GENERALIZATION OF VISUOMOTOR ADAPTATION ACROSS SPATIAL REFERENCE FRAMES

by

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ABSTRACT

Motor learning is a neurological process in which movement practice or experience leads to a change in motor behavior. Prism adaptation (PA) is an early form of one type of motor learning, in which motor patterns change due to a displacement of visual information. During PA people perform a visuomotor task (e.g., reaching or throwing to a target) while wearing prism lenses over the eyes. Initial performance errors, occurring in the direction of the prism shift, are corrected through trial and error practice. When the prisms are subsequently removed, errors occur in the opposite direction and are known as aftereffects. Aftereffects indicate that the adaptation has been stored by the central nervous system.

PA has been shown to generalize (i.e., transfer to untrained contexts) in some cases, but not all. In addition, PA has been shown to improve the symptoms of some patients with the neuropathology known as neglect, a disorder of spatial representations in which patients fail to detect stimuli in the contralesional hemispace. Neglect can occur in allocentric (world-centered) or egocentric (self-centered) spatial reference frames or both. Interestingly however, most intervention studies using PA treatment have not evaluated its efficacy differentially with respect to these.

In order for PA treatment to be beneficial there must be adequate generalization to the reference frames (e.g., allocentric, egocentric) affected by the disorder. To determine how PA generalizes with respect to these spatial reference

frames, healthy participants adapted to rightward displacing prisms by throwing a ball at a target while in either a seated or side-lying position. Following adaptation participants rotated to the alternate position and were tested for aftereffects. The rotation decoupled the allocentric and egocentric reference frames, and the direction of the aftereffects was used to determine the reference frame of PA generalization.

During PA internal models of motor control are modified in response to a visual sensory prediction error that may be represented in either allocentric or egocentric coordinates, or both. Therefore aftereffects could have appeared along the same axis as the initial visual displacement (allocentric generalization), along the axis perpendicular to this (egocentric generalization), or in the region between these two axes (mixed generalization).

Results showed that when participants adapted their throwing to prisms while in a seated position, significant aftereffects appeared when side-lying, and they were expressed egocentrically. This egocentric generalization suggests PA may only be effective for treating egocentric forms of neglect. Surprisingly however, participants who adapted while lying on their side showed no significant aftereffects, in either reference frame, when tested in the seated position (i.e., the adaptation did not transfer from side-lying to seated). This lack of transfer suggests that adaptation during side-lying throwing was context specific, and this may have been due to the novelty of the throwing position.

Chapter 1

INTRODUCTION

1.1 Internal Models for Motor Control and Motor Learning

1.1.1 Motor Control

Motor control refers to the processes within the central nervous system (CNS) that are responsible for coordinated and purposeful movement. Fundamental to motor control is the successful integration of motor apparatus with sensory information received from multiple modalities regarding the current state of the world and of the body. The CNS receives this sensory information from receptors located in the peripheral nervous system and uses it to plan movements and correct movement errors. For example, reaching movements can be corrected based on either proprioceptive or visual feedback, or both. However, because of delays caused by sensory transmission time, this feedback is only effective in correcting motor errors during ongoing movements if the movement is relatively slow (Imamizu et al. 1995; Shadmehr et al. 2010). Thus, because of our demonstrated ability to perform fast movements that are highly accurate, the CNS must have some way to control movement through predictive mechanisms (Shadmehr et al. 2010; Wolpert and Miall 1996).

A prominent theory in the field of motor control that explains predictive control states that movement is planned, controlled, and learned through the use of internal models, defined as neural representations that mimic sensory to motor transformations and their inverses (Kawato 1999; Scott and Norman 2003; Wolpert and Ghahramani 2000; Wolpert et al. 1998). There are two types of internal models: forward and inverse. Inverse models are used to determine the motor commands needed to accomplish a desired movement given current sensory input (Kawato 1999; Wolpert et al. 1998). Forward models are used to predict the consequences of the motor output (Shadmehr et al. 2010; Wolpert and Miall 1996).

Motor behavior is controlled by both inverse and forward models. Inverse models control movement in a feed-forward manner through the issuance of motor commands. Forward models control movement by providing feedback to the inverse model. Specifically, forward models combine information regarding the current state of the system with efference copies of motor commands to form predictions about the sensory consequences of motor output. This information is fed back into the inverse model where it is used to control movement in a feed-forward manner (Shadmehr et al. 2010; Wolpert and Ghahramani 2000; Wolpert and Miall 1996). One benefit of forward models is that they provide feedback to the inverse model that arrives more quickly than feedback from the peripheral nervous system. This forward feedback cycle is especially important for the control of fast movements (Imamizu et al. 1995; Shadmehr et al. 2010). Another benefit is that forward models can be used to adapt inverse models to changes in the body or environment, through the comparison of predicted sensory feedback with actual sensory feedback (Shadmehr et al. 2010; Tseng et al. 2007).

1.1.2 Motor Learning

Motor learning can be defined as a neurological process, brought about through experience and practice, that leads to a relatively permanent change in one's ability to perform a motor task (Salmoni et al. 1984). As such, it is an important part of development, skill acquisition, and rehabilitation. The motor learning process culminates in simultaneous formation of the forward and inverse internal models that are subsequently used to control motor behavior (Flanagan et al. 2003; Kawato 1999; Wolpert et al. 1998).

Motor adaptation, considered to be the early stage of an error-based form of motor learning, refers to the adjustment of a previously acquired motor behavior in response to an actual or perceived change in the body or environment (Krakauer and Mazzoni 2011; Martin et al. 1996; Reisman et al. 2005). In contrast to motor learning, adaptation occurs relatively quickly and can be short term. Motor adaptation is driven by a neurophysiological error signal (Kawato 1999; Shadmehr and Krakauer 2008) that is generated as a result of a mismatch between the actual sensory feedback and the sensory feedback predicted by the forward internal model associated with a particular movement (Wolpert and Miall 1996). This error signal triggers updating of subsequent outgoing motor plans that will reduce the error (Wolpert and Ghahramani 2000) and is part of an iterative process that occurs with trial repetition until the actual and predicted sensory feedback match (Shadmehr et al. 2010; Tseng et al. 2007).

Once corrected, repeated performance of the movement leads to storage of the new motor pattern. This storage is demonstrated through the presence of aftereffects, defined as movement errors that are initially directed opposite to the original perturbation once the perturbation is removed (Shadmehr and Mussa-Ivaldi 1994; Wallace and Redding 1979; Weiner et al. 1983; Welch 1974). The existence of aftereffects is consistent with the notion that the process of motor adaptation results in the modification of an inverse internal model that is then used to control subsequent movement in a feed-forward manner (Imamizu et al. 1995; Shadmehr and Krakauer 2008).

An important aspect of both motor learning and motor adaptation is generalization, a term that refers to the ability of training in one context to transfer to other, untrained, contexts (Imamizu et al. 1995; Krakauer et al. 2006; Latash 1999; Wolpert and Miall 1996). Examples of generalization might be the ability to ride a mountain bike off road subsequent to learning how to ride a street bike, or the transfer of balancing skills developed while surfing to a new context such as snowboarding. Generalization occurs continuously throughout life and contributes to our ability to perform a large repertoire of motor behaviors in different contexts.

Interestingly, the contextual cues around which generalization of motor learning occurs are not always obvious (Krakauer et al. 2006); however they can be probed for through experiments in which subjects learn a new motor behavior, and then specific aspects of their learning are tested for transfer to unpracticed movements or conditions. This type of experiment is important for both basic and applied science. First, this knowledge can improve our overall understanding of how the CNS is functionally organized. Further, from an applied perspective, it can be helpful for developing rehabilitative interventions. For example, this information could be used to design simple, possibly single task, treatment protocols that improve performance on multiple tasks, provided the learning generalizes to the appropriate workspaces and movements. One paradigm that has been used to study generalization of motor learning for both purposes (i.e. for both basic and applied science) is prism adaptation.

1.2 Prism Adaptation

1.2.1 Paradigm and Generalization

Prism adaptation (PA) is a visuomotor adaptation in which motor patterns change based on a distortion or displacement of visual information induced by prismatic lenses (Redding et al. 2005; Newport and Schenk 2012). Adaptation to prisms was first discovered by Hermann von Helmholtz in the late 1880's (Helmholtz 1866, 1906/1962) and has been used extensively since then to study both sensorimotor organization and generalization of motor learning. Most notable is Stratton's (1897) series of experiments in which he only allowed himself to view the world through glasses designed to invert his visual field. He wore the glasses for several days and at night covered his eyes with patches. Regardless of the directional change imposed by the inverting lenses (either left to right or up to down), the results were the same - while initially his interaction with the environment was clumsy and effortful, within a few days, his movements became spontaneous. In other words, his visuomotor system adapted.

While Stratton's visual inversion took days to adapt to, adaptation to visual displacement through simple movements can occur within minutes (Harris 1963) and has been used in hundreds of experiments since Stratton's time. Typically in these studies wedge prisms are used to displace vision laterally. Initial movement errors in the direction of visual displacement are corrected through repeated performance of a simple task, such as reaching or pointing. If an adequate number of improved movements are performed, the adaptation is stored by the CNS. That is, following removal of the prisms, aftereffects appear in the direction opposite of the prismatic displacement indicating that the inverse internal model associated with the movement has been modified.

Studies designed to investigate generalization of this form of motor learning have shown that in some instances PA is highly specific, while in other cases it is generalizable. For example, it was shown that PA of reaching is velocity dependent (Kitazawa et al. 1997). That is, adaptation transfers incompletely between fast and slow reaching, with the amount of transfer decreasing as the difference in velocity increases. Additionally, ball-throwing adaptation to prisms was found to be specific to both the task and hand (Martin et al. 1996). That is, little transfer occurs between overhand and underhand ball throwing, and training with the right hand does not transfer to the left. In contrast, other studies have shown PA to generalize across both effectors and tasks. Specifically, adaptation of pointing movements was shown to transfer from the arms to the legs (Savin and Morton 2008), and participants who adapted to prisms while walking demonstrated generalization to reaching (Morton and Bastian 2004). Finally, in a study by Rossetti et al. (1998) it was shown that a brief session of PA using a pointing task and rightward deviating prism glasses improved the performance of patients with left hemispatial neglect on a standard battery of neuropsychological tests, suggesting PA may generalize in a manner that is useful in rehabilitation for neglect.

1.2.2 Prism Adaptation as a Treatment for Neglect

Neglect (also known as hemispatial neglect or unilateral neglect) is a broad term used to describe a wide spectrum of disorders in which patients demonstrate a lost or impaired ability to attend to stimuli presented in the contralesional hemispace. Neglect can affect different modalities including sensory (visual, auditory, tactile, olfactory), motor (demonstrated as a reduced use or nonuse of a contralateral extremity), or representational (affecting internally generated images) (Plummer et al. 2003), however it occurs independently of any sensory or motor deficits. This lost or impaired ability is the result of a lesion (often in the right parietal and/or temporal lobe) caused by stroke, tumor, or other brain damage, and is considered to be a disorder specific to spatial representations (Brain, 1941; Gainotti et al. 1972; Kerkhoff 2001). Patients with large right-side lesions may have severe, chronic, and multi-modal neglect that prevents independent living and return to former jobs (Kerkhoff 2001).

Since its introduction as an intervention, PA has been considered a promising treatment for neglect (Jacquin-Courtois et al. 2013; Mattingley 2002; Newport and Schenk 2012; Serino et al. 2007). The original idea, as proposed by Rossetti et al. (1998), was that adaptation to prisms might ameliorate neglect symptoms by stimulating the neural structures involved in sensorimotor transformations. Indeed, adaptation aftereffects resulted in improved performance on tasks such as line bisection, line cancelation, copying a simple drawing, drawing a daisy, and reading simple text. Further, improvement was still shown two hours following adaptation. However, despite extensive research since then (e.g., over forty published PA treatment studies) the efficacy of PA remains unclear, as study results have been mixed (Barrett et al. 2012; Fasotti and van Kessel 2013; Newport and Schenk 2012). While there are many possible reasons for different experimental outcomes, including inconsistent methodology, one reason may be the heterogeneity of the disorder itself. Not only can neglect manifest in different modalities, but it also can affect different types of spatial reference frames broadly categorized as allocentric or egocentric.

1.3 Spatial Reference Frames

1.3.1 Allocentric and Egocentric

It is generally accepted that the brain represents space according to a coordinate type system, i.e., through the use of reference frames (Lacquaniti et al. 1995; McCloskey 2001). These spatial reference frames can be either allocentric (i.e., world-centered) or egocentric (i.e., self-centered) (Calvanio et al. 1987; Caramazza and Hillis 1990; Farah et al. 1990; Ota 2001; Walker 1995). Allocentric frames of reference are centered on either the environment or specific objects within the environment and these reference frames are used to define where objects are in relationship to other objects in external (environment-based) space or where components are within an object (object-based space). In contrast, egocentric frames of reference are projected from the individual and therefore define where objects are located relative to oneself, based on a specific body part, e.g. head-centered, trunk-centered, etc. (Andersen et al. 1997; Burgess 2008; Galati et al. 2000).

It has been suggested that different brain regions use allocentric and egocentric spatial reference frames for different purposes. For example, in a model by Goodale and Milner (1992), it was proposed that two visual pathways known as the ventral and dorsal streams (Ungerleider and Mishkin 1979) can be differentiated based on functional roles of perception and action. More specifically, it was proposed that visual information of the perceptual-ventral stream (also known as the "what" pathway) is used to construct a detailed representation of the environment, including the specific characteristics of the objects therein, while that of the action-dorsal stream (also known as the "where" pathway) is used for planning and controlling goal-directed motor behavior. Further, based on these functional roles, it was suggested that the ventral stream (which travels from the occipital lobe to the inferior temporal region) uses allocentric representations, while the dorsal stream (which travels from the occipital lobe to the posterior parietal cortex), uses egocentric representations (Goodale and Milner 1992; Norman 2002).

While much of Goodale and Milner's (1992) perception-action model is still accepted today, we know that successful accomplishment of visually-guided movement is dependent on both egocentric and allocentric spatial perception (Colby 1998). For example, when reaching for a drinking glass, egocentric visual representations provide information necessary for judging the direction and distance the hand must travel in order to reach the glass, while allocentric representations are used to adjust grip size and shape to that of the object being grasped. Further, it is understood that non-target-directed movements, such as drawing or copying a diagram, also depend on both types of spatial representations. That is, egocentric representations are necessary for moving the hand-held drawing device from its current location to a desired location, while allocentric representations of the objects being viewed, and the relationship between them, are necessary for determining the direction and distance of this hand movement (Thaler and Goodale 2011). Therefore, the brain must have mechanisms for integrating both allocentric and egocentric spatial representations with motor output; presumably these would be within the internal models of motor control.

1.3.2 Spatial Reference Frames of Neglect and Prism Adaptation

Neglect can affect allocentric and egocentric spatial reference frames concomitantly or differentially (Hillis and Caramazza 1995; Marsh and Hillis 2008; Medina et al. 2009; Ota 2001). For example, patients with egocentric forms of left hemispatial neglect fail to attend to stimuli located to the left of the body (or body part) midline, while those with allocentric forms of the disorder fail to attend to the left side of an environmental stimulus or object regardless of where this is located in relation to the body midline. In order for PA to be effective as a treatment for neglect it must generalize with respect to the reference frame(s) being affected by the disorder. Interestingly however, many studies testing PA as a treatment do not address differences in efficacy related to different spatial reference frames. Generally, patients are not separated based on the type of neglect demonstrated (perhaps because many patients have more than one form of the disorder); nor is there much discussion as to which form(s) of neglect the behavioral outcome measures are assessing. For example, in a randomized clinical trial by Turton et al. (2010), the main outcome measure was the Catherine Bergego Scale (CBS), a clinical test of self-care in which it is difficult to dissociate which representational system (allocentric or egocentric) is being diagnosed. To date, only one intervention study (Gossman et al. 2013) has attempted to evaluate the efficacy of PA treatment relative to allocentric and egocentric reference frames and the results suggest that PA may only be effective in treating egocentric forms of neglect. Considering the importance of providing effective treatment for neglect, it seems prudent to determine if this specificity of PA generalization is correct.

During PA, internal models associated with a particular motor behavior are modified in response to a sensory prediction error that is visual. In other words, the adaptation is driven by a mismatch between actual and predicted visual feedback. However, since the brain represents visual information according to both allocentric and egocentric reference frames, modifications to the inverse internal model could be based on an error signal that is in an allocentric reference frame, an egocentric reference frame, or both. Therefore, theoretically, PA could generalize in one of three ways.

First, PA could generalize purely allocentrically. PA does not occur without knowledge of movement results (Kitazawa et al. 1995) and this information is allocentric in nature. For example, when a thrown ball misses the intended target, an error signal is generated. The direction and degree of error is represented by the allocentric relationship between ball impact location and target location. If changes to the internal model are based solely on this relationship in environmental (allocentric) space then the adaptation might generalize purely allocentrically.

The second possibility is that PA could generalize purely egocentrically. PA does not occur without self-initiated movement (Held and Freedman 1963) thereby reflecting the importance of motor command efference copies in the adaptation process. These efference copies are used by forward models to predict the sensory consequences of motor output, and motor commands are updated if these predictions do not match the actual sensory feedback. While visual feedback is represented in both allocentric and egocentric coordinates, motor command coordinates are only egocentric. Therefore changes to transformations between the two systems (visual and motor) may be based only on an error signal that is represented in the coordinate system common to both (i.e., egocentric).

The third and final possibility is that PA could generalize in a mixed fashion across both spatial reference frames. That is, error signals in both allocentric and egocentric coordinates may be used during adaptation, and generalization could be expressed with respect to each partially. Relative contributions of each type of spatial information would not have to be equal. While it is not known which of these three options (allocentric, egocentric, or mixed generalization) is correct, generalization of PA with respect to these reference frames is testable.

1.4 Purpose, Aims, and Hypotheses

1.4.1 Purpose

The purpose of this study was to determine how PA of a ball-throwing task generalizes in healthy individuals with respect to allocentric and egocentric spatial reference frames. To test this, participants adapted to laterally displacing prisms by throwing a ball at a wall-mounted target (Martin et al. 1996) from either a seated position or while lying on their side. Following adaptation (prism exposure) some participants were rotated to the alternate position before testing for aftereffects (i.e., some participants who adapted while seated were tested while side-lying, and vice versa). This 90-degree rotation of position decoupled the reference frames (Calvanio et al. 1987; Farah et al. 1990) and the existence of aftereffects in the new position was used to indicate generalization across postures. The direction of aftereffects, if they occurred, was used to indicate the reference frame in which generalization was expressed. We had two aims and hypotheses for this study.

1.4.2 Aims and Hypotheses

Aim 1: Determine if PA of a throwing movement generalizes across body positions (seated and side-lying).

Hypothesis 1: *Following PA of throwing, aftereffects will transfer from seated to side-lying and from side-lying to seated positions.*

Aim 2: Determine how PA of throwing generalizes with regards to allocentric and egocentric reference frames.

Hypothesis 2: *A 90-degree rotation of participant position following PA of throwing will result in aftereffects that occur along the axis perpendicular to the axis of visual displacement in extrinsic space (i.e., aftereffects will rotate with subject rotation), indicating generalization within an egocentric reference frame.*

It was expected that PA of ball-throwing would transfer bi-directionally, as the same throwing arm was used in both positions, and because the movement pattern of the arm relative to the trunk remained the same across positions. Further, it was expected that generalization would be expressed purely egocentrically, as this is the coordinate system common to both motor and visual systems.

Chapter 2

GENERALIZATION OF VISUOMOTOR ADAPTATION ACROSS SPATIAL REFERENCE FRAMES

2.1 Introduction

Motor learning is a process in which movement practice or experience leads to a relatively permanent change in motor behavior (Salmoni et al. 1984). This process culminates in the formation of internal models that mimic sensory to motor transformations and their inverses and are then used by the central nervous system (CNS) to control motor behavior (Kawato 1999; Scott and Norman 2003; Wolpert and Ghahramani 2000; Wolpert et al.1998). Inverse models control movement in a feed-forward manner by generating the motor commands necessary for a desired movement given current sensory input (Kawato 1999; Wolpert et al. 1998). Forward models use efference copies of these motor commands to predict the sensory consequences of motor output based on the current state of the system, and these predictions are used as feedback control for the inverse model (Shadmehr et al. 2010; Wolpert and Ghahramani 2000; Wolpert and Miall 1996).

Motor adaptation refers to an error-driven motor learning process in which the internal models associated with a particular movement are modified in response to an actual or perceived change in the body or environment (Krakauer and Mazzoni 2011; Martin et al. 1996; Reisman et al. 2005). In contrast to motor learning, motor adaptation occurs quickly, is short term, and is easily reversed. One form of motor adaptation is prism adaptation (PA).

PA is a type of visuomotor adaptation in which motor patterns change when visual information is distorted by prismatic lenses (Newport and Schenk 2012; Redding et al. 2005). For example, when an individual looks through wedge prisms, the images of all objects within the visual field shift towards the apex of the prisms (i.e. base left prisms shift visual images to the right). Consequently initial performance errors in target-directed movements, such as reaching or ball throwing, occur in the direction of the prism shift. This results in a sensory prediction error (i.e., a mismatch between actual visual feedback and the visual feedback predicted by the forward model). This error information is fed back to the inverse model and used to modify sensory input to motor output transformations, so that subsequent outgoing motor commands lead to a more accurate movement (Kawato 1999; Shadmehr et al. 2010; Tseng et al. 2007; Wolpert and Ghahramani 2000; Wolpert and Miall 1996). This adaptation process continues until there is no longer a sensory prediction error. Storage of the adaptation (i.e., the modified internal models) is demonstrated by aftereffects, defined as errors occurring in the direction opposite to visual displacement once the prisms are removed (Shadmehr and Mussa-Ivaldi 1994; Wallace and Redding 1979; Weiner et al. 1983; Welch 1974).

PA has been shown to generalize (i.e., transfer to untrained contexts) in some cases. For example, when people adapt to prisms while walking, the adaptation transfers to reaching (Morton and Bastain 2004). In addition, it has been suggested that PA may have potential as a treatment for the neurological condition known as hemispatial neglect, a disorder of spatial representations in which patients demonstrate a lost or impaired ability to attend to stimuli presented in the hemispace contralateral to a cerebral lesion (Brain 1941; Hillis and Caramazza 1995; Kerkhoff 2001). It has been shown that some patients with left-sided neglect who undergo PA of reaching movements while wearing rightward-shifting prism lenses can subsequently demonstrate aftereffects that manifest as improved movements in, or perception of, the neglected (left) side of space (Rossetti et al. 1998). However, the brain represents space in multiple reference frames (Colby 1998) and in order for PA to be beneficial as a treatment for patients with neglect there must be adequate generalization, or transfer of the learning, to the spatial reference frame(s) affected by the disorder.

Spatial reference frames are broadly categorized as allocentric (world-centered) or egocentric (self-centered). Allocentric reference frames are centered on the environment or on objects, and they are used to define the spatial relationship between objects in external (environment-centered) space, or between components within an object (object-centered space). In contrast, egocentric frames of reference are projected from the individual and used to define where objects are located relative to oneself (i.e, they are body-centered) (Andersen et al. 1997; Burgess 2008; Colby 1998; Galati et al. 2000). While neglect can occur in both types of representation concomitantly or differentially (Hillis and Caramazza 1995; Marsh and Hillis 2008; Medina et al. 2009; Ota 2001), surprisingly it has never been tested to determine how PA generalizes with respect to these categories. Therefore, the purpose of this study was to examine how PA generalizes with respect to allocentric and egocentric spatial reference frames in neurologically intact individuals.

To determine the spatial reference frame of PA generalization, a ball-throwing task was used to adapt healthy participants to rightward displacing prism lenses while they were either seated or lying on their side. Following adaptation they rotated to the alternate position and were tested for aftereffects. This 90-degree rotation was used to decouple the allocentric and egocentric reference frames (Farah et al. 1990). If PA transferred between the two positions (seated and side-lying), the reference frame of generalization was determined based on the direction of the aftereffects.

Since visual information is represented both allocentrically and egocentrically, the sensory prediction error driving adaptation to prisms could occur in either representation or both. Therefore, there were three ways in which generalization of PA could have been expressed (Figure 1). First, the adaptation could have generalized purely allocentrically, meaning that aftereffects were along the same axis as the original visual displacement in extrinsic space (i.e., along the horizontal axis if adapted while seated, and along the vertical axis if adapted while side-lying). PA does not occur without knowledge of movement results (Kitazawa et al. 1995) and this information is allocentric in nature. Here the indicator that motor commands needed updating (i.e., the mismatch between the actual and predicted sensory feedback), was the observation that the ball did not hit the target. If changes to the internal model were based on the relationship between target location and location of ball impact in allocentric space then the direction of aftereffects, in Cartesian coordinates, could have been 180 degrees from the direction of initial errors caused by the prismatic displacement.

Second, the adaptation could have generalized purely egocentrically, meaning that aftereffects rotated with the individual and appeared along the axis perpendicular to the original axis of displacement in extrinsic space (i.e., along the vertical axis if adapted while seated, and along the horizontal axis if adapted while side-lying). PA only occurs in response to self-initiated movement (Held and Freedman 1963) thereby reflecting the importance of motor command efference copies in the adaptation process. While visual feedback is represented in both allocentric and egocentric coordinates, motor command coordinates are only egocentric. Therefore PA could have generalized in the coordinate system common to both (i.e., egocentric).

Finally, the adaptation could have generalized in a mixed fashion across both spatial reference frames. In other words, the aftereffects could have appeared somewhere in the region between the horizontal and vertical axes based on visual feedback from *both* allocentric and egocentric representations, and the relative contributions of each type of spatial representation could have been unequal.

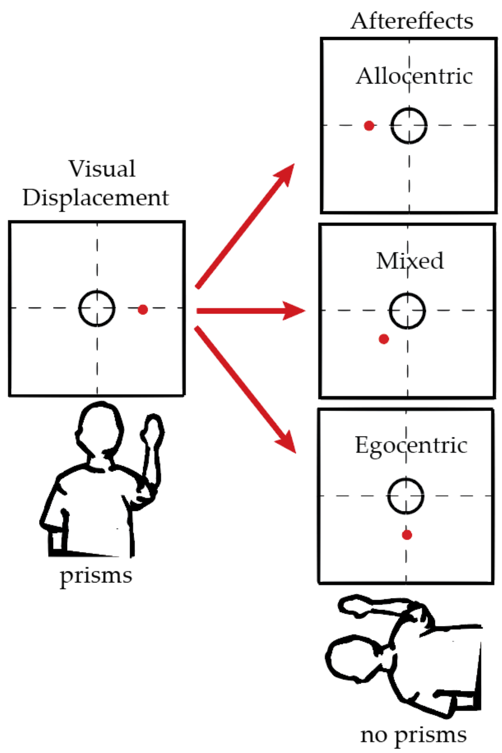

Figure 1 Illustration of Possible Experimental Outcomes. Illustration depicts a seated adaptation to rightward displacing prisms and a side-lying test of generalization.

It was predicted that PA of ball-throwing would transfer between seated and side-lying positions, and vice versa, due to the similarity of the task (i.e., the same throwing pattern and arm were used in both positions). Further, it was predicted that generalization would be expressed in the coordinate system common to both motor and visual systems. That is, generalization was expected to occur purely egocentrically.

2.2 Methods

2.2.1 Participants

Twenty-nine young healthy adults (22 female, 7 male) between the ages of 19 and 35 years were recruited for this study from the University of Delaware campus and surrounding community. Participants were right hand dominant, as assessed by the Edinburgh Handedness Inventory (Oldfield 1971), and had either normal vision or vision that was corrected to normal with contact lenses. Exclusion criteria were: past participation in a prism adaptation study, past or current neurological or neuromuscular disorder, including head injury (defined as any period of unconsciousness $\geq$ 5 min and/or requiring medical treatment), current medications affecting balance or vision, and any current musculoskeletal condition limiting the use of or feeling in the shoulder, arm, or hand. This study was approved by the University of Delaware Institutional Review Board. Subjects provided informed consent, were naïve to the purpose of the study, and were paid for their participation.

2.2.2 Paradigm

Participants were assigned to one of four groups (Figure 2). Two of these groups, Seated and Side-lying (n=5 for each), served as Control groups to verify that adaptation and aftereffects could be generated in either the Seated or Side-lying position. The other two groups, Transfer Seated to Side-lying (n=9) and Transfer Side-lying to Seated (n=10), were used to test for the existence of generalization across positions, and to determine the reference frame(s) in which generalization was expressed, should it occur.

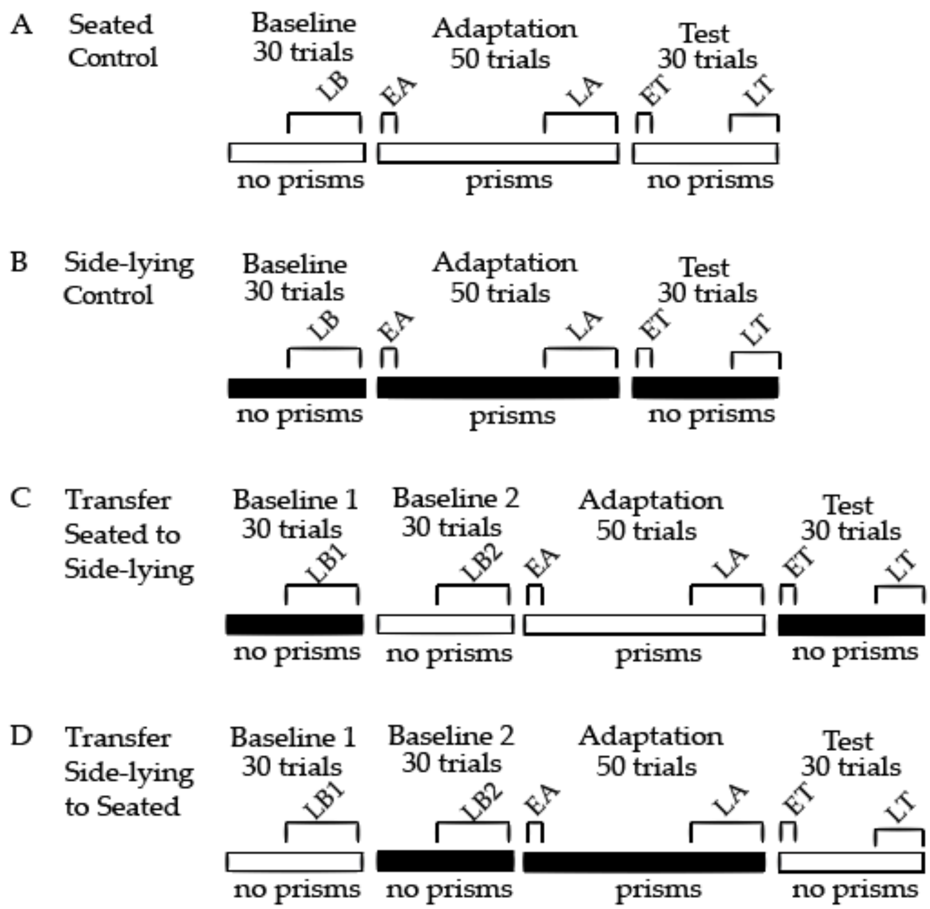

Figure 2 Schematic of Experimental Paradigm for Each Group. Open bars indicate the Seated position; filled bars indicate the Side-lying position. Key time periods for statistical analysis: Late Baseline (LB, LB1, LB2), Early Adaptation (EA), Late Adaptation (LA), Early Test (ET), Late Test (LT).

The task consisted of repeatedly throwing small (2.5 cm diameter) foam balls at a paper target mounted on the wall in front of the participants, from either a seated position or while lying on their side, depending on group assignment. The wall was otherwise void of any reference objects or visual cues. The prism deviation was applied via stick-on laterally-deviating prism lenses, 30 diopter base left (i.e., approximately 17 degree rightward deviating), mounted onto form-fitting swim goggles that could be easily donned and doffed.

The paradigm consisted of three phases: Baseline, Adaptation, and Test. Control group participants performed all three phases in the same position (Seated or Side-lying). Transfer group participants performed two Baselines (one in each position) and changed positions between Adaptation and Test phases. During each Baseline phase participants performed 30 trials of the throwing task without the goggles in order to assess each participant's individual throwing accuracy and variability. During Adaptation phase they performed 50 throws while wearing prism goggles. It was expected that during this phase participants would adjust their throwing (i.e., adapt) to the shifted visual target using trial-and-error practice. During Test phase they again performed 30 trials without the goggles. The Test phase was used to assess for the presence of aftereffects, the indicator of storage of the adaptation (Control groups), or the presence of generalization (Transfer groups). The directional shift of any generalized aftereffects obtained in the Transfer groups indicated how generalization occurred with respect to egocentric and allocentric reference frames.

In both positions and all phases, participants were located in the center of a height-adjustable cushioned table located 214 cm from the target. The target consisted of a yellow paper circle (15 cm diameter) with a 2.5 cm black square superimposed on its center. The target was securely fastened to the wall. The table height and position were adjusted such that the participant's sternal notch was in horizontal and vertical alignment with the center of the target whether in the Seated or the Side-lying position. Additionally people were positioned with their shoulders square to the wall on which the target was mounted. When Seated, the participants' feet were placed on the floor or a stool depending on the height of the table. When on their side (always the left side), the head was positioned on a foam pillow such that the midlines of the head, neck, and trunk were aligned. Additionally an assistant stood behind the participants and ensured that the head did not rise off the pillow and that the head, neck, and shoulders did not rotate. This was done by keeping a hand lightly placed on the head and/or trunk for cueing, as there is a natural tendency to want to raise the head and view the target vertically. In both the Seated and Side-lying positions the neck and trunk were kept in "neutral" alignment, meaning that there was no rotation, side-bending, or flexion/extension from the anatomical position. Participants in the Transfer groups wore a blind-fold between the Adaptation and Test phases while the table and their position on it were being adjusted. Measurements for each individual's position set-up (proper table height and location that aligns sternal notch with target) were made and recorded prior to Baseline in order to ensure that the repositioning between Seated and Side-lying positions would occur quickly and accurately.

During all phases, a small basket containing the foam balls was placed in front of each participant's trunk such that they could reach into it without looking. They used their right arm and hand to throw the balls. The experimenter instructed participants on when to throw each ball to ensure that the throws occurred approximately 2 seconds apart. Participants were instructed to keep their eyes fixed on the center of the target throughout the trials and to throw the ball to where they *saw* the target. Prior to each Baseline session participants were given 5 practice throws in order to familiarize them with the task. There were no practice throws in the Adaptation and Test phases.

2.2.3 Data Collection

An 8-camera Vicon MX (Edgewood, NY) motion capture system recorded three-dimensional position data of reflective markers using a sampling rate of 120 Hz. The throwing balls themselves were covered with reflective tape, thus the ball trajectory from the time of release to contact with the wall was recorded. The position of the target was calculated by temporarily placing a reflective marker on the center of the target and recording its location; after which the marker was removed from the target. Additionally, one reflective marker was securely attached to the participants face directly anterior to the tragus of the ear in order to track head movement grossly. This was to verify that participants did not raise their head from the pillow, or twist the neck during the Side-lying trials.

2.2.4 Data Analysis

Motion capture data was initially processed using Vicon Nexus 1.8.4 software to obtain the location coordinates of the target and head marker, as well as the location of ball impact. This information was exported for further analysis. Custom-written MATLAB (Mathworks, Natick, MA) code was used to identify key time and position values. The time of ball impact was identified as the data frame with the lowest value along the axis between the target and the participant (i.e., when the ball contacts the wall).

The primary outcome measure was throwing endpoint error (i.e., constant error) defined as the distance between the center of the target and the center of the ball at the time of impact, and calculated separately using the horizontal and vertical coordinates. Positive values represented errors to the right or above the target, and negative values represented errors to the left or below the target. Horizontal and vertical errors values were recorded for all trials. Measures were computed for each participant over these key time periods: Late Baseline (LB), the average of the last 15 trials of the Baseline phase; Early Adaptation (EA), the average of the first 3 trials of the Adaptation phase; Late Adaptation (LA), the average of the last 15 trials of the Adaptation phase; Early Test (ET), the average of the first 3 trials of the Test phase; and Late Test (LT), the average of the last 10 trials of the Test phase. While it is the first trial of Adaptation that is the most important for assessing the size of the perturbation, in order to minimize the possibility of an aberrant throw biasing the results, Early Adaptation was computed by averaging the first three Adaptation trials. Likewise, the first three trials of Early Test were averaged to assess the size of aftereffects. All values were normalized by subtracting the average of the entire (30 trials) Baseline from each.

Two additional variables were measured for secondary analyses. First, to determine if the speed of throwing changed over time, ball velocity, defined as the instantaneous velocity of the ball in the forward dimension as it left the hand, was calculated for each trial using the motion capture data. No kinematic data were collected for the arm, however, an assumption can be made that a difference in arm velocity would be reflected in a difference in ball speed. Ball velocity was averaged over the same key time periods as endpoint error: Late Baseline, Early Adaptation, Late Adaptation, Early Test, and Late Test.

Next, to determine if performance variability changed due to phase, dimension, or position, the standard deviation of endpoint error was used as a measure of movement variability (i.e., variable error). Because variability was expected to be abnormally high during the early portions of the Adaptation and Test phases, variability was computed using the last 10 trials of each phase, for each individual, and then averaged within groups. Variability was computed separately for each dimension (horizontal and vertical), as well as for the resultant endpoint error vector.

2.2.5 Statistical Analysis

Statistical analyses were done using Statistica software (StatSoft, Tulsa, OK). Because of the relatively small sample sizes (n=5 in some cases), non-parametric statistics were employed throughout. The level of statistical significance was set at $p<0.05$ with Bonferroni corrections for multiple comparisons applied when appropriate.

For the main analysis, performance (endpoint error values) was compared across the key time periods separately for each dimension (horizontal and vertical) using the Friedman Test for repeated measures. If the test yielded positive results, a priori post hoc analyses were done using the Wilcoxon signed rank test. For this analysis, between-groups comparisons were not conducted because each group was being used to test a different question. The Seated and Side-lying Control groups were used to establish that adaptation to throwing could occur normally in each position. This was done so that if a Transfer group showed no aftereffects we would be able to attribute this to a lack of generalization rather than a lack of adaptation. The

Transfer groups were used to test for generalization and type of reference frame(s), if generalization occurred. To do this, the direction and magnitude of aftereffects in the Early Test period were compared with each Late Baseline performance within each group. Aftereffects could have occurred along the same axis (in extrinsic space) as Early Adaptation errors (allocentric generalization), along the axis perpendicular to Early Adaptation errors (egocentric generalization), or in the region between the horizontal and vertical axes (mixed generalization).

As part of the secondary analyses, within-group comparisons using the Friedman Test for repeated measures and Wilcoxon signed rank test for post hoc analyses were done for ball velocity, across the key time periods, for all groups. Additionally, endpoint error variability (computed separately for horizontal and vertical dimensions) was compared within groups, across phases using the Friedman Test for repeated measures, and across dimensions (horizontal and vertical) or axes (parallel or perpendicular to the long axis of the body) using the Wilcoxon signed rank test. Resultant endpoint error was used to assess variability across positions (Seated and Side-lying). Specifically, at each phase, the resultant error was compared between the two Control groups and between the two Transfer groups using the Mann-Whitney U test.

2.3 Results

2.3.1 Main Analysis

Results of the main outcome measure, endpoint error (distance from target center to point of ball impact), decomposed into horizontal and vertical components, are presented below.

2.3.1.1 Control Groups

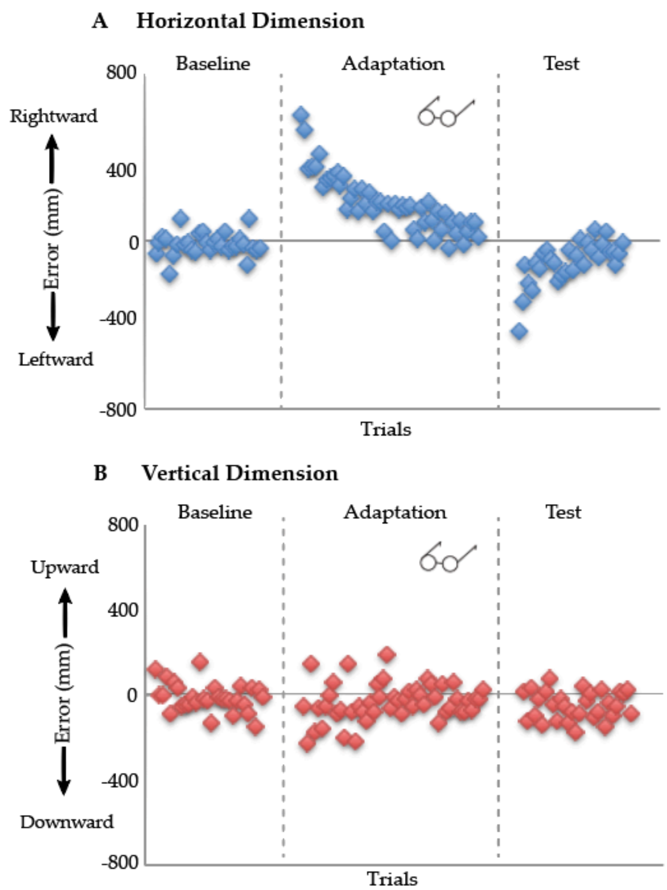

Figure 3 Endpoint Errors for a Single Participant in the Seated Control Group: Horizontal Dimension (A), Vertical Dimension (B). Each point indicates a single trial. Target center is at zero.

Overall, the data indicate that participants adapted throwing to the prisms in both the Seated and Side-lying postures. Individual data from a Seated Control group participant are shown in Figure 3, and those of a Side-lying Control group participant are shown in Figure 4. For both Control participants, initial errors during Early

Adaptation were largely corrected by Late Adaptation, and aftereffects were seen in Early Test. The direction of the errors in Early Adaptation was consistent with the direction of the visual displacement (to the right when Seated; upward when Side-lying) and the aftereffects occurred in the opposite direction along the same dimension as the displacement (to the left when Seated; downward when Side-lying).

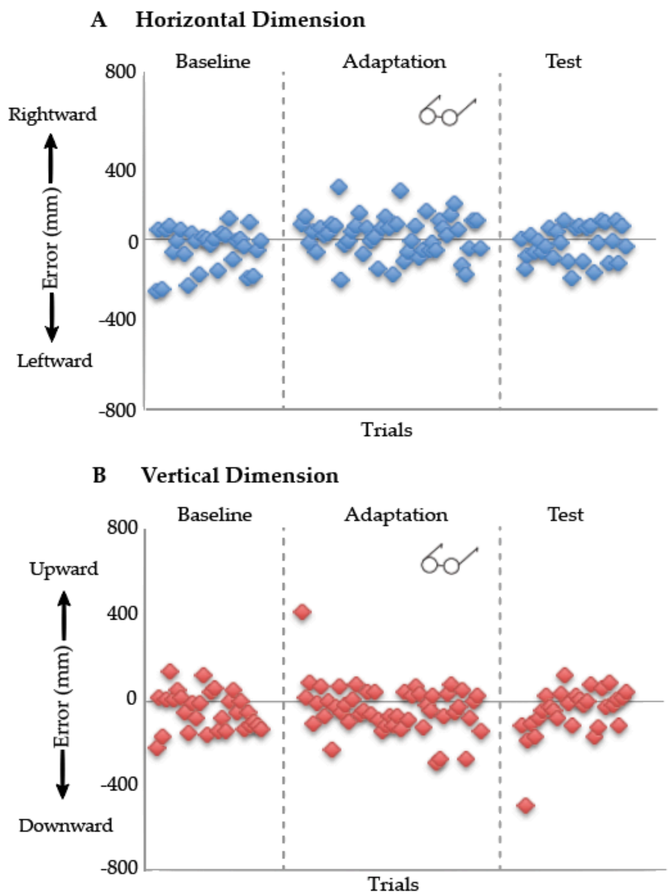

Figure 4 Endpoint Errors for a Single Participant in the Side-lying Control Group: Horizontal Dimension (A), Vertical Dimension (B). Each point indicates a single trial. Target center is at zero.

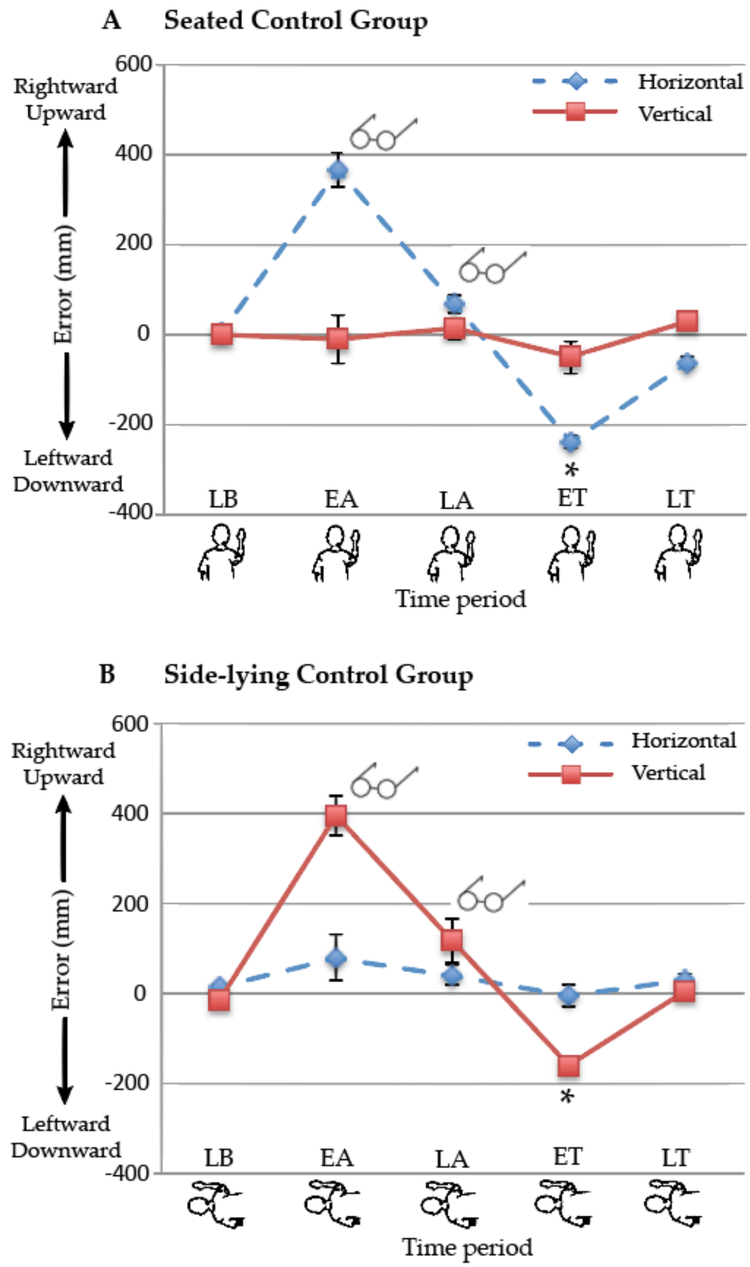

Figure 5 Group Average Endpoint Errors for the Control Groups over all Key Time Periods: Seated Control (A), Side-lying Control (B). Comparison of group means across key time periods: Late Baseline (LB), Early Adaptation (EA), Late Adaptation (LA), Early Test (ET), Late Test (LT). Error values indicate deviation from the target center. Error bars represent SEM. *Significantly different from LB, $p<0.05$ from post hoc analysis.

Group results for both the Control groups are shown in Figure 5 for all key time periods. For both groups there was a statistically significant effect of time period on error along the axis of visual displacement only (i.e., the horizontal axis for Seated and the vertical axis for Side-lying, both $p<0.01$), but not the other dimension (vertical axis for Seated $p=0.364$, and horizontal axis for Side-lying $p=0.193$). Post hoc analyses for the a priori comparison of Late Baseline versus Early Test revealed there were significant aftereffects in both Control groups: differences in error between Late Baseline and Early Test along the horizontal axis for the Seated Control group and the vertical axis for the Side-lying group were each significant at $p<0.05$ (both $p=0.043$). Recall that the sole purpose of the Control groups was to verify that adaptations acquired while Seated or Side-lying could be stored. The presence of aftereffects indicated that PA was stored by both groups.

2.3.1.2 Transfer Groups

Participants in the Transfer groups completed two Baseline phases (one in each position), an Adaptation phase, and a Test phase in the position opposite to their Adaptation phase position. Individual data from a Transfer Seated to Side-lying participant are shown in Figure 6. This participant adapted while Seated, and similar to those in the Seated Control group, had Early Adaptation errors along the horizontal axis that were reduced by Late Adaptation. Following Adaptation, the participant was rotated to the Side-lying position and then tested for aftereffects. No aftereffects appeared along the horizontal axis; however they did occur along the vertical axis suggesting that the adaptation generalized to the new position egocentrically. Figure 7 shows individual data from a participant in the Transfer Side-lying to Seated group. This participant adapted while lying on their side, and similar to those in the Side-lying Control group, had Early Adaptation errors along the vertical axis that were reduced by Late Adaptation. Following Adaptation, the participant was rotated to the Seated position and then tested for aftereffects. In contrast to those of previous groups, this participant showed no aftereffects along either axis suggesting that the adaptation did not generalize to the new position.

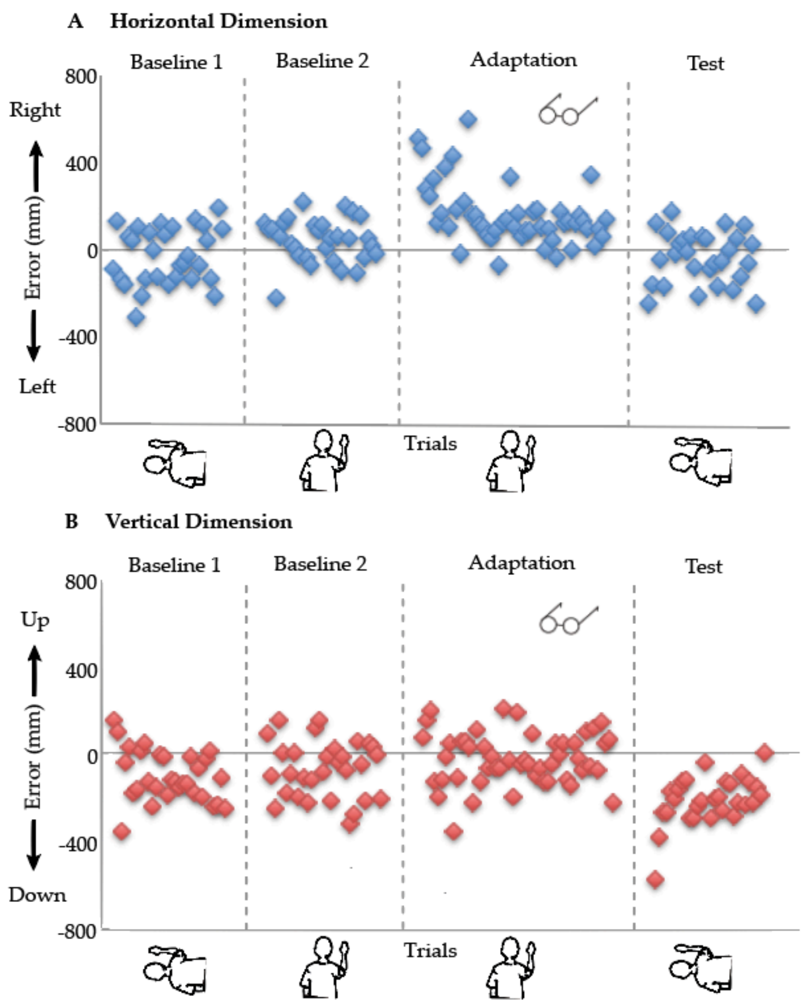

Figure 6 Endpoint Errors for a Single Participant in the Transfer Seated to Side-lying Group: Horizontal Dimension (A), Vertical Dimension (B). Each point indicates a single trial. Target center is at zero.

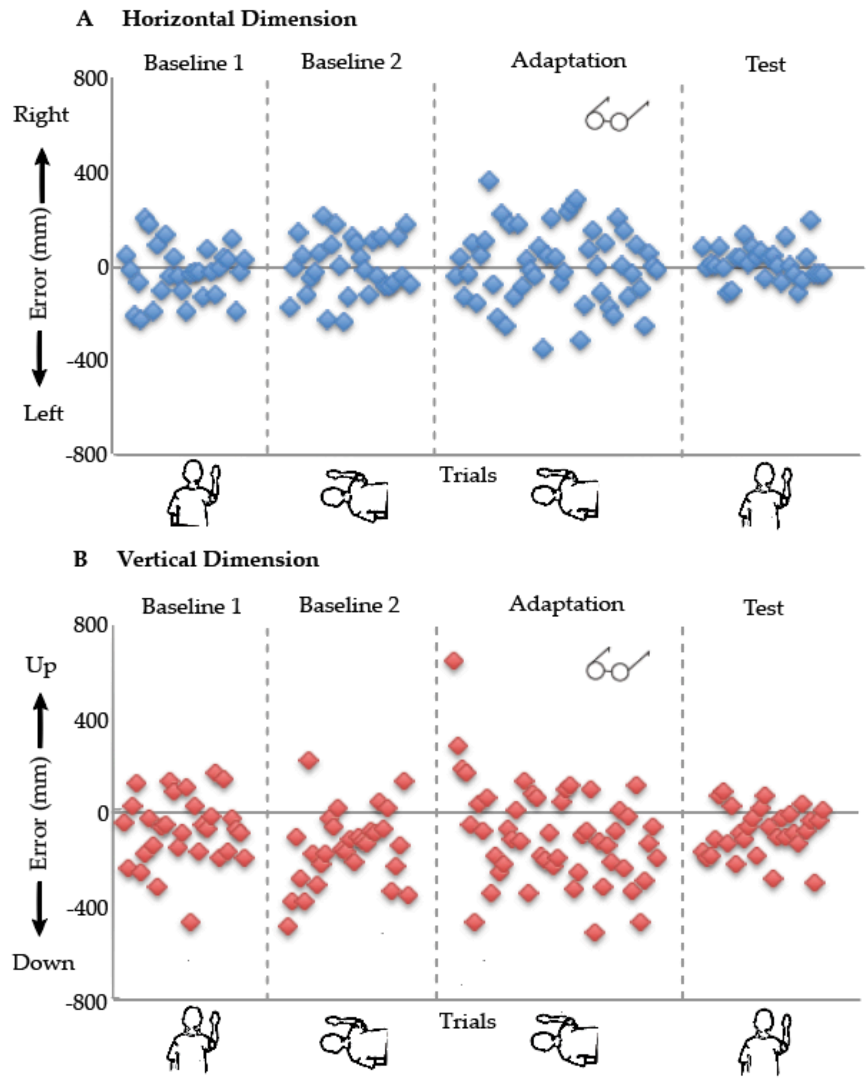

Figure 7 Endpoint Errors for a Single Participant in the Transfer Side-lying to Seated Group: Horizontal Dimension (A), Vertical Dimension (B). Each point indicates a single trial. Target center is at zero.

Averaged data for both Transfer groups are shown in Figure 8 for all key time periods. Like the Control groups, both Transfer groups showed statistically significant effects of time period. Post hoc analyses were done for four a priori comparisons (Bonferroni statistical correction $p<0.0125$). Early and Late Adaptation performance were compared with Late Baseline performance in the same throwing position (LB2 v EA, LB2 v LA) and, to test for generalization, Early and Late Test were compared to the Late Baseline that matched the Test throwing position (LB1 v ET, LB1 v LT). For the Transfer Seated to Side-lying group, both the horizontal error and vertical error showed differences across time periods (both $p<0.001$). The post hocs within the horizontal dimension showed significant differences between Late Baseline 2 and both Early and Late Adaptation (both $p<0.008$), and the direction of error was consistent with the lateral displacement caused by the prisms. In addition, Late Test was no different than Late Baseline 1 ($p=0.173$) indicating performance returned to Baseline. However, unlike the Seated Control group, here the Early Test period was no different than Late Baseline 1 (LB1 v ET, $p=0.515$). On the other hand, for the vertical dimension, the post hocs showed a significant difference between Late Baseline 1 and Early Test ($p=0.008$) indicating that aftereffects did occur in this dimension. There was also a significant difference between Late Baseline 2 and Late Adaptation ($p=0.011$) but no difference between Late Baseline 2 and Early Adaptation ($p=0.678$), or between Late Baseline 1 and Late Test ($p=0.110$). For the Transfer Side-lying to Seated group the effect of time period occurred only in the vertical dimension ($p<0.001$); there was no effect of time period on error in the horizontal dimension ($p=0.141$). Post hoc analyses (vertical) revealed a significant difference between Late Baseline 2 and Early Adaptation only ($p<0.005$). No other comparisons were significantly different (all $p>0.0125$).

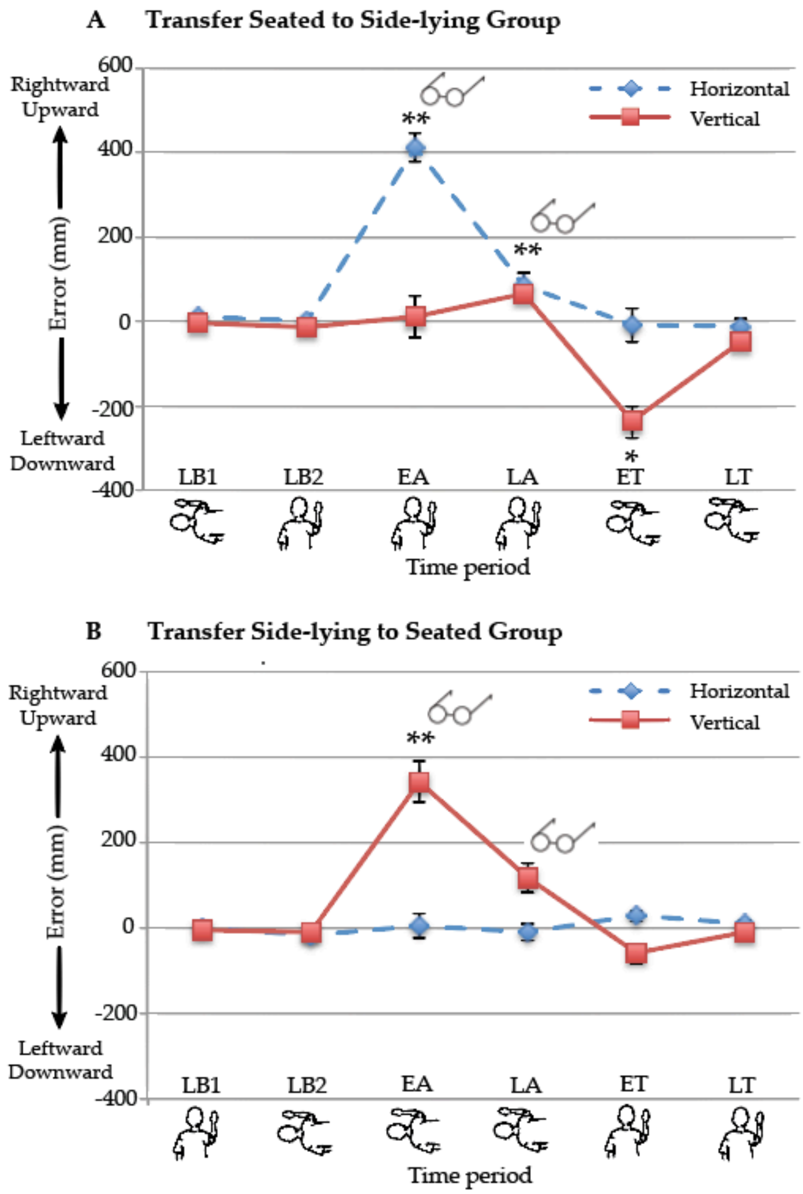

Figure 8 Group Average Endpoint Errors for the Transfer Groups over all Key Time Periods: Transfer Seated to Side-lying Group (A), Transfer Side-lying to Seated Group (B). Comparison of group means across key time periods: Late Baseline 1 (LB1), Late Baseline 2 (LB2), Early Adaptation (EA), Late Adaptation (LA), Early Test (ET), Late Test (LT). Error values indicate deviation from the target center. Error Bars represent SEM. Post hoc analysis results: *Significantly different from LB1, p<0.0125, **Significantly different from LB2, p<0.0125.

Thus, the Transfer Seated to Side-lying group (Figure 8A) had initial errors during Early Adaptation and, similar to Control groups, aftereffects were seen in Early Test. The presence of aftereffects in Side-lying indicates that generalization from Seated to Side-lying occurred. Because aftereffects were along the vertical axis and not at all on the horizontal axis, it appears that generalization was expressed in an egocentric reference frame and not in an allocentric reference frame. Interestingly, the results were different in the Transfer Side-lying to Seated group (Figure 8B). Although there was adaptation (i.e., Early Adaptation was significantly different from Late Baseline but Late Adaptation was not), no aftereffects appeared in either dimension, suggesting that the Side-lying prism throwing adaptation did not generalize to the Seated position.

In summary, the results indicate our hypotheses were partially correct. While the Transfer Seated to Side-lying group appeared to demonstrate a robust generalization in an egocentric reference frame, the Transfer Side-lying to Seated group did not seem to show any significant generalization at all.

2.3.2 Secondary Analyses

Several follow-up analyses were completed to examine factors that may have contributed in some way to the main results. Results of all additional analyses are presented below.

2.3.2.1 Velocity

Average ball velocities at the time of release from the hand were compared across the key time periods (Late Baseline 1, Late Baseline 2, Early Adaptation, Late Adaptation, Early Test, and Late Test) for each group (Figure 9). For the Control groups, there were no significant effects of time period on velocity (Seated Control, p=0.205; Side-lying Control, p=0.308). Likewise, velocity was consistent across time periods in the Transfer Side-lying to Seated group (p=0.541), indicating that this group's lack of generalization was not likely due to changes in movement speed.

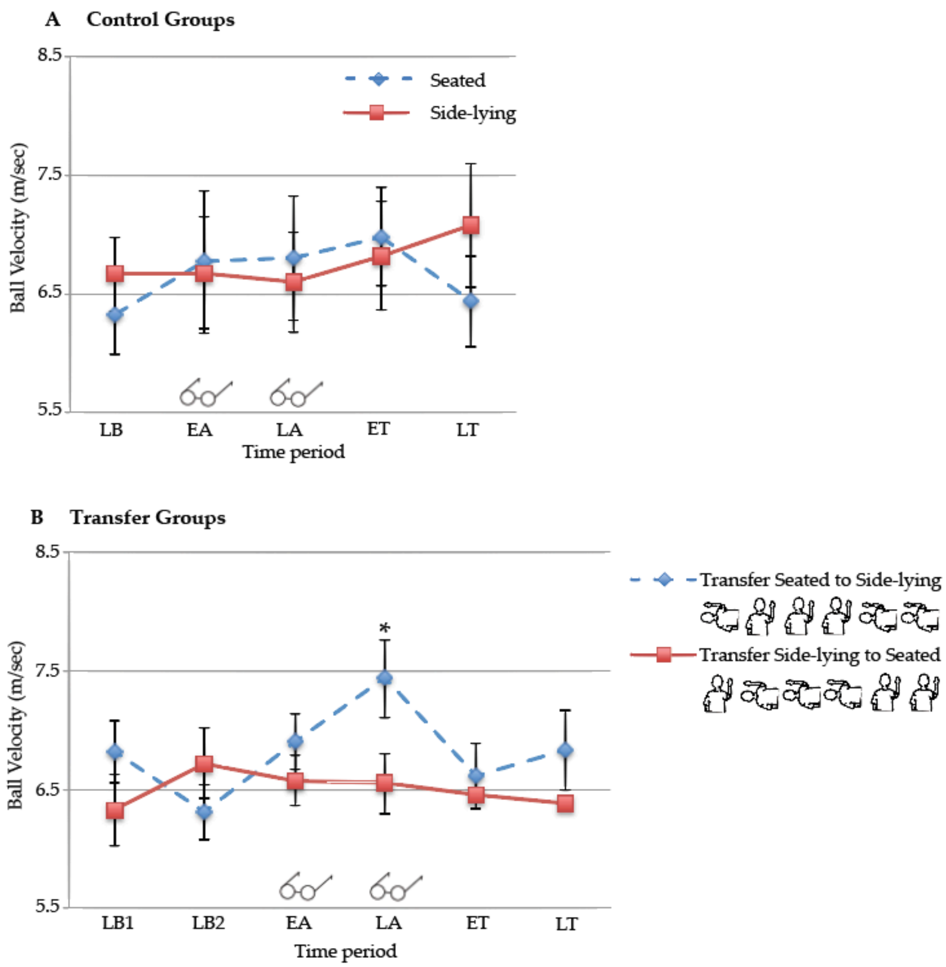

Figure 9 Group Average Ball Velocity over all Key Time Periods: Control Groups (A), Transfer Groups (B). Comparison of group means across key time periods: Late Baseline (LB, LB1, LB2), Early Adaptation (EA), Late Adaptation (LA), Early Test (ET), Late Test (LT). Error bars represent SEM. *Significantly different from LB2, p<0.0167 from post hoc analysis.

Surprisingly however, there was an effect of time period on velocity for the Transfer Seated to Side-lying group, ($p=0.012$). Three a priori post hoc comparisons with Bonferroni corrections ($p<0.0167$) were done: Early Test v Late Baseline 1, Early Test v Late Adaptation, Late Baseline 2 v Late Adaptation. No differences were found between Early Test and the two other time periods (ET v LB1, $p=0.314$; ET v LA, $p=0.028$). However, there was a significant difference between Late Baseline 2 and Late Adaptation ($p=0.011$) indicating that ball speed rose over the course of the Seated Adaptation in this group.

2.3.2.2 Endpoint Error Variability

A series of comparisons was done using the standard deviation of endpoint error, computed for the last 10 trials of each phase, as the endpoint error variability measure. Average endpoint error variability across phases and dimensions (horizontal and vertical) for the Control groups is shown in Figure 10. Neither the Seated Control group (Figure 10A) nor the Side-lying Control group (Figure 10B) showed any effect of phase for either dimension (for Seated Control, horizontal $p=0.247$ and vertical $p=0.549$; for Side-lying Control, horizontal $p=0.819$ and vertical $p=0.549$). That is, variability did not change over these three phases. However, for both groups, the variability appeared to be greater along the dimension aligned with the long axis of the body (i.e., the vertical axis for the Seated Control group and the horizontal axis for the Side-lying Control group). To determine if this effect was significant, the data were combined across phases, and within group comparisons were made between the horizontal and vertical axes for each Control group (Figure 10C). A significant difference between dimensions was found for the Seated Control group ($p=0.003$) and there was a similar (but non-significant) trend in the Side-lying control group ($p=0.069$).

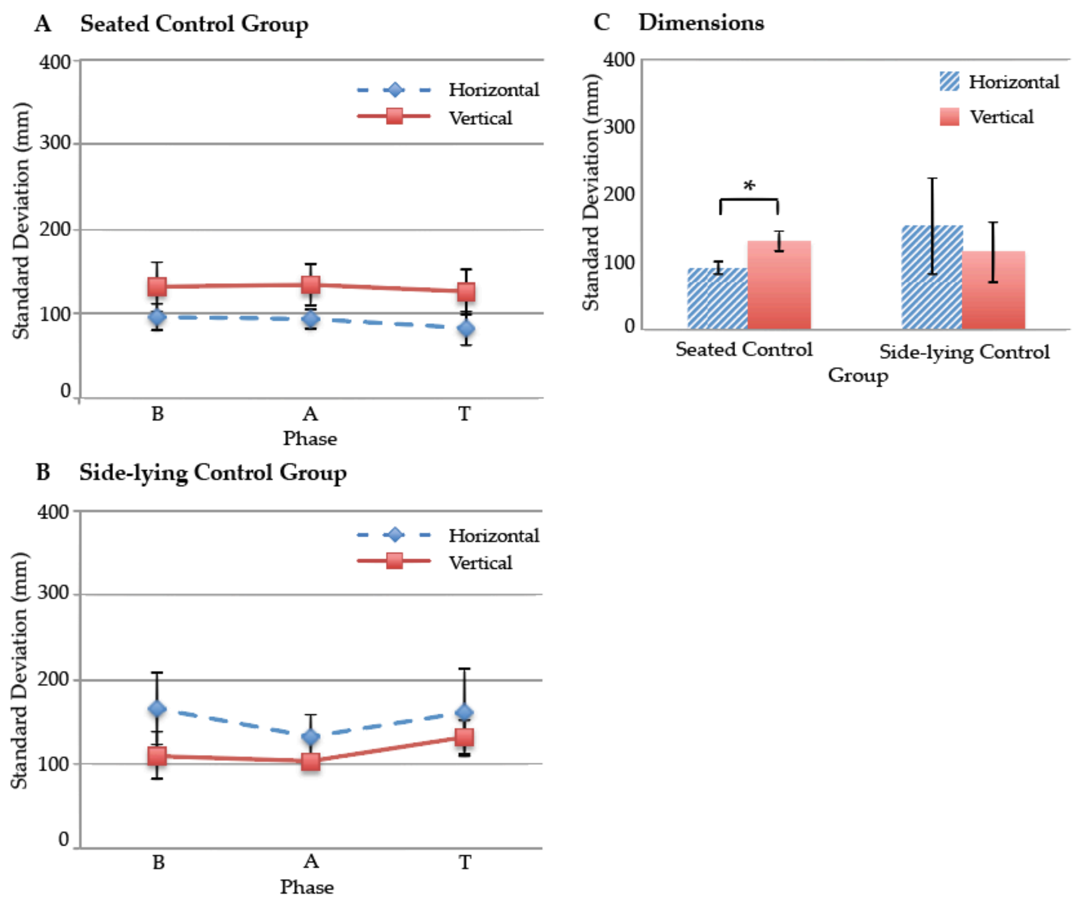

Figure 10 Group Average Endpoint Error Variability over Phases and Dimensions for Control Groups: Seated Control (A), Side-lying Control (B), Dimensions (C). For Figures A and B, group averages represent standard deviation of the last 10 trials of each phase: Baseline (B), Adaptation (A), Test (T). For Figure C, phase data are combined and compared between dimensions. Error bars represent SEM. *Significantly different $p<0.05$.

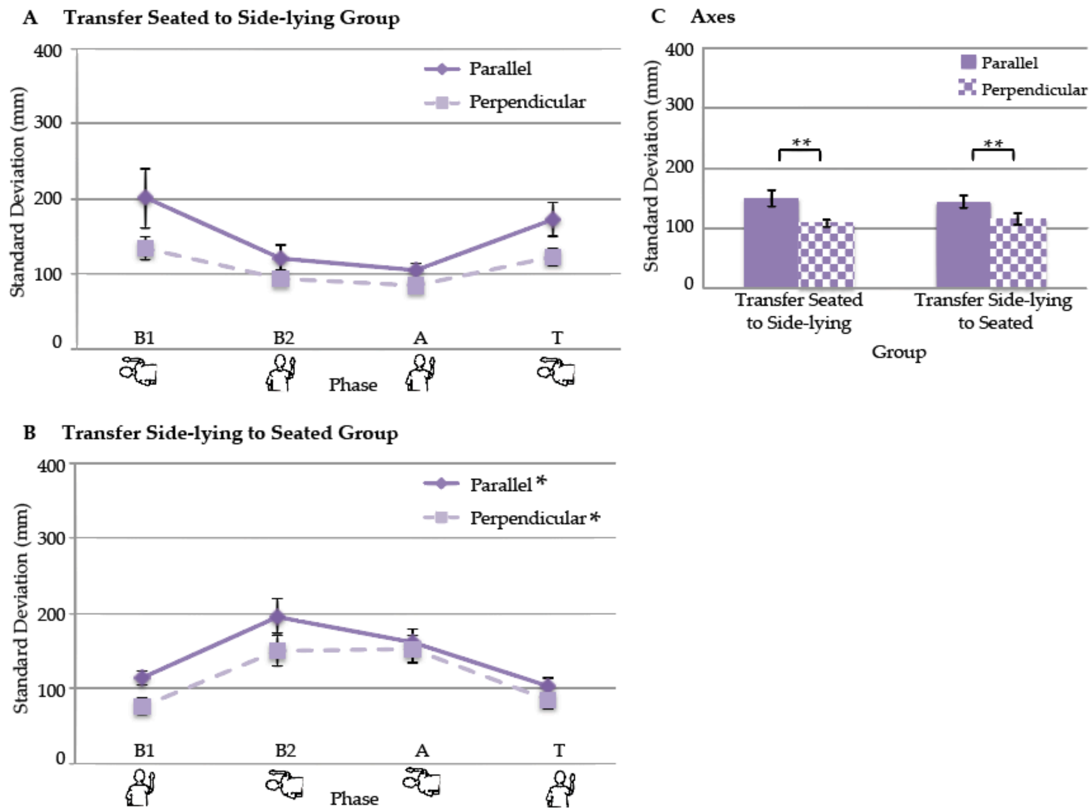

Figure 11 Group Average Endpoint Error Variability over Phases and Axes for Transfer Groups: Transfer Seated to Side-lying Group (A), Transfer Side-lying to Seated Group (B), Axes (C). For Figures A and B, group averages represent standard deviation of the last 10 trials of each phase: Baseline (B1, B2), Adaptation (A), Test (T). For Figure C, phase data are combined and compared between axes. Error bars represent SEM. *Indicates axes along which there is a significant effect of phase on standard deviation, $p<0.05$. **Significantly different $p<0.05$

In contrast, comparisons within the Transfer groups revealed a significant effect of phase on variability in the horizontal dimension for each group (both $p<0.001$). In addition there was a significant effect in the vertical dimension for the Transfer Side-lying to Seated group (Transfer Side-lying to Seated, $p=0.038$; Transfer Seated to Side-lying, $p=0.137$). These effects appeared to be because Transfer group participants rotate their position. Therefore, in order to determine if results of the Transfer groups were consistent with those of the Control groups, the data were reanalyzed based on orientation with the body (i.e., parallel or perpendicular to the body's long axis), rather than based on horizontal and vertical axes in Cartesian coordinates (Figure 11). Here, similar to the Control Groups, results for the Transfer Seated to Side-lying group (Figure 11A) showed no effect of phase on variability along either axis. That is, variability was not significantly different across phases for the axis aligned with the long axis of the body (parallel, $p=0.053$) or for the axis perpendicular to the long axis of the body (perpendicular, $p=0.0503$). However, variability did differ across phases for both axes (parallel and perpendicular, both $p<0.001$) in the Transfer Side-lying to Seated group (Figure 11B). When the data were combined across phases (Figure 11C), similar to those in the Control groups, Transfer group participants were more variable along the axis aligned (i.e., parallel) with the long axis of the body, and this comparison was significant for both groups (Transfer seated to Side-lying, $p<0.001$; Transfer Side-lying to Seated, $p=0.003$).

While differences across phases were only significant for the Transfer Side-lying to Seated group, in both Transfer groups variable error appeared to be greater along both axes (parallel and perpendicular) when participants were in the Side-lying position. To determine if there were significant differences in variability across positions overall, data for all groups were collapsed across the horizontal and vertical dimensions by computing the standard deviation of the resultant error vector. Again, this was averaged across the last 10 trials of each phase for each group. Comparisons were made between each of the two Control groups and the two Transfer groups, for each phase (Figure 12). For the Control groups (Figure 12A), the Side-lying participants appeared to be more variable, however this difference was not significant (BL, p=0.347; A, p=0.754; T, p=0.347). In contrast, there were significant differences between the two Transfer groups (Figure 12B) at each phase (BL1, p=0.009; BL2, p=0.022; A, p=0.014; T, p=0.004) and in each case, the group that was in the Side-lying position was more variable. Thus, it appears that for all groups, endpoint error was more variable when participants were in the Side-lying position and this difference was significant for the Transfer groups.

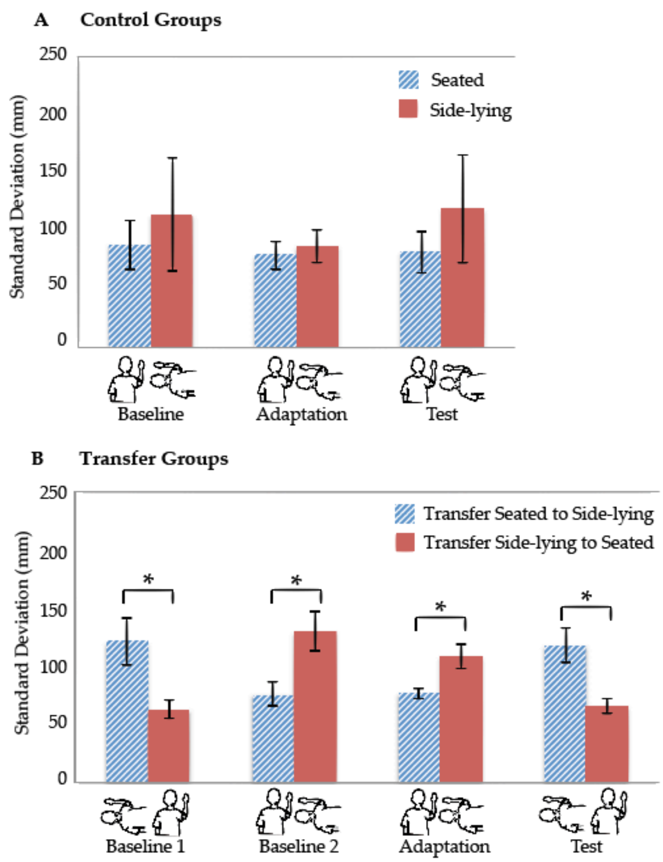

Figure 12 Group Average Resultant Endpoint Error Variability: Control Groups (A), Transfer Groups (B). Comparison of group means for standard deviation of resultant error averaged across last 10 trials of each phase. Error bars represent SEM. *Significantly different, p<0.05.

Overall, results of the variability analysis indicate participant throwing was more variable along the axis aligned with the long axis of their body, i.e., the vertical axis if Seated and the horizontal axis if Side-lying. In addition participants appeared to be more variable during Side-lying throwing.

2.3.2.3 Adaptation to Throwing Position Independent of Visual Perturbation

Finally, comparisons were done to determine if throwing in one position led to an adaptation that affected throwing in the other position, separate from any effects of the prism-induced perturbation. If Transfer group participants learned something during Baseline 1 that affected Baseline 2, this should be apparent as a difference between Baseline 2 performance of the Transfer groups and Baseline performance of the Control group throwing from the same position. To investigate this, group averages were computed for a new time period, Early Baseline (EB), defined as the first 3 Baseline trials, and for Late Baseline (LB) defined as the last 10 Baseline trials.

Average endpoint error during Early and Late Baseline of the Control groups, and Early and Late Baseline 2 of the Transfer groups, are depicted in Figure 13. It can be seen that Early Baseline 2 (EB2) performance in the Transfer groups was no different than that of Late Baseline (LB) in the Control group matched for throwing position, indicating that Baseline 1 had no negative impact on Baseline 2. To test this, a comparison of Early Baseline 2 (Transfer) to Late Baseline (Control) was done for each dimension within each of the two positions (Seated and Side-lying). No significant differences were found: for the Seated Baselines, EB2 (Transfer) v LB (Control), horizontal $p=0.205$, vertical $p=0.739$; for the Side-lying Baselines, EB2 (Transfer) v LB (Control), horizontal, $p=0.999$, vertical, $p=0.713$. Further, in the Transfer groups, it appears as if Baseline 1 may have provided a practice effect that led to reduced error during Early Baseline 2 as compared with Early Baseline of their Control group counterpart.

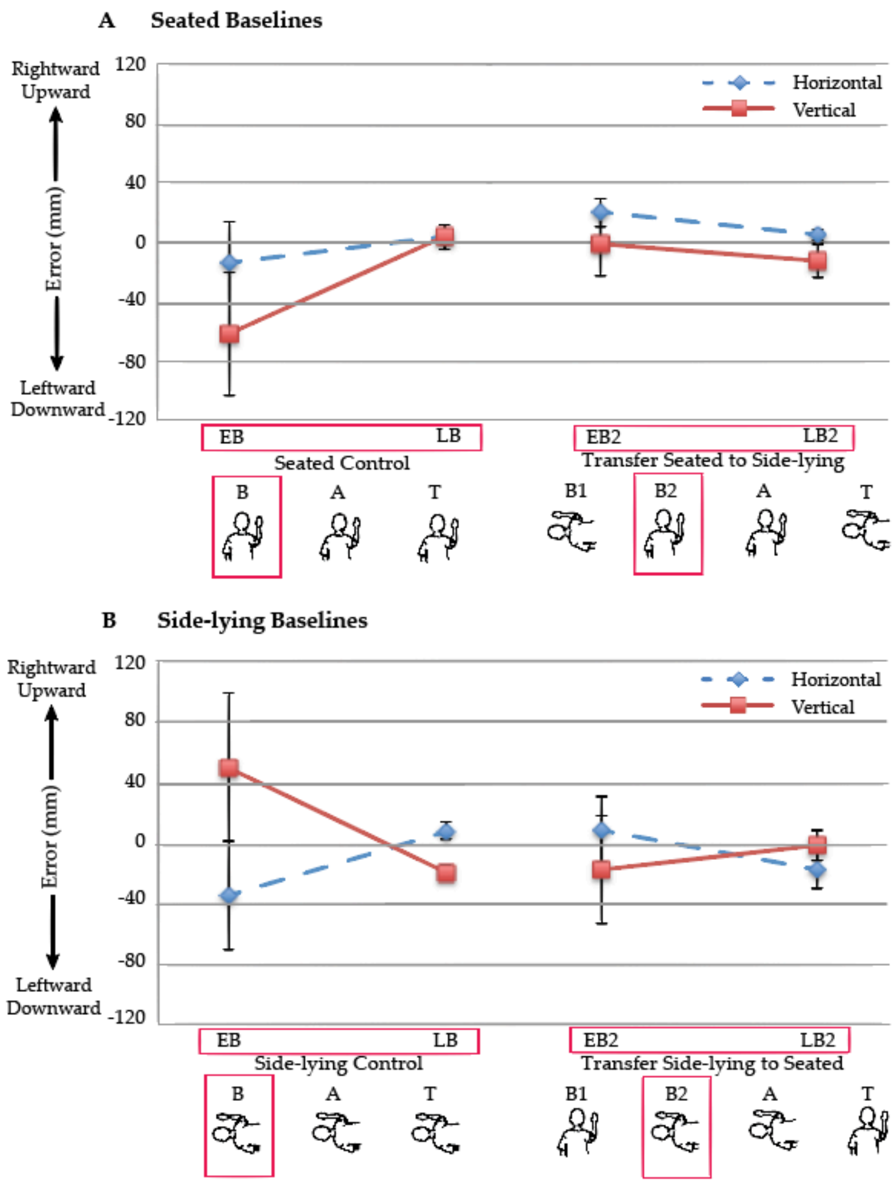

Figure 13 Group Average Early and Late Baseline Endpoint Errors for Control Groups and Transfer Groups: Seated Baselines (A), Side-lying Baselines (B): Early Baseline (EB, EB2), Late Baseline (LB, LB2), Baseline (B, B1, B2), Adaptation (A), Test (T). Error bars represent SEM.

2.4 Discussion and Limitations

2.4.1 Discussion

The primary purpose of this study was to determine how PA of ball-throwing generalizes with respect to spatial reference frames. It was predicted that, if generalization occurred, it would be expressed purely egocentrically. Our experimental results suggest that this hypothesis was correct. Significant aftereffects seen in the Transfer Seated to Side-lying group were to the left of the participant, not to the left of the target (i.e., transfer rotated with participant rotation).

While our results gave no indication of allocentric generalization, it is possible that a small allocentric generalization occurred, but was not detected. Results of the variability analysis suggest throwing movements were more variable along the axis aligned with the long axis of the body, and this is the axis along which allocentric generalization would be expressed. However, the size of vertical aftereffects in the Transfer Seated to Side-lying group was almost identical to that of the horizontal aftereffects in the Seated Control. Specifically, for the Transfer group, Early Test minus Late Baseline 1 in the vertical dimension was equal to (-)234.4 mm, and Early Test minus Late Baseline in the horizontal dimension for the Control group was equal to (-)242.7 mm. While caution should be taken when comparing these values, as they are from different groups of people, their consistency does lend support for a purely egocentric generalization.

An unexpected finding of this study was that only the Transfer Seated to Side-lying group demonstrated generalization of the adaptation. Thus, it appears that transfer of PA of ball-throwing was asymmetric; while participants who adapted in the Seated position showed robust aftereffects when Side-lying, there were no significant aftereffects in sitting for those who adapted while lying on their side. It is not known why the adaptation only transferred in one direction, however some factors that may have contributed were investigated through secondary analyses.

First, based on the findings of a study by Kitazawa et al. (1997), indicating that transfer of PA can be affected by movement speed, a velocity analysis was done. The instantaneous velocity of the ball as it left the hand was compared across the key time periods in each group. No significant effect of velocity on time period was found within the Transfer Side-lying to Seated group, therefore the lack of transfer seen in this group cannot be explained by differences in movement speed between Adaptation and Test periods. Interestingly however, there was an effect of velocity within the Transfer Seated to Side-lying group. Here, ball speed increased significantly between Late Baseline and Late Adaptation. This could be interpreted as a sign that these participants may have learned the throwing task better than those in the other groups. It also could indicate that Seated throwing was an easier task.

Interestingly, results of the variability analysis also indicate that there may have been differences in task difficulty related to throwing position. Here, it was found that variability was greater when participants threw while Side-lying. This was seen in the between-groups comparisons of the two Control groups, as well as that of the two Transfer groups. Remember however, that in the main analysis there was no significant difference between Late Adaptation endpoint error and that of Late Baseline 2 for the Transfer Side-lying to Seated group, so it appears that these participants were able to adapt in the Side-lying position. Further, there was no indication that any increased task difficulty affected storage of the adaptation, as the Side-lying Control group demonstrated significant aftereffects. Therefore, while it is possible that differences in task difficulty were responsible for the asymmetric transfer, there is no direct evidence to support this.

Another possible explanation is that differences in transfer were due to differences in the novelty of the task. In this study participants were required to throw a ball at a target while lying on their side and not raising their head from the horizontal plane. While throwing a ball was not a novel task, throwing it from this position was. Further, on the rare occasions when people do throw from this position it is usually done with the head rotated so it is vertical. While both the Side-lying Control group and the Transfer Side-lying to Seated group were able to adapt their movement when in the horizontal position, it is possible that the brain may not have utilized this learning when participants were repositioned into the Seated (vertical) posture that was more consistent with past experience. In other words, learning that occurred while throwing a ball in the Side-lying position, might have been outweighed by earlier learning (i.e., learning before this experiment) that was deemed more pertinent, once participants were rotated to a familiar and well-rehearsed position (Seated). This idea is supported by a visuomotor rotation study in which an arm adaptation, that had been shown to transfer to the wrist, was blocked if the wrist was previously adapted in a different direction. That is prior wrist experience blocked transfer of the arm adaptation to the wrist (Krakauer et al. 2006). On the other hand, when individuals in the current study were Seated during Adaptation, a position more consistent with normal throwing, the learning may have been considered relevant to throwing in general (i.e., not context specific) and therefore the adaptation was reflected in the Side-lying position.

While speculative, this explanation is consistent with results of a different PA study in which pointing movements were found to transfer asymmetrically between the arms and legs (Savin and Morton 2008). Specifically, when participants adapted to prisms during arm pointing movements, the adaptation transferred to leg pointing, but not vice versa. Again, pointing is not a novel task, however pointing with the leg is, when compared to pointing with the arm. Therefore leg learning may have been context specific. In contrast, pointing with the arm is a well-learned task, which has been practiced in many contexts, and therefore arm learning may have been considered relevant to all pointing movements.

In conclusion, there are two main findings from this study. First, it appears that when PA of ball-throwing generalizes, it does so with respect to egocentric spatial reference frames. This result implies that the error signal driving PA is egocentric. That is, modifications to internal model transformations are based on a comparison of actual and predicted visual feedback that is in egocentric coordinates. Our finding of egocentric generalization in healthy participants is consistent with the results of a recent intervention study in which PA treatment was shown to improve patient performance only on egocentric tasks (Gossman et al. 2013). While studies of patient populations must always be viewed with caution due to the wide variability in patients, the difficulty in isolating the functional locus of damage, and the ability of the brain to compensate, the results of both studies combined suggest that PA, as a rehabilitative intervention, may be most useful for individuals with egocentric forms of neglect.

The second, and unexpected, finding of this study is that PA of ball-throwing appears to transfer asymmetrically between Seated and Side-lying positions, and this may be due to the novelty of a Side-lying throwing position. This novelty may have resulted in learning that was context specific and not considered relevant to throwing while Seated.

2.4.2 Limitations

There are several limitations to this study. First, the brain uses many different egocentric reference frames to encode space (i.e., head centered, trunk centered, arm centered, etc.) (Colby 1998; Galati 2010). This study does not address which of those reference frames the adaptation might have occurred within; however this could be addressed in future studies by designing experiments that decouple the various reference frames. Next, kinematic data of the movement were not collected. While steps were taken to maintain the consistency of the task across positions (same arm, same overall configuration of the arm, trunk, and head relative to each other) it cannot be said definitively that the movement patterns in external space were identical across positions. In addition, the actual arm velocity cannot be compared across movements; it can only be inferred based on the velocity of the ball at ball release. Future studies should be done using reflective markers on the arm, head, and trunk to capture these data. Further, it is possible that the study design was not sensitive enough to detect a small allocentric generalization. To guard against this, sample size could be increased, or follow-up studies could be done using tasks that are more easily controlled (i.e., less variable) than ball-throwing. In addition, future studies could be designed with catch trials, so that a percent-transfer measurement could be computed. A high percent-transfer would support a purely egocentric transfer. Finally, the context(s) in which transfer of learning occurs are not clearly understood; therefore, extrapolating the results of this study to other movements or other types of visuomotor adaptations should be done with caution. Future studies could be done to test whether these results extend to different tasks.

Chapter 3

DISCUSSION

3.1 Discussion and Lessons Learned

In this study, generalization of visuomotor adaptation was examined from a novel perspective. Specifically, the study was designed to test for generalization of PA across reference frames involved in spatial cognition (i.e., allocentric and egocentric). In order to do this, it had to first be determined if PA would transfer across body positions that decouple the two spatial reference frames.

3.1.1 Aim 1

Thus, the first aim of this study was to determine if PA of a throwing movement generalizes across Seated and Side-lying positions. It was predicted that following adaptation, aftereffects would transfer from both Seated to Side-lying and from Side-lying to Seated. Surprisingly, the adaptation did not transfer in both directions; it only transferred from the Seated position to Side-lying. This lack of transfer from Side-lying to Seated cannot be attributed to an inability to adapt while in the Side-lying position because adaptation was demonstrated in this Transfer group. In addition, the significant aftereffects seen in the Side-lying Control group indicate Side-lying adaptation can be stored by the CNS.

The failure to transfer also cannot be explained by changes in movement velocity between the Adaptation and Test phases, because these were not significantly different. It also does not appear that variability of throwing between phases, across dimensions, or across positions could have led to an undetected transfer because most of the variability was along the axis aligned with the long axis of the body, and based on the results of the Transfer Seated to Side-lying group, this was not the axis of interest (i.e., egocentric generalization would have been demonstrated by aftereffects along the axis perpendicular to the long axis of the body, not parallel to it).

Interestingly, the results of this study may reflect the importance of context in the expression of motor learning. While ball-throwing is not a novel task, throwing from the Side-lying position is. Thus the context in which learning occurred was novel for the group showing no transfer, and familiar for the other group. Therefore, while both the Side-lying Control group and the Transfer Side-lying to Seated group were able to adapt their throwing movement while lying of their side, it is possible that when repositioned into the Seated (vertical) posture, a position more consistent with past experience, earlier Seated learning was recalled. In other words learning to throw a ball in the Side-lying position may have been context specific due to the novelty of the task. Conversely, when individuals were Seated during Adaptation the brain may have considered the learning relevant to all throwing contexts since this vertical position is consistent with past experience. Therefore, the adaptation was not only stored, but also expressed in the Side-lying position.

One important lesson learned from conducting this experiment was that the kinematics of the movement itself should have been captured through the use of reflective markers placed along the arm and trunk. This would have allowed us to examine potential differences in the arm configuration relative to the body, across the different positions. Further, the velocity of the arm could have been calculated directly from this data, rather then being inferred from ball speed.

3.1.2 Aim 2

The second, and primary, aim of the study was to determine how PA of throwing generalizes with regards to allocentric and egocentric reference frames. It was predicted that a 90-degree rotation of participant position following PA of throwing would result in aftereffects that occurred along the axis perpendicular to the axis of visual displacement in extrinsic space (i.e., aftereffects would rotate with subject rotation), indicating generalization within purely egocentric reference frames. Consistent with predictions, transfer within the Transfer Seated to Side-lying group was expressed egocentrically, with no indication of allocentric generalization. The rightward visual displacement caused by the prisms led to initial errors to the right of the target and to the right of the individual during Early Adaptation. Aftereffects in the Side-lying position were not to the left of the target but rather to the left of the individual (i.e., below the target).

Based on this result, it appears that the error signal used during PA is in egocentric coordinates. While the adaptation was not expected to transfer purely allocentrically, there was reason to believe there might be partial allocentric generalization. It has been shown that the brain represents space through the use of both allocentric and egocentric reference frames. Further allocentric perception is important for at least some (if not all) goal-directed movements. An alternative explanation for not seeing any allocentric generalization could be that the task used was not sensitive enough to detect a relatively small allocentric transfer. A task in which people are less variable in their accuracy might be a better choice for future studies. Additionally, in this study we were not able to quantify the extent of transfer between the two positions. If the study had been designed to do this, then the value found might indicate whether it was reasonable to believe that there was no allocentric transfer (e.g., a 95 % egocentric transfer would be stronger support for a purely egocentric transfer than a 75% transfer). Future studies could be designed to capture this information through catch trials.

Additionally, similar to the intervention study by Gossman et al. (2013), the finding that PA in healthy participants did not generalize allocentrically suggests that PA treatment may only be helpful for patients with egocentric forms of neglect. However, the results should not be taken to indicate that allocentric representations are not important for goal-directed movements, they only suggest that prism adaptations may not generalize with respect to them.

Finally, there is no indication that the results of this study were influenced by a secondary adaptation related to changes in participant throwing position.

3.2 Future Directions

While the primary purpose of this study was to investigate generalization of PA across spatial reference frames, an unexpected asymmetric transfer across throwing positions was found. We have suggested that this result may be due to differences in novelty of throwing position. It appears that when individuals adapt to prisms while in a position consistent with past throwing experience, adaptation transfers to a novel position; however, when they adapt in a novel position, it does not transfer to a well-practiced position. This finding has important implications for the design of rehabilitative interventions, which are often performed in clinical settings using specialized equipment. It suggests that if the clinical environment is too novel, the training may not transfer to daily activities outside the clinic (i.e., the learning may be context specific). Therefore, an important focus for future work is to determine how training environments need to be designed in order for learning to transfer to natural environments.

It has been suggested that generalization of motor adaptation depends on estimates of the source of the motor error (Berniker and Kording 2008). That is, motor errors may be the result of either changes within the body (e.g., fatigue, injury), or changes within the environment (e.g., external forces) and the source (body or world) to which the CNS attributes the error may affect how it generalizes. For example, Torres-Oviedo and Bastian (2012) have suggested that assignment of motor error to world/environmental (exogenous) factors reduces transferability across contexts (i.e., learning is considered context specific), whereas assignment of error to oneself (endogenous) may allow adaptation to transfer to other contexts. If this is true, then treatment protocols need to be designed in ways that minimize the possibility of error being assigned to environmental conditions.

One approach that has been suggested for reducing the likelihood of context specific learning during perturbation training, is to generate errors that are within a person's natural range (i.e., small errors that could be attributed to natural systems) rather than large or abrupt errors that are more likely to be considered environmentally induced and therefore specific to the environmental context (Torres-Oviedo and Bastian 2012). Another approach might be to perturb the system in settings that more closely resemble natural settings. If the environment appears consistent with past experience, then errors may be more likely to be assigned to the self rather than the environment. This approach might be accomplished through the use of virtual reality technology that masks the clinical setting. Finally, perturbing the system in multiple contexts may promote greater transferability of learning. That is, it is less likely learning will be considered context specific if it is brought about in a variety of settings. By applying similar perturbations across multiple contexts, assignment of the error source may shift from the environment to the self, and cause the adaptation to be more transferable.

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Appendix

IRB Approval and Permissions

This appendix includes two documents. The first document states University of Delaware IRB approval for the study outlined in this thesis. The second document, entitled "Human Subjects Protocol" lists the thesis author as an approved investigator.

UNIVERSITY OF DELAWARE RESEARCH OFFICE

210 Hullihen Hall
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DATE:	May 7, 2014
TO:	Susanne Morton, PT, PhD
FROM:	University of Delaware IRB
STUDY TITLE:	[594836-1] Prism Lens Adaptation
SUBMISSION TYPE:	New Project
ACTION:	APPROVED
APPROVAL DATE:	May 7, 2014
EXPIRATION DATE:	May 6, 2015
REVIEW TYPE:	Expedited Review
REVIEW CATEGORY:	Expedited review category # *(4)*

Thank you for your submission of New Project materials for this research study. The University of Delaware IRB has APPROVED your submission. This approval is based on an appropriate risk/benefit ratio and a study design wherein the risks have been minimized. All research must be conducted in accordance with this approved submission.

This submission has received Expedited Review based on the applicable federal regulation.

Please remember that informed consent is a process beginning with a description of the study and insurance of participant understanding followed by a signed consent form. Informed consent must continue throughout the study via a dialogue between the researcher and research participant. Federal regulations require each participant receive a copy of the signed consent document.

Please note that any revision to previously approved materials must be approved by this office prior to initiation. Please use the appropriate revision forms for this procedure.

All SERIOUS and UNEXPECTED adverse events must be reported to this office. Please use the appropriate adverse event forms for this procedure. All sponsor reporting requirements should also be followed.

Please report all NON-COMPLIANCE issues or COMPLAINTS regarding this study to this office.

Please note that all research records must be retained for a minimum of three years.

Based on the risks, this project requires Continuing Review by this office on an annual basis. Please use the appropriate renewal forms for this procedure.

If you have any questions, please contact Nicole Farnese-McFarlane at (302) 831-1119 or nicolefm@udel.edu. Please include your study title and reference number in all correspondence with this office.

HUMAN SUBJECTS PROTOCOL
University of Delaware

Protocol Title:
Prism Lens Adaptation

Principal Investigator

Name:	Susanne M Morton, PT, PhD
Department/Center:	Physical Therapy
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Advisor (if student PI):

Name:
Contact Phone Number:
Email Address:

Other Investigators: Jennifer H W Barnes
Xin Li

Investigator Assurance:

By submitting this protocol, I acknowledge that this project will be conducted in strict accordance with the procedures described. I will not make any modifications to this protocol without prior approval by the IRB. Should any unanticipated problems involving risk to subjects occur during this project, including breaches of guaranteed confidentiality or departures from any procedures specified in approved study documents, I will report such events to the Chair, Institutional Review Board immediately.

1. Is this project externally funded? □ YES **X** NO

2. Research Site(s)

X University of Delaware
□ Other (please list external study sites)

Is UD the study lead? **X** YES □ NO (If no, list the institution that is serving as the study lead)

1

3. Project Staff
Please list all personnel, including students, who will be working with human subjects on this protocol (insert additional rows as needed):

NAME	ROLE	HS TRAINING COMPLETE?
Susanne M Morton	Principal Investigator	Yes
Jennifer H W Barnes	Co-investigator (graduate student)	Yes
Xin Li	Co-investigator (graduate student)	Yes

4. Special Populations
Does this project involve any of the following:

Research on Children? NO

Research with Prisoners? NO

Research with Pregnant Women? NO

Research with any other vulnerable population (e.g. cognitively impaired, economically disadvantaged, etc.)? please describe NO

5. RESEARCH ABSTRACT
The prism adaptation (PA) paradigm will be used to help understand how the nervous system learns to integrate new sensory information from different sources and different reference frames to produce coordinated movements; i.e., sensorimotor organization. PA has been used as both an experimental tool and as a therapy for neurologic disorders (for review see Redding, Rossetti, & Wallace, 2005). PA occurs when a person performs a motor task while wearing special goggles that contain prismatic wedges. The goggles shift or invert the visual field, and this can be done either horizontally (left /right) or vertically (up /down). Initial movement errors are gradually reduced through trial-by-trial repetition. When the goggles are later removed, errors occur in the opposite direction, called negative aftereffects, which indicate that the sensorimotor system has learned and stored a “realignment” of spatial reference frames. However, research has not determined which reference frames are realigned. In this study, healthy adults will perform one of several PA tasks to help answer this question.

6. PROCEDURES
We will recruit and enroll up to 100 participants in this study. Participants will be asked to complete 1 testing session that will last 1-2 hours. All testing will take place in the

Physical Therapy Department in STAR - Health Sciences Complex.

Recruitment and Enrollment Procedures:
We will recruit healthy participants through posted flyers in and around campus (see attached sample flyer) and through the UD classified ads. People interested in participating will then contact the lab, either by phone or email, for details and to sign up for the study. During the initial contact period, we will inform each potential subject about the purpose and procedures for participation, inclusion and exclusion criteria, and potential risks and benefits. We will also answer any remaining questions anyone may have at that time.

Also during the initial contact, we will screen participants to determine whether they may be eligible to participate. They will be asked: 1. Have you ever participated in a prism adaptation study before? 2. Are you generally healthy and between 18-40 years? 3. Are you right-handed? 4. Do you have normal or corrected to normal vision? 5. Do you have any medical conditions that limit use of or feeling in your neck, shoulder, arm, or hand, or interfere with normal walking? 6. Have you been diagnosed with any neurological or neuromuscular disorder?

If the potential subject is interested and appears able (eligible) to participate, we will schedule an appointment to come to the lab for testing. A reminder email and/or phone call will be placed to the potential subject the day before testing.

Testing Procedures:
At the time of testing, a member of the research team will go over the informed consent document with the potential subject in detail. This includes explanation of the purpose and procedures for participation, inclusion and exclusion criteria, potential risks and benefits, privacy and confidentiality, and the voluntary nature of their participation. After answering any remaining questions, if the individual is still willing and able to participate, we will ask him/her to sign the consent document. After the consent document, we will have the subject complete some additional information to document eligibility, to record demographics, and to arrange for compensation. These are the Edinburgh Handedness Inventory (Oldfield 1971), Participant demographics, and Participant compensation forms, respectively (see attached). The participant will then be asked to perform the Prism Adaptation Paradigm for one of the following tasks outlined below: Throwing Task, Reaching Task, Target Slide Task, Walking Task.

1) Throwing Task: For this task participants will be asked to repeatedly toss a small diameter (less than 2 inches) foam or clay ball at a target that is located no more than 15 feet away. They will be asked to do this from either the standing position or while lying on their side on a cushioned platform. Their performance may be recorded using motion capture equipment.
2) Reaching Task: For this task participants will be seated at a table and asked to reach for a designated target(s). There may or may not be obstacles in the direct path to navigate around. During the task, portions of their arm and/or hand may be occluded. Their performance may be recorded using motion capture

equipment.

3) Target Slide Task: For this task participants will be seated at a table and asked to slide and release a small object (less than 2 inches in diameter) toward a designated target(s). During the task, portions of their arm and/or hand may be occluded. Their performance may be recorded using motion capture equipment.
4) Walking Task: For this task participants will be asked to walk back and forth over a short distance (less than 30 feet). They may need to navigate around a large, obvious obstacle. Their performance may be recorded using motion capture equipment.

Prism Adaptation Paradigm: The prism adaptation paradigm consists of three phases.

Phase 1: During this phase the participant will perform the assigned task and baseline measurements will be recorded.

Phase 2: During this phase the participant will perform the assigned task while wearing prism goggles that laterally displace the optical field in either the right or left direction.

Phase 3: During this phase the participant will remove the goggles and perform the assigned task. Compensatory aftereffect measurements, reflecting the level of adaptation, will be recorded.

7. STUDY POPULATION AND RECRUITMENT

Up to 100 healthy adults will be recruited to participate in this project. We will not recruit individuals from vulnerable populations. We will attempt to recruit individuals who are representative of the local population, i.e., we will strive to recruit relatively equal numbers of men and women and persons of racial and ethnic backgrounds similar to the racial and ethnic demographics of the state of Delaware. This demographic information is used so that we can be compliant with federal funding agency (e.g., NIH) requirements that we recruit and enroll individuals who fairly represent the area in terms of gender, race, and ethnicity.

The specific subject inclusion and exclusion criteria are:

INCLUSION:

1. Healthy adult, age 18-40 years
2. Right-hand dominant (as assessed by the Edinburgh Handedness Inventory)
3. Normal or corrected to normal vision
4. Willing and able to participate in the single testing session

EXCLUSION:

1. Past participation in a prism adaptation study
2. Any neurological or neuromuscular disorder
3. Any musculoskeletal or other condition that limits use of or feeling in the neck, shoulder, arm, or hand, or which interferes with normal walking

The inclusion and exclusion criteria are discussed at the initial screening and again on the first testing day when the informed consent document is reviewed. Determining whether all criteria are met is based on the subjects' individual responses to each question. Additionally, the Edinburgh Handedness Inventory will be completed immediately after the consenting process and anyone not scoring as a right-hand dominant individual will subsequently be removed from the study and not be allowed to participate.

Participation in the study is voluntary. Any subject may withdraw from the study at any time without any negative consequences. In addition, the PI may terminate a subject's participation if the subject is viewed by the PI to be placing him/herself at risk. This is not expected, since the task is not at all strenuous, but could potentially occur if a subject were to report any distress for any reason. Termination could also occur if there is some technical difficulty with the experimental equipment that disrupts data collection and makes the data unusable.

8. RISKS AND BENEFITS

There is a small (unlikely to occur) potential physical risk of mild fatigue or muscle soreness. There is a small (unlikely to occur) potential physical risk of mild skin irritation from adhesive if motion capture markers are used and affixed to the skin with adhesive. There is a very small (very unlikely to occur) potential psychological risk of frustration. These risks will be minimized by frequently inquiring as to each subject's condition throughout testing and encouraging subjects to say if/when they feel their arm begin to get tired or sore. Skin irritation will be minimized by adhering markers to clothing rather than skin whenever possible and using latex-free tape. Frustration will be minimized by informing subjects that the task is intended to be difficult and that feeling like it is hard is a normal response.

The risks associated with participation are, in the PI's opinion, minimal, and do not constitute any risk above that encountered in routine physical or psychological testing.

If fatigue or muscle soreness is experienced, it is expected to last no more than 12-24 hours. If the skin is irritated, it can be reduced by gently cleansing the exposed skin and should resolve within 24 hours. Likewise, frustration is not very likely, and can be minimized through a thorough explanation of the design.

There will be no direct benefits to participants. However, results from this study are expected to lead to a better understanding of how the central nervous system organizes sensory and motor system information. This knowledge will benefit delivery of rehabilitation in physical therapy settings in the future.

9. COMPENSATION

Participants will be provided $15 in compensation after participation.

10. DATA

Subjects will not be anonymous to the researchers. As part of the consent process and verification of eligibility, subjects must provide their name, date of birth and other identifying information to members of the research team. However, identities will be kept confidential to the extent possible (see Confidentiality section below). De-identified data may be presented in abstract, poster, presentation, or published manuscript format. Data with identifying information will be saved until the project is complete or the data are published, whichever comes first. Raw de-identified data will be stored for at least 5 years and may be used in future related studies. If after 5 years, it is determined that the data can be destroyed (for space-saving purposes) all electronic data will be wiped from hard-drives and servers and all paper data will be shredded. We have no current plans to share the data with anyone outside of the research team. If in the future, it serves a research purpose to share the data with another investigator, we will share only de-identified information and transfer the information over secure electronic means (personal delivery of hard drives or exchange over a secure network).

Data will be analyzed and reported to the public in the form of abstracts, invited talks, poster presentations, and/or as a peer-reviewed publication. Specifically, we will test for differences in performance between phases 1, 2 and 3 of the prism adaptation paradigm in order to assess the levels of adaptation and compensatory aftereffects reflecting storage and generalization of adaptation.

11. CONFIDENTIALITY

Motion capture recordings of the participant may be collected. All participant identifying information will be stored in a locked file cabinet (paper forms) or on password-protected computers or servers (electronic forms) and will be utilized only by investigators on the protocol who have a specific need for the identifying information. All data collection sheets and all data will be de-identified and, instead, coded using a numerical system, the key to which will be maintained on a password-protected computer. All de-identified data and data collection sheets will also be stored in a locked file cabinet (paper forms) or on password-protected computers or servers (electronic forms) that are kept separate from the identifying information.

Is there a Certificate of Confidentiality in place for this project? (If so, please provide a copy). NO

12. CONFLICT OF INTEREST

Do you have a current conflict of interest disclosure form on file through UD Web forms?
YES

Does this project involve a potential conflict of interest*? NO

13. CONSENT and ASSENT

_X___ Consent forms will be used and are attached for review (see Consent Template under Forms and Templates in IRBNet)

____ Additionally, child assent forms will be used and are attached. (NO)

____ Waiver of Documentation of Consent (attach a consent script/information sheet with the signature block removed). (NO)

____ Waiver of Consent (Justify request for waiver) (NO)

14. Other IRB Approval
Has this protocol been submitted to any other IRBs? NO
If so, please list along with protocol title, number, and expiration date.

15. Supporting Documentation
Please list all additional documents uploaded to IRBNet in support of this application.

- Handedness form
- Participant compensation form
- Participant demographics form
- Recruitment flyer

REFERENCES

Redding, G. M., Rossetti, Y., & Wallace, B. (2005). Applications of prism adaptation: a tutorial in theory and method. *Neurosci Biobehav Rev, 29*(3), 431-444.

Oldfield RC. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 1971 9: 97-113.