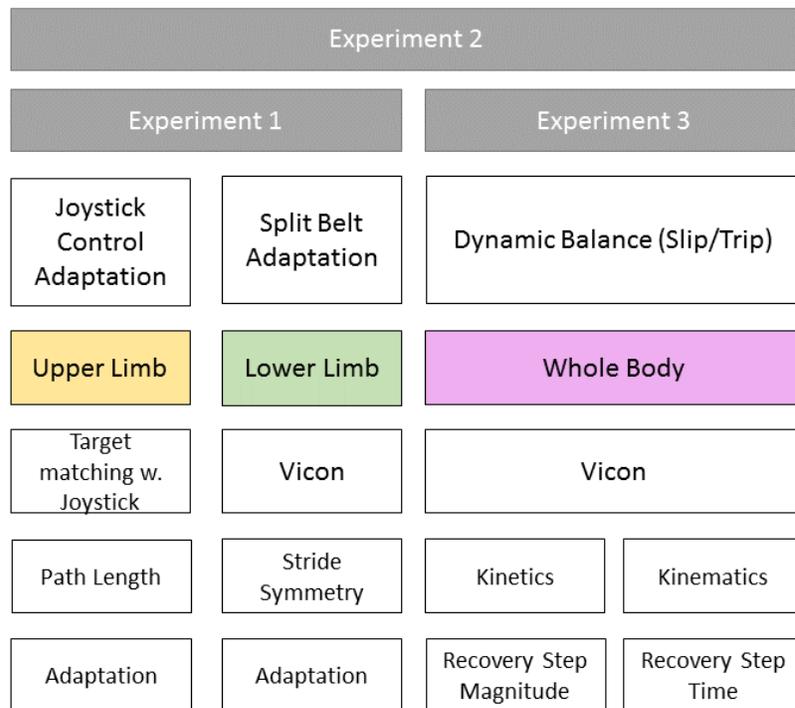


Figure 2: Outline of experimental protocols performed in pursuit of Specific Aims 1, 2 and 3. Protocol order was randomized among participants to minimize adaptive generalization between tasks.

III.II Power Analyses

A set of *a priori* power analyses were performed in preparation for this study using the G*Power 3.1 (Kriel University, Germany) software package. For Aim 1, a fixed model regression analyses was powered to estimate the required participant population (Rindskopf, 1984), see Equation 1.

$$y = \beta_1(k_{manual}^{-1}) + \beta_2(k_{locomotor}^{-1}) + c$$

Equation 1: Multiple regression equation predicting the relationship among manual and locomotor adaptation performance upon postural recovery outcome, representing recovery step reaction time, maximum recovery step force or perturbation time-to-recovery.

Two predictors were identified in this model, including the coefficient of manual adaptation and the coefficient of locomotor adaptation, where y represents the postural recovery outcome variable of interest, and c , the unaccounted for error in the model. A medium effect size ($f^2 = 0.15$) was adopted based on the limited number of comparable studies in this domain of motor control. To achieve an $\alpha = .05$ significance with approximate power $(1-\beta) = .80$ with two predictors, 55 participants were suggested, see Figure 3.

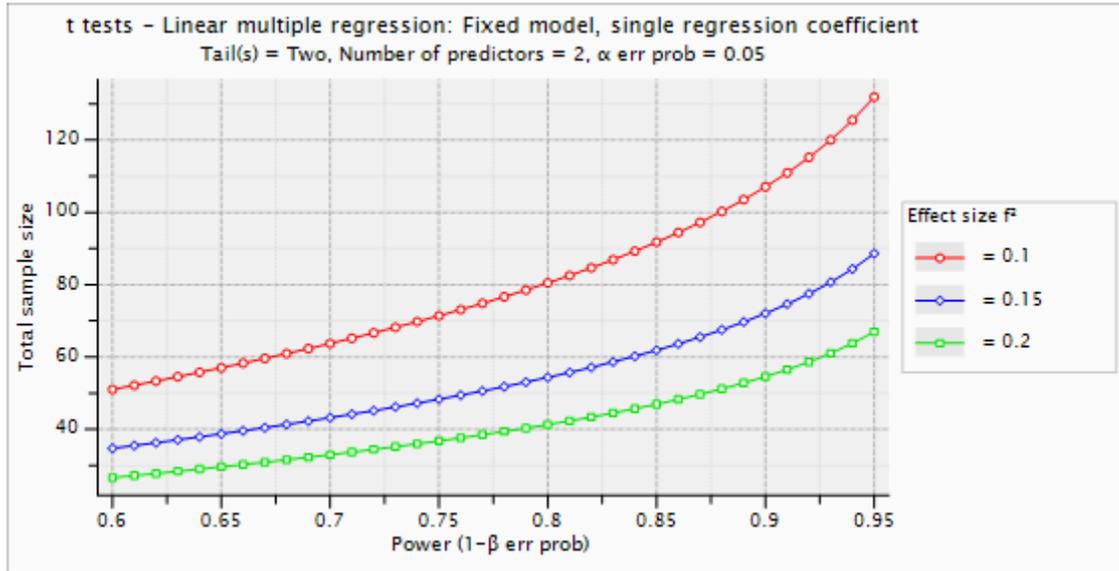


Figure 3: Power analysis trade space for a fixed model, single regression coefficient model with two predictors, including manual adaptation and locomotor adaptation coefficients. Reproduced in G*Power 3.1.3 (Faul, Erdfelder, Lang, & Buchner, 2007)

For Aim 2, *sensitivity* power analyses were performed to characterize the ability of a linear multiple regression model to detect an R^2 change from zero. This analyses estimated a required effect size of $f^2 = 0.1693$ (medium) to detect a significant relationship between adaptation performance and postural recovery, with an approximate power $(1-\beta) = .80$ and $\alpha = .05$.

III.III Inclusion and Exclusion Criteria

Prior to participation, individuals were screened for musculoskeletal, neurodegenerative and vestibular/balance related disease via self-report through the use of a modified Physical Activity Readiness Questionnaire (PAR-Q), see Appendix A. Participants were also excluded if they were taking medication for dizziness/nausea, or require an assistive device for walking (e.g. cane, walker). Those unable to maintain posture without support of pharmaceuticals or walking devices would significantly impact subject safety and negatively affect data collection. Furthermore, participants who were considered obese (BMI

> 30kg/m²), who wore corrective lenses for vision (and were unable to wear contacts), and those who were unable to identify a dominant hand or foot were excluded. Obese individuals represent a special population who have shown signs of balance impairment (Menegoni et al., 2009), as well as increased energy expenditure (Browning, Baker, Herron, & Kram, 2006), which increases the risk of fatigue. Individuals who can not identify a dominant hand or foot represent a special population and may bias results in a population of normal healthy individuals. Participants self-identified handedness and foot dominance.

III.IV Procedures

The experiment began with participants having anthropometric information collected, such as height, weight and a series of limb measurements, including: leg-length, ankle and knee width, shoulder offset, elbow and wrist width, and hand thickness, in accordance with guidelines by Vicon Motion Systems Ltd. (Vicon, Centennial, USA). Dominant foot was determined by self-identification of preferred kicking leg. Subjects then completed each of the three motor control protocols in randomized order, to control for the impact of adaptive generalization to minimize learning and performance bias among tasks.

III.IV.I Manual Rotated-input Joystick Matching Task (JOY)

The rotated-input joystick matching task (JOY) included a set of baseline and perturbation position matching trials, as well as a re-adaptation set of matching trials. Participants were positioned standing, at arm's length, comfortably in front of a computer monitor, which was adjusted to eye level. A video game style controller (Logitech F310, Logitech, USA) with dual potentiometer joystick inputs, see Figure 4, was secured to a table, approximately 1.1m (43") above the ground, and positioned midline with the participants and

a 22" LCD computer monitor (Dell E2210h, Dell, USA), in order to maintain constant shoulder and elbow flexion. Actuation of the joystick was performed with only the thumb and index finger of the dominant hand, to minimize gross arm movements. For each position matching trial, a target appeared in one of four locations: above, below, left or right of the centered start position. Targets were 4.0cm from the center, in each of the four directions, and 0.8cm in diameter. In pilot work, no participants expressed issues with acuity or difficulty tracking the cursor or target. Participants were instructed to move the on-screen cursor towards target using the joystick, with the goal of matching their centers and maintaining this position, as accurately as possible. Targets disappeared within 2 sec. of appearing, and participants were instructed to move as quickly as necessary to reach the target, while focusing on accuracy. Targets were presented in a random fashion. Participants were not required to bring the joystick back to center and were instead instructed to simply release the joystick such that it can re-center itself. Targets were presented every 3 sec., resulting in a total of 5 sec. per stimulus and target matching trial.



Figure 4: Spring actuated dual-joystick controller used as the input device for position matching task. Only the right joystick was used during matching attempts.

During baseline attempts, cursor output was mapped directly to joystick input. During adaptation attempts, cursor output was rotated by 45° with respect to joystick input, resulting

in immediate deviations requiring corrections, see Figure 5. Participant performed 28 baseline target matching attempts, 108 adaptation target matching attempts and 28 re-adaptation attempts to observe path length (total distance travelled by cursor in cm) (Seidler, 2004, 2006). The total time required to complete all trials was approximately 7 minutes.

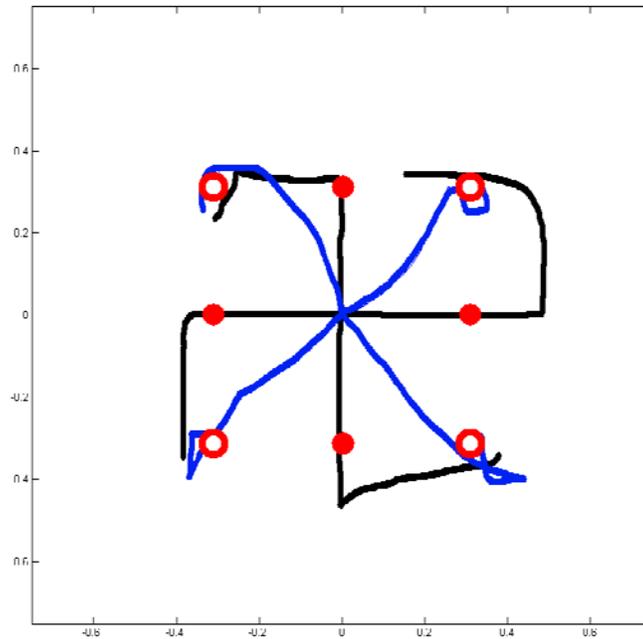


Figure 5: Example data from the 45° target matching adaptation task. Early attempts (black) and later, adapted, attempts (blue) are presented for a representative subject. Target locations in display screen coordinates are presented as filled red circles, while target locations in joystick coordinates are presented as open red circles. Path length is calculated as the total cursor distance travelled during an attempt to match the target, and is represented here in its joystick coordinate system. Participants would have viewed the paths above in real-time, rotated at 45°.

In the baseline condition, where the input is unperturbed, the path length should be no less than 4.0 cm (minimum distance between start point and target). To establish reliability statistics for these measures, baseline pilot data were collected from three participants who completed only the first 28 (baseline) target matching attempts. The mean path length travelled was found to be 4.31 ± 0.8 cm (mean+SD) across all pilot participants. Within individuals, a high correlation was observed (Pearson's $r > 0.85$) independently for baseline (non-adaptation) path length, suggesting high stability in the measure.

III.IV.II Locomotor Split-belt Adaptation Task (SBA)

To perform the split-belt adaptation task, participants were suited with reflective markers on their head, trunk, legs, arms and feet, in accordance with the Vicon lower body Plug-in-Gait model, to capture lower body movement during each trial using a Vicon motion capture system (Vicon, Centennial, USA). The subject was then outfitted with a safety harness attached by a pair of load bearing ropes to a rigid support structure and load sensing system, located overhead. A calibrated S-Beam load sensor (Omega Engineering, Connecticut, USA) was placed in-line with the safety harness ropes, and measured the force exerted upon the ropes by the subject in the event of a near-fall event. Rope lengths were adjusted so that the subject was in no danger of coming in contact with the treadmill in the case of a loss of balance.

At this point, subjects were instructed that the treadmill would start at 1.0m/s and they began walking. The split-belt adaptation protocol estimated step symmetry (SS), see Equation 2, and had three phases: baseline, adaptation and re-adaptation. Step symmetry is defined as the difference in step length (SL) between the ‘fast’ and ‘slow’ moving leg during a split-belt paradigm (L. A. Malone et al., 2011), normalizing for individual step length(s). This normalization accounts for varying height across participants by scaling the step symmetry difference by the sum of step lengths for both the ‘fast’ and ‘slow’ moving legs. During baseline walking (belts-tied condition), step symmetry should be 0, indicating no difference in the size of step length.

$$SS = \frac{SL_f - SL_s}{SL_f + SL_s}$$

Equation 2: Calculation of step-symmetry (SS) based on the step lengths of the fast (SL_f) and slow (SL_s) legs. In perfect symmetry, where the step lengths of each leg are equal, $SS = 0$.

A positive SS suggests the stride length of the ‘fast’ step was larger than that of the ‘slow’ step. This relationship is reversed for negative SS trials. As adaptation occurs through continuous exposure to asymmetric belt velocities, it is expected that SS will reduce, thereby becoming more symmetric and achieve a steady state (but not necessarily returning to a SS of 0).

Prior to data collection, participants were introduced to a split-belt protocol to minimize any ‘surprise’ reactions which may confound the adaptation process (L. A. Malone et al., 2011). The split-belt treadmill was accelerated to a walking speed of 1.0m/s, where the speed of each belt was tied for 2 minutes of baseline walking. After 2 minutes of baseline walking, subjects were exposed to split-belt walking for 20 seconds, where the dominant leg speed was increased by 25% (1.25m/s) and the non-dominant leg speed was decreased by 25% (0.75m/s). The belts were then re-tied for a washout period of 2 minutes at 1.0m/s to minimize the carryover effects of the initial exposure to the data collection trial. A minimum of 5 minutes of rest time was required after introduction before beginning data collection.

In the data collection trial, participants were centered on the split-belt treadmills, and walked for 3 minutes with the belts tied at 1.0m/s. They were not informed of the speed at which the split belts would be set, however they were informed when the split was to occur. A 3:1 ratio (Reisman, 2005) was adopted for this protocol, resulting in the dominant leg being set to 0.5m/s (L. A. Malone et al., 2011) and the non-dominant leg set to 1.5m/s (a

decrease and increase of 50%, respectively). Participants were instructed not to look at the belts throughout the trial and attempt to maintain their gaze on a fixed marker, located at eye level. To achieve adaptation, participants walked on the split treadmill for 10 minutes. At the end of the adaptation trial, to induce re-adaptation, the split-belts were re-tied in speed, and reset to 1.0m/s for a minimum of 3 minutes.

Kinematic data, specifically the position of the motion capture markers arranged according to the lower-body Plug-in-Gait model, were captured using Vicon Nexus software (Vicon, Centennial, USA). Motion capture data were sampled at 100Hz. Ground reaction force and harness loading data (kinetics) were collected from force plates located under each tread of the split-belt treadmill (Bertec Corporation, Columbus, USA) and sampled at 1000Hz. All data processing and analysis was performed using MATLAB 2015 (Mathworks Inc., Natick, MA, USA), using custom scripts. All data were low-pass filtered using a zero-phase, second-order Butterworth filter with 15Hz cutoff frequency. Outcome measures during SBA included step length in both the left and right leg, calculated as the distance from the heel during foot strike to the toe during toe-off portions of gait. Ground reaction forces were used to determine the specific phases of gait, and motion capture was used to determine the position of the feet.

Split-belt gait analysis using motion capture technology has been validated to provide a suitable comparison to over-ground kinematics (Tesio & Rota, 2008), where a maximum of 8% difference was observed in split-belt step length. As step symmetry is a comparison of step lengths between the left and right legs during split-belt walking, performed during post-processing and data analysis, no significant error is expected to be introduced to reduce the reliability of this measure.

III.IV.III Treadmill Induced Slip and Trip Perturbations (STP)

Prior to beginning the experiment, subjects were prepared in a similar manner as the SBA protocol, however the full-body Vicon Plug-in-Gait model was used to define reflective marker positions. Safety harness rope lengths were adjusted so that the subject was in no danger of coming in contact with the treadmill during an uncontrolled trip or slip recovery. Subjects were instructed that the treadmill would slowly accelerate (0.2m/s^2) to 1.0m/s – the maximum walking speed which was maintained across all subjects prior to perturbations.

The trip or slip perturbations occurred at approximately 10% of their gait cycle which corresponds with the period of double-limb support, where the subject's foot (heel) comes in contact with the ground and body weight is transferred to this limb. This loading phase was detected using measured ground reaction forces (2% of subject body weight) obtained by the force plates (Bertec Corporation, Columbus, USA) located under each of the treadmill belts. The first of each perturbation was recorded as the novel exposure to the dynamic postural stability stressors.

During the trip perturbations, the tread below the perturbed foot decelerated rapidly, coming to a stop (velocity = 0m/s), and did not begin again until a recovery step was detected by the un-tripped foot (2% of subject body weight). During slip perturbations, the tread below the perturbed foot accelerated rapidly (accelerated by -12m/s^2 to -1m/s in approximately 0.16sec), in the opposite direction of normal treadmill walking, resulting in forward translation of the slipped foot. This foot was slipped until a recover step was taken upon the opposite (unperturbed) belt.

Dynamic perturbations were provided after a minimum of 20 steps, randomly selected between 20-40 steps. Participants experienced 10 perturbations of each type, slip or trip, which were presented successively, in a block randomized fashion. In this way, a sample participant received 10 slip perturbations then 10 trip perturbations, or vice versa. 10 repetitions of each perturbation were selected for three reasons: 1) pilot data collection during trip perturbations resulted in anecdotal expressions of comfort and familiarity in participants after 6-8 perturbations; 2) recent work published by Lee et al. (B.-C. Lee, Martin, Thrasher, & Layne, 2016) show adaptation and familiarity to repeated trip perturbations after 4-8 recovery attempts and 3) Bhatt and Pai et al. (Bhatt et al., 2013; Pai & Bhatt, 2007; Pai et al., 2010; Pai, Bhatt, Yang, & Wang, 2014) routinely perform blocks of 6-8 over-ground slip or trip perturbations, totaling upwards of 20 perturbations during an experimental session, with no reported concerns of fatigue among young, aged and elderly populations. A total of 20 perturbations, balanced equally, were selected in consideration of these guidelines.

Kinematic data were captured using Vicon Nexus software (Vicon, Centennial, USA). Ground reaction force and harness loading data (kinetics) was collected from force plates located under each tread of the split-belt treadmill (Bertec Corporation, Columbus, USA) and harness load cell data (Omega Engineering, Connecticut, USA) was collected using custom software designed in C++ by Dr. Beom-Chan Lee (B.-C. Lee et al., 2016). This custom software was used to control the treadmill and force plate system in order to produce trip and slip perturbations. All data were sampled at 100 Hz, and was synchronized to the Vicon system. All data processing and analysis was performed using MATLAB 2015

(Mathworks Inc., Natick, MA, USA), using custom scripts. All data were low-pass filtered using a zero-phase, second-order Butterworth filter with 15Hz cutoff frequency.

Recovery step reaction time and the associated ground reaction forces were collected from the twin force plates. Recovery time was estimated as the amount of time elapsed after the perturbation before step forces returned to within 1.2 standard deviations of the baseline step force, see Figure 9.

III.V Outcome Measures

III.V.I Specific Aim 1

The primary outcome measure from the protocols in Specific Aim 1 yield observations of sensorimotor adaptation to a novel situation or environment including: joystick target matching path length (total cursor displacement), and changes in step length symmetry during split-belt walking.

In order to quantify the performance of these adaptations, the time course of adaptation was quantified as an adaptation coefficient (k), that is, the inverse of the number of stimuli required to achieve a steady state of performance in the perturbed condition ($1/k$). An exponential function of the form:

$$y = ae^{-xk} + c$$

Equation 3: Standard form exponential equation, where a and c represent free fitting parameters related to the initial and plateau regions of performance respectively; y and x representing the predicted fit and input factors, respectively; and k the adaptation coefficient, representing the constant learning rate observed to achieve adaptation.

was fit to the adaptation curves to identify the settling period (k) required to reach $(1-e^{-1})$ or ~63% of the steady state set of performance, see Figure 6 (Fernandez-Ruiz, Wong,

Armstrong, & Flanagan, 2011; L. A. Malone et al., 2011; Reisman, 2005; M. A. Smith et al., 2006), a technique derived from linear systems engineering to assess a constant exponential change in response to a step input.

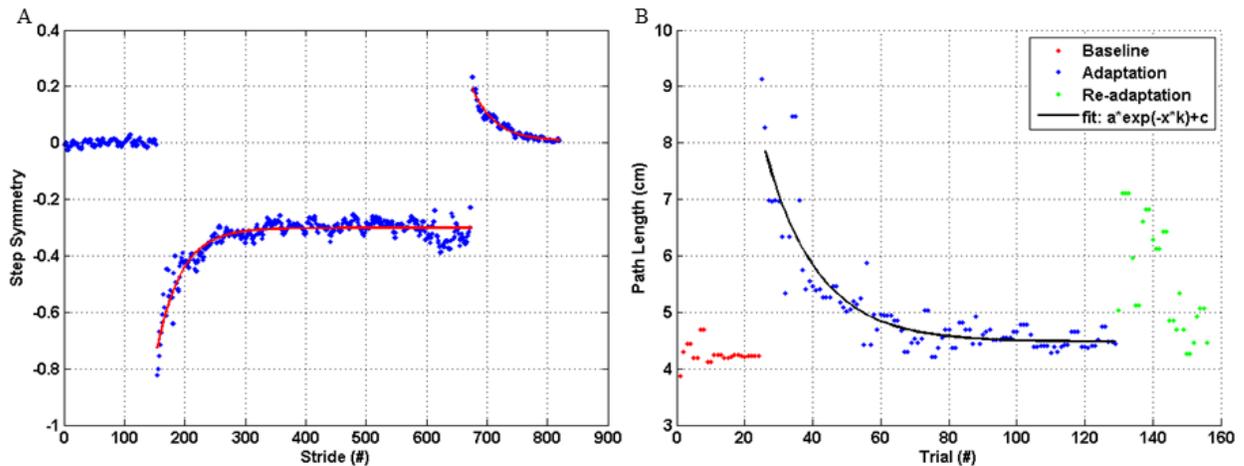


Figure 6: Example curve fitting for (A) split-belt step symmetry adaptation and (B) rotated input joystick matching adaptation. Re-adaptation behavior is also observed post adaptation, as expected. In both figures, baseline performance is observed with minimal variability, followed by a period of large error as the environmental change, either treadmill belt speed split or input rotation, is initiated. This is followed by a period of error reduction, resulting in a reduction in variability and steady state performance. Finally, a third period where the initial conditions are reenstated, resulting a rapid re-adaptation to baseline performance.

Assessing Curve Fit

The technique of fitting adaptation data, a complex form of motor learning or ‘practice’, whereby a decrease in performance error is expected to occur during a motor task throughout repeated attempts, or trials, is not uncommon in the field of motor control (Fernandez-Ruiz et al., 2011; Flanagan, Vetter, Johansson, & Wolpert, 2003; Heathcote & Brown, 2004; Heathcote, Brown, & Mewhort, 2000; Liu, Mayer-Kress, & Newell, 2003; L. A. Malone et al., 2011; Newell, Liu, & Mayer-Kress, 2001), however it is typically performed on averaged data. The inherently noisy nature of human performance makes fitting individual learning and performance data very challenging, and specific guidelines have been suggested to ensure appropriate consideration of the individual noise is included and not lost due to

averaging (Heathcote et al., 2000; Newell et al., 2001). The noisiness of the data, although characteristic of individuals, reduces the certainty of curve fit parameter estimations. These limitations are rarely discussed in the literature, and this study provided an opportunity to explore the implications of curve fit estimates and the estimated error associated with them.

Two approaches were taken to better understand the influence of curve fit performance and error in the estimation of model parameters: an assessment of the curve fit ‘goodness-of-fit,’ represented as an R^2 value, and as assessment of the influence of measurement error (standard error, SE) upon model predictions (adaptation coefficient, k). In both cases, an exploration of the sensitivity of the analyses described in Specific Aim 1 (see III.VI.I Specific Aim 1) to predication error was performed and is presented as a table Appendix B for reference, with subsequent analyses detailed in Appendix C.

Goodness-of-fit estimates, represented as R^2 , were calculated for each individual who successfully completed the manual joystick matching task and/or the locomotor split-belt matching task. Statistically, R^2 provides an estimate of the overall variance explained in a model, and intuitively, gives a sense of how well a set of data fit a model. Nonlinear regression, such as an exponential curve fitting model, is notorious for the misinterpretation of R^2 (Spiess & Neumeyer, 2010) regularly resulting in incorrect model selection, and heavy reliance upon these values for the evaluation of data/construct fit is cautioned in the seminal works of Newell et al. (2001) and Heathcote et al. (2000). Despite these warnings, the only information available to compare the quality of fits observed in this study to other attempts at the assessment of motor learning, or adaptation, using exponential models takes the form of these R^2 values. Heathcote et al. (2000) provides some guidance, observing an average $R^2 = 0.489$ after the analyses of thousands of individual motor learning tasks. Average R^2 values

were calculated for joystick and split-belt adaptation curves to support these comparisons. Sensitivity estimates were then performed with cut-off thresholds of $R^2 = 0.25$ and 0.5 , related to Cohen's d levels of high and very high correlations ($r = 0.5$ and 0.707 , respectively) (J. Cohen, 1992) to assess the impact of these poorer fits on the average fit quality and interpretation of the results in Specific Aim 1.

To estimate the uncertainty associated with each individual curve fit, 95% confidence intervals (95CI) and standard errors (SE) were calculated using the MATLAB 2015 Curve Fitting Toolbox (Mathworks Inc., Natick, USA) for each adaptation coefficient (k) and the subsequent adaptation performance estimate ($1/k$). To linearize the SE for comparison, the relative standard error (RSE) was calculated with respect to the estimated predictor, represented as a percentage (%RSE). To simplify interpretation, analyses were performed only on the adaptation performance estimate ($1/k$) only. No guidelines for acceptable error thresholds have been identified in the literature, therefore some inspiration was drawn from CDC guidelines for data suppression (Klein, Proctor, Boudreault, & Turczyn, 2002), which suggest a mean RSE of less than 30% is desired in qualitative assessments. As with the exploration of R^2 , sensitivity estimates were then performed with cut-off thresholds of %RSE $< 100\%$ and $< 50\%$ to assess the impact of these poorer estimates on the average parameter uncertainty (mean %RSE) and interpretation of the results in Specific Aim 1. Appendix B presents all subject data for manual and locomotor tasks described above, including R^2 , ($1/k$) estimates with 95% confidence intervals, standard error and %RSE for reference. Mean and standard deviation values are presented for each observed threshold, for both R^2 cut-offs and %RSE cut-offs.

To evaluate the impact of model fit and parameter estimate uncertainty, two sets of dummy-coded multiple linear regressions were performed to test for significant differences among the slopes and intercepts of models estimating the relationship among manual and locomotor adaptation performance (Specific Aim 1). Each set of dummy-coded regression compared three models, differing in the range of data included, based upon: 1) increasing goodness-of-fit (i.e. all R^2 vs. $R^2 > 0.25$ vs. $R^2 > 0.5$) or 2) increasing parameter estimate certainty (i.e. all %RSE vs. %RSE < 100% vs. %RSE < 50%). Dummy-coding in regression allowed for the testing of the null hypothesis that no significant differences in intercept or slope existed among models with increasing goodness-of-fit or increasing parameters estimate certainty. The details of these analyses are found in Appendix C.

Incorporating Measurement Uncertainty

As observed in Appendix B, a set of 95% confidence intervals and standard errors (SE) were generated for each adaptation coefficient estimate and expressed as a relative standard error (%RSE), for both manual and joystick matching tasks. To estimate the overall effects of this uncertainty, an average of this %RSE was calculated for each task, manual and joystick, respectively, and used to perturb the regression analyses outlined in Specific Aims 1 and 2. Inspiration for this technique was derived from discussions of measurement error outlined in Hutcheon et al. (2010), which describe the phenomena of regression dilution as a function of noisy or unreliable measurements during regression. To perturb the input variables to regression analyses, the data were sectioned into quartiles, where the top and bottom quartiles, which represent the most extreme values in the regression, were perturbed in opposite fashion, based on the average %RSE for that measure. These perturbations result in

two new sets of data, described in Table 3 and visually outlined using example data in Figure 7.

Table 3: Perturbation of adaptation data by relative standard error, represented as a percentage, resulting in two data sets (Perturbation 1 and Perturbation 2), influencing the 1st and 4th quartiles of the dependent variable in regression.

	1 st Quartile	4 th Quartile
Perturbation 1	+ %RSE	- %RSE
Perturbation 2	- %RSE	+ %RSE

In Perturbation 1, the location of the first and fourth quartiles on the horizontal axis became stretched towards their extremes, while Perturbation 2 served to compress the results closer to the mean. In both scenarios of regression bias, it was expected that the strength of the relationship would dilute, regressing towards 0. Cause for concern was noted if the interpretation of the perturbed data sets, such as identification of statistical significance, differed from the reported unperturbed data set in both of the perturbation cases.

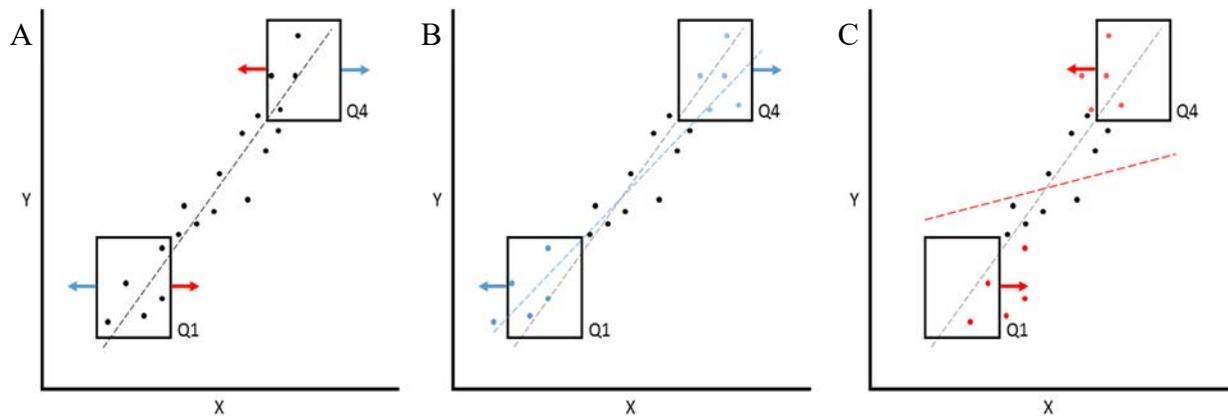


Figure 7: A) Example data highlighting the process of ‘stretch’ing or ‘compress’ing an adaptation performance data set based on %RSE. B) Perturbation 1, ‘stretch,’ is observed in blue, while C) Perturbation 2, ‘compress,’ is observed in red. In both cases, the strength of the relationship is expected to decrease, and regress towards the mean.

III.V.II Specific Aim 2 and 3

For Aim 2 and 3, the outcome measures quantifying the postural response to perturbations of dynamic stability in the form of slips and trips were: time to recovery step (RT), maximum recovery step ground reaction force (maxRSF) and time to recovery (TTR). RT represents the reaction ability for an individual to respond to a novel, fall inducing perturbation, which was expected to be minimized in healthy individuals who are less prone to falling. maxRSF represents the propensity for secondary injury as a result of a slip or trip perturbation, where strategies minimizing joint loading, such as knee flexion to absorb a sudden recovery step, were expected to be observed in healthy individuals, see Figure 8. In analyses, maxRSF is expressed as a function of body weight (maxRSF/mg) to allow for a normalized comparison.

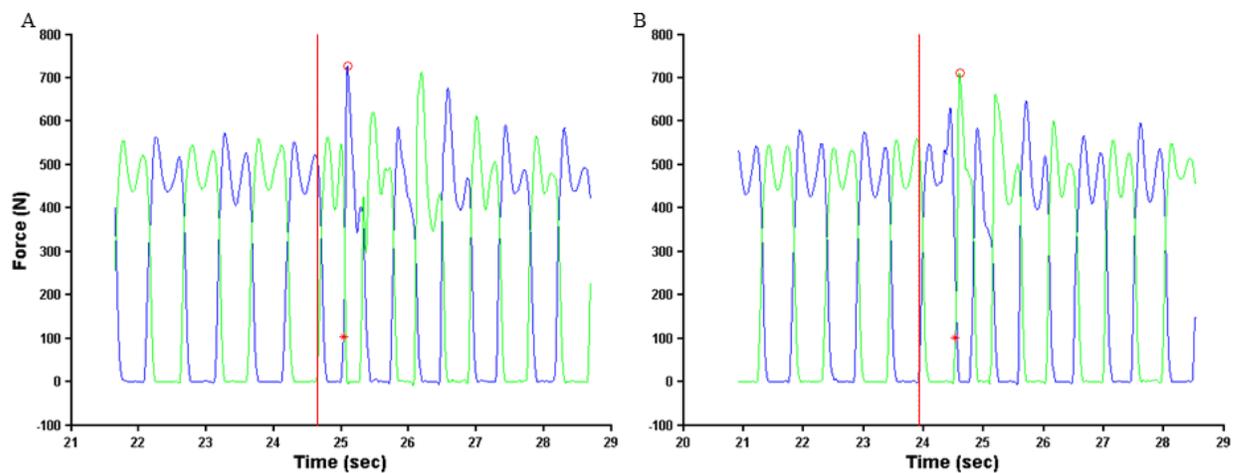


Figure 8: Max recovery force and reaction step time in response to a perturbation (vertical red dashed line) for an example subject, female with a body mass of 54kg. (A) shows the max recovery force (red circle) and recovery step reaction time (red asterisk) to a slip perturbation. (B) shows the max recovery force (red circle) and recovery step reaction time (red asterisk) to a trip perturbation.

TTR is a measure of the amount of time elapsed during postural recovery, which was observed to be completed as step forces return within a threshold comparable with pre-perturbation step force variability. For the purposes of this study, this threshold has been set

to be 1.2 standard deviations of the average peak step force during the four steps prior to the perturbation, see Figure 9.

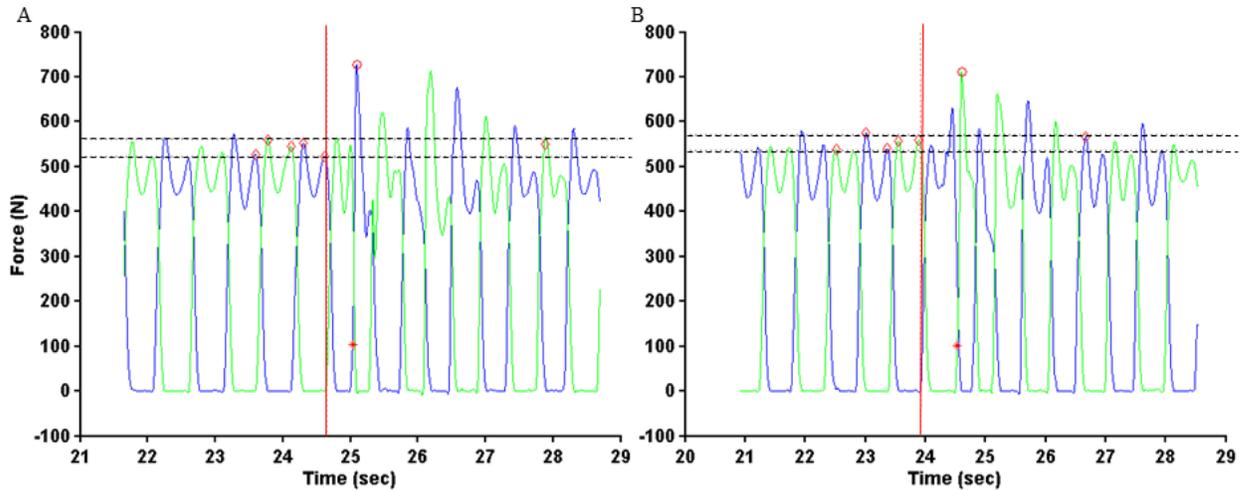


Figure 9: Recovery time for a treadmill induced (A) slip and (B) trip. The recovery time is defined as the time the recovery step forces return within a threshold of 1.2 standard deviations (black dashed lines) of the average maximum step force for the 4 steps (red diamonds) prior to the perturbation (red dashed line). (A) shows the recovery time for a slip perturbation at approximately 27.9 sec. (red diamond). (B) shows the recovery time for a trip perturbation at approximately 26.7 sec. (red diamond).

III.VI Data Analyses

III.VI.I Specific Aim 1

The goal of Specific Aim 1 was to determine the strength of the relationship between individual adaptation performance across two different modalities: manual and locomotor control. Two experimental protocols were performed, including one upper-extremity manual control task and one lower-extremity locomotor task: a computer controlled rotated-input joystick target matching task and a split-belt treadmill walking task. A regression analysis, see Equation 4, was performed observing the strength of the relationship between manual adaptation performance (k_{manual}) and locomotor adaptation ($k_{\text{locomotor}}$) performance among a population of healthy adults, distributed equally between males and females. It was hypothesized that the calculated manual task adaptation coefficient will be significantly

correlated ($r > 0.3$ (Mukaka, 2012; Wu et al., 2014)) with calculated locomotor adaptation coefficients.

$$k_{locomotor} = \beta_1(k_{manual}) + C$$

Equation 4: Simple linear regression equation, predicting the relationship between locomotor adaptation performance and manual task adaptation performance.

Adaptation coefficients were transformed from a unit-less coefficient to represent the number of attempts (joystick target matching attempts) or strides (step symmetry between fast and slow foot) required to achieve adaptation by taking the inverse of k (i.e. $1/k$).

Regression assumptions of normality (normalized residuals) and homoscedasticity were assessed through visual inspection of frequency and residual figures.

During preparation for statistical analyses, these adaptation outcome measures were log transformed (natural logarithm) using standard practices (J. Cohen, 1988, pp. 227–228; Field, 2009, pp. 156–158) to ensure assumptions of normality using Kolmogorov-Smirnov and Shapiro-Wilk tests, as well as visual inspections of frequency and residual distributions.

III.VI.II Specific Aim 2

The goal of Specific Aim 2 was to estimate the relationship between whole-body postural recovery performance during treadmill induced slip and trip perturbations, including recovery step reaction time, recovery step force and recovery time, and relate this performance to individual adaptation performance from Specific Aim 1. The novel locomotor perturbation paradigm was developed to produce consistent and repeatable fall perturbations to treadmill walking, while maintaining difficulty by minimizing the ability to predict and prepare for the perturbations.

During preparation for analyses, normality was verified for postural recovery measures through using Kolmogorov-Smirnov and Shapiro-Wilk tests, and well as visual inspections of frequency and residual distributions. Due to high correlation ($r = 0.799$) between manual and locomotor adaptation, multicollinearity was determined to be a source of issue, therefore multiple regression was not performed. To quantify the relationships between adaptation performance and postural recovery, three approaches were taken: 1) Pearson's correlations were performed among all adaptation measures (adaptation coefficients (k) and adaptation performance ($1/k$)) and postural recovery measures (recovery step reaction time, recovery step reaction force and recovery time) for Perturbation 1 (novel perturbation) and Perturbation 10 (final attempt), for slips and trips, respectively. 2) Pearson's correlations were performed among all adaptation measures and the percent change in postural recovery performance between the novel (1st) and final (10th) perturbations, for slips and trips, respectively and 3) A composite score of adaptation performance was generated using the sum of the unit-weighted z-scores for both the adaptation coefficient (zk) and adaptation performance ($z(1/k)$) (Ackerman & Cianciolo, 2000). Kolmogorov-Smirnov and Shapiro-Wilk tests, and well as visual inspections of frequency and residual distributions were performed to ensure composite scores did not violate the assumption of normality. Pearson's correlations were performed between the composite scores and all postural recovery metrics to identify significant linear correlations with the previous time points, and overall percent performance change. Where significant correlations ($r > 0.3$) were identified, linear regression was performed to predict changes in postural recovery performance based on manual or locomotor adaptation performance, after exposures to slip or trip perturbations, respectively.

III.VI.III Specific Aim 3

The goal of Specific Aim 3 was to quantify and assess the novel slip and trip protocol for its ability to produce repeatable and sufficiently challenging gait perturbations, while minimizing skill transfer between opposing tasks. To test the effects of multiple perturbation exposures and their impact upon a novel opposing gait perturbation, the participant population was stratified based on the order they received the slip or trip perturbations, either a block of 10 trip perturbations first (*Trip Group*) or a block of 10 slip perturbations (*Slip Group*), resulting in a crossover experimental design. The three outcome measures used to quantify postural recovery were tested among *Groups* using one-way ANOVA, comparing: (1) the novel exposure of a slip after trip training with the first (novel) slip in the slip-training group, as well as (2) the novel exposure of a trip after slip training with the first (novel) trip in the trip-training group, see Figure 10 below.

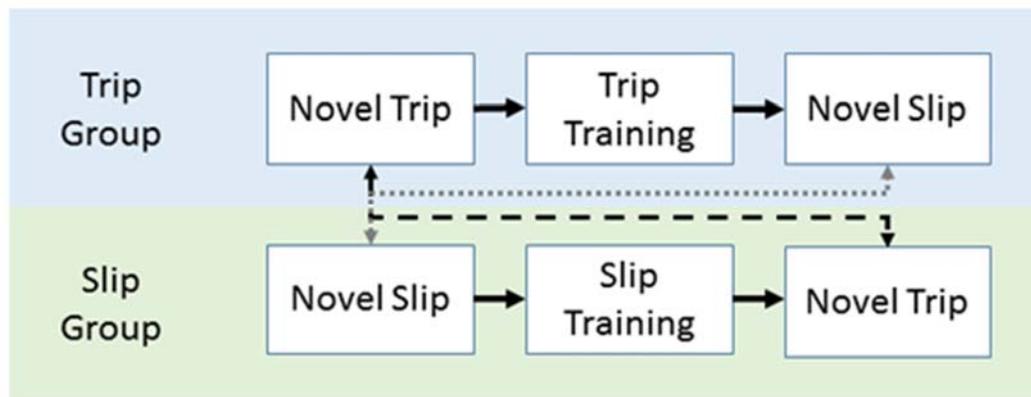


Figure 10: The participant population was randomly stratified into two groups: those who received 10 trips before slips (Trip Group) and those who received 10 slips before trips (Slip Group). The first comparison (black dashed line) tests for significant differences in recovery performance between the first trip in the Trip Group and the first trip in the Slip Group, after receiving treadmill slip training. The second comparison (grey dotted line) tests for significant differences in recovery performance between the first slip in the Slip Group and the first slip in the Trip Group, after receiving treadmill trip training.

To characterize the impact of repeated perturbations to recovery performance across the population, three linear mixed models for repeated measures were performed. The main

effects of *Perturbation* (Two levels: slip and trip), *Trial* (10 repeated perturbations) and the interaction of *Perturbation* and *Trial* were observed to identify any changes in the rate or structure of learning as participants become more familiar with each gait perturbation. A repeated LMM approach was selected over a traditional repeated measures designs to handle the situation of missing data as a result of slip or trip falls, where measurements of recovery reaction step, recovery step force and recovery time became unreliable to quantify. An autoregressive covariance structure was adopted for these analyses, which assumes the correlation among repeated measurements decrease with time, which we propose is representative of the familiarization associated with learning. Maximum likelihood modelling, as suggested by Shek et al. (2011) was adopted as an appropriate modelling strategy for measurements repeated over time.

In preparation for statistical analyses, the assumption of normality was tested primarily using the Kolmogorov-Smirnov and Shapiro-Wilk statistics at all time points for both groups, slips and trips, respectively. In cases where normality was violated (2/10), visual inspections of histogram and normal probability plots of the residuals showed mostly normal distributions, often offset by an outlier value. In these cases, normality was determined to be acceptable without transformation, as transformation for some repeated trials, and not others, would make interpretation challenging, and mixed model analyses are typically robust to this type of error (B. Winter, 2013). Bonferroni adjustments were adopted to evaluate post-hoc comparisons, when necessary.

IV. Results

This section details the results of the three experiments performed in this dissertation. A brief description of the young, healthy, experimental population is provided, followed by three sections outlining the results of Specific Aim 1, Specific Aim 2 and Specific Aim 3, respectively. Specific Aim 1 focused on the results of the manual (joystick matching) and locomotor (split-belt walking) adaptation tasks. Specific Aim 2 focused on the postural recovery to treadmill induced gait perturbations in the form of repeatable slips and trips, as well as the relationship between recovery performance and motor adaptation from Specific Aim 1. Finally, Specific Aim 3 served to assess the novel slip and trip protocol developed during the course of this dissertation, quantifying the effects of familiarization within a perturbation style (slip or trip) and recovery performance transfer between styles (slip and trip), using a crossover experimental design. All results are presented as means \pm standard deviations (unless otherwise indicated), and statistical significance is defined at $\alpha = 0.05$.

IV.I Participant Demographics

Results from 58 participants are presented in this dissertation. Of the 58 participants, 54 completed all experiments, while 4 participants completed only 1 adaptation task (2 completed split-belt adaptation while the other 2 completed the joystick matching), however all 58 participants completed the slip and trip protocol. General participant demographics are described below in Table 4, while participant demographics specific to perturbation order stratification for Specific Aim 3 are described in Table 23. All demographic data are presented as means and standard deviations ($\bar{x} \pm \sigma$).

Table 4: Participant demographic information including sex distribution, age, body mass and height.

	Male	Female	Total
N	28	30	58
Age (years)	25.9 ± 4.8	22 ± 4.3	23.9 ± 4.9
Mass (kg)	84.24 ± 14.0	61.25 ± 8.6	72.35 ± 16.3
Height (cm)	178.2 ± 7.9	162.1 ± 7.3	169.9 ± 11.1

IV.II Experiment 1

Adaptation performance was quantified during an upper extremity, manual control, joystick target matching task and a lower body, locomotor control, split-belt walking task. Adaptation coefficients were derived using curve fitting techniques, resulting in an adaptation coefficient (k) representing $(1-e^{-1})$ or approximately 63% of the total number of attempts required to reach a steady-state performance, described as a unit-less coefficient. The inverse of this coefficient ($1/k$) represents the actual number of attempts – number of target matching attempts for joystick or the number of strides while split-belt walking– required to achieve a steady state of performance. Linear regression analyses were performed to estimate the strength of the relationship among manual and locomotor adaptation performance. All results are presented as means and standard deviations ($\bar{x} \pm \sigma$).

IV.II.I Exponential Curve Fitting

An exploration of the quality of curve fitting ('goodness-of-fit', R^2) and the error associated with adaptation parameter estimates (standard error (SE) and relative standard error (%RSE)) was performed to estimate the impact of uncertainty on the interpretation of adaptation performance, and is presented in detail in Appendix C. For manual task adaptation, the mean R^2 was 0.485 ± 0.19 and the mean estimated measurement uncertainty was approximately $48.7 \pm 55.6\%$. For locomotor task adaptation, the mean R^2 was $0.589 \pm$

0.22 and the mean estimated measurement was approximately $13.7 \pm 10.5\%$. Overall, the curve fit quality among manual and locomotor tasks were deemed sufficient, based on other reported R^2 values in the literature, however the %RSE of the manual task was of concern.

To assess the impact of this uncertainty upon the linear regression results of Experiment 1, the adaptation estimates (I/k) with greatest uncertainty were removed and the impact of this removal was assessed by comparing the regression model parameters (intercept and slope) among three levels of increasing estimate confidence. The results of these comparisons are detailed in Appendix C and showed no significant differences among regression model intercept estimates ($F_{2,137} = 0.011, p = 0.990$) or slopes ($F_{2,135} = 0.025, p = 0.976$), suggesting the equality of intercepts and equality of slopes null hypotheses, both, could not be rejected. These findings supported the analyses of all exponential curve fitting adaptation estimates for manual and locomotor tasks, therefore no data were excluded.

Although no data were excluded, an attempt to better incorporate this measurement uncertainty was performed by assessing the stability of correlation results when data is exposed to perturbations, based on the average %RSE for the adaptation measure input into regression, see Table 3.

IV.II.II Manual Rotated-input Joystick Matching

Descriptive statistics are summarized below in Table 5. On average, participants required 20 ± 1.2 ($k = 0.059 \pm 0.003$) manual joystick matching attempts to adapt to the 45° rotated input.

Table 5: Average adaptation performance among participants during manual adaptation task

Manual	
Coeff (k)	0.059±0.003
Attempts ($1/k$)	20.0±1.2
Ln(k)	-2.91±0.06
Ln($1/k$)	2.91±0.06

IV.II.III Locomotor Split-belt Adaptation

Descriptive statistics are summarized below in Table 6. On average, participants required 88.8±5.5 ($k = 0.0144±0.0011$) strides to adapt to a 3:1 ratio split-belt treadmill walking challenge.

Table 6: Average adaptation performance among participants during locomotor adaptation task

Locomotor	
Coeff (k)	0.0144±0.0011
Strides ($1/k$)	88.8±5.5
Ln(k)	-4.37±0.07
Ln($1/k$)	4.37±0.06

IV.II.IV Relationship between Manual and Locomotor Adaptation

A set of linear regression analyses were conducted to estimate a linear relationship which predicts adaptation performance during a rotated-input joystick matching task based on an individual's adaptation performance during a challenging split-belt treadmill walking task. Two equations were generated, relating adaptation coefficients (k) and the number of attempts required to adapt ($1/k$) between manual and locomotor tasks. Prior to conducting the analysis, descriptive statistics and graphs were generated to examine the requisite test assumptions. It was determined that, due to issues of data skew, natural logarithm transformations would be used to achieve the linear regression assumptions of normality, see Figure 11. Results for the natural log transformed linear regression are presented.

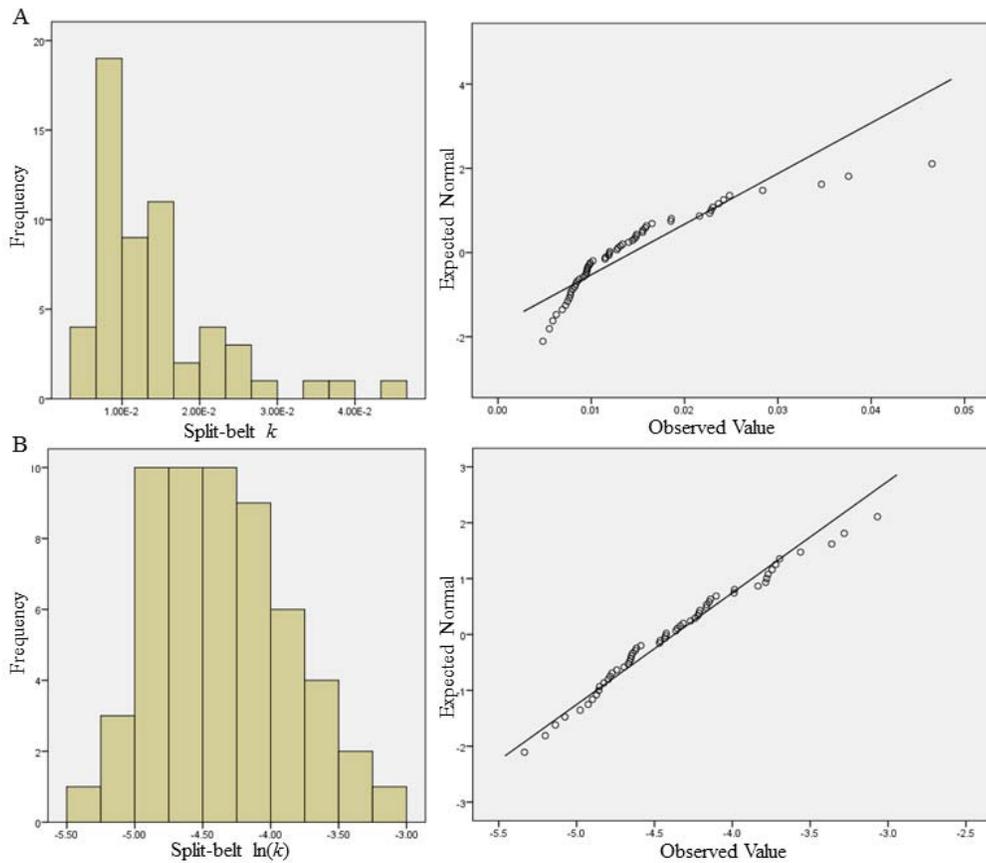


Figure 11: Histogram and normal Q-Q plots for split-belt adaptation coefficients (k). A) The histogram and Q-Q plot for the raw coefficient (k) values show very high positive skew and a clearly non-normal distribution. B) Natural logarithm transformation of the skewed data greatly improves the histogram and Q-Q normality plots for split-belt data.

Relationship between Natural Logarithm Transformed Adaptation Coefficient for Manual and Locomotor Tasks

A Pearson's correlation coefficient and scatterplot, see Figure 12, show a significant linear relationship ($r = 0.799$, $p < 0.01$) between adaptation coefficients from a manual joystick matching task and a locomotor split-belt walking task.

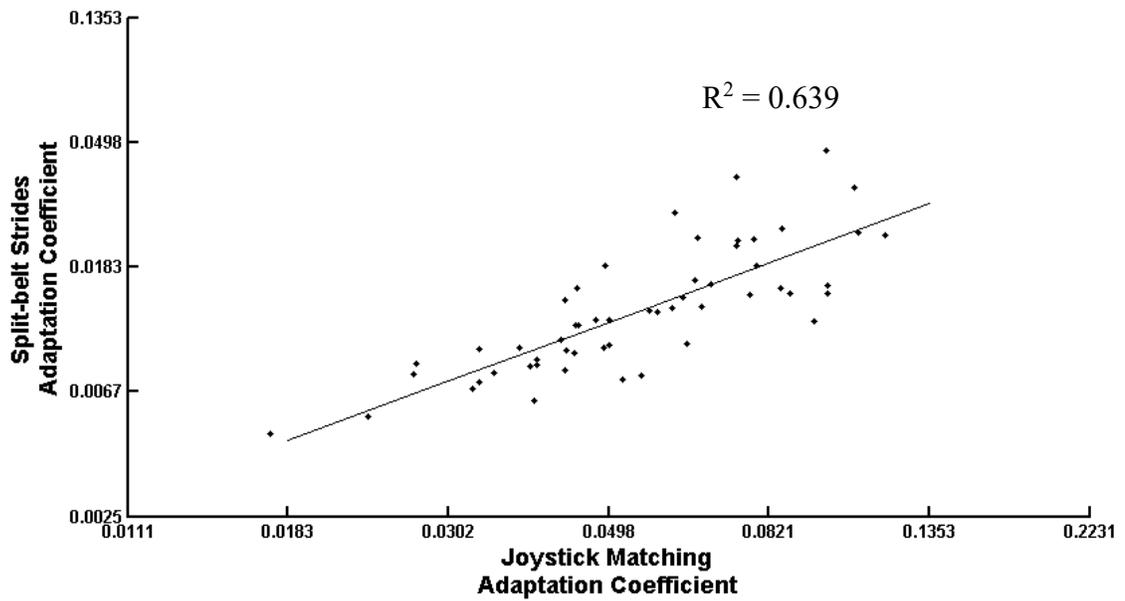


Figure 12: Scatter plot of the natural logarithm transformed manual task adaptation coefficient versus locomotor task adaptation. A linear trend is observed with a significant Pearson's r correlation of 0.799. Axes are presented in the exponential (untransformed) representation of the data to aid interpretation of coefficient values.

Inspections of both the histogram and normal probability plots of the residuals indicate that errors were normally distributed. A scatterplot of the predicted and residual scores showed no trend about the centerline, satisfying the assumption of homoscedasticity, see Figure 13.

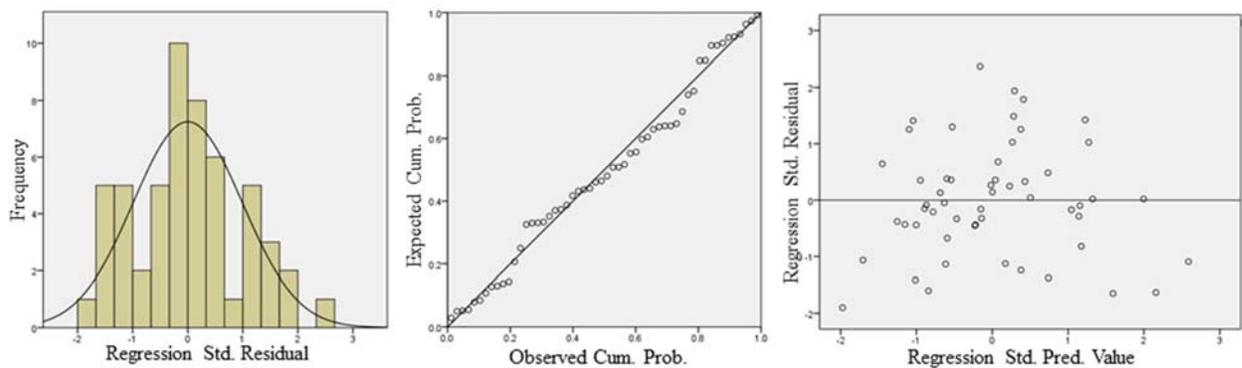


Figure 13: Histogram, P-P plot and scatterplot of the residuals for the simple linear regression estimating the impact of joystick adaptation coefficient upon split-belt adaptation coefficients. All plots are observed to withhold the assumptions of normality for simple linear regression.

The results of the linear regression analysis are presented below, see Table 7. These findings suggest a significant correlation between manual and locomotor adaptation performance ($F_{1,52} = 91.8, p < 0.01$). With a beta of 0.80 ($t_{52} = 9.59, p < 0.01$), joystick adaptation performance accounted for approximately 64% of the variance in split-belt adaptation, suggesting that those who are effective at adapting to challenging manual tasks may perform similarly during locomotor challenges.

Table 7: Results of linear regression analysis for manual and locomotor adaptation coefficients, after correcting for normality via natural logarithmic transformation. * denotes significance at $p < 0.05$.

Factor	R	R^{2a}	β	F	p
Joystick _{ln} (<i>k</i>)	0.799	0.639	0.799	91.87	0.000*

^aAdjusted R² = 0.632

Relationship between Natural Logarithm Transformed ‘Number of Attempts to Adapt’ for Manual and Locomotor Tasks

The inverse transformation from adaptation coefficient (*k*) to a representation of the number of actual attempts (or strides) results in no significant differences from the previous regression analyses. A Pearson’s correlation coefficient and scatterplot, see Figure 14, show a significant linear relationship ($r = 0.799, p < 0.01$) between the number of attempts required to achieve adaptation during a novel manual joystick matching task and a locomotor split-belt walking task. Assessments of normality mirror those previously observed above, see Figure 13.

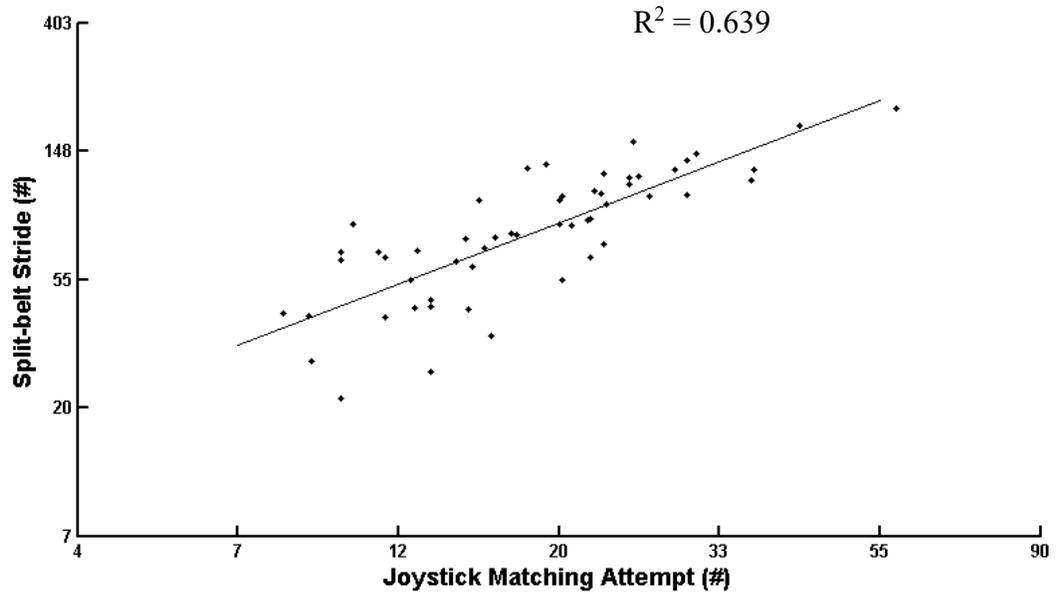


Figure 14: Scatter plot of the natural logarithm transformed inverse of k (i.e. $1/k$), representing the real number of attempts (or strides) required to achieve adaptation during a joystick matching or split-belt walking task, respectively. A linear trend is observed with a significant Pearson's r correlation of 0.799. Axes are presented in the exponential (untransformed) representation of the transformed data to aid interpretation of adaptation performance.

The results of the linear regression analysis are presented below, see Table 8. These findings suggest a significant correlation between manual and locomotor adaptation performance ($F_{1,52} = 91.8, p < 0.01$). With a beta of 0.80 ($t_{52} = 9.59, p < 0.01$), joystick adaptation performance accounted for approximately 64% of the variance in split-belt adaptation, suggesting that those who require less attempts to adapt to a novel manual task will also require fewer steps, and may adapt rapidly to a locomotor challenge.

Table 8: Results of linear regression analysis for manual and locomotor adaptation performance represented as the number of attempts (or strides) required to achieve adaptation, after correcting for normality via natural logarithmic transformation. * denotes significance at $p < 0.05$.

Factor	R	R^{2a}	β	F	p
Joystick Attempts $_{\ln(1/k)}$	0.799	0.639	0.799	91.87	0.000*

^aAdjusted $R^2 = 0.632$

Incorporating the estimated 49%RSE for the joystick matching, manual adaptation task, see Figure 15 shows that in the case of Perturbation 1, the strength of the relationship among joystick adaptation and split-belt adaptation decreases ($r = 0.771$), but is still considered significant ($p = 0.00$). Perturbation 2, however, shows the loss of a significant relationship among split-belt and joystick matching adaptation ($r = 0.261$, $p = 0.057$), suggesting that in the worst case scenario, it is possible that average measurement uncertainty may be a driving factor in the interpretation of this relationship.

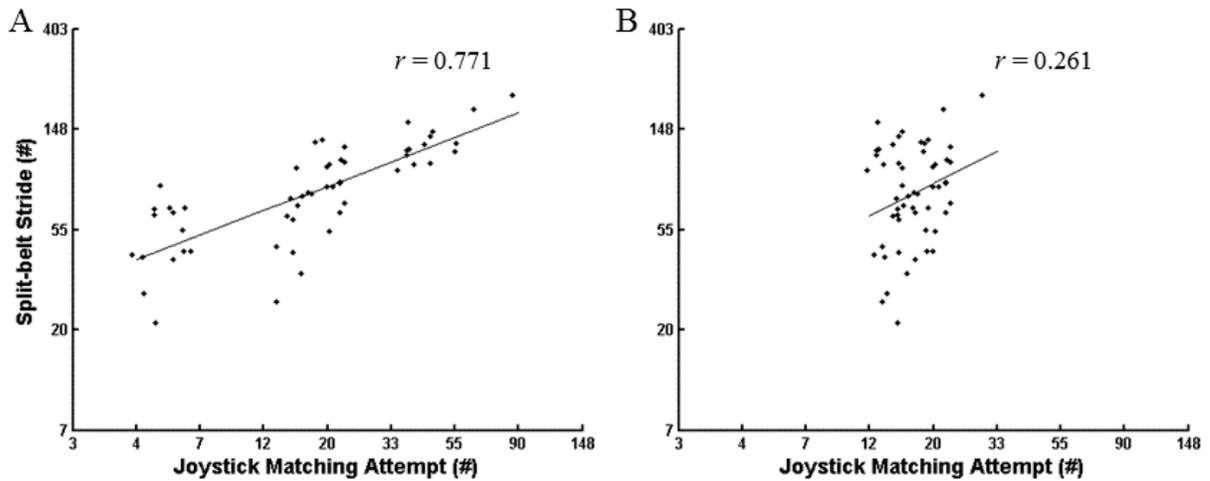


Figure 15: Scatter plot of the relationship among locomotor adaptation and manual adaptation performance, as perturbed by the 49%RSE measurement uncertainty of the manual task. A) Shows the results of Perturbation 1, where the 1st and 4th quartiles are stretched along the horizontal axis while B) shows the results of Perturbation 2, where the 1st and 4th quartiles are compressed along the horizontal axis.

IV.III Experiment 2

Postural recovery performance was measured using whole body motion capture and ground reaction forces via force plates in response to treadmill induced slips and trips. Outcome variables included: recovery step reaction time (RT), a measure of an individual's ability to rapidly produce a recovery step; recovery step reaction force (maxRSF), a measure of an individual's posture-correcting force production; and perturbation recovery time (TTR),

a measure of the time required to achieve normal walking after recovering from a gait perturbation. Population means and a performance summary describing the first and final perturbations is presented in Table 9, below.

Table 9: Measures of trip and slip performance on the first (novel) and final perturbations.

	Recovery Step Reaction Time (msec)	Recovery Step Reaction Force (N/kg)	Recovery Time (msec)
Trip Perturbations			
Trial 1 (novel)	625.5 ± 91.4	1.507 ± 0.177	2748.4 ± 570
Trial 10	642.0 ± 98.7	1.255 ± 0.110	2377.3 ± 578
Slip Perturbations			
Trial 1 (novel)	348.1 ± 43.6	1.485 ± 0.232	2969.8 ± 662
Trial 10	364.3 ± 61.2	1.407 ± 0.214	2514.7 ± 799

Calculations of Pearson’s correlation among adaptation performance and postural recovery performance during Trials 1 and 10 for slips and trips are described in Table 10. No significant correlations ($r > 0.3$) were observed among manual or locomotor adaptation measures and postural recovery during a novel (1st) exposure to a slip or trip perturbation. These findings suggest there is no relationship between adaptation performance during a continuous motor task and a novel exposure to a discrete, whole-body gait perturbation. Observing the final slip recovery attempts, however, yielded a significant linear relationship between split-belt adaptation coefficients and slip recovery time ($r = -0.338, p < 0.05$), which was mirrored in split-belt adaptation performance (l/k). No relationships were observed among final trip recovery and adaptation performance.

Table 10: Pearson’s r correlation calculations between adaptation performance measures and measures of recovery step reaction time (RT), maximum recovery step force (maxRSF) and recovery time (TTR) during the 1st (novel) and 10th (final) attempt to recovery from a slip or trip perturbation. Significant linear relationships are denoted with *.

	Trip RT	Slip RT	Trip maxRSF	Slip maxRSF	Trip TTR	Slip TTR
Perturbation 1 (Novel)						
Joystick Adaptation Coeff.(k)	$r = 0.067$ $p = 0.625$	$r = -0.206$ $p = 0.132$	$r = 0.074$ $p = 0.586$	$r = 0.120$ $p = 0.383$	$r = 0.283$ $p = 0.036^*$	$r = -0.167$ $p = 0.247$
Split-belt Adaptation Coeff(k)	$r = 0.133$ $p = 0.330$	$r = -0.137$ $p = 0.320$	$r = 0.247$ $p = 0.067$	$r = 0.065$ $p = 0.639$	$r = 0.196$ $p = 0.151$	$r = -0.069$ $p = 0.640$
Joystick Attempts (1/k)	$r = -0.067$ $p = 0.625$	$r = 0.206$ $p = 0.132$	$r = -0.074$ $p = 0.586$	$r = -0.120$ $p = 0.383$	$r = -0.283$ $p = 0.036^*$	$r = 0.167$ $p = 0.247$
Split-belt Strides (1/k)	$r = -0.133$ $p = 0.330$	$r = 0.137$ $p = 0.320$	$r = -0.247$ $p = 0.067$	$r = -0.065$ $p = 0.639$	$r = -0.196$ $p = 0.151$	$r = 0.069$ $p = 0.640$
Perturbation 10 (Final)						
Joystick Adaptation Coeff.(k)	$r = 0.081$ $p = 0.558$	$r = -0.108$ $p = 0.438$	$r = -0.027$ $p = 0.843$	$r = -0.099$ $p = 0.475$	$r = -0.043$ $p = 0.753$	$r = -0.068$ $p = 0.628$
Split-belt Adaptation Coeff.(k)	$r = 0.081$ $p = 0.555$	$r = -0.041$ $p = 0.770$	$r = -0.001$ $p = 0.993$	$r = -0.209$ $p = 0.129$	$r = -0.284$ $p = 0.035^*$	$r = -0.338$ $p = 0.013^*$
Joystick Attempts (1/k)	$r = -0.081$ $p = 0.558$	$r = 0.108$ $p = 0.438$	$r = 0.027$ $p = 0.843$	$r = 0.099$ $p = 0.475$	$r = 0.043$ $p = 0.753$	$r = 0.068$ $p = 0.628$
Split-belt Strides (1/k)	$r = -0.081$ $p = 0.555$	$r = 0.041$ $p = 0.770$	$r = 0.001$ $p = 0.993$	$r = 0.209$ $p = 0.129$	$r = 0.284$ $p = 0.035^*$	$r = 0.338$ $p = 0.013^*$

To capture the change in performance associated with strategic learning after multiple perturbation exposures, the difference between the first and last perturbations, represented as percentage change (% change), was calculated for each postural recovery measure. A negative percent change describes improved performance between initial and final perturbations. Population means and a performance summary is described in Table 11, below.

Table 11: Measures of trip and slip performance, represented as percent change from the first perturbation to the last perturbation. Negative percent change is interpreted as an improvement in performance, where reaction time, force production or recovery time are decreased after repeated exposure, or training, to either gait perturbation.

	Total		Male		Female	
	Trip % Change	Slip % Change	Trip % Change	Slip % Change	Trip % Change	Slip % Change
Step Reaction Time	3.3 ± 2.1	5.2 ± 2.7	4.0 ± 3.1	6.8 ± 4.2	2.7 ± 2.8	3.6 ± 3.4
Reaction Force	-16.1 ± 1.4	-3.1 ± 2.4	-14.0 ± 2.2	-0.9 ± 4.3	-18.0 ± 1.8	-5.1 ± 2.4
Recovery Time	-11.7 ± 2.6	-13.8 ± 3.8	-11.8 ± 3.8	-11.5 ± 5.1	-11.6 ± 3.5	-15.6 ± 5.4

Overall, reaction force and recovery time improved across participants, evidenced by a negative percent change. Recovery step reaction time was minimally different between the first and last perturbations, and on average increased. Calculations of Pearson’s correlation between adaptation performance and changes to postural recovery performance after repeated exposures are described in Table 12, below. Significant and meaningful ($r > 0.3$) linear relationships were identified between split-belt adaptation coefficients and trip recovery time ($r = -0.43, p < 0.05$) as well as slip recovery time ($r = -0.31, p < 0.05$). These were also mirrored between split-belt adaptation performance ($1/k$) and recovery time in trips ($r = 0.43, p < 0.05$), and slips ($r = 0.31, p < 0.05$), respectively.

Table 12: Pearson's r correlation calculations between adaptation performance measures and measures of the change in recovery step reaction time (RT), maximum recovery step force (maxRSF) and recovery time (TTR) after repeated exposure to slip and trip perturbations. Significant linear relationships are denoted with *.

	Trip RT %Change	Slip RT %Change	Trip maxRSF %Change	Slip maxRSF %Change	Trip TTR %Change	Slip TTR %Change
Joystick Adaptation Coeff.(<i>k</i>)	<i>r</i> = -0.029 <i>p</i> = 0.835	<i>r</i> = 0.019 <i>p</i> = 0.893	<i>r</i> = -0.100 <i>p</i> = 0.466	<i>r</i> = -0.217 <i>p</i> = 0.119	<i>r</i> = -0.293 <i>p</i> = 0.032*	<i>r</i> = -0.053 <i>p</i> = 0.718
Split-belt Adaptation Coeff(<i>k</i>)	<i>r</i> = -0.121 <i>p</i> = 0.379	<i>r</i> = 0.051 <i>p</i> = 0.716	<i>r</i> = -0.201 <i>p</i> = 0.140	<i>r</i> = -0.269 <i>p</i> = 0.051	<i>r</i> = -0.427 <i>p</i> = 0.001*	<i>r</i> = -0.312 <i>p</i> = 0.033*
Joystick Attempts (1/ <i>k</i>)	<i>r</i> = 0.029 <i>p</i> = 0.835	<i>r</i> = -0.019 <i>p</i> = 0.893	<i>r</i> = 0.100 <i>p</i> = 0.466	<i>r</i> = 0.217 <i>p</i> = 0.119	<i>r</i> = 0.293 <i>p</i> = 0.032*	<i>r</i> = 0.053 <i>p</i> = 0.718
Split-belt Strides (1/ <i>k</i>)	<i>r</i> = 0.121 <i>p</i> = 0.379	<i>r</i> = -0.051 <i>p</i> = 0.716	<i>r</i> = 0.201 <i>p</i> = 0.140	<i>r</i> = 0.269 <i>p</i> = 0.051	<i>r</i> = 0.427 <i>p</i> = 0.001*	<i>r</i> = 0.312 <i>p</i> = 0.033*

As a result of multicollinearity between the two measures of adaptation, a pair of statistically standardized estimates of composite adaptation coefficient (zk) and adaptation performance ($z(1/k)$) were calculated (Ackerman & Cianciolo, 2000). Calculations of Pearson's correlation coefficient showed no significant correlations between the composite adaptation coefficients and postural recovery during the novel (1st) or final (10th) slip or trip perturbations, see Table 13.

Table 13: Pearson's r correlation calculations among standardized adaptation performance measures and measures of recovery step reaction time (RT), maximum recovery step force (maxRSF) and recovery time (TTR) during the 1st (novel) and 10th (final) attempt to recovery from a slip or trip perturbation. Significant linear relationships are denoted with *.

	Trip RT	Slip RT	Trip maxRSF	Slip maxRSF	Trip TTR	Slip TTR
Perturbation 1 (Novel)						
Adaptation	$r = 0.054$	$r = -0.181$	$r = 0.168$	$r = 0.095$	$r = 0.243$	$r = -0.122$
Coeff.($z(k)$)	$p = 0.697$	$p = 0.194$	$p = 0.223$	$p = 0.501$	$p = 0.079$	$p = 0.409$
Adaptation	$r = -0.054$	$r = 0.181$	$r = -0.168$	$r = -0.095$	$r = -0.243$	$r = 0.122$
Performance ($z(l/k)$)	$p = 0.697$	$p = 0.194$	$p = 0.223$	$p = 0.501$	$p = 0.079$	$p = 0.409$
Perturbation 10 (Final)						
Adaptation	$r = 0.060$	$r = -0.096$	$r = -0.017$	$r = -0.179$	$r = -0.190$	$r = -0.200$
Coeff.($z(k)$)	$p = 0.670$	$p = 0.496$	$p = 0.906$	$p = 0.205$	$p = 0.173$	$p = 0.160$
Adaptation	$r = -0.060$	$r = 0.096$	$r = 0.017$	$r = 0.179$	$r = 0.190$	$r = 0.200$
Performance ($z(l/k)$)	$p = 0.670$	$p = 0.496$	$p = 0.906$	$p = 0.205$	$p = 0.173$	$p = 0.160$

Observing the percent change in postural recovery performance between first and final perturbations yield significant linear correlations between composite adaptation coefficients and trip recovery time improvements after repeated perturbations ($r = -0.39, p < 0.05$), see Table 14 below. These results are mirrored for the composite measure of adaptation performance ($z(l/k)$).

Table 14: Pearson's r correlation calculations between composite adaptation performance measures and measures of the improvement in recovery step reaction time (RT), maximum recovery step force (maxRSF) and recovery time (TTR) after repeated exposure to slip and trip perturbations. Significant linear relationships are denoted with *.

	Trip RT %Change	Slip RT %Change	Trip maxRSF %Change	Slip maxRSF %Change	Trip TTR %Change	Slip TTR %Change
Adaptation Coeff. (zk)	$r = -0.028$	$r = 0.022$	$r = -0.159$	$r = -0.269$	$r = -0.378$	$r = -0.194$
	$p = 0.840$	$p = 0.880$	$p = 0.255$	$p = 0.057$	$p = 0.006^*$	$p = 0.191$
Adaptation Performance ($z(l/k)$)	$r = 0.028$	$r = -0.022$	$r = 0.159$	$r = 0.269$	$r = 0.378$	$r = 0.194$
	$p = 0.840$	$p = 0.880$	$p = 0.255$	$p = 0.057$	$p = 0.006^*$	$p = 0.191$

Relationship between Slip Recovery Time (TTR) and Natural Logarithm Transformed Adaptation Coefficients for Manual and Locomotor Tasks

The results of a linear regression analysis, summarized in Table 15 below, identified locomotor adaptation coefficients as significant predictors of slip recovery time (TTR), after a training bout of 10 slip perturbations ($F_{1,51}=6.57, p < 0.05$). With a beta coefficient of -0.338 ($t = -2.27, p < 0.05$) individual locomotor adaptation performance was identified to account for 11.4% of the total variance in slip recovery time after repeated perturbations. A scatter plot of these results, see Figure 16, suggest a limited relationship between locomotor adaptation and slip recovery, wherein those adept at locomotor adaptation will show improved performance after slip training i.e. decreased time to recover.

Table 15: Results of linear regression analysis for the prediction of slip recovery while controlling for locomotor adaptation coefficient, after correcting for normality via natural logarithmic transformation. * denotes significance at $p < 0.05$.

Factor	<i>R</i>	<i>R</i>^{2a}	β	<i>F</i>	<i>p</i>
Split-belt Coeff. $\ln(k)$	0.338	0.114	-0.338	6.57	0.013*

^aAdjusted $R^2 = 0.097$

These results are mirrored in linear regression predicting slip recovery time by locomotor adaptation performance ($1/k$), as summarized in Table 16, below. No significant influence of manual adaptation was observed upon postural recovery improvements after repeated slip training.

Table 16: Results of linear regression analysis for the prediction of slip recovery time while controlling for locomotor adaptation performance. Adaptation performance is represented as the number of attempts (target matches or strides) to achieve adaptation after correcting for normality via natural logarithmic transformation. * denotes significance at $p < 0.05$.

Factor	R	R^{2a}	β	F	p
Split-belt Strides $\ln(1/k)$	0.338	0.114	0.338	6.57	0.013*

^aAdjusted $R^2 = 0.097$

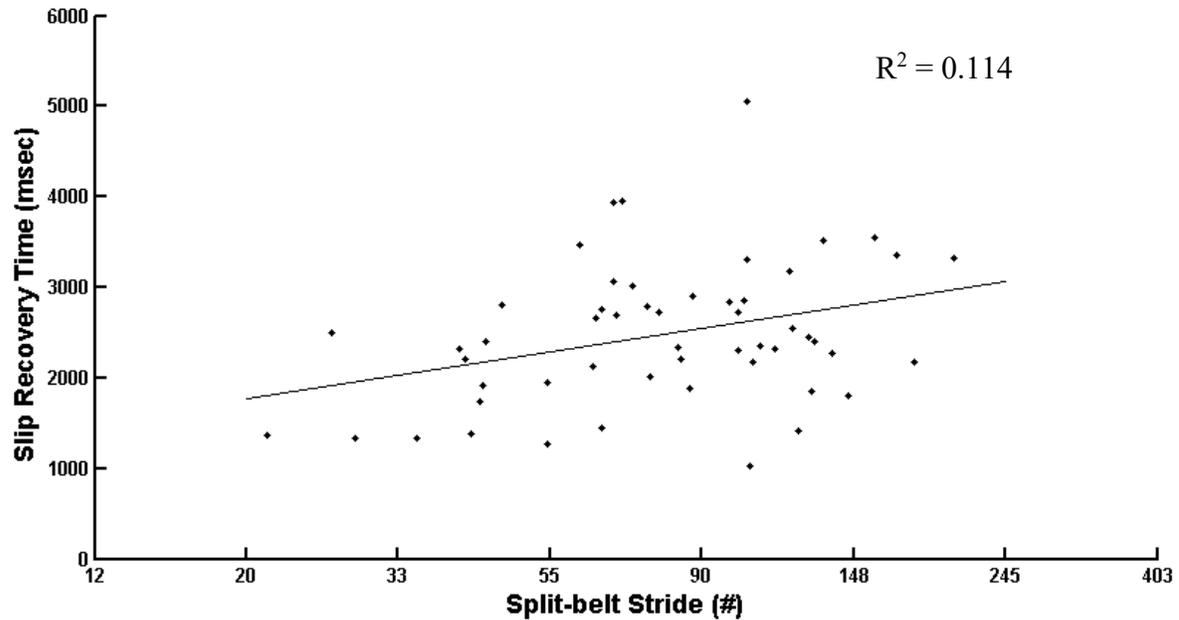


Figure 16: Scatter plot of the natural logarithm transformed locomotor task adaptation performance ($1/k$) versus time to recovery (TTR) on the final (10th) slip perturbation. A weak linear trend is observed with a significant Pearson's r correlation of 0.338. The horizontal axes is presented in the exponential (untransformed) representation of the data to aid interpretation of coefficient values.

Incorporating the estimated 16%RSE for the split-belt, locomotor adaptation task, see Figure 17, shows that in the case of Perturbation 1, the strength of the relationship among slip recovery time after bout of slip training and split-belt adaptation performance increases slightly ($r = 0.345$), and is still considered significant ($p = 0.011$). The relationship resulting from Perturbation 2 also maintains a significant linear correlation ($r = 0.335$, $p = 0.014$), suggesting that estimate uncertainty resulting from noise in the split-belt walking task did not influence the stability of the reported results.

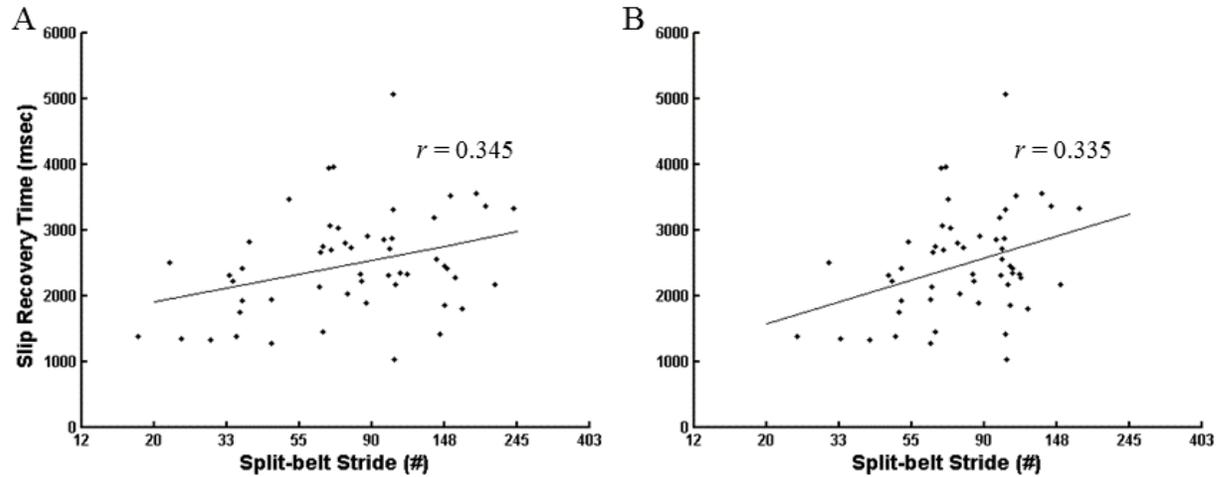


Figure 17: Scatter plot of the relationship among locomotor adaptation and slip recovery time (TTR) after training, as perturbed by the 16%RSE measurement uncertainty of the locomotor task. A) Shows the results of Perturbation 1, where the 1st and 4th quartiles are stretched along the horizontal axis while B) shows the results of Perturbation 2, where the 1st and 4th quartiles are compressed along the horizontal axis.

Relationship between Trip Recovery Time (TTR) % Change and Natural Logarithm

Transformed Adaptation Coefficients for Manual and Locomotor Tasks

The results of a linear regression analysis, summarized in Table 17 below, revealed a significant correlation between locomotor adaptation coefficients and changes in trip recovery time performance after training ($F_{1,52} = 5.79, p < 0.05$). With a beta value of -0.43 ($t = -3.40, p < 0.05$), the coefficient of split-belt adaptation was identified to account for approximately 18% of the variance in treadmill induced trip perturbation percent change after repeated perturbations. A scatter plot of these results, see Figure 18, indicate that those more adept at locomotor adaptation (greater adaptation coefficient) will, on average, show a greater change in recovery performance after repeated treadmill trip perturbations.

Table 17: Results of linear regression analysis for the prediction of trip recovery time % change while controlling for locomotor adaptation coefficient, after correcting for normality via natural logarithmic transformation. * denotes significance at $p < 0.05$.

Factor	R	R^{2a}	β	F	p
Split-belt Coeff. $\ln(k)$	0.427	0.182	-0.427	11.57	0.001*

^aAdjusted $R^2 = 0.166$

These results were mirrored in the transformation of adaptation coefficients to adaptation performance ($1/k$), as in Experiment 1, representing the number of repeated perturbations required to achieve plastic adaptation, see Table 18. No meaningful significant correlations ($r > 0.3$) were observed between manual adaptation and changes in postural recovery performance after repeated trip perturbations.

Table 18: Results of linear regression analysis for the prediction of trip recovery time % change while controlling for locomotor adaptation performance. Adaptation performance is represented as the number of attempts (target matches or strides) to achieve adaptation after correcting for normality via natural logarithmic transformation. * denotes significance at $p < 0.05$.

Factor	R	R^{2a}	β	F	p
Split-belt Strides $\ln(1/k)$	0.427	0.182	0.427	11.57	0.001*

^aAdjusted $R^2 = 0.166$

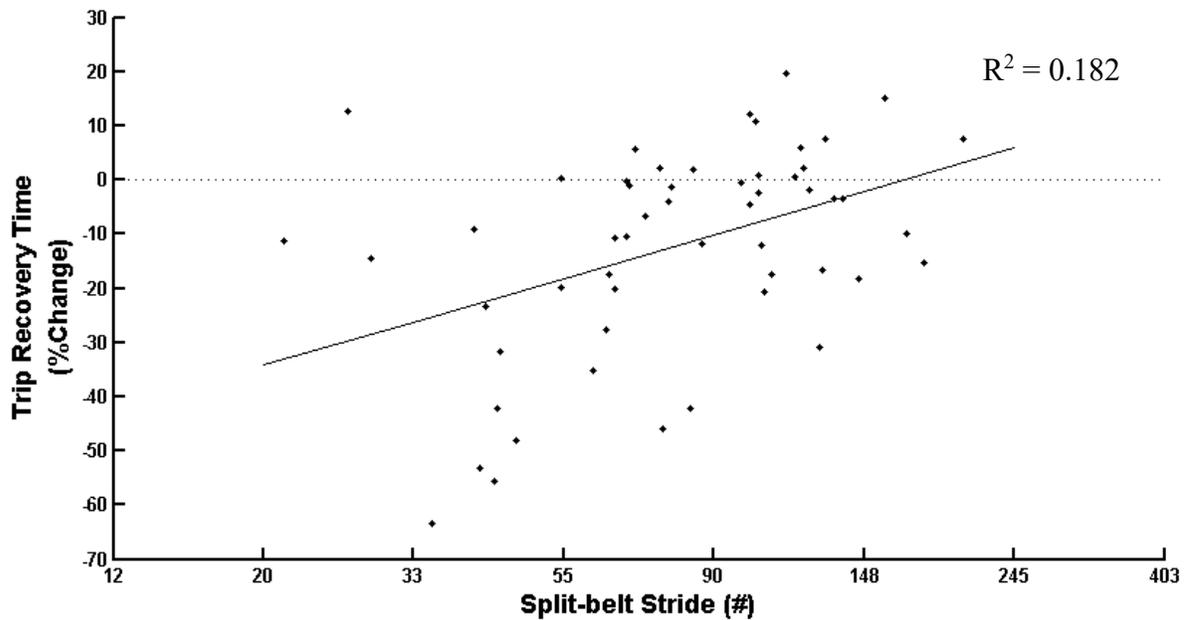


Figure 18: Scatter plot of the natural logarithm transformed locomotor task adaptation performance (l/k) versus percentage change in the time to recovery (TTR) for trips, between the first and final (10th) trip perturbation. The dashed line at 0% differentiates among participants who improved TTR (-ve % change) and those who took longer to recover from a trip after 10 perturbations (+ve % change). A moderate linear trend is observed with a significant Pearson's r correlation of 0.427. The horizontal axes is presented in the exponential (untransformed) representation of the data to aid interpretation of coefficient values.

Incorporating the estimated 16%RSE for the split-belt, locomotor adaptation task, see Figure 19, shows that in the case of Perturbation 1, the strength of the relationship among trip recovery time improvement (% change) and split-belt adaptation performance decreases slightly ($r = 0.406$), and is still considered significant ($p = 0.002$). The relationship resulting from Perturbation 2 results in an improved significant linear correlation ($r = 0.440$, $p = 0.001$), suggesting that estimate uncertainty resulting from noise in the split-belt walking task did not influence the stability of the reported results.

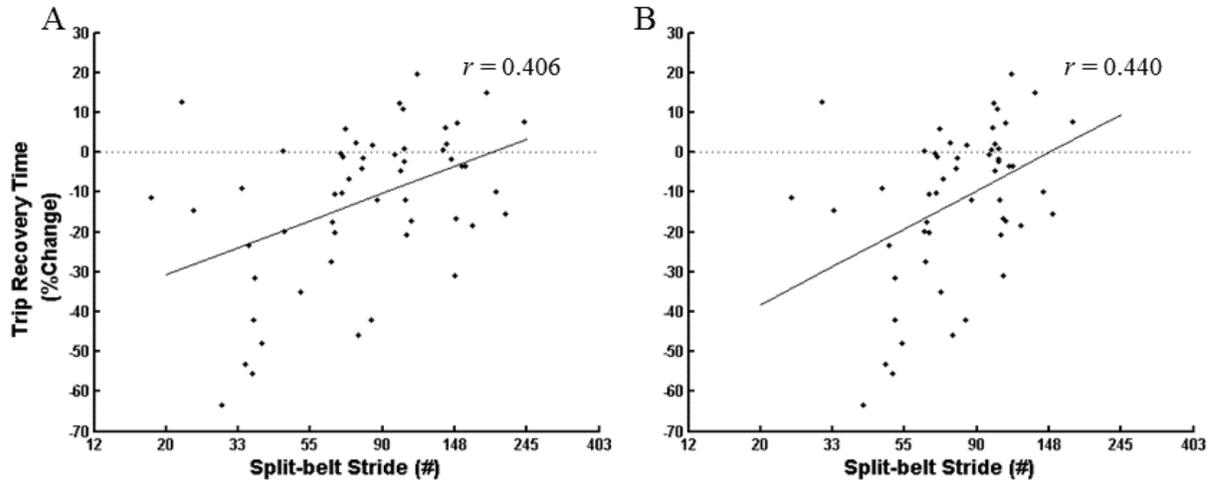


Figure 19: Scatter plot of the relationship among locomotor adaptation and trip recovery time (TTR) represented as percent change, as perturbed by the 16%RSE measurement uncertainty of the locomotor task. A) Shows the results of Perturbation 1, where the 1st and 4th quartiles are stretched along the horizontal axis while B) shows the results of Perturbation 2, where the 1st and 4th quartiles are compressed along the horizontal axis.

Relationship between Slip Recovery Time (TTR) % Change and Natural Logarithm

Transformed Adaptation Coefficients for Manual and Locomotor Tasks

The results of a linear regression analysis, summarized in Table 19 below, identified locomotor adaptation coefficients as significant predictors of changes in slip recovery performance after training ($F_{1,45}=4.84$, $p < 0.05$). With a beta coefficient of -0.31 ($t = -2.20$, $p < 0.05$) individual locomotor adaptation performance was identified to account for only 9.7% of the total variance in slip recovery time percent change after repeated perturbations. A scatter plot of these results, see Figure 20, suggest a weak relationship between locomotor adaptation and slip recovery, wherein those adept at locomotor adaptation may show increased improvement in slip recovery time with training.

Table 19: Results of linear regression analysis for the prediction of slip recovery time % change while controlling for locomotor adaptation coefficient, after correcting for normality via natural logarithmic transformation. * denotes significance at $p < 0.05$.

Factor	R	R^{2a}	β	F	p
Split-belt Coeff. $\ln(k)$	0.312	0.097	-0.312	4.84	0.033*

^aAdjusted $R^2 = 0.077$

These results are mirrored in linear regression predicting slip recovery time change by locomotor adaptation performance ($1/k$), as summarized in Table 20, below. Although the explained variance is low, the results imply that those who perform more effectively during adaptation to a novel locomotor task will exhibit greater postural recovery performance changes after treadmill slip training. No significant influence of manual adaptation was observed upon changes to postural recovery performance after repeated slip training.

Table 20: Results of linear regression analysis for the prediction of slip recovery time % change while controlling for locomotor adaptation performance. Adaptation performance is represented as the number of attempts (target matches or strides) to achieve adaptation after correcting for normality via natural logarithmic transformation. * denotes significance at $p < 0.05$.

Factor	R	R^{2a}	β	F	p
Split-belt Strides $\ln(1/k)$	0.312	0.097	0.312	4.84	0.033*

^aAdjusted $R^2 = 0.077$

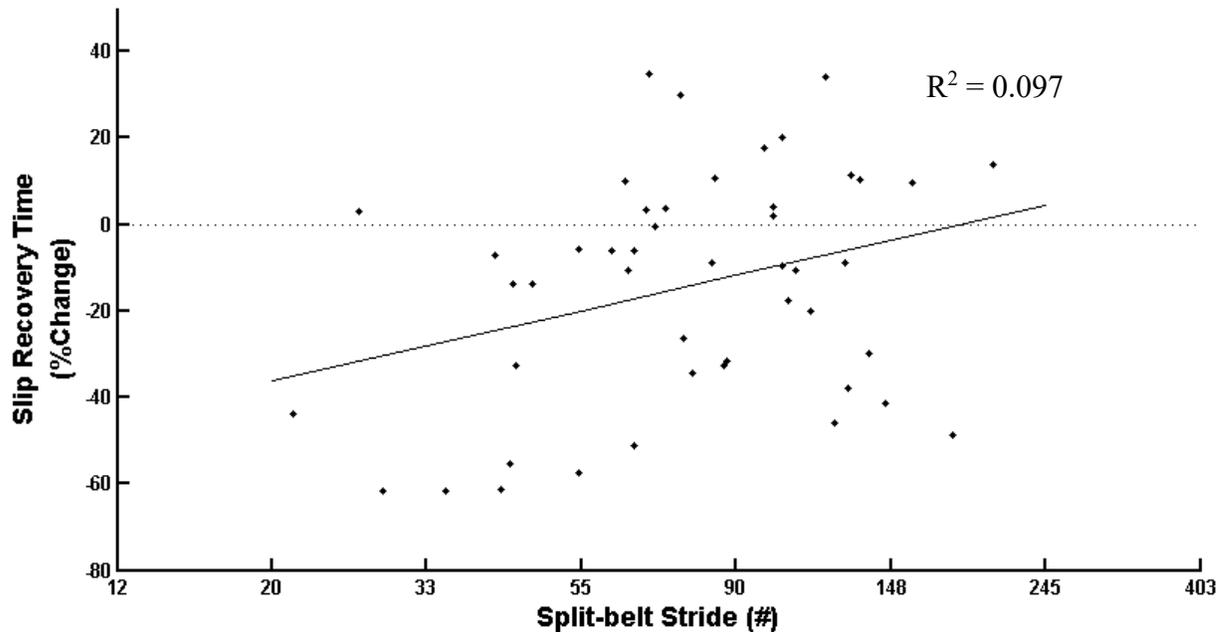


Figure 20: Scatter plot of the natural logarithm transformed locomotor task adaptation performance (I/k) versus percentage change in the time to recovery (TTR) for slips, between the first and final (10th) slip perturbation. The dashed line at 0% differentiates among participants who improved TTR (-ve % change) and those who took longer to recover from a slip after 10 perturbations (+ve % change). A weak linear trend is observed with a significant Pearson's r correlation of 0.312. The horizontal axes is presented in the exponential (untransformed) representation of the data to aid interpretation of coefficient values.

Incorporating the estimated 16%RSE for the split-belt, locomotor adaptation task, see Figure 21, shows that in the case of Perturbation 1, the strength of the relationship among slip recovery time improvement (% change) and split-belt adaptation performance remains mostly constant ($r = 0.311$), and is still considered significant ($p = 0.033$). The relationship resulting from Perturbation 2 also maintains a similar significant linear correlation ($r = 0.315$, $p = 0.031$), suggesting that estimate uncertainty resulting from noise in the split-belt walking task did not influence the stability of the reported results.

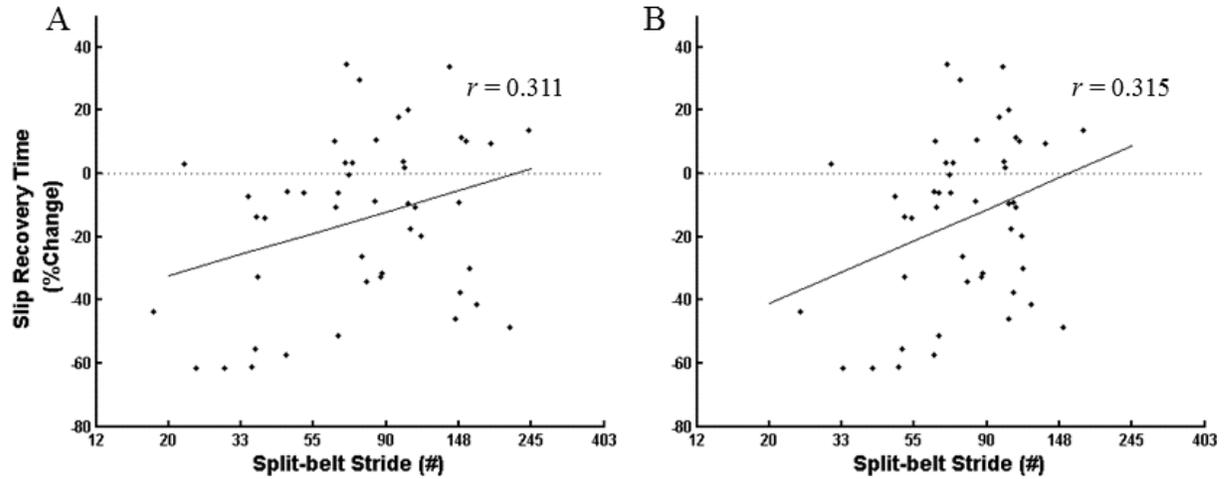


Figure 21: Scatter plot of the relationship among locomotor adaptation and slip recovery time (TTR) represented as percent change, as perturbed by the 16%RSE measurement uncertainty of the locomotor task. A) Shows the results of Perturbation 1, where the 1st and 4th quartiles are stretched along the horizontal axis while B) shows the results of Perturbation 2, where the 1st and 4th quartiles are compressed along the horizontal axis.

Relationship between Trip Recovery Time (TTR) % Change and Standardized Adaptation Coefficients

The results of a linear regression analysis, summarized in Table 21 below, identified the standardized adaptation coefficient, a combined score of manual and locomotor adaptation coefficients, as a predictor of changes in trip recovery time after repeated exposure to treadmill trip perturbations ($F_{1,50}=8.31, p < 0.05$). With a beta of -0.38 ($t = -2.88, p < 0.05$), a standardized adaptation coefficient accounted for 14.3% of the total variance in treadmill induced trip recovery percent change over multiple exposures. A scatter plot of these results, see Figure 22, suggest a weak relationship between adaptation performance during novel manual and locomotor tasks and trip recovery improvement during repeated treadmill trip perturbations, wherein trip recovery improvement may be predicted to increase with greater adaptation performance.

Table 21: Results of linear regression analysis for the prediction of trip recovery time % change while controlling for a standardized adaptation coefficient of manual and locomotor adaptation, after correcting for normality via natural logarithmic transformation. * denotes significance at $p < 0.05$.

Factor	<i>R</i>	<i>R</i>^{2a}	β	<i>F</i>	<i>p</i>
Adaptation Coeff. $\ln(k)$	0.378	0.143	-0.378	8.31	0.006*

^aAdjusted $R^2 = 0.125$

These results were also mirrored in the standardized adaptation performance measure ($z(1/k)$), where the results of linear regression, described in Table 22 below, identified a significant predictive relationship upon trip recovery improvement after treadmill training. These relationships, although limited in their ability to explain the variance in trip recovery improvement, do suggest an intuitive link between adaptation task performance and task performance improvement during repeated attempts at a strategic learning task.

Table 22: Results of linear regression analysis for the prediction of trip recovery time % change while controlling for a standardized measure of adaptation performance to manual and locomotor tasks. Adaptation performance is represented as the sum of z-scores for the number of attempts (target matches or strides) to achieve adaptation after correcting for normality via natural logarithmic transformation. * denotes significance at $p < 0.05$.

Factor	<i>R</i>	<i>R</i>^{2a}	β	<i>F</i>	<i>p</i>
Adaptation Perf. $\ln(1/k)$	0.378	0.143	0.378	8.31	0.006*

^aAdjusted $R^2 = 0.125$

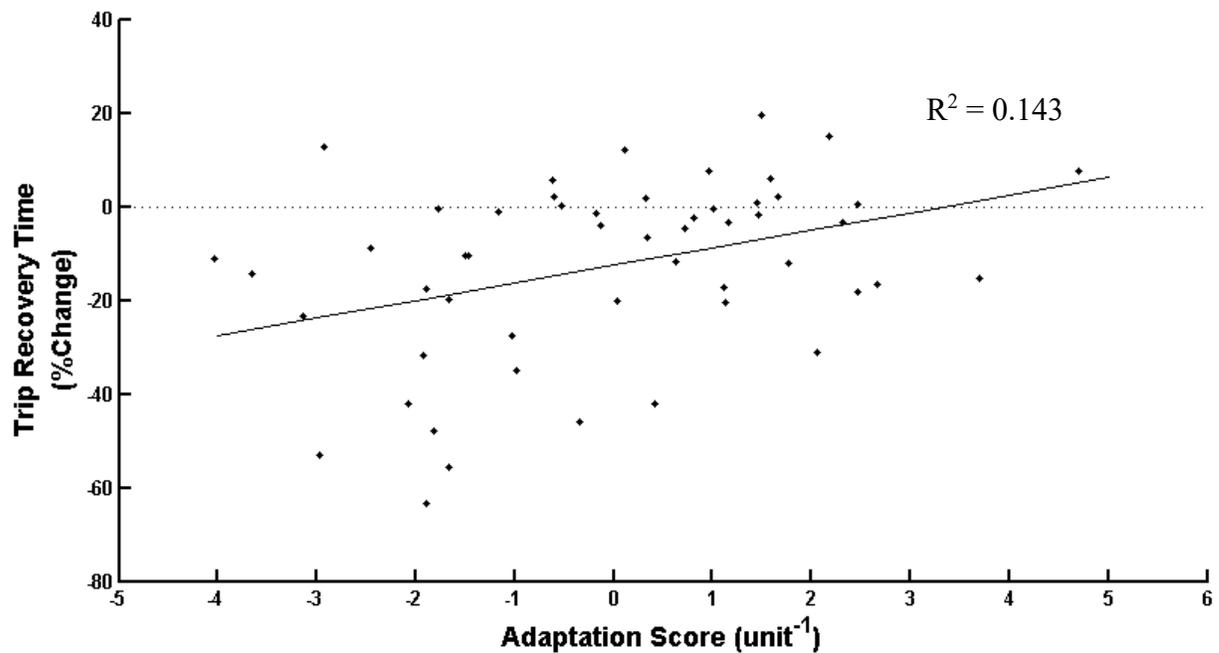


Figure 22: Scatter plot of composite adaptation performance ($z(I/k)$) versus percentage change in the time to recovery (TTR) for trips, between the first and final (10th) trip perturbation. The dashed line at 0% differentiates among participants who improved TTR (-ve % change) and those who took longer to recover from a trip after 10 perturbations (+ve % change). A moderate linear trend is observed with a significant Pearson's r correlation of 0.378. The horizontal axes is presented as a standardized z -score (unit^{-1}).

No attempt was made to incorporate the estimated %RSE for the composite measurement, as the composite score would require a multi-dimension perturbation to account for uncertainty in both the manual and locomotor adaptation performance measurements. This analysis was considered outside the scope of this study, therefore no inference is available to describe the stability of these results, making their interpretation limited.

IV.IV Experiment 3

Three repeated measures linear mixed models observing the main effects of repeated trip and slip *Perturbations* upon postural recovery, measured as recovery step reaction time (RT), recovery step maximum force (maxRSF) and recovery time (TTR), through the course of a training session, consisting of 10 repeated perturbations (*Trial*) were performed. To quantify

the transfer effect of recovery performance after training on one perturbation (i.e. trip training) upon response to the opposite perturbation (i.e. a slip), a one-way ANOVA was performed to observe the effect of *Group* (slip or trip training first) upon the novel exposures to slip and trip perturbations, respectively. The counterbalanced design, described in Figure 10, allows for the initial perturbation of each *Group* (per *Perturbation*) to be compared directly and observe any transfer effects, i.e. A comparison of recovery time for Trip 1 of *Slip Group* with Trip 1 of *Trip Group* would demonstrate the transfer effect of repeated slip perturbations (*Slip Group*) upon a novel trip perturbation within a group (*Trip Group*) who are naïve to any treadmill perturbations.

Recovery Step Reaction Time (RT)

A significant main effect of *Perturbation* ($F_{1,174.9} = 929.4, p < 0.05$) was observed for RT, however no effects of *Trial* or *Perturbation* Trial* interactions were observed, see Figure 23. Over 10 repeated perturbations, the mean recovery step reaction time for trips was significantly greater than slip recovery step reaction time (635.4 ± 6.5 vs. 356 ± 6.5 msec., respectively). Recovery step reaction time was observed to be maintained consistently throughout repeated exposures to gait perturbations.

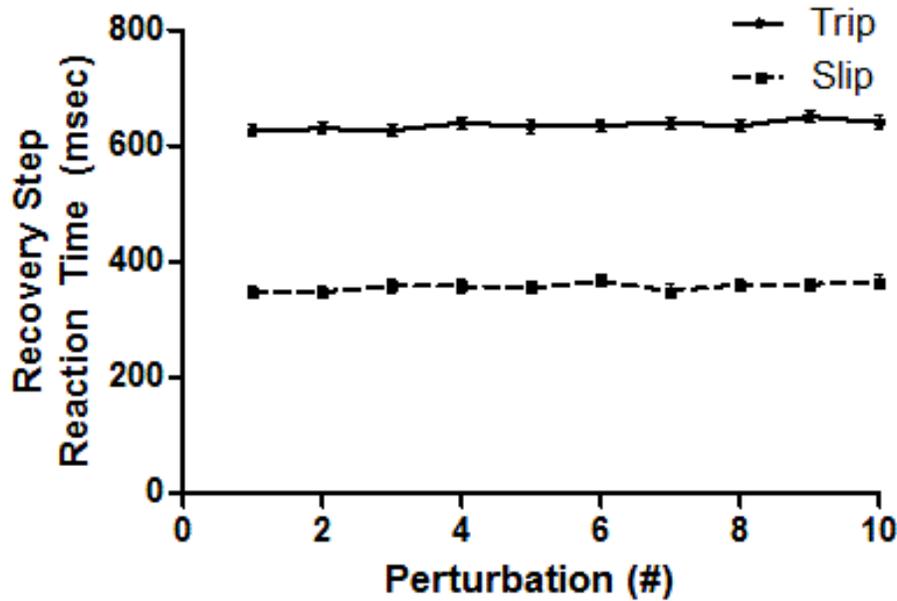


Figure 23: Recovery step reaction time (RT) measured in milliseconds, signifying the time between perturbation onset and the first recovery step with the non-perturbed foot. Trip reaction time is described by the solid line, while slip reaction time is described by the dashed line. Reaction time is maintained consistently over repeated perturbations, although significant different between perturbations.

Recovery Step Reaction Force

Significant main effects of *Perturbation* ($F_{1,223.5} = 19.0, p < 0.05$), *Trial* ($F_{9,745.5} = 9.74, p < 0.05$) and the interaction of *Perturbation***Trial* ($F_{9,745.5} = 2.26, p < 0.05$) were observed for recovery step maximum force in response to repeated treadmill induced gait perturbations, see Figure 24. Reaction forces were normalized to participant body weight, to account for some individual variability. Mean reaction forces for slips and trips across all time points were 1.328 ± 0.012 and 1.401 ± 0.12 , respectively. Over time, average reaction force decreased from 1.495 ± 0.017 to 1.331 ± 0.017 , or an average decrease of 11.1%. The significant interaction between *Perturbation***Trial* occurs as result of the change in slope among slip force and time, which initially decreases, but levels off after perturbation 6/7. Trip perturbations continue to produce decreased force during recovery over time, appearing to

plateau around perturbation 9/10, meaning participants continued to improve performance (decrease step force) longer during trips than slips.

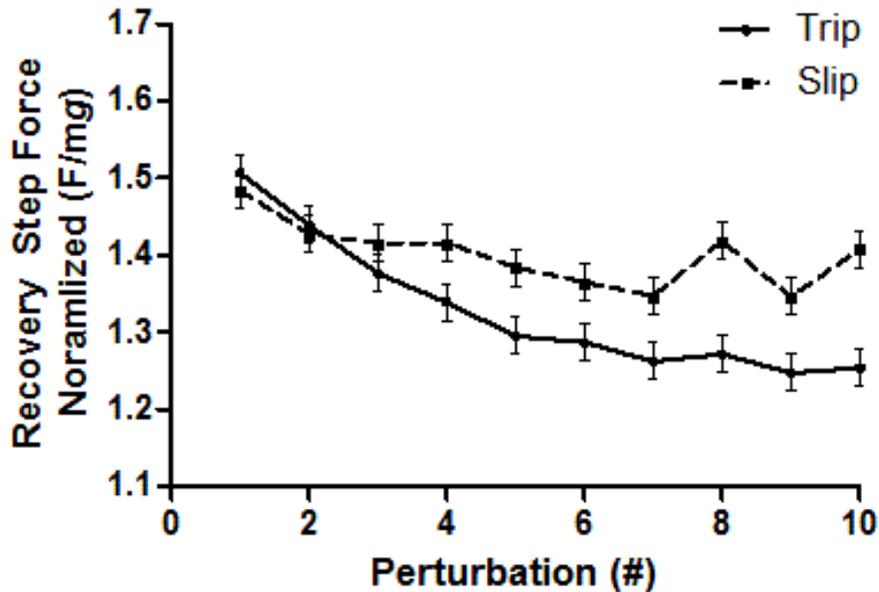


Figure 24: Recovery step maximum reaction force (maxRSF), normalized to body weight (mg), identified as the maximum force produced during recovery to a slip or trip perturbation by the non-perturbed foot. Trip maxRSF is described by the solid line, while slip maxRSF is described by the dashed line. Trip maxRSF decreases throughout repeated perturbations, while slip maxRSF appears to decrease initially, but plateaus at approximately perturbation 6/7.

Gait Perturbation Recovery Time

Significant main effects of *Perturbation* ($F_{1,191.1} = 10.5, p < 0.05$) and *Trial* ($F_{1,704.0} = 4.79, p < 0.05$) were observed for the time required to recover after a treadmill induced gait perturbation, see Figure 25. The interaction of *Perturbation***Trial* was not observed to be significant for recovery time. Mean recovery time for trip and slip perturbations were 2581.2 ± 44.2 msec. and 2786.8 ± 45.4 msec., respectively, suggesting trips were recovered from more quickly than slips. On average, recovery times improved (decreased) after repeated perturbations, regardless of the perturbation, from an average recovery time of 2866.6 ± 62.1 to 2430.4 ± 61.0 , or an improvement of 15.2%.

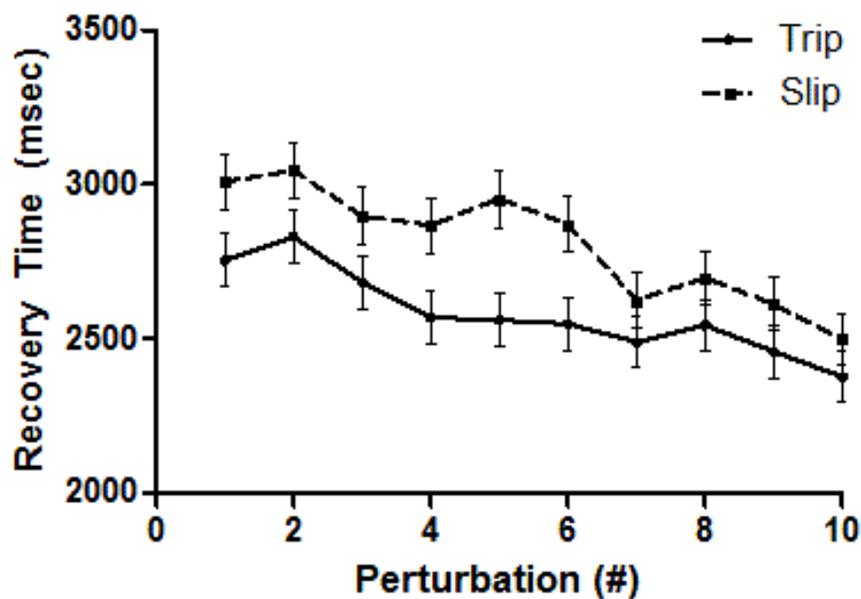


Figure 25: Treadmill induced gait perturbation recovery time, identified as the time (milliseconds) required to return to normal treadmill gait after receiving a slip or trip perturbation. This time was defined based on the return of gait kinetics post-perturbation to a threshold of ± 1.2 standard deviations of the baseline gait kinetics. Trip recovery time is described as the solid line, while slip recovery time is described as the dashed line. Recovery time improvement is observed in a similar fashion between both slips and trips as a result of repeated perturbations.

Transfer Effects of Perturbation Training upon Novel and Opposite Gait Challenge

The results of one-way ANOVA of *Groups* (*Trip Training* and *Slip Training*) upon postural recovery to novel exposures to slip and trips are summarized in Table 23 and Figure 26, below. Mean recovery step reaction time was significantly increased in the *Group* receiving slip training prior to their first novel trip ($F_{1,56} = 5.87, p < 0.05$), from 595.6 ± 96.4 msec. to 651.5 ± 91.4 msec. No other significant changes in postural recovery performance are observed as a result of training transfer between repeated perturbations and novel trips or slips.

Table 23: Participant demographic information including age, body mass and height stratified for perturbation training and novel perturbation exposure. Mean and standard deviations for trip and slip training groups upon novel perturbations are presented. * denotes significance at $p < 0.05$.

	Trip Training Group	Slip Training Group	<i>F</i>	<i>df</i>	<i>p</i>
N	27	31			
Age (years)	23.4 ± 5.3	24.3 ± 4.6	0.538	56	0.466
Mass (kg)	68.9 ± 13.6	75.4 ± 17.9	0.362	56	0.550
Height (cm)	1689.5 ± 102.8	1707.2 ± 118.7	2.369	56	0.129
Trip Perturbations	Novel Trip	Trip after Slip Training			
Reaction Time (RT)	595.6 ± 96.4	651.5 ± 91.4	5.869	56	0.019*
Recovery Force (maxRSF)	1.536 ± 0.189	1.481 ± 0.166	1.372	56	0.246
Recovery Time (TTR)	2672.9 ± 570.7	2816.3 ± 570.2	0.898	55	0.347
Slip Perturbations	Slip after Trip Training	Novel Slip			
Reaction Time (RT)	356.4 ± 48.4	340.7 ± 38.1	1.869	55	0.177
Recovery Force (maxRSF)	1.485 ± 0.227	1.485 ± 0.240	0.000	55	0.997
Recovery Time (TTR)	2980.4 ± 765.6	2907.3 ± 620.8	0.139	48	0.711

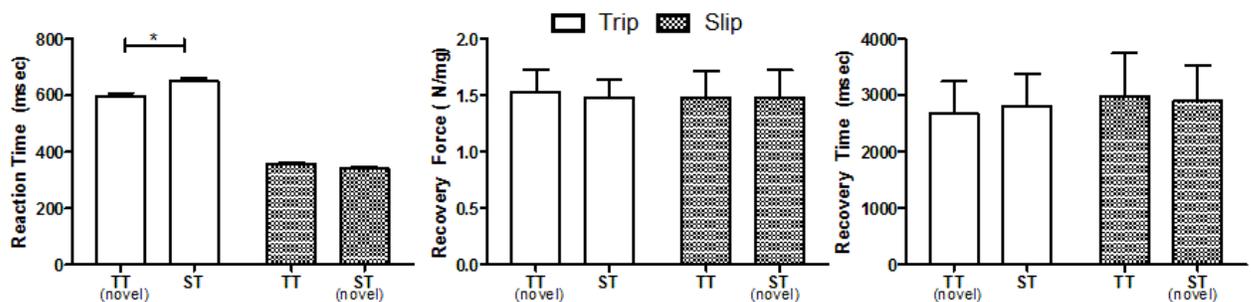


Figure 26: Recovery step reaction time, maximum recovery force and time to recover comparing trip-training group (TT), who experienced a naïve trip and training prior to their first slip and the slip-training group (ST), who received a naïve slip and training prior to their first trip. Significant differences are denoted with *.

V. Discussion

The individualization of adaptation to spaceflight has made it nearly impossible to produce a single countermeasure to minimize the perceptual and motor risks for astronauts during their return to gravity transitions. Sensorimotor adaptability, and the training of adaptation, is a novel paradigm currently being explored to prepare astronauts to better adapt and re-adapt to changes in their environment, as opposed to minimizing the effects of adaptation itself – typically the goal of other spaceflight countermeasures. This dissertation strove to better understand adaptation within an individual, for the purposes of guiding future countermeasure development and begin to understand the relationship among environmental adaptation and discrete postural stressors during locomotion, to better understand how adaptation may relate to fall risk. A novel system to repeatedly and consistently generate these dynamic postural perturbations, in the form of treadmill induced trips and slips, was developed during this dissertation to pursue this understanding of individualized adaptation performance and fall risk.

Formally, the three aims of this dissertation were: 1) to measure and quantify plastic adaptation performance across two adaptation paradigms within an individual and determine the relationship that exists between manual and locomotor adaptation performance; 2) to observe and quantify whole-body postural recovery to treadmill induced gait perturbations, in the form of slips and trips, and identify if adaptation performance predicted novel or experienced recovery performance, or if the strategic learning, or strategic adaptation, employed during blocks of repeated challenges was related to within-individual plastic adaptation performance; and finally, 3) to quantify and assess the effectivity of this novel split-belt slip and trip system to produce challenging and unexpected perturbations, such that

exposure, or training, of one type of perturbation (i.e. slips) did not significantly influence performance on the opposite perturbation (i.e. trips).

With respect to the first aim, it was hypothesized that a common mechanism, likely based on online error-checking (Peterburs & Desmond, 2016; Wolpert & Kawato, 1998) and located in the cerebellum (Imamizu et al., 2000, 2003; Izawa et al., 2012; Reisman, 2005, p. 200; Reisman et al., 2010), is employed when performing adaptation tasks, such as rotated input joystick target matching (Imamizu et al., 2000, 2003; Seidler, 2004) or split-belt walking (L. A. Malone et al., 2011; Reisman et al., 2010; Vazquez, Statton, Busgang, & Bastian, 2015). These adaptation tasks are considered plastic-adaptive, as they produce observable after-effects (Seidler et al., 2015). These after-effects are considered a consequence of a semi-permanent changes to the forward-model motor program for the adapted movement (Peterburs & Desmond, 2016; Reisman et al., 2010; Ullsperger, Danielmeier, & Jocham, 2014), resulting in an over-correction and biased performance when the stressor is removed and conditions are returned to baseline (Seidler, 2004, 2006; Torres-Oviedo et al., 2011). Quantifying these individual adaptations using an exponential curve fitting model provided an adaptation coefficient (k), representing the continuous course of performance change during exposures to a novel stimuli, which can be described also as the discrete number of attempts required to achieve adaptation ($1/k$). This adapted state was identified as the point at which an individual achieved $(1-e^{-1})$ or $\sim 63\%$ of their steady-state performance in the task, a technique derived from the analyses of linear systems in engineering, whose seminal work in the domain of motor control was explored by Newell et al. (2001) and Heathcote et al. (2000). Linear regression analyses predicting the performance of manual adaptation based on locomotor adaptation performance was observed to be highly

correlated ($r = 0.799$), previously untested in the literature within-individuals. These results support the primary hypothesis of Specific Aim 1, and provide support for the notion that a common mechanism exists to generalize adaptation between two distinct motor control modalities – manual (upper extremity) and locomotor (lower extremity) adaptation – within an individual.

The second aim of this dissertation hypothesized that the generalized plastic adaptation performance captured within individuals in Specific Aim 1 would predict postural recovery performance when challenged by discrete gait perturbations and provide insight into the relationship between plastic adaptation performance and the strategic adaptation developed through repeated slips and trips. This hypothesis theorized that individuals with a greater predisposition towards adaptation performance would navigate postural recovery during a novel (1st) and experienced (10th) perturbation more effectively, and express greater improvement after repeated exposures to treadmill induced postural stressors. Two opposing postural stressors were created for this dissertation, based upon a split-belt treadmill system, capable of providing unpredictable and challenging backward slip perturbations, as well as forward trip perturbations. All subjects performed bouts of each of the 10 perturbations in a block-randomized fashion. Due to the high correlation between manual and locomotor adaptation performance observed in Experiment 1, attempts to predict postural recovery changes using multiple regression, as they relate to manual and locomotor adaptation performance, were challenging due to violations of the assumptions of multicollinearity, therefore they were analyzed individually, and a combined adaptation measure was also generated.

Pearson's correlation coefficients were calculated among the adaptation performance measures (manual and locomotor) and postural recovery measures for the novel (1st) perturbation, the final (10th) perturbation and the percentage change within an individual between the last and first perturbations, for both slips and trips, respectively. No significant linear correlations were observed among adaptation and postural recovery during the first slip or first trip, suggesting there is no relationship between adaptation performance and whole-body responses to novel, discrete, gait perturbations. Observing performance on the final perturbation attempts yielded a significant correlation among split-belt adaptation and slip recovery time. Analysis of the percent change between the first and final perturbations exposed significant linear correlations between locomotor adaptation and postural recovery time for both trip and slip perturbations. All significant linear correlations ($r > 0.3$) were followed up with simple linear regression. These results suggest that individuals who performed more effectively during split-belt walking, exhibiting more effective plastic adaptation during a locomotor task, were capable of navigating slip perturbations more effectively after some practice, and were capable of improving their overall performance in the recovery of trips and slips after a training session of repeated perturbations. Although the explained variance predicting slip recovery time (11.4%) and changes in recovery performance for trips and slips predicted by adaptation performance (18% and 9.7%, respectively) are not particularly impactful, these results do support a notion that, within an individual, a relationship exists between continuous plastic adaptation performance and one's ability to develop a strategy to navigate discrete whole-body challenges. This suggests strategic adaptation performance is related to individual plastic adaptation performance.

In response to violations of the assumption of multicollinearity, a statistical transformation of manual and locomotor adaptation performance was performed to generate a composite measure of individual adaptation performance, using a summation of within-individual *z*-scores (Ackerman & Cianciolo, 2000). No significant linear correlations were observed between this composite measure of adaptation performance and postural recovery during first or final exposures to slip or trip perturbations. It was observed to relate significantly with changes in trip perturbation recovery performance, however, accounting for 14.3% of the variability in the change of trip recovery time between first and final perturbations. This measure did not significantly predict postural recovery performance during repeated slip perturbations.

These results provide a mixed set of support for the hypotheses associated with Specific Aim 2. No statistically significant predictions were observed to support the hypothesis that novel slip or trip recovery can be estimated by measuring performance in a joystick or locomotor adaptation task. After a bout of training, however, it was identified that a statistically significant, although limited, relationship exists between slip recovery time (TTR) and adaptation performance during a 10 minute split-belt walking task. Quantifying the overall change in performance between the first and final perturbations exposed statistically significant relationships among slip and trip recovery time with split-belt adaptation performance. These findings support the hypothesis that individuals who possess improved plastic adaptation performance may be more likely to effectively generate strategic responses to discrete motor perturbations over the course of a short training session. The results of the analyses of the standardized composite adaptation scores highlight the relative contribution of manual adaptation prediction as that of a moderating effect, which decreases

the total explained variance when compared with that of split-belt alone (18.2% split-belt adaptation vs. 14.3% standardized adaptation). It is important to note the intuition associated between improved plastic adaptation performance and improved strategic learning is supported by a negative relationship (split-belt adaptation $\beta = -0.43$) among plastic adaptation performance and trip recovery time improvement. This suggests a unit decrease in the percentage change between first and final perturbation (a greater decrease represents improved performance, i.e. less time is required to recover after training) results in a unit improvement in plastic adaptation performance (increased adaptation coefficient (k) or decreased number of attempts to adapt ($1/k$)).

The final aim of this dissertation served to quantify and assess performance among a large sample of young, healthy individuals experiencing gait perturbations on a custom-built slip and trip perturbation system. This aim also allowed for the ability to systematically quantify improvement to postural recovery performance after repeated exposures to gait perturbations, and ensure that the ability to transfer this performance from one perturbation task to the other was minimized. Overall, it was observed that typical familiarization and learning was present during repeated exposures to the gait perturbations, with a consistent decrease in recovery step force production (maxRSF) and recovery time (TTR) throughout the 10 perturbations. Responses to slip perturbations were observed to loosely follow this trend, as recovery performance plateaued more rapidly than in the trip perturbations. This is believed to be due to the increased difficulty of this task, where the ability of participants to minimize maxRSF and TTR was limited due to fewer successful recoveries. On average, approximately 8.0 ± 3.6 participants ($14 \pm 6\%$) fell per slip throughout the 10 successive

perturbations, with all but 18 participants (69%) experiencing at least 1 fall. These falls typically occurred within the first 5 perturbations (64.3% of total falls).

Unlike the recovery step force production (maxRSF) and recovery time (TTR), recovery step reaction time (RT) was observed to be maintained mostly constant throughout repeated perturbations. This is believed to be a result of the biomechanical constraints associated with producing a postural recovery response. Trip recovery reaction time was significantly higher than slip recovery, primarily due to the response strategies employed during each perturbation. During trips, the perturbed foot (trip-foot) was rapidly stopped via the split-belt upon heel-strike, while the recovery foot (non-trip foot) was continued through the swing phase before attempting a recovery maneuver. Slips, on the other hand, which accelerated the split-belt of the perturbed foot (slip-foot) *away* from the participant (producing a rapid anterior translation of the slip-foot), typically resulted in participants stepping their recovery foot (non-slip foot) immediately downwards, halting the natural progression of gait to attempt recovery. It was interesting to note that, despite within-and-between participant consistency throughout repeated perturbations, regardless of trips or slips, RT was the only measure of postural recovery impacted by the transfer effects, or generalization, of experiencing a bout of the opposite perturbation prior to a novel perturbation.

V.I Assessment and Testing of a Novel Split-belt Treadmill Gait Perturbation System

It was hypothesized that the difficulty of the perturbations designed for this healthy population would minimize any transfer effects of experiencing a series of perturbations (i.e. a bout of 10 trips) prior to receiving a novel, opposite, perturbation (i.e. an unexpected slip). Bhatt et al. (2013) describe some generalization between their two over-ground gait

perturbation systems, one capable of producing a trip by rapidly injecting an obstacle into one's walking path and one capable of producing a slip by releasing a sliding plate on the floor during locomotion. The authors observed that slip training 'primed' individuals for their first novel trip perturbation, resulting in the elimination of a compensatory recovery step, which was typically observed in control participants. To provide a more clear comparison to the findings of this dissertation, these results would suggest that those 'primed' for recovery after receiving over-ground slip training were capable recovering more quickly, therefore exhibiting a significantly decreased time to recovery (TTR). A similar set of 'priming' was observed in this dissertation, although the results themselves were contradictory. Participants who received a bout of slip training prior to their first novel trip expressed significantly *increased* recovery step reaction timing (RT), when compared to participants whose first gait perturbation was a novel trip (7.8% increase) while naïve to the experimental setup. It is hypothesized that this is due to the familiarity of the Slip Training Group (those who received slips before a novel trip) with the treadmill perturbation system, and it was the participants who had not yet received any perturbation, still naïve to the type of perturbation (slip or trip) they would experience first, who reacted more instinctively upon experience of their first trip perturbation (Trip Perturbation Group). After slip perturbation training, individuals appeared to, on average, expressed a blunted instinctive 'startle' response during novel trips, as evidenced by this decrease in RT. The maximum recovery step force (maxRSF) and the overall time to recover (TTR) were not significantly different between the two groups, however, implying that the 'priming' observed by Bhatt et al. (2013) did not result in significant changes to the postural recovery strategies employed on our perturbation system.

The counterbalanced design of this experiment allowed for the inverse relationship to also be tested: identifying the transfer effects of repeated trip training upon a slip perturbation, when compared with a naïve population experiencing a novel slip. Overall, no significant differences were observed as a result of ‘priming’ or generalized postural recovery strategies in measures of the time to produce a recovery step (RT), the maximum force produced to attempt postural recovery (maxRSF) or the amount of time required to return to normal gait following the perturbation (TTR). These results supported the hypothesis that the slip and trip protocol designed for this dissertation was tuned sufficiently to produce challenging and opposing gait perturbations which did not allow for notable generalization or transfer of postural recovery strategies. In other words, a protocol which incorporates both slips and trips can be considered an acceptable design, as they do not significantly impact participant responses between one another.

Although collected, no clear patterns were observed in the analyses of basic kinematic measures during slip and trip postural recovery, owing primarily to the dramatic variability in recovery strategies observed during this study. While in-depth analyses of these kinematics were outside the scope of the present study, a generalized set of responses for each, slip and trip, were observed as they relate to an individual’s attempt to maintain their center of pressure within their dynamic base of support during locomotion. During trip perturbations, many individuals rapidly straightened their posture, driving their center-of-mass forward, and used this momentum to continue the trajectory of their recovery foot through their current gait cycle, yielding a greater RT which was maintained with consistency. Less frequently, participants would adopt a strategy of rapid trunk flexion, leaning forward and using momentum to drive the center of pressure towards the forward edge of their base of support,

in order to continue their current gait cycle. This resulted in a similar RT response, making the two strategies difficult to differentiate without in-depth analyses of the hip and trunk angles. During slips, as the slip-foot – and base of support, together – were driven in the anterior direction, a more rapid and dynamic set of movements were required to drive the center-of-mass forward to follow suit. A center-of-mass counter-rotation was generated through a set of rapid arm swings, flexing forward at the shoulder joint, in order to straighten posture and maintain the center of pressure within the base of support. This was followed by the immediate termination of the current gait cycle, consistently evidenced in RT, serving to instantaneously widen the base of support in the anterior/posterior direction, before taking a further set of recovery steps to return to normal gait. The magnitude and rate of arm swing varied dramatically among participants, as some would attempt to grab the safety harness, while others would not – making detection of a recovery pattern or strategy challenging.

Limitations

Although effective for the purposes of this set of studies, the split-belt treadmill based gait perturbation system was not without its limitations. A significant challenge, common with split-belt treadmill experimentation, was limb-crossover during operation—an issue exacerbated during gait perturbation recovery. The open-loop and ballistic postural recovery responses observed during slip recovery were virtually impossible to predict, and extremely variable from participant to participant. The programmed belt-dynamics to produce the slip perturbation were sourced from the in-depth analyses of Redfern et al. (2001), however the motivation for the design of the slip perturbation was sourced from observation of, and personal experience with, frozen and slippery surfaces. In this way, if a participant were to produce a high force recovery step upon the perturbed surface (the slipping belt), they would

continue slipping and likely experience a fall, much like someone who continues to step on a patch of ice. This was designed to best mimic real-life situations and responses as closely as possible in an experimental setting, however, it resulted in a very challenging perturbation. In these situations, the safety harness was loaded and the treadmill was rapidly stopped to protect the participant, classifying the perturbation response as a 'fall.' It is possible that a wider split-belt treadmill may assist in minimizing the recovery-step crossover during perturbation responses. Throughout data collection, it was observed that the positioning of the participant with respect to the midline of the split-belt treadmill was critical to predicting the foot placement of the recovery step. For many participants, especially those who fell multiple times, this recovery step foot position was often posterior and midline, placed directly upon the split between the two belts.

To improve the predictability of responses, which would assist in quantifying a more common strategy for overcoming the slip perturbations, time limiting the perturbation, as done by Yang et al. (2013) may help to decrease difficulty. Their system may not be directly comparable, however, as they employ a single-belt treadmill during their gait perturbations, but the results from this dissertation suggest there may be value in exploring this approach using the split-belt treadmill system. Another limitation to this system, not uncommon to other perturbation systems, is the confounding factor of the whole-body harness system, used for subject safety. During perturbation recovery, many participants would instinctively reach for the harness support straps, in an attempt to seek stability guidance and support from their environment. This phenomenon is well documented (Horak, 2006; Redfern et al., 2001), but little researched, and represents a very interesting aspect of unconscious motor control. Unfortunately, the inconsistent fashion with which participants interacted with these supports

– or more closely followed instructions to ‘not grab the harness’ – limited the ability to generalize observed strategies among participants. A common issue observed throughout this study, typical in the measurement of postural control, is the interpretation of ‘falls.’ In this study, falls were treated as failed conditions and omitted from analyses, as the derived metrics for postural recovery could only be assessed when recovery was observed. That said, these outcomes represent a real action and response to a slip or trip perturbation whose impact was lost on the observed data set, but may have been highly influential in the development of a strong error signal and updating of the internal model necessary for recovery. Future studies should look to quantify some, or categorically include, fall data to better understand their impact on sensorimotor adaptation and strategic motor learning.

Future Work

Bhatt and Pai et al. (Pai, Bhatt, et al., 2014; Pai et al., 2003; Pai, Yang, Bhatt, & Wang, 2014; Yang & Pai, 2014) have lead the effort to better understand how gait perturbation training, using treadmill and over-ground slip and trip training techniques, can be utilized to minimize fall risk in at-risk populations, such as the elderly. They have shown that motor learning and the improved performance required to navigate these challenging perturbations can be attained in elderly participants, laying the foundation for a new paradigm of fall avoidance and rehabilitation training. The perturbation system used here may be useful for training, especially as it does not appear to produce significant transfer effects between perturbation types – slip or trip – as observed by Bhatt et al. (2013). Fall injury has also become a major concern for obese populations (Himes & Reynolds, 2012; Mitchell, Lord, Harvey, & Close, 2014), who represent another population who may benefit from training and intervention protocols designed using the gait perturbation system used during this

dissertation. Future work should focus on the transfer of treadmill slip and trip recovery performance to over-ground perturbations, as well as the form and frequency of training required to improve fall risk factors. Here, a focus on the assessment of rate of falls and the kinematics or kinetics of experienced falls becomes important to ensure comparison and generalizability among treadmill induced and over-ground locomotor perturbations.

V.II Quantifying the Relationship between Manual and Locomotor Adaptation Performance

The results of Experiment 1 strongly support the hypothesis that adaptation performance within an individual is related across multiple tasks, and that this relationship can be attributed to a single set of neural mechanisms or sources. Typically, in the study of motor adaptation, experimental frameworks focus on a single task, such as movements of the arm during perturbed position matching tasks (Mattar, Darainy, & Ostry, 2013; Shadmehr et al., 2010), matching a cursor to a target (Seidler, 2004, 2006), or performing a ballistic target matching task, such as throwing an object, under the influence of vision-shifting prisms (T. A. Martin, Keating, Goodkin, Bastian, & Thach, 1996; Roller et al., 2001, 2002).

Dichotomously, an equally large body of literature has focused on similar motor adaptation during split-belt walking (Choi & Bastian, 2007; Choi, Vining, Reisman, & Bastian, 2009; L. A. Malone et al., 2011; Laura A. Malone & Bastian, 2010; Reisman, 2005; Reisman et al., 2010; Vazquez et al., 2015). In both domains, the predominant theory driving this plastic adaptation, or motor recalibration (Vazquez et al., 2015), is one of error detection and correction based on a set of expected outcomes, requiring an update of the forward model used to predict the sensorimotor consequences of a movement (Izawa et al., 2012; Reisman et al., 2010; Seidler et al., 2015).

Numerous imaging studies (Imamizu et al., 2000, 2003; Seidler, 2010; Synofzik, Lindner, & Thier, 2008), and more recently transcranial neural stimulation studies (Doppelmayr, Pixa, & Steinberg, 2016), provide extensive support for the role of the cerebellum, specifically the cerebellar thalamocortical pathways (Seidler et al., 2015), as a key neural structures employed during adaptation tasks requiring manual control. Imaging while performing gait, especially in the cerebellar region, is challenging, therefore models of cerebellar dysfunction during split-belt walking (Morton, 2006; Morton & Bastian, 2007; Reisman et al., 2010, 2007; Torres-Oviedo et al., 2011) have been used infer the role of the cerebellum during adaptation. The results of this dissertation provide a link between these two domains of motor control, independently hypothesized to rely on the cerebellum for error processing and adaptation. This provides support for models of the cerebellum as a whole-body performance monitoring apparatus (Peterburs & Desmond, 2016; Ullsperger et al., 2014), expanding its influence beyond task-specific error correction to generic forward model updating.

Until recently, quantifying individual performance during a motor adaptation task as performed in this study, regardless of motor location (upper/lower extremity) or movement type (manual/locomotor), was uncommon. In a recent review, McDougle et al. (2016) refer to the canonical shape of motor adaptation in response to a novel environment as a monotonic gradient, well understood in the literature, but to the best of our ability, only four recent studies (Babič, Oztop, & Kawato, 2016; Erkelens, Thompson, & Bobier, 2016; Fernandez-Ruiz et al., 2011) have attempted to quantify individual performance using continuous modelling of these functions – specifically a decaying exponential function – and discuss their results within the context of motor control. Significant work has been accomplished in the field of identifying and testing the best models for approximating the

behavior of learning during different tasks, and resoundingly, models of an exponential nature have been recommended, despite their limitations (Heathcote & Brown, 2004, p. 200; Heathcote et al., 2000; Liu et al., 2003; Newell et al., 2001). Recent work by Simon and Bock (2016) have identified the time course of adaptation to be related most strongly to the number of attempts to perform a task successfully, rather than the true time spent exposed to a novel environment. Representing adaptation as a function of the number of attempts to achieve a steady-state performance ($1/k$) therefore provides researchers with the ability to characterize adaptation, not simply the differences in performance as a *result* of adaptation, which is much more common (Batson et al., 2011; Roller et al., 2001; Seidler, 2004, 2006; Shadmehr & Moussavi, 2000). Characterizing adaptation performance allows for greater generalizability of this behavior and facilitates comparison with other tasks. In fact, the strength of the relationship observed in this study suggests a predictive relationship, wherein the expected performance of an individual exposed to a challenging split-belt protocol could be estimated by their performance during a novel joystick target-matching task, or vice-versa.

Seidler et al. (2015) recently have published a well-detailed review of potential individualized predictors of sensorimotor adaptation, with particular emphasis on microgravity adaptation as a source of environmental perturbation. Although the quantification of individual adaptation performance via exponential modelling is a technique absent from this review, the benefits to predicting adaptation performance are well described, especially within the context of human spaceflight. Bloomberg et al. (2015) provides complimentary insight into the current attempts to achieve adaptive generalization throughout the past 15 years. These studies have primarily focused on different modalities of sensorimotor adaptability training, which has shown to be effective at improving

performance to novel environments with high levels of long-term retention. The techniques and results described in this dissertation may provide a new avenue for the quantification and application of these already observed generalization effects. If it is possible to improve (generalize) adaptation performance to novel environmental stressors, and adaptation performance, or adaptability, is measurable within an individual, it may be possible to predict and individualize training in preparation of expected environmental shifts. Mentioned only briefly, the novel avenue of adaptation enhancement via transcranial direct current stimulation (tDCS) (Doppelmayer et al., 2016) further combined with these recent advancements in the understanding and manipulation adaptive generalizability could usher in a new paradigm of astronaut preparedness for spaceflight, training before return to Earth or exploration of Mars, as well as new approaches to rehabilitation therapy.

Limitations

Curve fitting to individual data were a challenging aspect of this study, as individual variation is the most typical source of noise in a population sample. In 4 of the participants, no adaptation was observed in one of the two tasks (2 did not adapt to target matching and 2 did not adapt to split-belt treadmill walking). ‘No adaptation’ was identified when the adaptation coefficient, or adaptation performance ($1/k$), calculated for a task was observed to be greater than the number of actual attempts performed, i.e. an estimated adaptation performance greater than 108 attempts to achieve adaptation to the rotated joystick input. In these situations, it was observed that participants were either unfocused or unmotivated, or simply did not follow directions during the task. In all cases, it was the first of the two adaptation tasks which were performed that showed limited focus and poor adaptation performance. A recent study by Gajda et al. (2016) underscores the importance of motivation

on the study of sensorimotor adaptation, showing that financial remuneration significantly improved task compliance and adaptation performance when compared to a control group who did not receive a financial incentive.

As with all measures in experimentation, consideration of the accuracy and uncertainty (error) associated with an observation is critical to informing one's interpretation of the results. When approximating real-world data with mathematical models, even those based on previous exploration and theory, is it easy to take for granted the estimates of discrete model parameters without accounting for the context of human behavior, especially as they are affected by individual variability. In the modelling of motor learning, Newell et al. (2001) and Heathcote et al. (2000) provide a set of seminal exploration into the use and appropriateness of an exponential model to understand the time course of this behavior. They caution reliance upon goodness-of-fit estimates (R^2) to quantify the representativeness of the model fit to individual or group (mean) motor performance, suggesting that individual variability and noise in the data collection will severely impact R^2 estimates and does not necessarily imply a lack of model relevancy. They do not – nor do others – however, comment on the uncertainty of the model parameter estimates, as described by the standard error (SE), or 95% confidence intervals, associated with these fits. In fact, in the review of the literature which attempts to model and study motor learning, practice, or adaptation through the use of exponential curve fits, no description of the quality of these estimates, for individual curve fits, have been presented.

Variability in parameter estimates were theorized to stem from two primary sources: curve fit quality (described as R^2) and performance variability (described as %RSE). Careful selection of the tasks to be performed, based on the available literature observing practice

and adaptation performance helped to, *a priori*, serve as the foundation for the selection of an exponential model for this analyses. Multi-rate models, such as bi-exponential or linear time invariant (LTI) models, were investigated as a potential alternative to quantifying adaptation performance to novel motor tasks, however in the study of motor control, these models are typically reserved for behavior where multiple rates of motor learning are expected to be observed, such as re-adaptation studies (M. A. Smith et al., 2006; Stratton, Liu, Hong, Mayer-Kress, & Newell, 2007) and others, focused on quantifying ‘savings’ among related motor learning tasks (Zarahn, Weston, Liang, Mazzoni, & Krakauer, 2008). A tertiary exploration of the relevancy of bi-exponential modelling to fit the joystick and split-belt behavioral data were performed, and was concluded to not significantly improve model fit (R^2) or improve the interpretation of motor adaptation performance. Furthermore, no theoretical explanation could be determined from an exploration of the literature to support the inclusion of a secondary learning rate (k_2) during exposure to a novel task, as they are typically associated with fast and slow learning portions of the second, and subsequent, exposure to a task. By selecting tasks with classically observed performance curves, and ensuring novel exposure, the model selection and fit was considered theoretically appropriate. A further exploration of the effects of R^2 upon the results of Experiment 1 showed no significant differences in the results of regression, including the slope or model intercepts, therefore all samples, regardless of R^2 , were included throughout analyses.

Performance variability was explored in greater detail due to limitations in the literature, and observed to vary widely in the joystick matching task, ranging from 7% to 328% (!) relative standard error (RSE), with a mean uncertainty of $48.9 \pm 55.6\%$. Split-belt adaptation was found to be considerably less variable, ranging from 4% to 49% RSE, with an overall

mean uncertainty of $13.7 \pm 10.5\%$. As insinuated by the high mean and standard deviation of %RSE in the joystick matching task, a few very highly uncertain adaptation parameter estimates dominated this average error (see Appendix B) and this uncertainty prompted a deeper exploration into the effects of these uncertain measurements upon the interpretation of results in Experiment 1. The overall mean uncertainty in the joystick matching task was decreased from 48.9% to 31.0% and finally 24.5% through the exclusion of highly uncertain adaptation performance estimates (removal of %RSE>100% and %RSE>50%, respectively), and the effects of these omissions upon the results of Experiment 1 were calculated and compared observing the linear regression parameters of slope and model intercept (see Appendix C). No significant differences were observed when removing the highly uncertain points from model generation using dummy-coded comparisons, suggesting these highly uncertain measurements were not significantly influencing the shape, position or strength of the observed relationship among the two motor adaptation tasks performed in this population. These results supported the decision of including the entire data set, including highly uncertain measurements, to maintain population power throughout analyses. This decision should not be taken to justify or support the use of mathematical models, such as an exponential or power law estimates, for the prediction of adaptation performance without an assessment of uncertainty in the parameter estimates – in fact, the alarmingly high level of uncertainty associated with highly variable or noisy individual performance necessitates consideration of these limitations and exploration of their implications upon the results. It is strongly suggested that a description of these uncertainties be presented in future studies employing similar techniques to quantify learning and motor adaptation.

To gain a better understanding of the impact of the estimated average measurement uncertainty— approximately 49% in the manual adaptation task and 16% in the locomotor adaptation task – the adaptation data sets used in regression were perturbed to ‘stretch’ or ‘compress’ the first and fourth quartiles of the population’s performance. Measurement error, resulting from a noisy or poor measurement device or technique, is particularly impactful when observed in the regressor variable, as noise or uncertainty in the experimental variable can be accounted for within the error term of a regression equation (Hutcheon et al., 2010). The first (Q1) and fourth (Q4) quartiles were selected as they contain the most extreme high and low performing scores, expected to drive the strength of a correlation estimate.

Analyzing the sensitivity of the results from Experiment 1 by perturbing the predictor variable (manual adaptation performance) by 48%RSE showed: Perturbation 1 (‘stretch,’ Q1-%RSE, Q4+%RSE) maintained a significant correlation, although decreased compared to unperturbed measures, while Perturbation 2 (‘compress,’ Q1+%RSE, Q4-%RSE) resulted in the loss of a significant correlation among manual adaptation and locomotor adaptation performance. These results suggest that it is possible that the data noisiness and parameter estimate uncertainty associated with manual adaptation performance may make the suggested relationship among manual and locomotor adaptation less impactful, as measurement uncertainty may be a driving force underlying the observed significant linear correlation.

Future studies employing these techniques should attempt to minimize individual performance noise by increasing motivation and attentional focus upon the task, perhaps through the use of incentives (Gajda et al., 2016); adopt alternative data cleanup and reduction techniques, perhaps more aggressive filtering or averaging, with more target matching attempts collected (greater than the 108 used in this study); or improving the

joystick interface by making the user input more intuitive, such as a traditional joystick handle, as opposed to a video-game style controller input, such as the one used in this study.

An alternative interpretation of the results presented in Experiment 1 may be related to the inherent difficulty within each of the tasks, requiring a high level of focus and cognitive resources. These cognitive resources would be expected to enlist the prefrontal (PFC) and motor cortices, thereby bringing into question the importance of the contribution of the cerebellum to the strategic and plastic adaptation observed during performance. In fact, the numerous imaging studies performed on upper extremity adaptation (Galea, Vazquez, Pasricha, de Xivry, & Celnik, 2011, p. 201; Imamizu et al., 2000, 2003; Synofzik et al., 2008) describe cortical activity of these regions in detail, supported in models of animal (Shik & Orlovsky, 1976; Yanagihara, Udo, Kondo, & Yoshida, 1993) and human (Hoogkamer et al., 2015; Reisman et al., 2007; Serrao et al., 2012; Mitsuo Suzuki et al., 2004) walking with neurological impairments. This cortical interplay is explored in the literature, differentiating between strategic and plastic adaptive performance, and summarized most parsimoniously as a distinct difference in roles: the cerebellum is thought to provide feedforward sensory prediction to the prefrontal areas, where the PFC provides the outcome comparison feedback (error) signal to the cerebellum (Peterburs & Desmond, 2016). As behavior changes to optimally minimize the error signal, the cerebellum, acting in its performance monitoring role, provides updates to the internal model (efference copy) associated with this movement goal. The adaptation coefficient quantified in this study is hypothesized to provide a measure of this internal model updating, where error is minimized through repeated feedforward comparisons with the predicted model.

A significant limitation to this study is the inclusion of only young, healthy participants. This limits generalizability of the study findings to populations outside that of college-aged adults, however provides support for expanding the study methodology into other age groups. The decision to include only young, healthy participants was grounded in the novelty of the study design and the analytical techniques proposed. Further, the findings of Roller et al. (2002) suggest that the ability to produce the expected motor adaptation and after-effects behavior is retained, therefore, provided the participants are healthy enough to perform the tasks (the 3:1 split-belt protocol performed in this study may not be the most appropriate), their adaptation performance is expected to be quantifiable.

Another limitation to this study included the exclusion of neuronal imaging techniques to better understand the cortical activity present during these adaptation tasks. A deeper understanding of the relationship proposed from the results of this study would be available with electroencephalography (EEG) or functional near-infrared spectroscopy (fNIRS) observing prefrontal, motor or premotor cortices during multiple sensorimotor adaptation tasks, distributed across manual and locomotor movement goals. Providing consistent instructions between participants was not observed to produce consistent behavior in this study, with some participants adopting unexpected strategies which limited their ability to navigate the adaptation tasks effectively, such as running or jogging on the split-belt treadmill instead of walking, or talking and expressing frustration during the challenging joystick matching task. Only task instruction was attempted to be controlled-for in this study, but due to the impact of motivation on sensorimotor performance (Gajda et al., 2016), future explorations of this area may require better control for motivation, such as standardized remuneration requirements, or assessing motivation using social psychology techniques

(Touré-Tillery & Fishbach, 2014). Attentional focus is a classically cited source of measurement error and variability in the study of motor control (Barthelemy & Boulinguez, 2001; Lohse, Jones, Healy, & Sherwood, 2014, p. 20; Newell, 1991; Pashler, Johnston, & Ruthruff, 2001; Schneider & Shiffrin, 1977; M. Woollacott & Shumway-Cook, 2002), and is proposed as the primary source of measurement uncertainty observed during the joystick matching task. It was interesting to note the discrepancy in measurement uncertainty, as previously discussed, between the joystick matching task and the split-belt walking task. It seems logical, here, that increased variability in the joystick matching task should be expected, as individuals possess considerably greater control over performance during a fine motor task, increasing the impact of loss-of-motivation and distracted attention on their performance. When compared with the split-belt task, where walking is a requirement driven by the treadmill belts, there is an inherent motivation to maintain upright posture and avoid the risk of a fall, which would certainly occur if attention is unfocused upon walking on the treadmill. Within this context, future studies using this manual control task should pay special attention to ensuring attention and motivation, as discussed by Gajda et al. (2016), in order to minimize participant variability and increase the certainty of adaptation performance measurement. Conversely, these paradigms may also be perfect candidates for systematically observing the effects of distracted attention *upon* the variability of adaptation performance within a population, such as those with attentional deficits stemming from a neurological disorder (attentional disorders, stroke (Loetscher & Lincoln, 2013)), injury (concussion (Howell, Osternig, Van Donkelaar, Mayr, & Chou, 2013) or traumatic brain injury (Stierwalt & Murray, 2002)) or changes in cognition as a result of aging (Commodari & Guarnera,

2008; Mather & Carstensen, 2005; Verhaeghen & Cerella, 2002), Alzheimer's disease (Perry & Hodges, 1999) or dementia (Ballard et al., 2001), for example.

Future Work

Despite the evidence in the literature, which the results of this study further support, it is possible, however, that these two tasks may be related for an unforeseen reasons, unrelated to the role of the cerebellum and plastic adaptation. By coupling the protocols tested in this study with cerebellar stimulation (i.e. transcranial magnetic stimulation (TMS) or tDCS), future studies could more effectively pursue the mechanistic role of the cerebellum in sensorimotor adaptation. A stimulation-sham design wherein participants complete the same joystick matching and split-belt adaptation tasks, divided into three groups: those receiving TMS prior to joystick matching; others receiving sham-TMS; and a third control group receiving neither. It would then be possible to determine if the slopes of the relationships are modified by cerebellar stimulation, providing further evidence to support the role of the cerebellum as a performance monitoring and forward modelling system. It would also provide greater context for the findings of Doppelmayr et al. (2016), who have observed increased adaptation performance after tDCS to the cerebellum, and also begin to answer questions about the transfer and generalizability of these improvements to other tasks.

V.III Examining the Role of Strategic Motor Learning and Motor Adaptation during Repeated Gait Perturbations

The results of Experiment 2 provide some support for the hypothesis that a predictive relationship exists between individual plastic adaptation performance and strategic adaptation, within the context of discrete, whole-body, locomotor challenges. This

relationship would imply that those individuals who are adept at navigating and improving their performance during a simple, novel sensorimotor task also possess the innate ability to identify and act upon strategies to effectively navigate complex, whole-body, sensorimotor challenges. The underlying motivation of this dissertation to observe discrete motor challenges served as an attempt to conceptualize abstract interpretations of motor adaptation, such as the time-course of learning during simple and laboratory-conceived tasks, with a set of tasks that are common to the human experience and have real-world consequences, such as slip and trip related injuries. Unfortunately, the results of this study did not provide a parsimonious set of relationships between motor adaptation and postural recovery to gait perturbations – novel or otherwise – however they did present an interesting glimpse into the within-individual relationships among plastic motor adaptation and compensatory motor strategies, sometimes referred to as a motor heuristics (McDougle et al., 2016).

These heuristics, or compensatory motor strategies as described by McDougal et al. (2016), are often considered a nuisance in the study of motor learning, whereby explicit instructions are typically used by investigators to ensure participants perform a motor task in a way that discourages this behavior. An ‘aiming strategy’ is an example of this type of behavior, sometimes observed during studies of prism-adaptation, such as in a ballistic target matching (ball throwing) task (Roller et al., 2001, 2002), where instead of throwing a ball to ‘where the target appears,’ some participants will attempt to estimate the visual deviation (ex. 20° horizontal shift) produced by the prism and generate a compensatory counter-movement, instead of incrementally reducing the error between attempts (producing the canonical human motor-learning curve). Typically, investigator feedback is provided to correct this counter-strategy, however in this study, minimal explicit feedback was provided to participants

during the slip and trip perturbations, and they were simply instructed to “do their best to recover from the perturbation,” while “staying on the treadmill” and “refraining from grabbing the support harness.” In this way, participants were required to rapidly plan and execute their own implicit motor strategies to maintain upright postural stability while exploring their dynamic region of stability (Pai et al., 2003). Among subjects, these responses were wildly variable, and included all manner of injury avoidance strategies; in some cases, attempting to jump off the treadmill system itself. Simple laboratory style tasks and the complex action of postural recovery may not be immediately comparable; however, the compensatory approach to incorporating environmental feedback in either a predictive (estimating experimentally induced environmental error) or reactive (unconsciously identifying environmental postural support surfaces) manner similarly biases performance away from the expected iterative approach to error reduction and goal achievement, suggestive of a heuristic strategy. Attempts to plan and execute these heuristic strategies may account for the observed increase in recovery time for both slips and trips during the 2nd exposure to the gait perturbations, see Figure 25, thereby sacrificing recovery time performance to allow participants to decrease recovery step force production and minimize the chance of injury, Figure 24. Through repeated perturbation attempts, these strategies were refined to improve performance in both time to recover and recovery step force production, which were observed to improve (decrease) in both slips and trips, respectively.

Although these strategic approaches result in confounding motor adaptation observations during traditional laboratory motor tasks – such as the split-belt walking or joystick matching tasks performed in this study – they represent a very real and very effective method of error minimization, planning, and motor execution to overcome a discrete challenge. In the

planning and execution of manual motor tasks, Anguera et al. (2007) and Seidler et al. (2010) describe the neural correlates associated with the early stages of the attainment of strategies, highlighting the role of the basal ganglia thalamocortical loops, medial cerebellum, anterior cingulate cortex, and visual and parietal cortical areas during the same adaptation task performed in this study: rotated input joystick matching. In locomotion, including split-belt walking, identifying the neural correlates, or areas of activity in the brain, to the same degree as manual tasks, is very challenging with current technology, however advances in near-infrared spectroscopy (fNIRS) provide glimpses into these functional networks (Mihara, Miyai, Hatakenaka, Kubota, & Sakoda, 2008; Mitsuo Suzuki et al., 2004).

Another common technique in the neuroimaging of locomotion employs fMRI (functional magnetic resonance imaging) during imagined walking (Bakker, Verstappen, Bloem, & Toni, 2007; Jahn et al., 2008). A review by Nutt et al. (2011) summarizes the hypothesized neural circuitry associated with the initiation and termination of gait, as well as the assessment of spatial orientation and planning of navigation, to involve a similar network as those involved in the manual control task: the frontal cortex, including the premotor and supplemental motor area (SMA), basal ganglia, brain stem/mesencephalic locomotor region and the cerebellum. When this network is disturbed, typically as a result of neurological dysfunction, i.e. Parkinson's disease (Akram, Frank, & Jog, 2013; Halliday et al., 1998; Stolze et al., 2004), cerebral stroke (Harris, Eng, Marigold, Tokuno, & Louis, 2005; Kajrolkar et al., 2014; Reisman et al., 2010, 2007), or in exclusionary animal models, such as the well-investigated decerebrate cat (T. G. Brown, 1911; Shik & Orlovsky, 1976; Yanagihara et al., 1993), breakdowns are observed in the ability to produce, maintain or adapt locomotion to changes in one's environment. These breakdowns do not completely halt

the ability to walk, however, owing to the theorized function of the central pattern generator (CPG) (Duysens & Van de Crommert, 1998; Kiehn & Butt, 2003; MacKay-Lyons, 2002), or involvement of lower spinal control, for the production of rhythmic and continuous, unconscious-but-coordinated, movement. Bhatt et al. (2005) and Pai et al. (2007) hypothesize, however, that in response to postural perturbations during locomotion, the automaticity of gait generated by CPGs are overridden by conscious control, which is consistent with the hypothesis that the PFC generates a sensorimotor error signal in response to a rapid environmental change (Shadmehr et al., 2010), resulting in a feed-forward motor response (Pavol & Pai, 2002) independent of cerebellar moderation.

In the context of motor adaptation, it is hypothesized that these cognitive resources are responsible for the production of the error signals used to re-evaluate sensory predictions and update the internal forward model at the cerebellar level (Nutt et al., 2011; Schlerf, Ivry, & Diedrichsen, 2012; Seidler, 2010). It stands to reason that improvements in this overall architecture of motor performance refinement towards a steady-state performance requires both: effective updating of the forward model, hypothesized to occur at the lateral cerebellum in the 'later stages' of adaptation (Seidler, 2010); and effective production of error signal estimates *to* update this model – better estimates of the magnitude of the error and the appropriate response to correct that error will theoretically minimize the number of comparisons required to optimize performance towards a predictable steady-state (Wolpert & Kawato, 1998; Wolpert, Miall, & Kawato, 1998). In this way, individuals who possess increased ability to optimize motor outputs during novel sensorimotor adaptation tasks derive this skill from increased performance at *both* effector-affecter sensory comparisons and error estimation, as well as forward model updating and sensory prediction.

Quantifying the total change in individual recovery performance between the first and final slips and trips as percent change (% change) provided some support for this interpretation, suggesting that individuals who produced large changes (improvements) in recovery time (TTR) were predicted to perform more effectively during locomotor adaptation. Intuitively, the ability to navigate a split-belt gait adaptation task effectively would transfer to a gait perturbation task, such as a slip or trip, and this intuition is supported by the lack of relationship observed between changes in recovery performance and manual adaptation. Producing a composite measure of adaptation performance, calculated via statistical standardization of the manual and locomotor adaptation coefficients (zk) (and adaptation performance ($z(l/k)$)), was shown to reduce the strength of the relationship with trip recovery time; abolishing it completely in slip recovery time. This suggests a moderating effect exists between manual and locomotor adaptation with respect to locomotor perturbations. Interestingly, although a strong relationship exists between manual and locomotor adaptation performance (Experiment 1), tasks that are more related to locomotion are more finely tuned to predict postural recovery to locomotor perturbations, suggesting that although there is some similarity in how these manual and locomotor tasks are handled in general – through cerebellar updating of the forward model – the differences in cortical and subcortical production of error signals are likely handled very differently, despite each demanding attention and cognitive resources.

These results provide further insight into the results of Experiment 1 by contextualizing these findings within the greater scope of within-task motor adaptation. Previous studies have shown consistent within-task improvements, theorized to be a result of adaptation generalization (Bhatt & Pai, 2009; Reisman, 2005; Reisman et al., 2010; Seidler, 2004; T.-Y.

Wang et al., 2011), however no attempt has been made to generalize these results to discrete motor tasks, which present limited opportunities for learning and high consequences for error. The relationships identified in Experiment 2 between motor adaptation performance and task improvement during repeated, high-risk, gait perturbations reinforce these classical within-task improvements by expanding them to relate to within-class (i.e. performance among locomotor tasks) generalizations. These results suggest that the constant rate of motor adaptation estimated during Experiment 1 captures, to some degree, an individual's ability to improve performance within a task-class (i.e. locomotor stability) during both discrete (strategic) and continuous (plastic) motor learning. These results also highlight the limited utility of across-class (manual vs. locomotor) motor performance estimates, suggesting that although it may be possible to predict continuous, or plastic, motor adaptation within an individual, it may not be feasible to predict early, strategic or heuristic-mediated, adaptation performance.

Limitations and Future Work

A possible limitation to the interpretation of performance change (% change) within individuals is described by Schmidt et al. (2011, pp. 341–345), who cautions this approach to minimize the contributions of 'high performers' who exhibit small improvements over repeated attempts, and emphasizes those who produce large errors early and improve their performance over time. This bias is evident when comparing the relationships between adaptation performance (manual and locomotor) and the first and final perturbations, against those relationships identified with the % change between the first and final perturbations. Little impact of adaptation performance is observed in raw performance, highlighting only a weak relationship between slip recovery time after training and split-belt adaptation

performance. A stronger relationship, however, exists when we observe the change in performance, or motor learning achieved, during repeated perturbations. Two interpretations of these findings as they relate to the limitations are described: 1) since no relationship was observed among adaptation performance and the initial slip or trip perturbations, there were no significant 'skills' associated with motor adaptation performance present in the population, suggesting that the task was sufficiently challenging to minimize this bias. Although these findings do not strongly support the primary hypotheses of Specific Aim 2, they do provide confidence that observing overall performance changes are not misrepresenting 'high performance' among the participants since no underlying relationship between adaptation performance and novel perturbation recovery was observed; and 2) individuals who performed more effectively at motor adaptation produced larger initial errors relative to their final performance than those who performed less effectively during motor adaptation. The significant relationships observed among % change and motor adaptation performance suggests that adopting increased variability during early movements may be a strategy for participants to rapidly minimize their errors and improve performance, a phenomenon recently suggested by Wong and Shelhamer (2014) and Wu et al. (2014) to aid in, and be predictive of (Seidler et al., 2015), sensorimotor adaptation. By representing postural recovery performance as % change, it is possible to account for the relative variability between the novel performance and the 'trained' end-point performance, highlighting the efficacy of the individual motor learning strategy employed.

To account for measurement uncertainty and test the stability of results obtained in Experiment 2, the regressor variable of locomotor adaptation was perturbed based on the estimated average %RSE (approximately 16%RSE), similar to that of Experiment 1. In

general, the inclusion of 16%RSE in the first and fourth quartiles of performance data for the trained (final) slip time-to-recover (TTR) and overall improvements in trip and slip TTR performance (% change) produced no significant changes to the interpretation of the results. Neither ‘stretching’ nor ‘compressing’ the observed locomotor adaptation performance by 16%RSE resulted in the loss of a significant linear correlation, suggesting the results of Experiment 2 were not sensitive to measurement error during analyses of locomotor adaptation performance.

Despite the results of this study providing limited ability to predict discrete responses to slip and trip perturbations through the assessment of individual motor adaptation, the findings which imply that training improvements, such a reduction in the time to recover from a perturbation, can be predicted by relatively simple laboratory tasks represent a real-world application of this research to the field of rehabilitation and therapy. Yang et al. (2013) and Patel and Bhatt (Patel & Bhatt, 2015) have shown promising results generalizing the training of treadmill induced slips to over-ground slips, including early work in elderly populations to increase dynamic postural stability and minimize fall risk. Although the slip and trip protocol assessed in this dissertation has not been compared with over-ground performance, these results are promising and identify a clear set of future studies, including trip and slip training interventions for at-risk populations, estimations of the efficacy of these interventions with respect to motor adaptation performance and retrospective or prospective studies of fall history as they relate to controlled slip and trip performance.

Many of the technical limitations to the study of postural recovery during treadmill induced slip and trip perturbations have been discussed previously, however other experimental limitations require highlighting. Common with Experiment 1, no attempt to

observe neuronal activity was performed in this study, therefore all relationships between neural correlates and the findings of this study can only be discussed within the context of findings in the literature. A combination of EEG and fNIRS would provide insight into both the time course of cortical activation as well as estimates of the localization of that activity during the observed open-loop postural recovery responses. To standardize the analyses of perturbations in this study, participants always experienced a slip perturbation on their self-identified non-dominant leg, while always receiving trips on their self-identified dominant leg. Although no differences are expected between legs, Bhatt et al. (2005) has observed some differences in compensatory stepping strategies during sliding-platform slip perturbations, depending on the slipped foot, within individuals. A set of future studies where the perturbed foot is randomized or leg dominance is balanced among ‘left footed’ and ‘right footed’ participants through inclusion criteria will help provide insight the impact of this experimental constraint. Repeated trips and slips, especially, were challenging perturbations for participants, and anecdotally increased stress and anxiety in some participants. Controlling for, or quantifying stress (especially if fNIRS or similar systems are to be employed (Ogoh et al., 2005; Villringer & Chance, 1997)) was not performed in this study, and measures of heart rate (at minimum) are suggested for future studies. After the first perturbation, especially if a bout of slip perturbations were experienced first, participants were encouraged to attempt to walk as normally as possible, however many exhibited signs of muscle stiffness, reduced arm swing and other strategies to decrease the available degrees of freedom (Bongaardt & Meijer, 2000) as they attempted to anticipate the upcoming perturbation. A significant strength of the treadmill based system when compared with the over-ground systems used elsewhere is grounded in the ability to truly randomize

perturbation onset. Sliding platforms suffer from being fixed in a location, and despite the capability to randomize the trials in which they are released, knowledge of its location allows participants to adopt anticipatory strategies (Cham & Redfern, 2002) that may influence their behavior. With the treadmill based system, participants could be perturbed at any time during locomotion, and as a consequence of this, it was observed that they were always in a heightened state of stress or anticipation during testing. Future studies employing a dual or secondary task may help to redistribute cognitive loading to a more real-world state, limiting participant ability to focus solely upon postural recovery, thereby making observations theoretically more comparable with day-to-day trip and slip responses.

Finally, ensuring participant motivation during the study of motor control is a common problem, however when comparing two very different scenarios of motor control, namely a set of simple experimental tasks and very challenging tasks associated with previous experiences of injury, motivation becomes very important. The greater risk involved with gait perturbations was considered to be one of the main sources of the high variability in responses observed among individuals as they attempted to navigate the slips and trips, where 'survival' likely provides very different set of motivations than those experienced during the performance of a simple motor adaptation task. The recent results of Gajda et al. (2016) highlight these issues, and it is suggested that greater care be taken when considering individual motivation during future studies of motor adaptation and its relationship with fall risk.

V.IV Conclusions

The set of studies presented here are the first to demonstrate a strong within-individual relationship among upper-extremity manual and lower-extremity locomotor adaptation performance. The results of Experiment 1 support hypotheses of a common mechanism responsible for plastic adaptation, that is, the achievement of a steady-state motor performance after errors are introduced due to a change in the environment. The cerebellum is typically believed to control this behavior, acting as a performance monitoring system responsible for the comparison between predicted and actual sensorimotor consequences in order to update one's internal model and optimize performance. This provides support for the theory of adaptive generalizability in a novel and unexplored experimental framework.

Experiment 2 was the first study to explore the relationship between plastic and strategic adaptation across different task domains, within the same individual. The motivation here was to bring the understanding of motor adaptation out of the laboratory and relate these findings to the real-world application of locomotor challenges and dynamic fall risks. These results were preliminary and not decisively conclusive. No relationships were observed between postural recovery performance during slips or trips and individual sensorimotor adaptation performance during initial exposure to the perturbations. After a bout of 10 postural recovery attempts, a weak relationship emerged among locomotor adaptation performance and the total time required to recover from a slip perturbation and return to normal walking. No relationships were observed between adaptation performance and trip recovery performance after training (repeated trips). Re-interpreting performance as a percent change (% improvement) between the first and final perturbations served to highlight moderate predictive relationships between individual adaptation performance and postural

recovery time during slips and trips. It is hypothesized that these relationships represent a deeper connection between short-term strategic adaptation and traditional plastic adaptation observed during simple motor adaptation tasks than previously observed. These interpretations are preliminary and require significant future work.

Given the novelty of the gait perturbation system used, an assessment of its functionality to produce repeatable and challenging trips and slips was performed. In terms of postural recovery, individual recovery step reaction time (RT), maximum recovery step reaction force (maxRSF) and the time required to return to normal gait (time to recover, TTR) were measured for all slips and trips. RT measured between perturbation onset and the first self-righting recovery step were mostly unchanged with repeated exposure, suggesting a biomechanical limitation to this response. maxRSF and TTR were both observed to decrease with repeated exposures to the slip and trip perturbations, as expected. These results are important, because it shows that, on average, participants can improve their responses to the perturbations and support future notions of using it as a tool for training or for rehabilitation purposes. The ability to transfer this training from trips to slips, and vice versa, was estimated using a crossover design. No transfer effects upon maxRSF or TTR were observed during novel slip recovery after a training session of trips, or novel trip recovery after a training session of slips. RT, however, was observed to be improved when recovering from a trip after a training bout of slips, suggesting some ‘priming’ of the response was generated during the challenging slip perturbations, which was not ‘primed’ after trip training.

Anecdotally, the slip perturbations were described by participants, and observed by investigators, to provide a significant challenge to maintaining postural stability. It is unknown how well this level of difficulty will transfer to other populations, especially those

inherently at greater risk of falling, such as the elderly, or those with balance and gait impairment. After a significant amount of use, it is strongly suggested that more pilot work be done to determine the best slip protocol for different populations using the split-belt treadmill system.

Despite the limitations, these results provide exciting new support for the application of adaptive generalizability to improve the current efforts of adaptability training as a sensorimotor spaceflight countermeasure. The results from Experiment 1 suggest that individuals can be assessed for their adaptation performance using simple laboratory based measurements, and it is possible this performance can be used to help guide and design individualized sensorimotor training paradigms to improve adaptation to more challenging environments. Furthermore, the relationships among locomotor adaptation and postural recovery training suggest that adaptation performance is indicative of those who will benefit most from repeated trip and slip simulations. These findings have real-world implications for a novel preparatory training regimen, useful while en-route during exploration-class missions, such as a mission to Mars, where fall related injuries after landing would be catastrophic. The results from these studies lay the groundwork for the development of these training and assessment protocols, and support the continued exploration of adaptation performance assessment and improvement through cerebellar stimulation studies, as well as better understanding how postural recovery from treadmill induced perturbations relates to over-ground locomotor challenges.

From a rehabilitation point of view, these studies support the notion of exploring the effects of aging and other fall-risk related pathologies, upon the relationship among locomotor adaptation performance and treadmill induced gait perturbations. Treadmill slip

training is already gaining some traction as a viable rehabilitation tool for aging individuals, and if locomotor adaptation performance is predictive of the efficacy of this slip training, or its transfer to opposing perturbations or over-ground challenges, these results may provide the foundation for a new set of training tools to improve postural recovery performance in individuals at-risk for falling.

VI. References

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Appendix A

Modified Physical Activity Readiness Questionnaire (PAR-Q)

Participant Code:	Date:
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For most people physical activity should not pose any problem or hazard. PAR-Q has been designed to identify the small number of adults for whom physical activity might be inappropriate or those who should have medical advice concerning the type of activity most suitable for them. Common sense is your best guide in answering these few questions. Please read them carefully and mark the yes or no opposite the question as it applies to you.

Yes	No	1) Has a physician ever said you have a heart condition <u>and</u> you should only do physical activity recommended by a physician?
Yes	No	2) When you do physical activity, do you feel pain in your chest?
Yes	No	3) In the past month have you had chest pain when you were not doing physical activity?
Yes	No	4) Do you lose your balance because of dizziness or do you ever lose consciousness?
Yes	No	5) Do you have a joint or a bone condition or problems with your feet? If so, specify:
Yes	No	6) Do you have insulin dependent diabetes or related conditions? If so, specify:
Yes	No	7) Do you have any breathing difficulties or suffer from asthma?
Yes	No	8) Do you suffer from epilepsy?
Yes	No	9) Do you have any neurological conditions? If so, specify:
Yes	No	10) Have you had a major operation? If so, specify (what, when):
Yes	No	11) Do you suffer from any other medical conditions? If so, specify:
Yes	No	12) Do you know of any other reason you should not exercise or increase your physical activity?
Yes	No	13) Are you using any medication currently or have been using any in the last week? If so, what kind of medication did you use?
Yes	No	14) Do you require vision correction?
Yes	No	15) If Yes to 14) Are you willing/able to wear contact lenses?

Appendix B

Table 24: Individual subject adaptation curve fit parameters for each manual and locomotor task, including R² ('goodness-of-fit') and standard error (SE). Adaptation performance is represented in number of attempts (manual task) and number of strides (locomotor task) with 95% confidence intervals [95%CI]. Relative standard error (%) is provided as a percentage ratio of the SE and adaptation performance measure (1/k). Mean and standard deviation (SD) of the population are provided below. Sensitivity Analysis outlines changes in the mean/SD at different thresholds of estimate exclusion, based on either R² or %RSE, including the number of samples included in each threshold defined estimate.

Subject	Manual Task (Joystick Matching)				Locomotor Task (Split-belt Walking)			
	R ²	1/k [95%CI]	SE	RSE(%)	R ²	1/k [95%CI]	SE	RSE(%)
1601	0.2467	18.17 [-23.53 59.87]	21.28	117.10	0.7895	130.62 [117.72 143.52]	6.58	5.04
1602	0.5221	11.74 [-23.37 46.85]	17.91	152.62	0.2327	64.50 [43.76 85.24]	10.58	16.41
1603	0.2844	8.46 [-4.49 21.41]	6.61	78.10	0.4921	42.29 [11.79 72.79]	15.56	36.79
1604					0.5335	170.10 [100.43 239.76]	35.54	20.90
1605	0.6003	15.03 [9.27 20.79]	2.94	19.55	0.3801	74.85 [36.87 112.84]	19.38	25.89
1606	0.4090	13.50 [-22.86 49.86]	18.55	137.39	0.4833	46.30 [34.70 57.90]	5.92	12.78
1607	0.1767	11.42 [-8.99 31.83]	10.41	91.16	0.8062	67.60 [57.10 78.10]	5.36	7.92
1608	0.1883	10.58 [1.55 19.61]	4.61	43.55	0.7494	84.25 [68.25 100.25]	8.16	9.69
1609	0.5378	9.34 [5.12 13.56]	2.15	23.05	0.1212	28.84 [18.31 39.37]	5.37	18.63
1610	0.3726	15.94 [-32.03 63.91]	24.47	153.53	0.8081	69.41 [62.88 75.94]	3.33	4.80
1611					0.3513	103.65 [66.35 140.95]	19.03	18.36
1613	0.6001	10.13 [6.41 13.85]	1.90	18.71	0.4882	63.37 [48.93 77.81]	7.37	11.63
1615	0.3611	25.31 [-137.80 188.41]	83.22	328.84	0.5718	159.90 [110.88 208.92]	25.01	15.64
1616	0.4905	19.89 [6.62 33.16]	6.77	34.03				
1618	0.5221	19.23 [6.59 31.87]	6.45	33.54	0.6444	134.05 [77.81 190.28]	28.69	21.40
1619	0.6580	15.72 [7.62 23.82]	4.13	26.29	0.2045	101.09 [64.89 137.29]	18.47	18.27
1620	0.4058	57.61 [-3.56 118.78]	31.21	54.18	0.7487	207.47 [178.55 236.39]	14.76	7.11
1621	0.5939	20.35 [8.20 32.50]	6.20	30.46	0.7531	104.73 [93.39 116.07]	5.79	5.52
1622	0.7301	13.44 [5.51 21.37]	4.05	30.09	0.4070	44.08 [34.70 53.46]	4.79	10.86
1623	0.5759	18.09 [10.37 25.81]	3.94	21.77				
1624	0.4870	20.30 [9.65 30.95]	5.43	26.77	0.8028	53.83 [47.91 59.75]	3.02	5.61
1625	0.3970	10.17 [6.91 13.43]	1.66	16.35	0.8213	21.50 [10.17 32.83]	5.78	26.89
1626	0.4493	12.76 [9.59 15.94]	1.62	12.68	0.5517	43.79 [22.19 65.39]	11.02	25.17
1627	0.4842	14.59 [6.99 22.19]	3.88	26.57	0.5880	62.80 [53.84 71.76]	4.57	7.28
1628	0.8295	16.35 [-1.36 34.06]	9.04	55.27	0.5456	35.25 [16.13 54.37]	9.76	27.68
1629	0.5347	22.06 [14.10 30.03]	4.06	18.42	0.7930	86.77 [71.41 102.13]	7.84	9.03
1630	0.3406	23.04 [12.63 33.45]	5.31	23.05	0.6636	71.37 [58.53 84.21]	6.55	9.18
1631	0.1716	36.52 [11.51 61.53]	12.76	34.94	0.7882	118.16 [106.06 130.26]	6.17	5.22
1634	0.0845	15.24 [-32.06 62.53]	24.13	158.34	0.7078	43.41 [38.02 48.80]	2.75	6.34
1636	0.2862	25.09 [-3.86 54.04]	14.77	58.86	0.8841	119.79 [111.59 127.99]	4.18	3.49
1637	0.8004	15.32 [12.08 18.56]	1.65	10.79	0.8034	60.56 [54.20 66.92]	3.24	5.36
1638	0.3582	30.07 [3.87 56.27]	13.37	44.45	0.5440	105.58 [91.91 119.24]	6.97	6.60
1640	0.4993	9.22 [2.80 15.64]	3.28	35.53	0.8535	41.33 [38.23 44.43]	1.58	3.83
1641	0.5580	22.14 [9.86 34.42]	6.27	28.30	0.6730	64.43 [58.07 70.79]	3.24	5.03
1642	0.8545	11.71 [8.44 14.98]	1.67	14.25	0.7042	40.29 [26.09 54.49]	7.24	17.98
1643	0.8522	17.67 [14.06 21.28]	1.84	10.43	0.2791	77.70 [3.00 152.40]	38.11	49.05
1644	0.2551	22.31 [10.67 33.95]	5.94	26.62	0.7532	109.38 [98.38 120.38]	5.61	5.13

Subject	Manual Task (Joystick Matching)				Locomotor Task (Split-belt Walking)			
	R ²	1/k [95%CI]	SE	RSE(%)	R ²	1/k [95%CI]	SE	RSE(%)
1645	0.4499	22.22 [-7.29 51.73]	15.06	67.77	0.5091	87.17 [57.81 116.53]	14.98	17.18
1646	0.5609	22.95 [14.13 31.76]	4.50	19.60	0.2876	106.49 [39.39 173.59]	34.24	32.15
1647	0.8290	17.24 [14.90 19.58]	1.19	6.93	0.7964	78.46 [68.40 88.53]	5.14	6.54
1649	0.4208	23.34 [18.92 27.76]	2.26	9.66	0.5683	98.21 [81.22 115.20]	8.67	8.83
1650	0.4072	36.89 [-77.96 151.75]	58.60	158.84	0.5561	128.73 [111.13 146.33]	8.98	6.98
1651	0.5121	42.55 [9.04 76.06]	17.10	40.18	0.7088	181.50 [163.70 199.30]	9.08	5.00
1653	0.2540	30.09 [11.25 48.93]	9.61	31.94	0.8260	137.82 [125.22 150.42]	6.43	4.66
1654	0.6922	10.15 [5.77 14.53]	2.23	22.02	0.8390	67.24 [58.64 75.84]	4.39	6.53
1655	0.2361	26.56 [20.12 32.99]	3.28	12.36	0.3930	104.47 [60.47 148.47]	22.45	21.49
1656	0.4383	13.47 [8.62 18.31]	2.47	18.34	0.0634	26.62 [7.25 45.99]	9.88	37.13
1657	0.4119	12.91 [7.04 18.77]	2.99	23.18	0.6427	68.16 [50.24 86.08]	9.14	13.41
1658	0.6269	20.07 [12.70 27.44]	3.76	18.73	0.0656	101.90 [27.50 176.30]	37.96	37.25
1659	0.5599	23.03 [15.18 30.88]	4.01	17.39	0.8313	124.57 [113.77 135.37]	5.51	4.42
1660	0.3832	30.75 [8.21 53.29]	11.50	37.40	0.6362	145.05 [117.15 172.95]	14.23	9.81
1661	0.3779	12.67 [3.86 21.48]	4.49	35.48	0.3736	53.98 [29.58 78.38]	12.45	23.06
1662	0.6184	28.71 [6.02 51.40]	11.58	40.33	0.7132	128.09 [108.69 147.49]	9.90	7.73
1663	0.6400	20.87 [9.76 31.98]	5.67	27.17	0.8859	83.44 [77.97 88.91]	2.79	3.34
1664	0.4474	20.07 [8.59 31.55]	5.86	29.18	0.5502	83.77 [60.67 106.87]	11.79	14.07
1665	0.6749	25.68 [17.43 33.93]	4.21	16.39	0.7435	121.15 [105.05 137.25]	8.21	6.78
1666	0.7769	16.50 [12.86 20.14]	1.86	11.24	0.3584	76.19 [58.51 93.87]	9.02	11.84
1667	0.3405	25.12 [-17.57 67.80]	21.78	86.71	0.8589	105.37 [123.97 4.74]	4.74	4.14
Total (N = 54)								
	R ²	1/k	SE	RSE(%)	R ²	1/k	SE	RSE(%)
Mean	0.4850	20.01	10.13	48.69	0.5983	88.76	11.02	13.73
Std.Dev.	0.1855	9.05	13.90	55.64	0.2200	40.84	9.14	10.47
Sensitivity Analysis								
0.25 > R² > 1.0 (N = 43)								
	R ²	1/k	SE	RSE(%)	R ²	1/k	SE	RSE(%)
Mean	0.5214	20.04	9.82	39.60	0.6439	91.13	10.49	12.57
Std.Dev.	0.1607	9.04	14.44	37.56	0.1709	40.77	8.67	9.81
0.50 > R² > 1.0 (N = 15)								
	R ²	1/k	SE	RSE(%)	R ²	1/k	SE	RSE(%)
Mean	0.6504	18.79	5.51	29.49	0.7137	96.36	8.67	9.68
Std.Dev.	0.1140	7.16	4.49	27.50	0.1137	42.97	7.00	6.74
0 > RSE > 100 (N = 47)								
	R ²	1/k	SE	RSE(%)	R ²	1/k	SE	RSE(%)
Mean	0.5056	20.07	6.52	31.02	0.5987	88.76	11.02	13.73
Std.Dev.	0.1833	9.17	5.84	19.36	0.2196	40.84	9.14	10.47
0 > RSE > 50 (N = 40)								
	R ²	1/k	SE	RSE(%)	R ²	1/k	SE	RSE(%)
Mean	0.5133	19.46	5.01	24.47	0.5987	88.76	11.02	13.73
Std.Dev.	0.1790	7.55	3.61	9.88	0.2196	40.84	9.14	10.47

Appendix C

To assess the impact of curve fitting quality (goodness-of-fit) and parameter estimate uncertainty (SE), exclusionary thresholds were selected to remove ‘poor-fit’ (decreased R^2) and ‘high error’ (increased %RSE) estimates, see Table 24 – Sensitivity Analysis. The impact of the exclusion of these estimates was assessed by observing the relative changes in the results of simple linear regression analysis proposed for Experiment 1. The goal here was to minimize poorer estimates and poorer fits (remove high %RSE and decreased R^2) and observe the changes in the relationship (R^2) and slope among manual and locomotor adaptation performance, estimated by Equation 4.

Evaluation of the R^2 values among manual and locomotor adaptation showed a decreased mean ‘goodness-of-fit’ in the manual task when compared with the locomotor task, 0.482 ± 0.19 and 0.598 ± 0.22 , respectively. When compared with values observed in the motor control literature, these fits appear to compare well. Heathcote et al. (2000) observed a mean $R^2 = 0.498$ over thousands of individual practice trials, and other published studies describe values ranging from $R^2 = 0.293$ (including all subjects, $R^2 = 0.48$ selectively) (Liu et al., 2003) to $R^2 = 0.60$ (Newell et al., 2001) provide support for the values observed. To better understand the impact of the weakest fits ($R^2 < 0.25$) upon the mean R^2 , they were removed, yielding increased values for both manual and locomotor adaptation, 0.523 ± 0.16 and 0.644 ± 0.17 respectively, reducing the total population to $N=43$. A final observation of the mean of the best fits ($R^2 > 0.5$) yielded averages for manual and locomotor adaptation of 0.650 ± 0.11 and 0.714 ± 0.11 , respectively, which are much higher than those typically reported in the literature, however reduced the sample population to $N=15$. These population reductions also impacted %RSE, which can be observed in Appendix B.

Evaluation of the mean error rates (%RSE) among manual and locomotor adaptation showed a higher rate in manual tasks than locomotor tasks, $48.7 \pm 55.7\%$ and $13.7 \pm 10.5\%$, when all samples were considered. The error rate in locomotor adaptation estimates was interpreted to be fairly low and mostly consistent, which was deemed acceptable. In the population sample of locomotor adaptation, only one extreme value was observed with a %RSE of 49.1% (Subject 1643), which did not appear to dramatically influence the overall observed uncertainty. Manual adaptation, however, exhibited 7 extreme values, the greatest of which suggested an uncertainty of 328% (Subject 1615). The adaptation curve and raw data for this participant is provided below, see Figure 27, for context. It is clear that the expected behavior of adaptation is observed over multiple trials, reinforced by the accelerated learning/improvement during re-adaptation (green dots), but within-individual variability and noise dramatically increase the uncertainty of this parameter estimate.

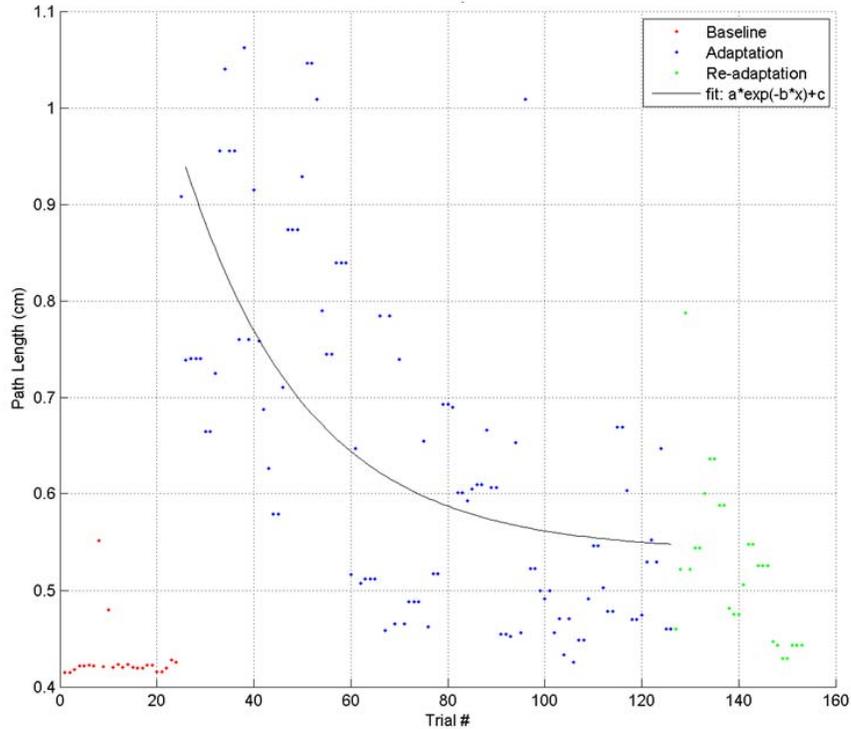


Figure 27: Manual task performance for Subject 1615 showing a clear learning trend and decent curve fitting performance $R^2 = 0.361$, however exemplifies high levels of noise and variability in performance. This dramatically increases the uncertainty of the adaptation coefficient estimate using curve fitting techniques.

Removal of all extreme %RSE values ($\%RSE > 100\%$) resulted in a decrease in mean %RSE to $31.0 \pm 19.4\%$ for manual adaptation, no change in locomotor adaptation (no extreme values), and an overall sample population of $N = 47$. This %RSE was determined to be fairly acceptable, and not far from the CDC guidelines of $RSE\% < 30\%$ (Klein et al., 2002) for data suppression in qualitative assessments. Some high outliers were still observed in the population at this RSE rate, therefore a final decimation was performed, removing all %RSE $> 50\%$, resulting in mean %RSE values of 24.47 ± 9.9 and 13.73 ± 10.5 (no change) in manual and locomotor adaptation estimates, respectively, and a resultant sample of $N = 40$. These population reductions also had effects on mean R^2 values, evidenced in Appendix B.

Two data sets were generated to estimate the strength of the relationship among locomotor adaptation ($1/k$) and manual adaptation ($1/k$) (Larsen, 2004; Weaver & Wuensch, 2013): one which varies inclusion of samples based on R^2 values (three levels: all R^2 , $R^2 > 0.25$ and $R^2 > 0.5$) and one which varies samples based on %RSE (three levels, all %RSE, %RSE < 100 and %RSE < 50). Dummy-coded linear regression, see Equation 5, was performed to test the null hypotheses that the intercept and slopes (parallelism) of each set of regressions are not significantly different, using the following generalized model:

$$Y = \beta_0 + \beta_1x + \beta_2z_a + \beta_3z_b + \beta_4x \times z_a + \beta_5x \times z_b + \varepsilon$$

Equation 5: Dummy coded multiple regression to test null hypotheses for the equivalence of intercept and slope among two sets of adaptation performance data. Z_a and Z_b are dummy variables.

Where:

$$Y = (k^{-1})_{locomotor} \text{ and } x = (k^{-1})_{manual}$$

Testing:

Equality of intercepts null hypothesis:

$$\beta_2 = \beta_3 = \beta_4 = \beta_5$$

Equality of slopes null hypothesis:

$$\beta_4 = \beta_5 = 0$$

For R^2 , where:

$$z_a = \begin{cases} 1 & \text{for all } R^2 \\ 0 & \text{otherwise} \end{cases}$$

$$z_b = \begin{cases} 1 & \text{for } R^2 > 0.25 \\ 0 & \text{otherwise} \end{cases}$$

Therefore:

$z_a = 1, z_b = 0$: all samples included in model

$z_a = 0, z_b = 1$: samples with $R^2 > 0.25$ included in model

$z_a = 0, z_b = 0$: samples with $R^2 > 0.50$ included in model

Simple linear regressions were performed for each model to ensure assumptions of normality of the residuals were met. Levene's test for equality of variance among the three models was found to not be significant, therefore this assumption was met. Figure 28 provides a scatter plot to visualize the distribution of data sets and their associated linear regressions.

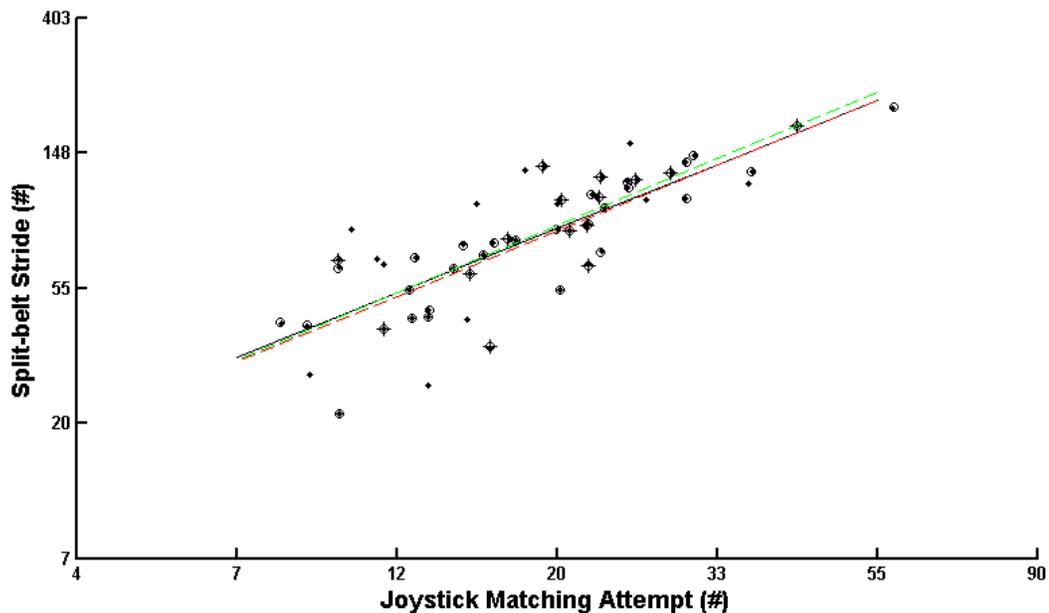


Figure 28: Scatter plots of the natural logarithm transformed $1/k$ for: 1) All R^2 values (black dots) and black solid line, $N = 54$, 2) $R^2 > 0.25$ (open circles) and red-dashed line, $N=43$, and 3) $R^2 > 0.50$ (+) and green-dashed line, $N=15$. Axes are presented in the exponential (untransformed) representation of the transformed data to aid interpretation of adaptation performance.

The full ANOVA table and SPSS Syntax are provided below in Table 25. No significant differences were observed among the 3 regression models, suggesting the relationship

observed among locomotor adaptation performance and manual adaptation performance was not influenced by increased manual task performance estimate certainty. It was observed that the intercepts were not observed to differ significantly from one another ($F_{2,108} = 0.045, p = 0.956$) suggesting the equality of intercepts null hypothesis could not be rejected, nor were the slopes observed to differ significantly ($F_{2,106} = 0.042, p = 0.958$), suggesting the equality of slopes null hypothesis could not be rejected.

Table 25: ANOVA table for dummy-value linear regression testing null hypotheses of equality of intercepts and parallelism of slopes among 3 models of adaptation performance with various levels of uncertainty based on model fit (R^2). No significant differences were observed among intercepts or slopes.

ANOVA^a

Model		Sum of Squares	df	Mean Square	F	Sig.	R Square Change	
1	Regression	17.225	1	17.225	216.860	.000 ^b		
	Residual	8.737	110	.079				
	Total	25.962	111					
2	Subset Tests	Za, Zb	.010	2	.005	.060	.942 ^c	.000
	Regression		17.234	3	5.745	71.092	.000 ^d	
	Residual		8.727	108	.081			
	Total		25.962	111				
3	Subset Tests	ZaX, ZbX	.007	2	.004	.043	.958 ^c	.000
	Regression		17.242	5	3.448	41.916	.000 ^e	
	Residual		8.720	106	.082			
	Total		25.962	111				

a. Dependent Variable: log_sb

b. Predictors: (Constant), log_joy

c. Tested against the full model.

d. Predictors in the Full Model: (Constant), log_joy, Zb, Za.

e. Predictors in the Full Model: (Constant), log_joy, Zb, Za, ZaX, ZbX.

For %RSE, where:

$$z_a = \begin{cases} 1 & \text{for all \%RSE} \\ 0 & \text{otherwise} \end{cases}$$

$$z_b = \begin{cases} 1 & \text{for \%RSE} < 100 \\ 0 & \text{otherwise} \end{cases}$$

Therefore:

$z_a = 1, z_b = 0$: all samples included in model

$z_a = 0, z_b = 1$: samples with %RSE less than 100% included in model

$z_a = 0, z_b = 0$: samples with %RSE less than 50% included in model

Simple linear regressions were performed for each model to ensure assumptions of normality of the residuals were met. Levene's test for equality of variance among the three models was found to not be significant, therefore this assumption was met. Figure 29 provides a scatter plot to visualize the distribution of data sets and their associated linear regressions.

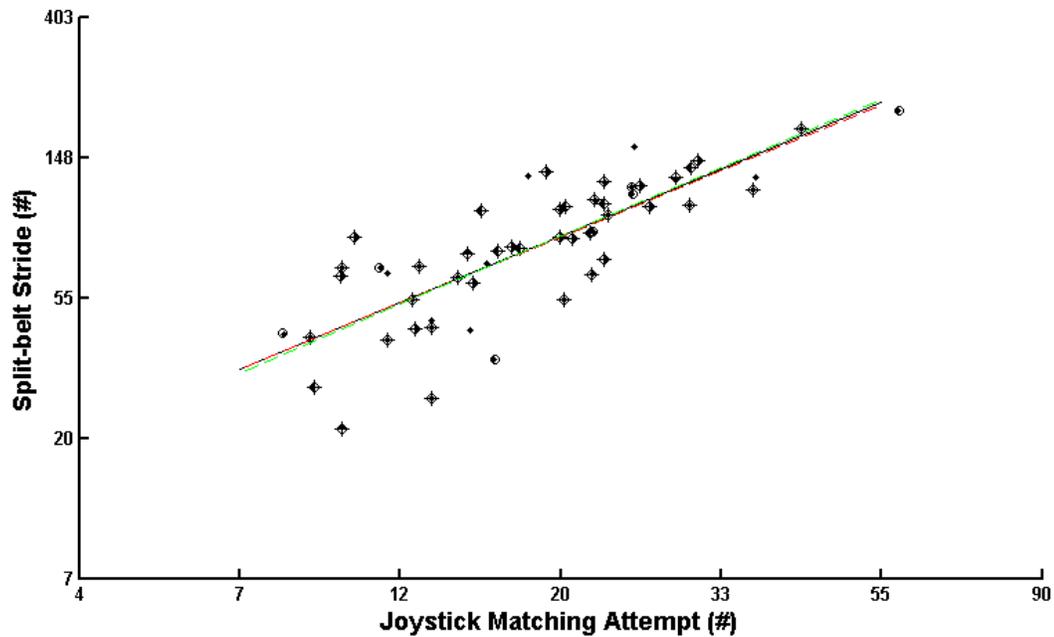


Figure 29: Scatter plots of the natural logarithm transformed $1/k$ for: 1) All %RSE values (black dots) and black solid line, $N = 54$, 2) %RSE < 100 (open circles) and red-dashed line, $N=47$, and 3) %RSE < 50 (+) and green-dashed line, $N=40$. Axes are presented in the exponential (untransformed) representation of the transformed data to aid interpretation of adaptation performance.

The full ANOVA table is provided below, see Table 26. No significant differences were observed among the 3 regression models, suggesting the relationship observed among locomotor adaptation performance and manual adaptation performance was not influenced by increased manual task performance estimate certainty. It was observed that the intercepts were not observed to differ significantly from one another ($F_{2,137} = 0.011, p = 0.990$) suggesting the equality of intercepts null hypothesis could not be rejected, nor were the slopes observed to differ significantly ($F_{2,135} = 0.025, p = 0.976$), suggesting the equality of slopes null hypothesis could not be rejected.

Table 26: ANOVA table for dummy-value linear regression testing null hypotheses of equality of intercepts and parallelism of slopes among 3 models of adaptation performance with various levels of uncertainty based on parameter standard error. No significant differences were observed among intercepts or slopes.

ANOVA^a

Model		Sum of Squares	df	Mean Square	F	Sig.	R Square Change
1	Regression	21.449	1	21.449	247.159	.000 ^b	
	Residual	12.063	139	.087			
	Total	33.512	140				
2	Subset Tests Za, Zb	.002	2	.001	.011	.990 ^c	.000
	Regression	21.451	3	7.150	81.220	.000 ^d	
	Residual	12.061	137	.088			
	Total	33.512	140				
3	Subset Tests ZaX, ZbX	.004	2	.002	.025	.976 ^c	.000
	Regression	21.455	5	4.291	48.048	.000 ^e	
	Residual	12.056	135	.089			
	Total	33.512	140				

a. Dependent Variable: log_sb

b. Predictors: (Constant), log_joy

c. Tested against the full model.

d. Predictors in the Full Model: (Constant), log_joy, Za, Zb.

e. Predictors in the Full Model: (Constant), log_joy, Za, Zb, ZbX, ZaX.

SPSS Syntax (IBM, SPSS v20.0.0)

```
compute Za = 0.  
compute Zb = 0.  
if Condition = 1 Za = 1.  
if Condition = 2 Zb = 2.  
compute ZaX = Za*log_joy.  
compute ZbX = Zb*log_joy.  
EXECUTE.
```

REGRESSION

```
/MISSING LISTWISE  
/STATISTICS COEFF OUTS CI(95) R ANOVA CHANGE  
/CRITERIA=PIN(.05) POUT(.10)  
/NOORIGIN  
/DEPENDENT log_sb  
/METHOD=ENTER log_joy  
/METHOD=test(Za Zb)  
/METHOD=test(ZaX ZbX)  
/SCATTERPLOT=(*ZRESID ,*ZPRED)  
/RESIDUALS HISTOGRAM(ZRESID) NORMPROB(ZRESID).
```

Appendix D

UNIVERSITY OF HOUSTON

CONSENT TO PARTICIPATE IN RESEARCH

PROJECT TITLE: Leveraging sensorimotor adaptive generalizability to minimize static and dynamic fall risk.

You are being invited to participate in a research project conducted by Stefan Madansingh from the Department of Health and Human Performance at the University of Houston. This project is in support of Mr. Madansingh's doctoral dissertation. It will be conducted under the supervision of Dr. Charles Layne.

NON-PARTICIPATION STATEMENT

Your participation in this study is completely voluntary. You do not have to participate if you don't want to. You may also leave the study at any time. If you leave the study before it is finished, there will be no penalty to you. You may also refuse to answer any question. If you are a student, a decision to participate or not or to withdraw your participation will have no effect on your standing.

PURPOSE OF THE STUDY

The purpose of this dissertation is to observe how individuals adapt to various sensory and motor stressors during upper extremity tasks, lower extremity tasks, static upright balance and dynamic balance during walking on a treadmill. Using these adaptation observations, predictive models of performance will be developed for static and dynamic balance, which are related to fall risk and one's ability to avoid fall-related injuries. We believe that a better understanding of individual responses to new and novel sensory or motor environments will help predict one's ability to avoid a life-threatening fall, and ultimately aid in the development of improved and individualized fall-risk minimization strategies.

PROCEDURES

You will be one of approximately 64 people to be asked to participate in this project. All experiments will be conducted at the Center for Neuromotor and Biomechanics Research (CNBR) at the National Center for Human Performance (NCHP) in the Texas Medical Center. The CNBR is one of the UH research labs associated with the Department of Health & Human Performance. Upon arriving for the study session, you will review this consent document, complete the PAR-Q, ask any questions you might have, and sign the consent form.

This experiment will take place over the span of one testing session, which will include 4 experimental protocols. A description of each task, is provided below, however the order in which you perform them will likely be different. All tasks must be completed to complete the study.

Following the consent process, we will ask your age and measure your height and body weight for the parameter setting, which will be used to calibrate our data collection systems. We ask that you wear athletic, non-reflective clothing, including a form fitting T-shirt and athletic shorts.

Joystick Matching Task (JOY)

For this task, you will be positioned in front of a laptop display and provided with a video game controller which has two joysticks. This controller will be fixed to the table, and in line with the laptop screen, both of which will be adjusted to a comfortable height. Throughout this trial, you will remain standing. To interact with the joystick controller, you will use your dominant hand and, at most, your thumb, index and middle finger in a pinch-style grip. A series of demonstration images and video will be provided to clearly explain the procedures for this protocol. In this protocol, you will attempt to move the joystick in order to move the on-screen cursor from the center of the screen to the target which is displayed either up, down, left or right of center. You will perform a series of baseline, adaptation and re-adaptation trials, all with the same goal of moving the centered cursor to the target. Once the cursor meets the target, you will let go of the joystick and allow it to return to center automatically. There will be one block of baseline target matches, four blocks of adaptation target matches and one block of re-adaptation target matches, which will take approximately 10 minutes.

Split-belt Adaptation Task (SBA)

Prior to beginning the SBA task, we will make sure that you are fitted correctly with a safety harness. Next, passive reflective markers will be taped to your feet, legs, torso, arms, wrists, and you will be given a marked headband to wear on your head. Once fully equipped, you will be attached to the harness safety ropes attached to a rigid support structure above the treadmill, such that any slackness in the ropes is minimized. A rectangular safety rope support structure will be customized to your height to provide information about where you are on the treadmill.

You will be experience walking on the split-belt treadmill at 1.0m/s, which is considered an average-to-brisk walking pace. You will be asked to practice walking at this speed with your vision fixed on an 'X' marker, at eye-level. You will be instructed to maintain your gaze at the fixed marker for the duration of the entire protocol. After 2 minutes of normal walking, you will be briefly introduced to the split-belt protocol. The belt speeds will be changed, where one belt speed is increased and one is decreased. This will last for approximately 20 seconds. After this introduction, the belt speeds will return to the original speed of 1.0m/s and you will walk here for another 2 minutes. The treadmill will then be stopped and you will have up to 5 minutes to rest before beginning the beginning of the trial. Throughout the trial, a spotter will be present with you near the treadmill and the PI will control a safety switch.

After the familiarization session and break, you will be repositioned on the treadmill and asked to walk at the same speed for 3 minutes, where both belts will move at the same speed (1.0m/s). After 3 minutes, the speed of the belts will be split, where one will increase in speed and the other will decrease. Here, you will walk for 12 minutes at two different speeds.

At the end of these 12 minutes, the belts will be returned to the original walking speed for a final 3 minutes. This will mark the end of the SBA protocol.

Sensory Organization Tests (SOTs) and Motor Control Tests (MCTs)

Prior to beginning the SOT and MCT tasks, we will make sure that you are fitted correctly with a safety harness. Next, the size and width of your feet will be measured using the standard Brannock device, similar to those found in shoe stores. These measures will be used during the SOT and MCT tests. At this point, you will be introduced to the NeuroCom EquiTest device, which is the gold standard for clinical balance measurements. In this device, you will complete 3 SOT tests and 1 MCT test.

Prior to every test, the instructions will be explained and asked to be repeated to ensure clear communication and understanding. For the first SOT test, SOT1, you will be asked to simply stand quietly with your arms at your side, facing forward, for 30 seconds. You will be asked to maintain your gaze as best as possible and refrain from any head or arm movements, as well as any talking or observing any distractions. For SOT2, you will complete a similar test, however your eyes will be closed during the 30 second trial. You will complete 2 trials of SOT2 before moving onto SOT5. In SOT5, you will complete a similar task to SOT2, where your eyes will be closed and you will need to try and maintain your upright balance, however in this situation the support surface you are standing on will be free to move. In this task, the support surface will be ‘sway referenced,’ which means that it will tilt upwards or downwards depending on your balance, and whether you are leaning forward or backward. In this position, you will attempt to maintain your balance as best as possible. If you feel the need to take a step to maintain your balance, please do so, however we will mark this trial as a fall, and will need to repeat it. You will, again, complete SOT5 two times.

After completing the SOT measures, you will be provided with an optional rest period of 5 minutes before continuing with the mMCT. Upon beginning the mMCT, you will be reattached to the harness of the NeuroCom system, and instructed that the support platform may shift rapidly forwards or backwards. In this protocol, you will experience 20 rapid forward translations, all with your eyes open, and your goal will be to maintain your upright posture as best as possible, similar to previous trials. After 20 exposures to this perturbation, you will be detached from the NeuroCom harness system and this will mark the end of the SOT/mMCT protocol.

Treadmill Induced Slip and Trip Perturbations (STP)

Prior to beginning the STP task, we will make sure that you are fitted correctly with a safety harness. Next, passive reflective markers will be taped to your feet, legs, torso, arms, wrists, and you will be given a marked headband to wear on your head. Once fully equipped, you will be attached to the harness safety ropes attached to a rigid support structure above the treadmill, such that any slackness in the ropes is minimized.

Once fully equipped, you will be attached to the harness safety ropes attached to a rigid support structure above the treadmill, such that any slackness in the ropes is minimized. At this point, you will be notified that the treadmill will begin to move. You will provide us with

information regarding your comfortable walking speed, indicating whether the treadmill walking speed should be increased or decreased until comfortable. You will be asked to practice walking at this comfortable walking speed with your vision fixed on an 'X' marker, at eye-level. At this point, a trip familiarization session will begin, whereby we will notify you of an upcoming treadmill based trip, upon which foot it will occur, and in how many steps. Trips will be accomplished by decelerating a treadmill belt under one foot until a recovery step has taken place with the un-tripped foot. We will repeat this familiarization on the opposite foot. Next you will begin the slip familiarization session in which you will be notified that a slip instead of a trip will occur. During a slip, the treadmill belt will accelerate rapidly in the opposite direction of normal walking, representing a slip. We will once again repeat this slip familiarization on the opposite foot prior to beginning the experiment. Data from familiarization sessions will be collected and used as a baseline performance measure.

When you are comfortable with the tripping and slipping protocols, we will begin the treadmill at your preferred walking speed. Throughout the experiment you will experience 10 trips trials and 10 slips trials. These will be performed in a block randomized order, meaning you will receive 10 trips then 10 slips, or vice versa. Following each perturbation, you will take at least 30 steps before another trip or slip is received. After every 10 trials, you will be given the opportunity to take an optional rest period of up to 5 minutes.

In the case of any non-recovery trips or slips, you will be asked to rest and assent before continuing the protocol. Non-recovery trips or slips will be recorded and labeled as a 'fall,' and another trip or slip will be included in the protocol. If you are unable to complete the trial, the PI will determine their suitability for continuation in the study. Upon the completion of 20 successful perturbations, the testing session will be complete.

This data collection session will take approximately 2.5 hours to complete.

CONFIDENTIALITY

Any records used in the study will only be accessed by the study team members. All data records will be identified by a code assigned to you. The key that matches this code to any personal identifiers, including your name, will be kept in a locked file separate from the data records. The coded research data will be stored in a locked cabinet in the laboratory. None of the research results will become part of your personal or medical record.

RISKS/DISCOMFORTS

The experiments we are planning to conduct involve walking and balance tasks which always pose a risk to maintaining balance and include the risk of falling. We will address these risks in the following ways: For all treadmill walking trials and static balance tests using the NeuroCom EquiTest device, you will be wearing a full body safety harness. This will prevent any potential fall related injuries. Additionally, there will be a spotter beside you who will stabilize you in the case of a loss of balance. Finally, for all treadmill tests, a set of load cells attached to the harness will provide an instantaneous alert to the PI in the case of a loss of balance, and will immediately shut down all experimental technology, mitigating potential risks.

A possible source of discomfort includes fatigue. To prevent this discomfort, opportunities for rest will be provided after every protocol, and during longer sessions, within the protocol itself at regular intervals. Throughout the testing sessions, the participants will be asked to express any feelings of fatigue, in which case extra rest can be provided. In addition, very minor skin irritation could result from the removal of the taped reflective markers, but this typically disappears within a few minutes.

In the unlikely event of unexpected events/problems during data collection, the principal investigator will immediately stop the protocol, assess the need for medical attention and if necessary, notify emergency medical services (EMS) and remain with you until arrival of EMS. In the event you do not need medical attention, the principal investigator will assist you to recover and exit the study. The principal investigator will immediately report the incident to the appropriate University of Houston authorities. In the event of any harm resulting from your participation in this study, the University of Houston does not provide any financial compensation including costs for medical treatment.

BENEFITS

There will not be any direct benefits associated with this study. However, your participation will influence the development of future protocols aimed and developing new technology and techniques presently being researched for advanced sensorimotor countermeasures to microgravity adaptation.

ALTERNATIVES

Participation in this project is voluntary and the only alternative to this project is non-participation.

INCENTIVES/REMUNERATION

There will not be any incentives associated with this study. You will be reimbursed for parking at the Texas Medical Center, in the form of a validated parking token.

PUBLICATION STATEMENT

The results of this study may be published in professional and/or scientific journals. It may also be used for educational purposes or for professional presentations. You will not be identified in any of these reports or presentations. However, no individual subject will be identified.

SUBJECT RIGHTS

1. I understand that informed consent is required of all persons participating in this project.
2. I have been told that I may refuse to participate or to stop my participation in this project at any time before or during the project. I may also refuse to answer any question.
3. Any risks and/or discomforts have been explained to me, as have any potential benefits.

4. I understand the protections in place to safeguard any personally identifiable information related to my participation.
5. I understand that, if I have any questions, I may contact Stefan Madansingh at 832-729-1397 or email at simadansingh@uh.edu
6. **Any questions regarding my rights as a research subject may be addressed to the University of Houston Committee for the Protection of Human Subjects (713-743-9204).** All research projects that are carried out by Investigators at the University of Houston are governed by requirements of the University and the federal government.

SIGNATURES

I have read (or have had read to me) the contents of this consent form and have been encouraged to ask questions. I have received answers to my questions to my satisfaction. I give my consent to participate in this study, and have been provided with a copy of this form for my records and in case I have questions as the research progresses.

Study Subject (print name): _____

Signature of Study Subject: _____

Date: _____

I have read this form to the subject and/or the subject has read this form. An explanation of the research was provided and questions from the subject were solicited and answered to the subject's satisfaction. In my judgment, the subject has demonstrated comprehension of the information.

Principal Investigator (print name and title): _____

Signature of Principal Investigator: _____

Date: _____

