ABSTRACT

Title of Thesis: SENSORY INTEGRATION DURING DE-ADAPTATION TO VISUOMOTOR DISTORTIONS

Bradley R. King, Masters of Arts, 2006

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Previous research has demonstrated that adults can adapt to novel sensorimotor perturbations, a process thought to be achieved by the gradual update of an adaptive internal representation. However, few research studies have investigated the persistence of a newly acquired representation, as assessed by the reduction of performance errors after the perturbation has been removed (i.e., de-adaptation). The primary objective of this thesis was to determine if the central nervous system (CNS) could flexibly utilize visual and proprioceptive afference to de-adapt to novel sensorimotor perturbations. It has been previously demonstrated that the CNS relies more heavily on visual information for hand localization in the azimuthal direction whereas proprioception is more heavily weighted for hand localization in the radial direction. Seventy-two right-handed adults executed reaching movements during exposure to either an incremental visuomotor rotation or gain distortion. Visual feedback provided during post-exposure was manipulated. Results indicate that the CNS predominantly utilized visual afference to de-adapt to both perturbations, despite the fact that rotation adaptation resulted in movement errors in the azimuthal direction whereas gain adaptation resulted in movement extent errors. These data suggest that the CNS did not flexibly re-weight proprioceptive afference in the absence of visual feedback during a center-out drawing task.

SENSORY INTEGRATION DURING
DE-ADAPTATION TO VISUOMOTOR DISTORTIONS

By

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Thesis submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Master of Arts
2006

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ACKNOWLEDGEMENTS

I would like to thank all of those who helped with this thesis, especially:

- My parents, Randy and Linda, for the incredible support, friendship, and love they provide.

- Jane E. Clark, for being my advisor, and providing a tremendous amount of support.

- Florian Kagerer, Marcio Oliveira, Jae Kun Shim and Jose Contreras-Vidal for serving on my committee and providing valuable feedback.

- Melissa Pangelinan, Li-Chiou Chen, and Jason Metcalfe for answering 1,344.2 questions per day. Additional thanks to Melissa and Li-Chiou for recruiting participants.

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CHAPTER I

Introduction

Reaching or pointing movements towards a specific object are essential in many everyday activities, such as using a remote control to change the television channel or obtaining a glass of water. Although these movements are often considered ‘simple’, the successful execution of such movements involves a complex process of sensorimotor transformations. It has been suggested this sequence of events includes the accurate sensory perception of both hand and target locations, and the generation of the appropriate joint torques that guide the hand to the desired target (Krakauer, Pine, Ghilardi, & Ghez, 2000; Shadmehr & Holcomb, 1997; Bullock & Grossberg, 1988). The accuracy of these sensorimotor transformations is thought to be based on an internal representation, or internal model (IM), acquired over time as relationships between the external environment and the intrinsic characteristics of the arm are learned (Tong & Flanagan, 2003; Wolpert & Kawato, 1998; Gandolfo, Mussa-Ivaldi, & Bizzi, 1996; Shadmehr & Mussa-Ivaldi, 1994). Familiar movements are generally executed with ease as the central nervous system (CNS) can rely on these internal representations, developed as a result of previous experiences, in order to produce the appropriate motor commands. If the relationship between the limb and the environment changes, or the arm is subject to novel task demands, then performance will suffer.

To investigate the acquisition of novel sensorimotor transformations, researchers manipulate conditions in the environment in which participants move; specifically, by introducing either visuomotor distortions or mechanical perturbations during the execution of movements such as point-to-point reaching. In order to produce accurate movements during exposure to these perturbations, the CNS adapts by updating an IM appropriate for moving in the distorted environment. Investigating these adaptive internal representations during sensory-guided reaching allows researchers to better understand how the CNS is able to efficiently learn and flexibly control everyday movements: an area of research with strong developmental and pathological implications.

Exposure to such novel sensorimotor distortions during a reaching task results in an initial decrease in performance, as indicated by a larger directional error, decreased movement smoothness, and increased movement time and length (Shadmehr & Wise, 2005). However, with practice, participants adapt to the imposed distortion and return performance levels to those demonstrated prior to exposure. This has been shown in previous research for visuomotor rotations (Wang & Sainburg, 2005; Buch, Young, & Contreras-Vidal, 2003; Krakauer, Ghilardi, & Ghez, 1999; Kagerer, Contreras-Vidal, & Stelmach, 1997; Conditt, Gandolfo, & Mussa-Ivaldi, 1997), gain adaptations (Prager & Contreras-Vidal, 2003; Krakauer et al., 2000) and dynamic force field perturbations (Shadmehr & Brashers-Krug, 1997; Gandolfo et al., 1996; Shadmehr & Mussa-Ivaldi, 1994). The CNS utilizes both proprioceptive and visual afference to help generate on-line corrective motor commands appropriate for the distorted environment; however, the existing time delays in the sensorimotor pathways potentially result in erroneous movement trajectories. Recent research has demonstrated that the CNS can better compensate for the perturbation by predicting the future state of the arm based on an efferent copy of the motor command and accurate sensory feedback (Ariff, Donchin, Nanayakkara, & Shadmehr, 2002; Witney, Goodbody, & Wolpert, 1999).

Motor adaptation is thought to be initiated by the central nervous system detecting a mismatch between this state prediction and the distorted visual feedback during visuomotor adaptation paradigms, or the state prediction and both proprioceptive and visual feedback during dynamic adaptation tasks (Wolpert & Ghahramani, 2000; Ingram et al., 2000; Wolpert & Kawato, 1998). The CNS uses these sensory feedback error signals to drive within-trial, on-line corrections of the movements executed immediately after the introduction of the perturbation (Thoroughman & Shadmehr, 1999). With continued practice, the corrective responses generated in response to the sensory error signals are utilized in a feed-forward process, altering the initial motor commands of subsequent movements (Thoroughman & Shadmehr, 1999; Wolpert & Kawato, 1998; Conditt et al., 1997). This feed-forward update becomes obvious when the perturbation is removed and subsequent movements contain movement errors that are opposite to those experienced during the early adaptation trials. The distorted trajectories are referred to as aftereffects, and provide a measure of the level of adaptation acquired during exposure conditions (Prager & Contreras-Vidal, 2003; Kagerer et al., 1997; Shadmehr & Mussa-Ivaldi, 1994).

Since adaptation is thought to be triggered by the CNS perceiving an error between internal signals, it should follow that accurate sensory input will play an essential role in the process. Recent investigations have examined the contribution of proprioception and vision during adaptation experiments. Participants with impaired peripheral proprioceptive feedback failed to adapt to a mechanical perturbation, suggesting that accurate proprioception is required in dynamic adaptation tasks (Pipereit, Bock, & Vercher, in press). Conversely, several studies have demonstrated that deafferented participants, either permanently or experimentally, were able to adapt to novel visuomotor distortions, and in some cases, these participants demonstrated more complete adaptation than control participants (Pipereit et al., in press; Balslev et al., 2004; Ingram et al., 2000). These data suggest that intact proprioception is not necessary for visuomotor adaptation. Rather, it is possible that the existing mismatch between the state predictor and the distorted visual feedback serves as a sufficient signal for the central nervous system to update the internal representation.

It should be noted that these results do not necessarily indicate that proprioceptive afference is entirely ignored, as its contribution can be dependent upon the context of the task. If redundant information is provided to the CNS, such as both proprioceptive and visual afference, an optimal integration model suggests that these signals would ideally be combined with differential weights to produce the most accurate estimate of limb position (van Beers, Wolpert, & Haggard, 2002b; van Beers, Sittig, & Gon, 1999). Traditionally, it has been thought that vision is weighted significantly higher than proprioception. However, recent evidence indicates that the relative weights of proprioception and vision are highly flexible, dependent upon the stage of motor planning (Sober & Sabes, 2003), as well as the direction of arm localization (van Beers et al., 2002b; van Beers et al., 1999). Specifically, proprioception provides a more precise estimate for localization depth, or magnitude, and vision provides a more precise estimate for the azimuthal (left-right) direction. This potentially suggests that proprioception could contribute more heavily during gain distortion tasks compared to a visuomotor rotation as gain adaptation results in movement errors in the radial direction.

As previously stated, successful adaptation is indicated by the presence of aftereffects once the imposed perturbation is removed. However, these altered trajectories are transient as participants ‘de-adapt’ and execute movements appropriate for the unperturbed environment. Existing research has largely ignored this de-adaptation process despite the fact that it can provide information related to the persistence of the updated representation. Furthermore, investigation of the de-adaptation process could provide further insight into the integration of proprioception and vision by the CNS following exposure to a visuomotor distortion. If an experimentally manipulated distortion is no longer consistently reinforced, how does the CNS utilize available afferent signals to ‘wash out’ the updated internal representation and return to moving accurately in the unperturbed environment?

This research study has three specific aims to address these issues. For the first aim, two separate visuomotor tasks will be used to characterize the persistence of updated internal representations following adaptation to a gradually introduced visuomotor rotation and a gradually introduced visuomotor display gain distortion. This will be accomplished by establishing the time course and final level of de-adaptation, as assessed by the reduction of performance errors after the rotation has been removed. Gradual, rather than abrupt distortions will be implemented to restrict the participants’ ability to use cognitive strategies. Moreover, previous research has demonstrated that exposure to an incrementally introduced perturbation results in an identical, or even more complete, level of adaptation (Klassen, Tong, & Flanagan, 2005; Caithness et al., 2004; Kagerer et al., 1997). The second aim is to determine how the persistence of the updated representations is affected by the systematic manipulation of the feedback provided during the post-exposure phase. To interfere with the existing error signals between sensory afference and the state predictor, some participants will have limited visual feedback. Although proprioception does not play a significant role during adaptation, it is expected that proprioceptive information may contribute to the de-adaptation process in the absence of salient visual feedback. Lastly, the third aim will compare de-adaptation to visuomotor rotations and gain distortions in terms of the persistence of the updated representations and the relative contributions of proprioceptive and visual afference. Based on existing research supporting direction-dependent precision, it should follow that the contribution of proprioception during de-adaptation to a gain distortion will be greater than its contribution following exposure to a visuomotor rotation.

In addition to this first introductory chapter (Chapter I), four additional chapters are included in this thesis. The second chapter contains a review of the relevant literature, including an examination of sensory-guided reaching movements, emphasizing the roles of, as well as the integration of multiple sensory stimuli. The third and fourth chapters outline the methodology of the proposed study and present the experimental results, respectively. The final chapter includes a discussion of the experimental findings and suggestions for future research.

CHAPTER II

Review of Literature

The central nervous system (CNS) is capable of initiating and controlling nearly an infinite number of goal-directed movements, each of which involves precise, coordinated activity among multiple muscle groups regulated by specific neuronal activity patterns. The level of complexity is further increased when considering the high level of contextual variability. Changes in the environment, the inertial properties of a body segment, and the interaction with an external object all need to be considered. Despite such an intricate process, the CNS accurately performs a wide variety of movements, many of which are executed within specific spatial and temporal constraints. Research conducted over the past few decades has provided compelling evidence that goal-directed movements are governed by internal representations, or internal models (IM), acquired by the CNS (Tong & Flanagan, 2003; Wolpert & Kawato, 1998; Gandolfo et al., 1996; Shadmehr & Mussa-Ivaldi, 1994).. These internal representations can be viewed as computational sensorimotor transformations that relate perceived sensory information, such as the locations of the body and intended target, to the motor commands necessary to achieve the desired movement. The first section of this review of literature discusses the importance of internal representations as related to sensory-guided reaching movements. Subsequent sections introduce the experimental paradigms used to investigate the update of such representations as well as the roles of both proprioceptive and visual afference during these processes. Lastly, this review discusses an optimal multi-sensory integration model previously demonstrated in arm localization tasks. A goal of this thesis is to extend this model with respect to the integration of visual and proprioceptive error signals in order to update an internal representation appropriate for moving within a novel environment.

Why are Internal Representations Necessary?

A fundamental problem in motor control is how the central nervous system integrates the available sensory information in order to generate the appropriate motor commands that will drive the limb from its current state (including both position and velocity) to a desired state. The complexity of this issue is best understood when examining the coordinate frames of the available sensory input and the appropriate motor output. For instance, it is thought that target location is predominantly encoded in gaze- or fixation-centered coordinates: a concept that has been demonstrated for targets perceived by audition, vision, and proprioception (Pouget, Ducom, Torri, & Bavelier, 2002). Information regarding hand location is often provided in two distinct coordinate frames as the hand can be localized via proprioceptive afference with respect to joint angles and by the visual system in a gaze-centered coordinate frame. The available proprioceptive and visual feedback is integrated in order to provide a single estimate of hand location in gaze-centered coordinates (Buneo, Jarvis, Batista, & Andersen, 2002), a concept that will be discussed in a subsequent section. In order to move the limb to the target, the CNS needs to accurately integrate the sensory input and transform this information into a coordinate frame appropriate for motor command generation.

These point-to-point reaching movements can be controlled by feed-forward and/or feedback control mechanisms. Feed-forward implies an open-loop control system in which the entire movement is pre-planned and executed without on-line corrective responses. Conversely, a feedback control strategy is dependent upon sensory afference as well as motor reafference in order to guide the hand to the desired target. The presence of on-line visual feedback significantly increases the accuracy of goal-directed reaching; however, movements executed within specific temporal parameters (i.e., rapid arm movements) may be off-line by the time corrective movements can be generated in response to visual feedback. It has been reported that corrective movements in response to visual or proprioceptive afference are subject to a delay of at least 80-100ms (Desmurget & Grafton, 2000) , although other studies have reported values up to 200-300ms (Wolpert & Miall, 1996). If a reaching movement is completed within 400 to 500ms, these time delays would be detrimental to the accuracy of the movement. In order to execute rapid movements, the CNS must be able to predict the consequences of its own actions. Rather than relying on the delayed, feedback-dependent sensorimotor pathways, the CNS can provide an internal feedback signal based on the predictions of the arm's future state, a process considerably faster than utilizing the available sensory feedback (Desmurget & Grafton, 2000; Wolpert & Miall, 1996). Experimental support for such a predictive mechanism has been provided in bimanual grip force modulation tasks (Witney, Goodbody, & Wolpert, 2000; Witney et al., 1999; Blakemore, Goodbody, & Wolpert, 1998) during which anticipatory responses of one hand are generated in response to self-producing perturbations caused by the other hand. This ability to modify efferent motor commands based on either predicted or previously obtained knowledge of the arm's interaction with the external environment is an example of a feed-forward control mechanism. It should be noted that feed-forward and feedback control are not entirely independent as the majority of our movements are regulated by both types of mechanisms.

Transformations among coordinate frames and the existing delays in the sensorimotor pathways introduce potential obstacles during the execution of reaching movements. However, such movements are thought to be regulated by internal representations acquired by the CNS. It is important to note that these representations should not be viewed as physical mechanisms located within the central nervous system. Rather, they are better conceptualized as neural networks capable of performing specific functions that allow for the accurate execution of a wide variety of movements, one of which is goal-directed reaching. IMs are often thought to contain two primary components: an inverse model and a forward model. The forward model can be best understood as a predictive mechanism that provides the future state of the arm based on its current state and the motor commands generated by the CNS. Therefore, the forward model is well suited to cope with the problems caused by sensorimotor feedback delays. Conversely, the inverse model is simply the inverse process as it generates motor commands that will move the limb from the current to the desired state (Smith & Shadmehr, 2005; Wolpert & Ghahramani, 2000; Wolpert & Kawato, 1998). The inverse model is thus responsible for the coordinate frame transformation between the sensory input and the appropriate motor output, a relationship that is developed as a result of previous experiences (Wolpert & Kawato, 1998; Shadmehr & Mussa-Ivaldi, 1994).

In order to predict sensory consequences of a given motor command (i.e., forward model) or to generate a command appropriate for a given change in state (i.e., inverse model), these representations have to consider the interaction between the intrinsic characteristics of the arm and the external environment. Therefore, IMs *must* be highly adaptive. A child’s arm increases in mass, length, and inertia during development; all changes that will impact the arm-environment interaction. Furthermore, if a movement involves the use of a particular tool, an additional mass has been added and the dynamics of the task are no longer the same. In these instances, the CNS must update an internal representation that is appropriate for the given movement conditions.

The use of internal representations allows the CNS to accurately execute a wide variety of movements in constantly changing environments. The development of accurate forward and inverse models helps alleviate obstacles resulting from conflicting coordinate frames and sensorimotor feedback delays. Most importantly, these representations are not innate, as they have to be acquired through motor experience. Researchers often investigate the acquisition of adaptive representations by manipulating the environment in which participants' move, an area of research referred to as sensorimotor adaptation.

Sensorimotor Adaptation Paradigms

Familiar movements such as point-to-point reaching are generally executed with a high level of accuracy as the CNS can rely on stable, previously acquired internal representations to move the hand to the desired target. When participants are presented with a distortion that impairs motor performance, the CNS must adapt by generating motor commands that will result in straight and accurate movements despite the presence of the external manipulation. In laboratory tasks, typical perturbations include exposure to either a visuomotor or mechanical distortion during a center-out reaching paradigm in which participants make movements from a centrally-located start circle to peripherally-positioned target circles. Visuomotor distortions manipulate the visual feedback of the movement path provided via a visual display so that it is no longer congruent with the participant’s actual movement. For example, visuomotor *rotation* experiments rotate the feedback of the movement trajectory a specified magnitude either in the clockwise (CW) or counterclockwise (CCW) direction.   If a movement is made in a direction that is 90° with respect to the start circle, the visual feedback will appear at a 60° angle if the visuomotor distortion is 30° CW. Participants need to move at a direction equal in magnitude but opposite in direction to the imposed rotation in order to accurately reach the target. Visuomotor *gain* experiments multiply the amplitude of the participant’s movement by a specified gain. If the gain is greater than one, smaller amplitude movements are necessary to avoid overshooting the target. Gains less than one require larger amplitude movements to avoid undershooting. *Mechanical* perturbations are intrinsically different from visuomotor tasks as participants operate a robotic manipulandum while exposed to either a velocity- or position-dependent force field. The force field ‘pushes’ the manipulandum away from the desired target, resulting in directional errors similar to visuomotor rotation tasks. Note that visuomotor tasks present a conflict between sensory afference as the visually perceived hand position (provided on the experimental display) does not match the ‘felt’ position of the hand. Exposure to a force-field does not present a sensory conflict; rather, visual and proprioceptive afference both detect the force field imposed on the hand.

Exposure to these types of perturbations results in an initial decrease in performance, as assessed by greater directional errors and increased movement time and length (Shadmehr & Wise, 2005). With continued practice, participants begin to make feed-forward and feedback adjustments to the motor commands in order to return performance levels to those achieved prior to perturbation exposure (Krakauer et al., 1999; Conditt et al., 1997; Gandolfo et al., 1996; Shadmehr & Mussa-Ivaldi, 1994). This adaptive process is thought to be triggered by the CNS detecting an error between internal signals, such as the visually perceived hand location and the forward model's state predictor during visuomotor adaptation, or the state predictor and both visual and proprioceptive afference during mechanical perturbations (Wolpert & Ghahramani, 2000; Ingram et al., 2000; Kawato & Wolpert, 1998). During this exposure phase, it is thought that the CNS updates an internal representation appropriate for moving in the distorted environment (Shadmehr & Mussa-Ivaldi, 1994). The acquisition of a representation becomes evident once the perturbation is suddenly removed as participants demonstrate distorted movement trajectories that are opposite in nature to those experienced during early exposure. These distorted trajectories are the result of movements executed under the feed-forward control of the newly updated representation. They are commonly referred to as aftereffects and provide a relative measure of the level of adaptation to the imposed perturbation (Shadmehr & Wise, 2005). If performance improvements demonstrated during the exposure phase were the result of feedback-dependent processes, aftereffects would not be evident. These results remained consistent whether participants adapted to abrupt or gradually introduced perturbations (Klassen et al., 2005; Kagerer et al., 1997). The updated internal representations acquired by the CNS are able to model the distorted external environment in order to accurately produce the motor output appropriate for moving in such an environment (Shadmehr & Mussa-Ivaldi, 1994).

The majority of existing sensorimotor adaptation research has investigated the adaptive process *during* exposure to visuomotor and mechanical perturbations. However, the characteristics of an updated internal representation following the adaptation process are also of interest. Recent research has investigated the stability of newly acquired representations as it has been suggested that updated IMs can be consolidated into long-term memory and subsequently reactivated if similar environmental conditions are again experienced (Krakauer & Shadmehr, 2006; Shadmehr & Holcomb, 1997; Shadmehr & Brashers-Krug, 1997). In addition to the consolidation research, the persistence of an updated representation can also be examined by assessing the reduction of aftereffects immediately following the exposure phase. The persistence of an acquired representation has largely been ignored with the exception of a few research studies, none of which have focused on a visuomotor reaching task. Robert Scheidt and colleagues investigated the persistence of aftereffects following adaptation to a mechanical perturbation (Scheidt, Reinkensmeyer, Conditt, Rymer, & Mussa-Ivaldi, 2000). Participants in the post-exposure phase were either provided with real-time feedback of their movement trajectories or with a simulated ‘channel’ feedback that always displayed a straight line from the start point to the desired target. Thus, the channel group did not perceive any visual movement errors. Results indicated that removal of the kinematic aftereffects prevented the rapid de-adaptation evident in the on-line visual feedback group, suggesting that visual kinematic errors are necessary in restoring movements that are appropriate for a null environment. A separate mechanical perturbation study concluded that rapid de-adaptation is not unique to the null environment as participants were quickly able to de-adapt to a novel force field that was smaller in magnitude than the original field (Davidson & Wolpert, 2004). This suggests that this process is not the result of a simple ‘switching’ mechanism from a newly updated representation to a previously acquired, stable representation already stored in long-term memory. Rather, de-adaptation reflects the rapid ability to scale down the required force output of a given movement, an explanation that is only valid for mechanical adaptation tasks.

Role of Sensory Afference During Adaptation

It has been well established that adult participants can adapt to novel perturbations during the execution of point-to-point reaching movements (Krakauer et al., 1999; Gandolfo et al., 1996; Shadmehr & Mussa-Ivaldi, 1994). Since adaptation is thought to be initiated as a result of existing internal error signals such as sensory afference, it is important to develop an understanding of how sensory feedback is utilized by the CNS during these adaptation tasks. The majority of this research has investigated deafferented participants during exposure to novel distortions. Ingram et al. (2000) exposed a single deafferented patient to both a gradual and abrupt visuomotor gain distortion. Although the participant's lack of proprioception resulted in a decrease of the overall accuracy of the pointing movements, the patient was able to adapt to the imposed distortion. Similarly, a different research group investigated the performance of a deafferented patient in a double-step paradigm (Sarlegna, Gauthier, Bourdin, Vercher, & Blouin, 2006). A peripheral target was presented to the participant. Following movement onset, the target was displaced laterally. Participants would have to execute corrective movements towards the displaced target. Control subjects were able to alter their movement paths during the course of the movement in. Interestingly, without any peripheral feedback, the deafferented participant was also able to modify the on-line trajectory after the target was displaced. Performance was similar to that of the control subjects, although the velocity profiles of the movement were altered. Results suggest that intact proprioception is not necessary to adapt to a visual distortion. However, experimental studies investigating the performance of deafferented participants are often equivocal as patients can develop unique control strategies in order to cope with the lack of peripheral feedback (Ingram et al., 2000).

More recent research has implemented methods designed to experimentally degrade proprioceptive acuity in ‘typical’ participants. Fifteen minutes of 1 Hz repetitive transcranial magnetic stimulation (rTMS) was applied over the somatosensory cortex, resulting in a ‘virtual lesion’ that significantly reduced proprioceptive precision (Balslev et al., 2004). Immediately following the rTMS, participants were asked to complete a computerized mirror-drawing task during which the position of the cursor was reversed in the vertical direction relative to the position of the computer mouse. An upward movement of the mouse resulted in a downward movement of the cursor. Those who received the rTMS were significantly more accurate than control subjects, providing further support that proprioceptive afference is not necessary, and possibly even detrimental, during visuomotor adaptation tasks. In a related study, (Pipereit et al., in press) placed vibration devices on the dominant wrist of participants, with one vibrator on the flexor tendon and one on the extensor tendon proximal to the wrist. Although proprioceptive afference was strongly reduced, participants demonstrated identical adaptation to a 60° visuomotor rotation as compared to control subjects. However, participants exposed to the same wrist vibration technique failed to adapt to a force-field perturbation, suggesting that intact proprioception is required for mechanical, but not visuomotor, adaptation. A possible explanation for the above findings is that deafferented patients, either permanently or experimentally, demonstrate higher levels of adaptation compared to controls because the existing visual-proprioceptive conflict during visuomotor tasks is reduced. Decreasing this existing conflict allows the CNS to decrease the existing visual errors during the task (Pipereit et al., in press). This would also suggest that in intact proprioceptive participants, adaptation will be faster and more complete if proprioceptive afference is eliminated or down-weighted. Recordings from muscle spindle afferents have demonstrated decreased activity during a visuomotor adaptation task, a result the authors attributed to a reduction of the existing visuo-proprioceptive conflict (Jones, Wessberg, & Vallbo, 2001).

This notion of down-weighting available proprioceptive information is largely supported by tasks in which the visual information is extremely salient. The goal of these tasks is to move the pen as straight as possible to the intended target. If direct vision of the hand is occluded (as it typically is), the only available visual information is the pen trace provided on the display screen. Therefore, the goal of the task is to move the distorted visual feedback on a straight line towards the intended target. If the visual feedback is reduced or removed altogether, will the previously down-weighted proprioceptive afference become up-weighted in order to generate accurate movements towards the target? A recent experiment sought to answer a similar question (Bernier, Chua, & Franks, 2005). Two groups of participants were exposed to a visuomotor rotation during which one group was provided full vision of the movement path. The second group was provided with only hand position relative to target location at the end of the movement. After the distortion was removed, movements were executed without on-line or end-point feedback. Results indicated that both groups of participants reduced movement errors during the exposure phase; however, the group with full vision demonstrated significantly smaller aftereffects and these aftereffects decayed at a faster rate. The authors suggested that the group with full vision during exposure adapted to the distortion primarily using visual feedback of the movement path rather than between-trial, feed-forward corrections. Thus, the full vision group failed to adequately calibrate proprioception during exposure, resulting in a smaller level of adaptation. Conversely, the end-point only feedback group resulted in proprioceptive calibration, indicative of an up-weighting in the absence of full vision.

Flexible Re-weighting of Proprioception and Vision

A central concept in motor control is the how the central nervous system is able to integrate sensory information from multiple modalities. Traditionally, it has been thought that vision is the dominant sense as it ultimately prevails when redundant sensory information is available. However, more recent research discounts the ‘vision is dominant’ notion and provides evidence demonstrating that the relative contribution of visual and proprioceptive information is dependent upon the stage of motor planning (Sober & Sabes, 2003), the sensory modality of the target (Sober & Sabes, 2005), and the spatial direction with respect to arm localization (Snijders, Holmes, & Spence, in press; van Beers, Baraduc, & Wolpert, 2002a; van Beers et al., 1999).

As discussed in a preceding section, a fundamental aspect of point-to-point reaching movements is accurate localization of both the target and the hand. The CNS is often provided with redundant information about the localization of the hand as it can be perceived through both proprioception and vision. In order to accurately localize the arm, the CNS needs to integrate the available information in order to reduce the noise or uncertainty in the estimate (van Beers et al., 2002a). Participants executed reaching movements in the horizontal plane to one of three targets: proprioceptive (P: the unseen right hand), visual (V), or proprioceptive and visual (PV) together (van Beers et al., 1999). Movements were analyzed by comparing the location of the pointing movements during condition PV to conditions P and V. Results indicated that movements during condition PV were not located on a straight line between conditions P and V. Rather, they were located in an area that would suggest that vision and proprioception are integrated with direction-dependent weights. Specifically, vision provides a more precise estimate in the azimuthal (left-right) direction whereas proprioception provides a more precise estimate in the radial direction. When the two sensory modalities are integrated in order to output a single localization estimate, the CNS will localize the hand in a position that will minimize the uncertainty in both directions. These results were further supported by a computational model (van Beers et al., 1999) and during the execution of reaching movements under the influence of a mirror illusion (Snijders et al., in press). These findings support an optimal integration model in which available sensory feedback is flexibly re-weighted in order to produce the most optimal or precise estimate of arm localization.

If the CNS can optimally integrate visual and proprioceptive information in order to localize the hand, is it also capable of integrating sensory afference in a manner that will decrease movement errors during or even after exposure to a visuomotor distortion? The present study wishes to extend the optimal integration model as a potential mechanism that could be used to accurately detect existing movement errors and use this sensory feedback in order to generate more accurate movements in subsequent trials.

CHAPTER III

Method

Participants

Seventy-two right-handed adults (36 males, 36 females) between 18 and 36 years old (mean age = 23.18 ± 3.20) with no known neurological or motor disorders were recruited from the University of Maryland at College Park. Handedness was determined using the preferred hand during writing and drawing activities, as indicated on an Edinburgh Handedness Inventory (Appendix I). An adult neurological health questionnaire (Appendix II) was also completed by each participant. Participants who failed to respond 'no' on items 3 through 7 did not participate in the current study. The experimental protocol was approved by the University of Maryland, College Park Institutional Review Board and all participants provided informed consent prior to participation (Appendix III). Participants were randomly assigned with stratification for gender into one of the six groups (12 participants per group). Detailed descriptions of each experimental group are included in the Experimental Design section. Each participant was required to make one visit to the Cognitive Motor Neuroscience Lab for approximately forty-five minutes. Upon completion of the testing session, participants received a small monetary compensation.

Experimental Design

The experiment employed a 3 x 2 between-subjects design, in which the independent variables were the feedback provided during the second baseline and post-exposure phases (3 levels) and the type of visuomotor distortion task completed by the participants (2 levels). The three feedback conditions included (1) on-line visual feedback with knowledge of end point position (FB1), (2) no on-line visual feedback, but with visual end point position (FB2), and (3) no on-line feedback or end point position (FB3). The two types of distortion were (1) an incremental visuomotor rotation (R), or, (2) an incremental visuomotor gain distortion (G). Gradually introduced visuomotor distortions were employed to decrease the likelihood of participants' using cognitive strategies (Klassen et al., 2005; Kagerer et al., 1997). Dependent variables consisted of behavioral measurements that assessed the overall performance of the reaching movements. Detailed descriptions of the procedures as well as the independent and dependent variables are included below.

Procedure

All participants were seated comfortably in a chair in front of a horizontally positioned computer monitor that rested on an elevated board designed to occlude vision of the participant's hand as he/she drew lines on a digitizing tablet with a digital pen (Figure 3.1).

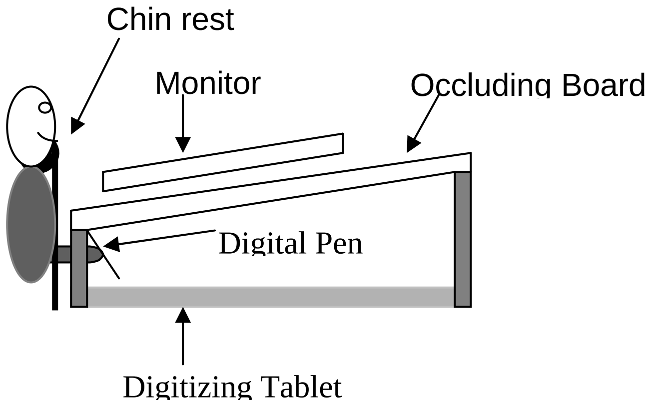


Figure 3.1. Experimental setup.

Chair height was adjusted in order to position the participant's chin in a rest located approximately 20.5 cm in front of and 9.5 cm above the computer monitor. The chinrest was implemented to ensure all participants viewed the monitor from the same angle throughout the course of the experiment. The chair was laterally positioned to center the computer monitor and the digitizing tablet with the participant's torso. Participants were asked to use a digital pen to draw lines on a digitizing tablet from a home position, located 4 cm in front of the center of the tablet, to a single peripheral target. The computer monitor positioned above the tablet provided the locations of both the start (0.25 cm radius) and target (0.35 cm radius) circles, as well as the appropriate visual feedback of the movement trajectory (Figure 3.2). The center of the target circle was located 10 cm from the center of the home position and displayed at 90° in a Cartesian coordinate system with respect to the home position.

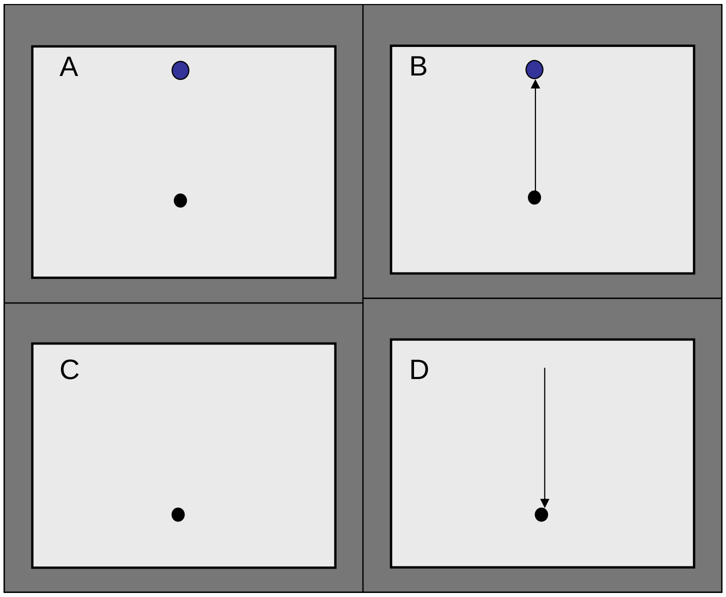


Figure 3.2. Task stimuli. A) Depiction of the start and target locations. B) Participants moved to the target. C) Once the target was reached, it disappeared. D) Participants returned to start position.

The target appeared when the participant's pen was motionless in the home position for 500ms. The participant then moved the pen towards the desired target and stopped the movement when he/she positioned the pen in the target circle. Once the pen was still for

750ms, the target circle disappeared and the participant returned to the home position to begin the next trial. Participants were instructed prior to and during the task to move to the target circle at a fast pace and as straight as possible. The position of the start circle was always provided via the monitor.

Data collection sessions (Figure 3.3) consisted of four experimental phases. During the first phase, visual baseline (VB: 24 trials), participants made point-to-point reaching movements from the start circle to the target with veridical, real-time visual feedback of the movement trajectory provided via the computer monitor.

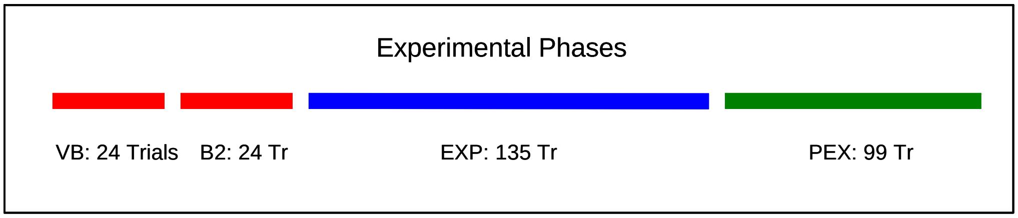


Figure 3.3. Experimental phases and their lengths expressed in number of trials. Red lines represent the baseline phases, blue represents exposure, and green represents post-exposure.

The second phase (baseline 2, B2: 24 trials) reflected the assigned visual feedback manipulation. Baseline 2 for FB1 groups was identical to the VB phase, in that accurate on-line visual feedback was provided throughout the reaching movement. FB2 groups were provided no on-line feedback of the movement trajectory. However, the participants were provided the position of the pen after the completion of each movement. Participants could view the end point position of their movement relative to the target location for 250ms. Any visual error that existed between the desired and final positions could be used to correct movements on subsequent trials. On-line feedback of the pen trace was also absent on the return path to the home position, except when the participant was within 3cm of the start circle. FB3 groups were not provided on-line feedback or end point position. On-line feedback of the pen’s return trajectory to the start circle was again absent outside the 3cm distance from the start circle. The third phase (exposure, EXP: 135 trials) of the experiment consisted of exposure to either an incremental visuomotor rotation or an incremental visuomotor gain, as determined by random group assignment. On-line visual feedback of the movement trajectory was again available for all groups but gradually manipulated dependent on the task.

For the visuomotor rotation, the visual feedback was rotated in the clockwise (CW) direction in 6 degree increments (27 trials per increment), up to a total of 30 degrees.

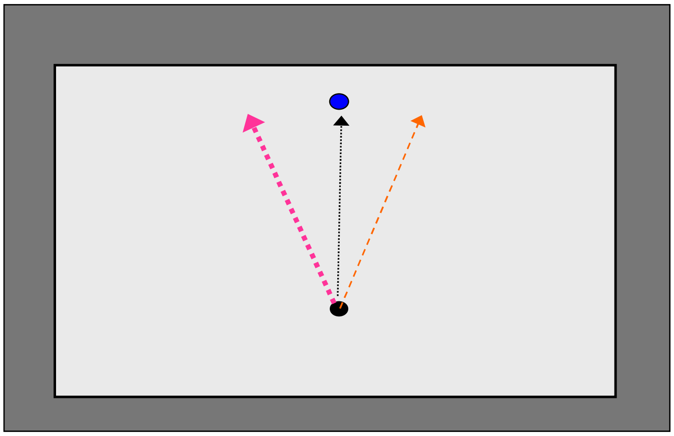


Figure 3.4. Visuomotor Rotation. Black arrow represents ideal movement trajectory. In the exposure phase, visual feedback of the trajectory was rotated in the CW direction (orange arrow). Participants had to move in the CCW direction equal in magnitude to the distortion (pink arrow) to accurately reach the target.

In order to adapt to the distortion, participants had to move in the counter-clockwise (CCW) direction equal in magnitude to the rotation, as demonstrated in Figure 3.4. Previous research has demonstrated that adults adapt to the gradual rotation by making feed-forward adjustments to the motor commands (Klassen et al., 2005; Kagerer et al., 1997). For the visuomotor gain distortion, the amplitude of the visual feedback was increased by a factor of 0.2 every 27 exposure trials, up to a total gain of 2.0. To adapt to this distortion, participants had to make progressively smaller movements as the exposure phase progressed. Previous research has demonstrated that participants are capable of adapting to an imposed gain distortion (Seidler, 2004; Prager & Contreras-Vidal, 2003; Krakauer et al., 2000; Ingram et al., 2000). The magnitudes of the rotation and gain distortions were selected to create nearly identical linear movement errors. Complete adaptation to the rotation would result in a linear error of 5.18 cm during post-exposure whereas complete gain adaptation would result in a 5 cm error. The final phase of the data collection session (Post-exposure, P-EX: 99 trials) was again specific to each feedback condition and was identical to B2. FB1 groups were provided on-line as well as end point visual feedback, FB2 groups were provided end point but not on-line visual feedback, and FB3 groups were not provided either form of feedback. This post-exposure phase was designed to measure the persistence of the updated internal representation as well as the contributions of visual and proprioceptive feedback during the de-adaptation process. In total, the experimental session consisted of 282 trials and lasted approximately 25-30 minutes.

Instrumentation

Data were collected using a digitizing tablet (12” x 12” WACOM In Tuos, Vancouver, Canada) that recorded pen position at a sampling rate of 200 Hz using software written in OASIS (Kikosoft, Nijmegen). Trials in which participants removed the digitizing pen from the tablet or failed to move from the home position in the appropriate amount of time were removed before data analysis. Less than 5% of trials were removed. Movement onset and offset were determined by an algorithm specified in previous research (Teasdale, Bard, Fleury, Young, & Proteau, 1993). MATLAB 7.0 software (The Mathworks Inc. ^{TM}) was used to visually inspect the marking of movement onset and offset for every trial in order to ensure the accuracy of the data prior to statistical analysis.

Dependent Measures

Performance for the visuomotor rotation task was assessed using initial directional error (IDE). It was calculated as the directional deviation of the movement path from the ideal trajectory vector 80 milliseconds following movement onset. IDE is considered indicative of the planning of the movement as it was calculated before corrective movements can be generated in response to the visual feedback provided via the monitor. Performance for the gain distortion task was assessed with initial amplitude error (IAE). IAE (cm) was calculated by subtracting the linear distance the pen traveled during the first ballistic movement from the ideal amplitude of the movement (10 cm for baseline and post-exposure trials). The end of the first ballistic movement was defined by either a change in the direction of the movement or the presence of a second ballistic movement, as determined by an examination of the velocity and acceleration profiles. IAE provided a linear error in the extent or magnitude of the planned movement trajectory. It is similar to a variable used in previous research and thought to be minimally affected by on-line visual feedback (Seidler, 2004). To draw comparisons between the two dependent measures, scores were standardized relative to individual baseline means by the following formula:

$$\textit{Standardized value} = (x - \bar{x}) \div s.d.$$

where x is the raw dependent measure score, $\bar{x}$ is the appropriate baseline mean, and *s.d.* is the appropriate baseline standard deviation (Prager & Contreras-Vidal, 2003). Exposure trials were standardized relative to VB and post-exposure trials were standardized relative to B2. Standardized IDE scores with a positive number indicate a value CCW of the ideal trajectory vector whereas standardized IAE values indicate either an undershooting of the target or the presence of a second corrective movement prior to reaching the target. Standardization allowed for statistical comparison between IDE and IAE for the rotation and gain groups, respectively.

Statistical Analysis

Before data analysis, trials considered statistical outliers, defined as dependent measure scores that exceeded 2.5 s.d. of the mean of that particular phase, were eliminated. Less than 5% of trials were eliminated prior to analysis. The final 18 trials of the visual baseline phase were averaged to calculate a single VB score to be used in the standardization of the exposure trials. Excluding the first 6 trials of the phase ensured participants were familiar and comfortable with the required task. The same procedure was completed with the B2 phase to ensure that the participants were familiar with the different feedback conditions. The 135-trial exposure phase was decomposed into fifteen blocks of 9 trials each. In order to accurately characterize the de-adaptation process, the 99-trial post-exposure phase was decomposed into 34 blocks. The first P-EX block included only the first post-exposure trial as the visual feedback provided to the participants could potentially contaminate the magnitude of the aftereffects of subsequent trials. The second block was an average of the next two P-EX trials. Each block thereafter consisted of 3 trials each. Exposure trials were standardized to the mean of the visual baseline phase whereas each post-exposure trial was standardized to the mean of B2. An average value was calculated for each exposure and post-exposure block.

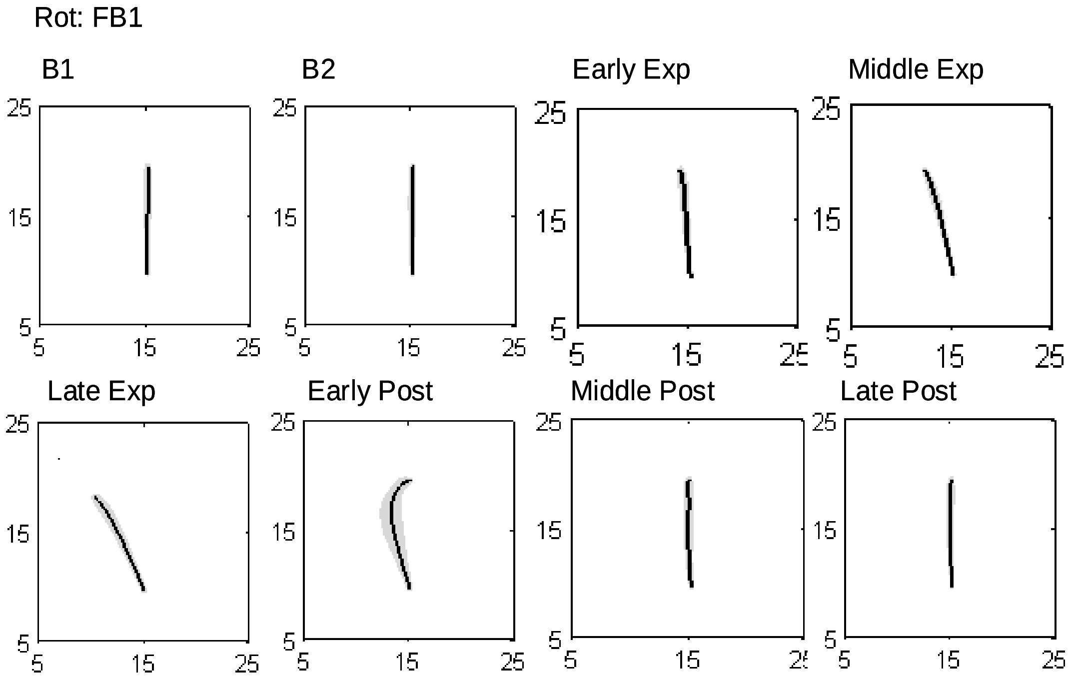
To demonstrate that all groups adapted to their respective distortions, the average dependent measure scores from the first post-exposure block were compared to a test value of 0 in six independent one-sample t-tests (with Bonferroni correction). One-sample t-tests with a test value of 0 were used since the post-exposure scores have been standardized to baseline performance. An additional 2 x 3 (visuomotor distortion x feedback condition) ANOVA was conducted to determine group differences for the first P-EX block. An examination of the group de-adaptation trends revealed a steep, near-linear decrease during the first 9 trials. In order to characterize this initial rate of de-adaptation, the standardized performance errors (IDE for the rotation groups and IAE for the gain groups) were linearly regressed with trial number as the independent variable for the first 9 trials of the individual data. The trial number regression coefficients were averaged across groups and analyzed using a 2 x 3 (distortion by feedback) ANOVA. This initial rate of de-adaptation was further analyzed with a separate 2 x 3 (distortion by feedback) ANCOVA with the standardized performance value from the fourth P-EX block as the dependent variable and performance from the first trial as a covariate. The ANCOVA was designed to indirectly assess the rate of de-adaptation by determining if the final level of this steep, near linear reduction of performance errors was statistically different among experimental groups. The first P-EX block was used as a covariate because the initial performance errors were not equal among experimental groups. This procedure statistically controlled for the existing initial performance differences among groups. A final 2 x 3 (distortion by feedback) ANOVA was used to analyze the standardized performance errors from the last post-exposure block to determine if the final de-adaptation levels were significantly different among groups.

CHAPTER IV

Results

Movement Trajectories

Movement paths for the three rotation groups are shown in Figure 4.1 for the following phases: visual baseline, baseline two, early, middle, and late exposure, and early, middle and late post-exposure. As expected, participants made straight and accurate movements to the target during both baseline phases regardless of the visual feedback provided. As the exposure phase progressed, the direction of the movement path gradually shifted in the counter-clockwise direction as participants adapted to the imposed visuomotor rotation.



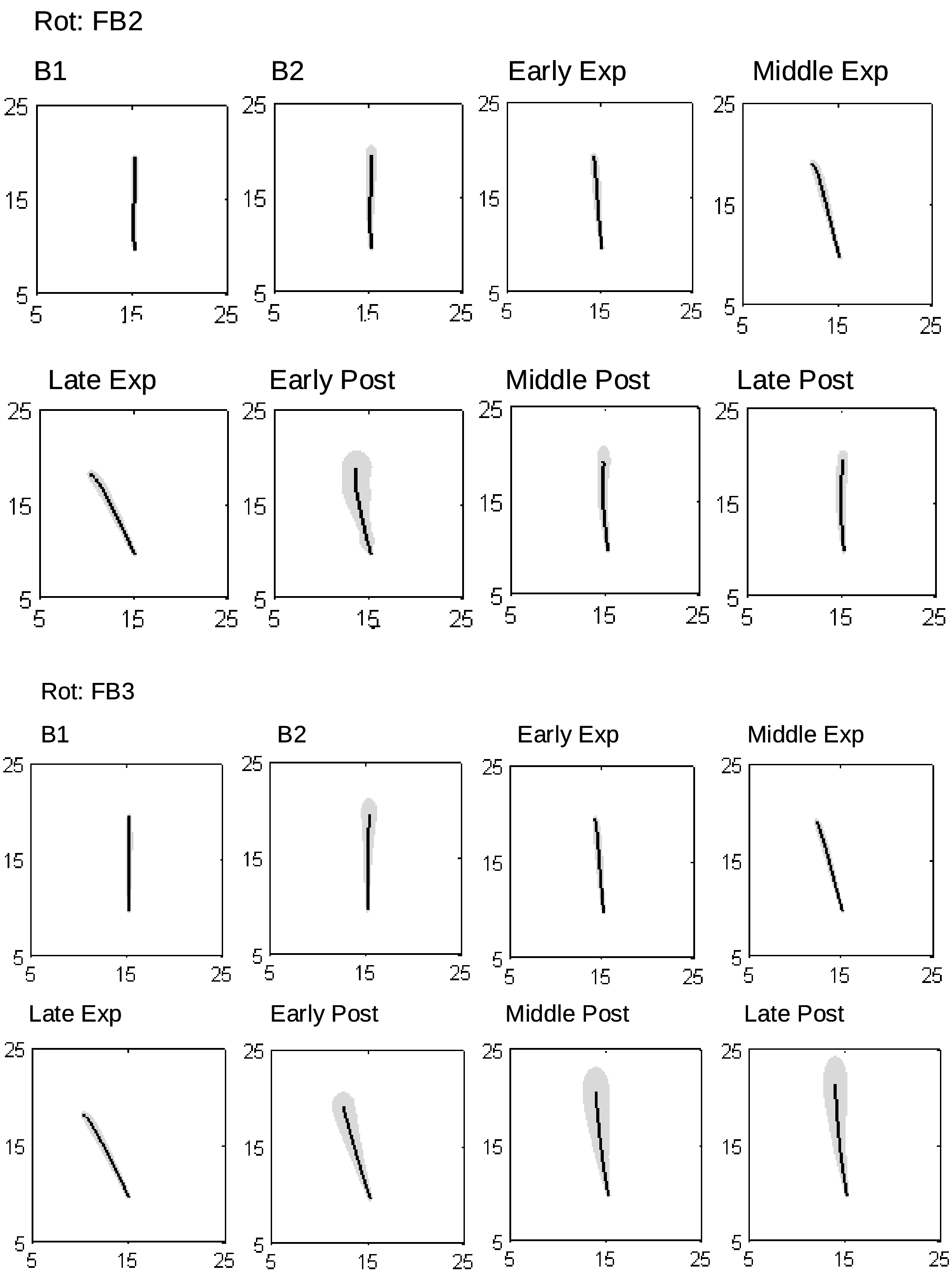
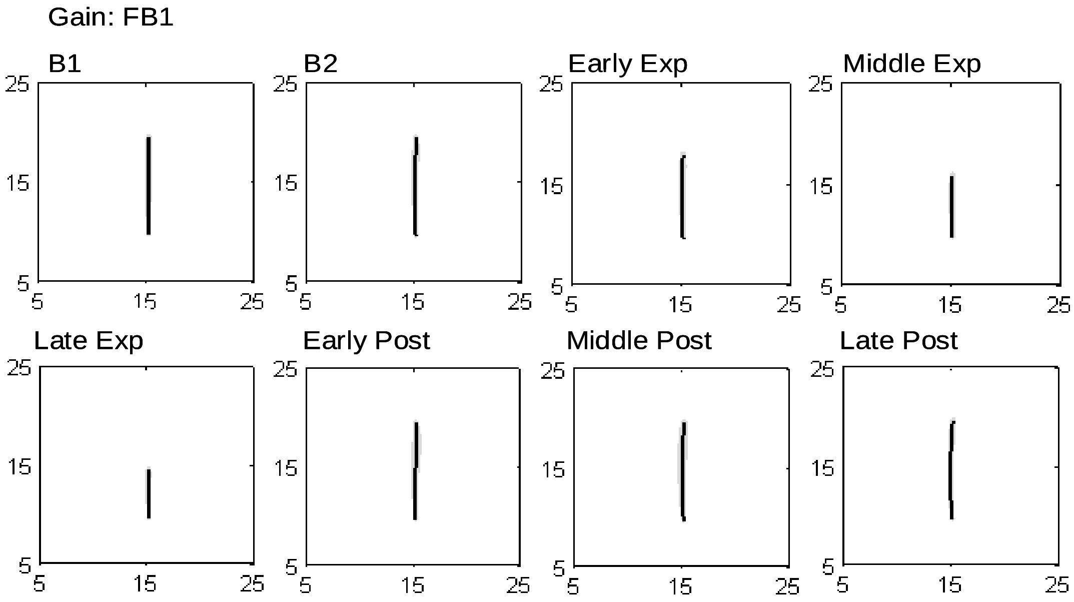


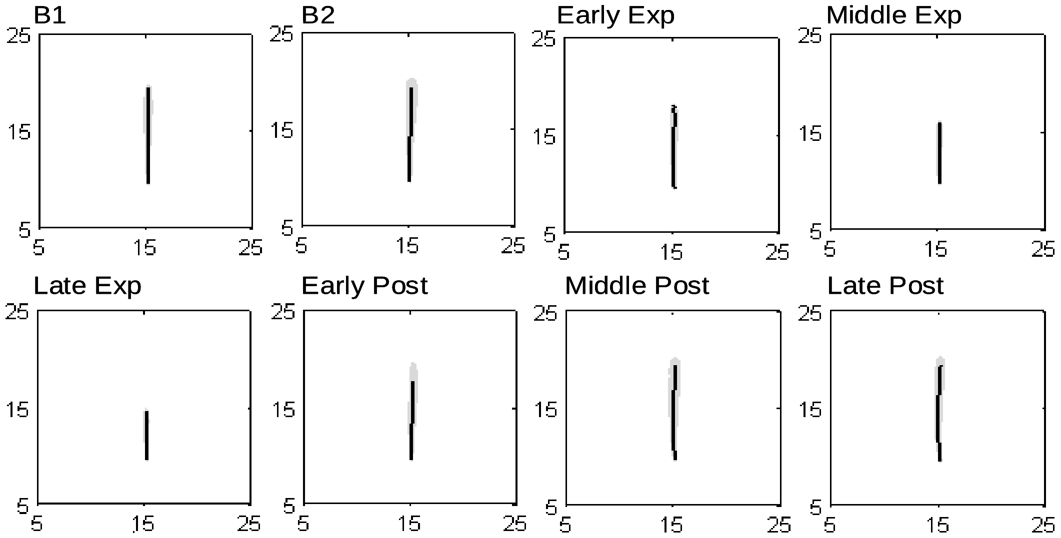
Figure 4.1. Movement trajectories: Rotation for the three feedback conditions. Averaged movement paths are shown for eight phases of the experimental session. Surrounding gray area represents one standard deviation. Horizontal and vertical axes are in units of cm. B1 = trials 7-24, B2 = trials 31-48, Early Exp = trials 49-75, Middle Exp = trials 103-129, Late Exp = trials 157-183, Early Post = trials 184-189, Middle Post = trials 229-234, Late Post = trials 277-282.

During the post-exposure phase, the visual feedback perturbation was abruptly removed and the feedback conditions returned to those experienced during the second baseline phase. For the R:FB1 group (top panel), the swirled movement trajectories during early post-exposure are indicative of aftereffects when on-line visual feedback is provided as participants make feedback-dependent corrective movements in order to reach the target. As the post-exposure phase progressed, all groups demonstrated some level of de-adaptation as the movement paths became straighter. However, note that the distorted trajectories indicative of aftereffects for group R:FB3 (bottom panel) remained during late post-exposure trials.

Movement paths for the three gain distortion groups are shown in Figure 4.2. Participants from each group made accurate reaching movements towards the desired target in both baseline phases. During the exposure phase, participants made progressively shorter movements as the visual feedback displayed on the monitor was multiplied by a gradually increasing gain.



Gain: FB2



Gain: FB3

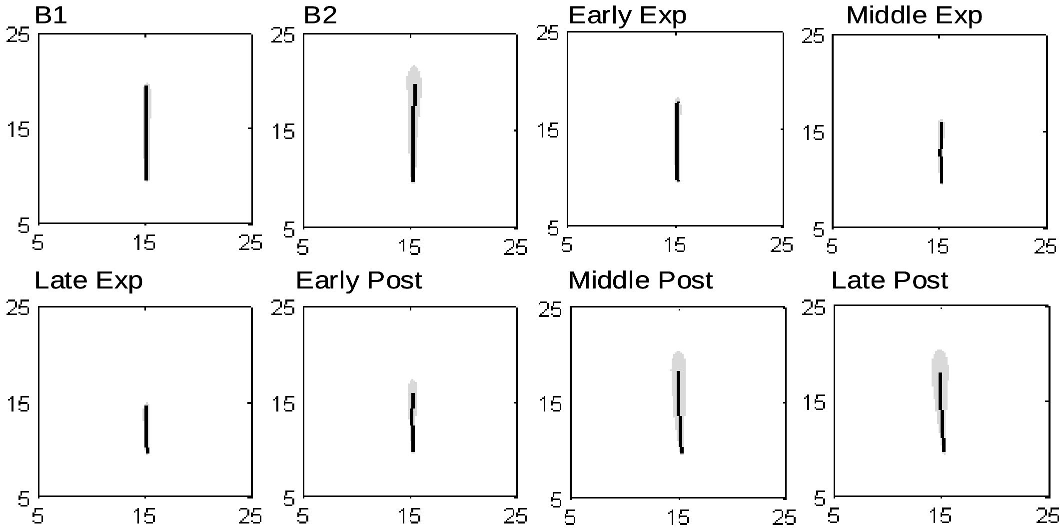


Figure 4.2. Movement trajectories: Gain distortion for the three feedback conditions. Averaged movement paths are shown for eight phases of the experimental session. Surrounding gray area represents one standard deviation. Horizontal and vertical axes are in units of cm. B1 = trials 7-24, B2 = trials 31-48, Early Exp = trials 49-75, Middle Exp = trials 103-129, Late Exp = trials 157-183, Early Post = trials 184-189, Middle Post = trials 229-234, Late Post = trials 277-282.

Following the removal of the visual distortion, participants in groups G:FB2 (middle panel) and G:FB3 (bottom panel) completed much shorter movements. These trajectories indicate that participants adapted to the distortion by executing movements appropriate for the manipulated environment. The movement paths for group G:FB1 (top panel) in Figure 4.2 are not indicative of aftereffects because vision of the movement path was provided during the post-exposure trials. Although participants planned and initiated movements appropriate for the distorted environment, the available on-line visual feedback prompted them to keep moving towards the desired target; thus, masking the presence of aftereffects in this figure.

Assessment of Adaptation Level

During the exposure phase, participants made feed-forward and feedback adjustments in order to accurately reach the target. As both IDE and IAE were calculated as deviations from the ideal trajectory for that particular exposure block, maintaining performance errors of zero would indicate optimal adaptation. Figure 4.3 depicts performance errors as a function of exposure trials for the visuomotor rotation experimental groups. The standardized performance values increased in magnitude as the exposure phase progressed because the rotation was introduced gradually and participants failed to fully adapt at each increment. The downward spikes represent the exposure blocks which contained an increase in rotation magnitude, resulting in a sudden increase in error magnitude followed by a gradual decrease. Despite the accumulation of performance errors during exposure, participants adapted to the distortion as indicated by the significant post-exposure aftereffects to be discussed in the subsequent section. Figure 4.4 depicts exposure phase performance for the experimental groups exposed to the gradual gain distortion. Note that the gain distortion participants were able to maintain small performance errors throughout the exposure phase as they exhibited significantly smaller (in magnitude) performance errors during the last exposure block as compared to the rotation participants (p < .001). However, these data do not necessarily indicate better or more complete adaptation.

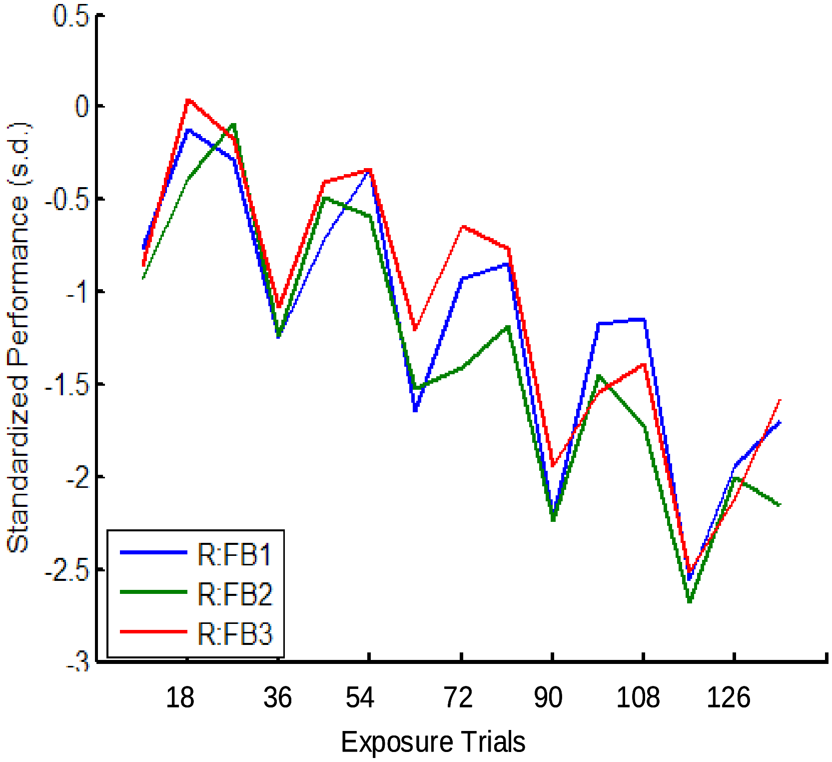


Figure 4.3. Rotation Exposure. Mean standardized IDE values as a function of exposure trials for the experimental groups exposed to visuomotor rotation. IDE measures directional error 80ms after movement onset. Values are standardized relative to performance during the VB phase. A standardized value of 0 indicates initial directional error identical to the baseline average.

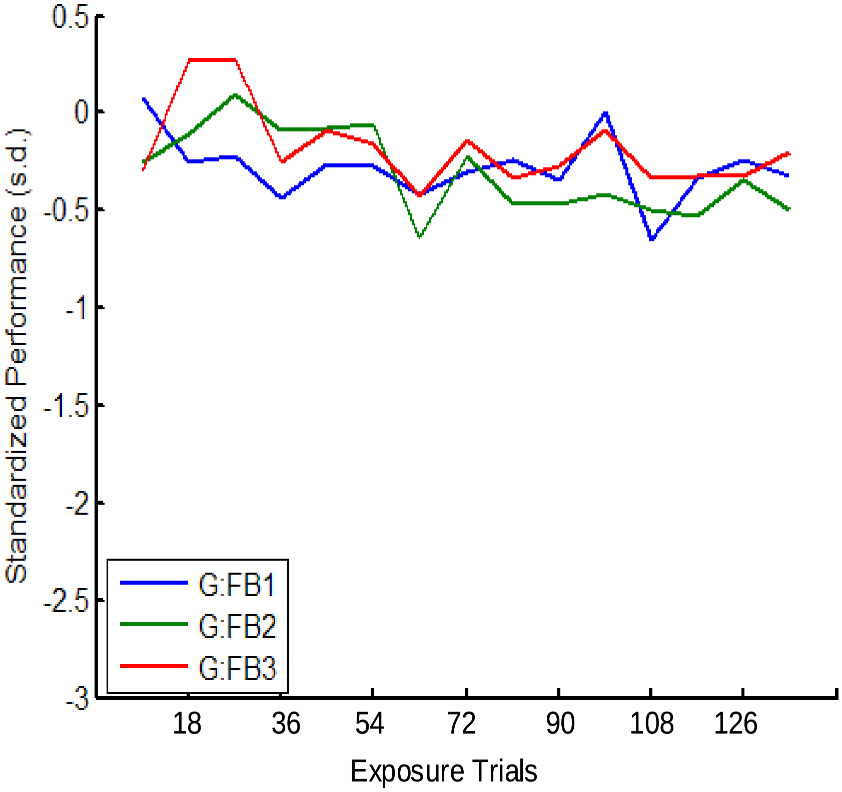


Figure 4.4. Gain Exposure. Mean standardized IAE values as a function of exposure trials for the experimental groups exposed to visuomotor gain distortion. IAE measures linear amplitude error after the first ballistic movement. Values are standardized relative to performance during the VB phase. A standardized value of 0 indicates initial amplitude error identical to the baseline average.

The feed-forward adjustments to the reaching movements became evident in the post-exposure phase when the visual perturbations were removed. Participants then exhibited distorted trajectories opposite in nature to the previously imposed perturbation. These aftereffects are quantified in order to provide a measure of the level of adaptation and are indicative of an acquisition of an internal representation appropriate for moving in the distorted environment. Figure 4.5 contains the non-standardized initial directional error values for the three experimental groups exposed to the visuomotor rotation. An aftereffect of 30° would indicate *complete* adaptation as participants were ultimately exposed to a 30° distortion

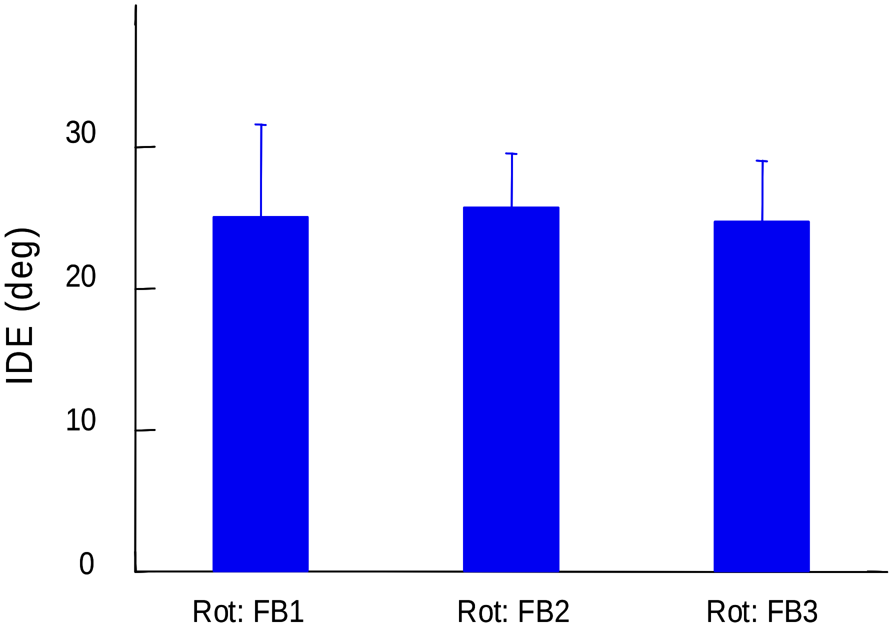


Figure 4.5. Aftereffects: Rotation. Mean non-standardized initial direction error (IDE) values by feedback condition for the experimental groups exposed to the visuomotor rotation. Error bars represent one standard deviation. Values were calculated from the IDE of the first post-exposure trial. An error of 30° would indicate complete adaptation as participants were exposed to a 30° CW rotation.

Only the first post-exposure trial was included in the assessment of aftereffects as subsequent trials may be contaminated due to the presence of visual feedback. All three experimental groups adapted to the rotation and exhibited IDE values greater than 24° in the first P-EX trial. Figure 4.6 depicts the IAE values for the first post-exposure trial following adaptation to a gain distortion. An IAE value of 5 cm represents complete adaptation since participants were ultimately exposed to a display gain of 2:1 for a 10 cm movement. All three gain groups successfully adapted to the distortion as indicated by IAE aftereffects greater than 4.5 cm.

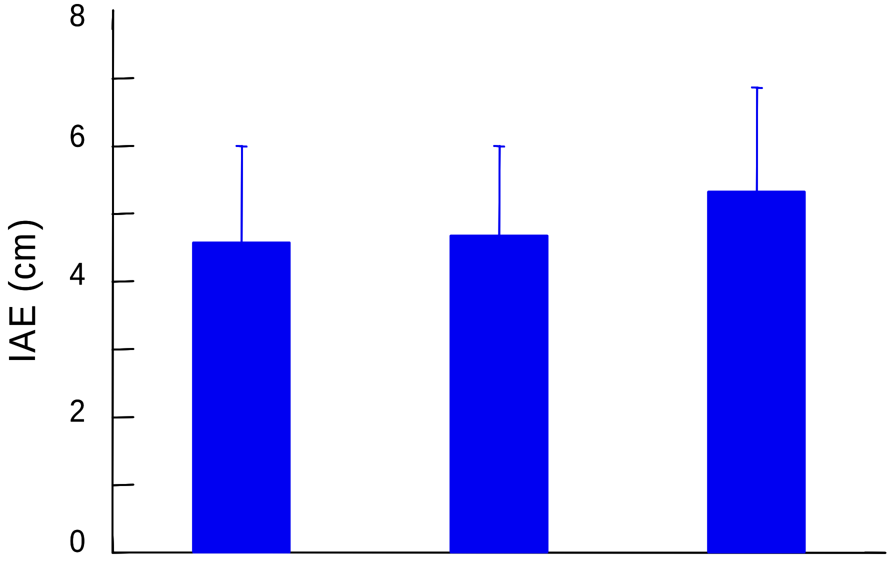


Figure 4.6. Aftereffects: Gain Distortion. Mean non-standardized initial amplitude error (IAE) values by feedback condition for the experimental groups exposed to the visuomotor gain distortion. Values were calculated from the mean IAE of the first post-exposure trial. An error of 5 cm would indicate complete adaptation.

In order to make comparisons between the six experimental groups, IDE and IAE values were standardized relative to individual baseline means, as detailed in the Methods section. Figure 4.7 contains the standardized dependent measure values for the first post-exposure trial. All IDE and IAE data presented herein are referred to as standardized performance errors and will be in units of standard deviations. No significant differences exist between the standardized performance aftereffects, indicating that the experimental groups experienced equivalent levels of adaptation during the exposure phase despite the apparent difference in the magnitude of performance errors during the last exposure phase displayed in Figures 4.3 and 4.4. The standardized aftereffects were compared to a test value of zero in six independent one-sample t-tests with Bonferroni correction for the level of significance. Each experimental group exhibited significant aftereffects in the first post-exposure trial ($p < 0.005$ for all groups). No significant differences existed among the six experimental groups.

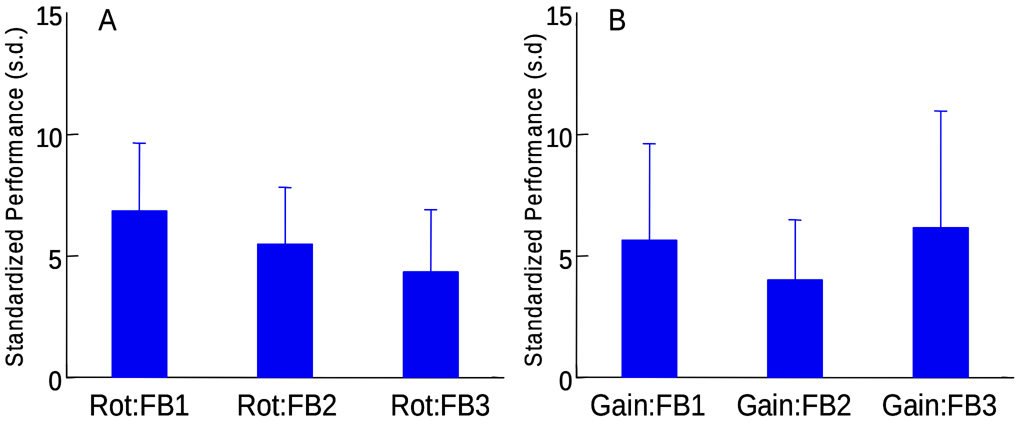


Figure 4.7. Aftereffects: Standardized. Mean standardized IDE (A) and IAE (B) values calculated from the first post-exposure trial standardized relative to performance during B2 for the three feedback conditions exposed to a visuomotor rotation (A) and gain distortion (B). Error bars represent one standard deviation. Standardized values allow for comparison between the two distortion conditions.

De-adaptation Primarily Occurs within First 9 P-EX Trials

Previous research has indicated that the presence of aftereffects following visuomotor distortion exposure is extremely transient as participants quickly de-adapt and execute movements that are again appropriate for the null environment (Davidson & Wolpert, 2004). The present study sought to: 1) characterize the rate of de-adaptation for two types of visuomotor distortions, and 2) to investigate the CNS's ability to flexibly re-weight the available proprioceptive and visual information in order to execute movements appropriate for a given environment. Figure 4.8 illustrates the reduction of standardized performance errors during post-exposure for the six experimental groups.

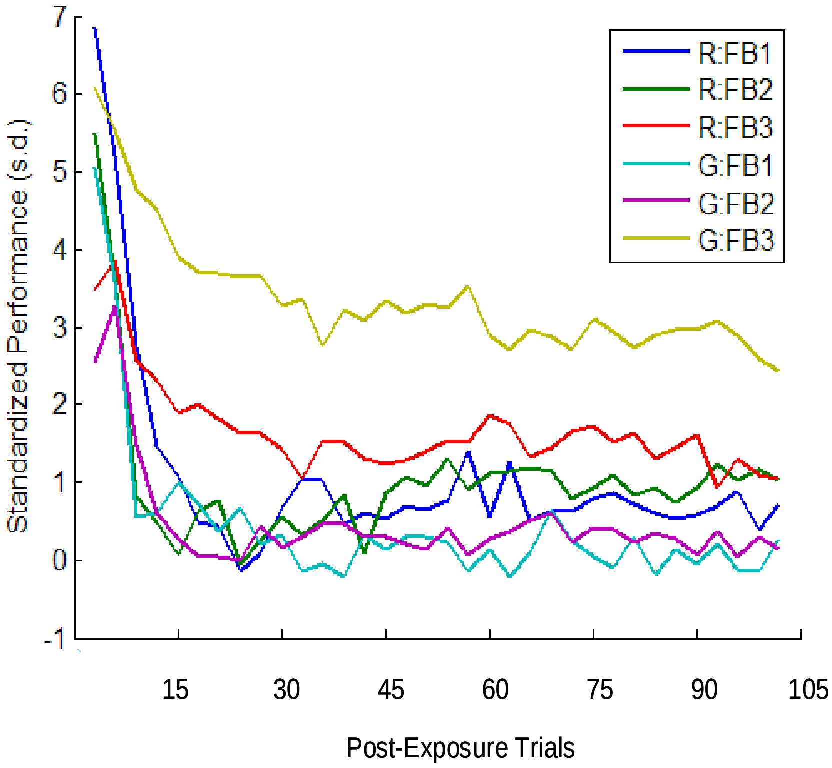


Figure 4.8. De-adaptation. Mean standardized performance errors in units of standard deviations as a function of post-exposure trials for the six experimental groups. Values were standardized relative to performance in the second baseline phase (B2). IDE standardized performance is depicted for the three experimental groups exposed to the visuomotor rotation whereas IAE standardized performance is depicted for the gain distortion experimental groups. Data were calculated with respect to P-EX blocks, not P-EX trial number.

An examination of Figure 4.8 reveals that participants quickly de-adapted with a fast, near-linear decrease in standardized error over the first 9 post-exposure trials. It is also evident that the experimental groups provided with visual feedback (R:FB1, R:FB2, G:FB1, and G:FB2) demonstrated similar rates of de-adaptation. Groups not provided with visual feedback (R:FB3 and G:FB3) appear to have slower rates of de-adaptation. In order to quantitatively characterize the return to the null condition, the first 9 post-exposure trials were linearly regressed for each individual with trial number as the independent variable and standardized performance errors as the dependent variable. A 2 x 3 (distortion by feedback) ANOVA revealed a significant main effect of feedback ($p < 0.005$).

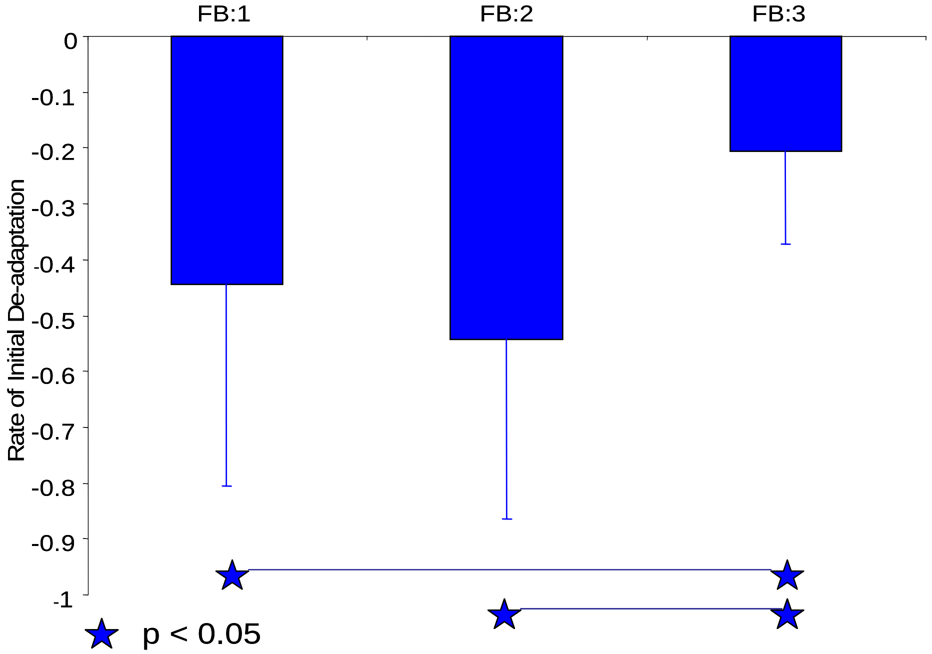


Figure 4.9. Rate of Initial De-adaptation. Linear regression coefficient with post-exposure trials as the predictor variable (included 9 P-EX trials) and standardized performance as the dependent variable by feedback group. Error bars represent one standard deviation. Standardized IDE was used as the dependent measure for the rotation groups and standardized IAE was used as the dependent measure for the gain distortion groups.

FB1 and FB2 experienced significantly faster rates of de-adaptation compared to group FB:3 ($p < 0.05$), as determined by a Tukey's post hoc test (Figure 4.9). A 2 x 3 (distortion by feedback) ANCOVA was used to further assess the rate of de-adaptation over the first 9 post-exposure trials. The standardized performance value for the fourth (trials 7-9) and the first (trial 1) P-EX blocks were used as the dependent variable and the covariate, respectively. ANCOVA results indicate a significant feedback main effect ($p < .001$) as group FB3 exhibited significantly larger error values as compared to the other two feedback groups (Figure 4.10). This indicates that the no visual feedback groups failed to de-adapt to the same level during the initial, fast reduction of performance errors, while statistically controlling for the initial level of aftereffects.

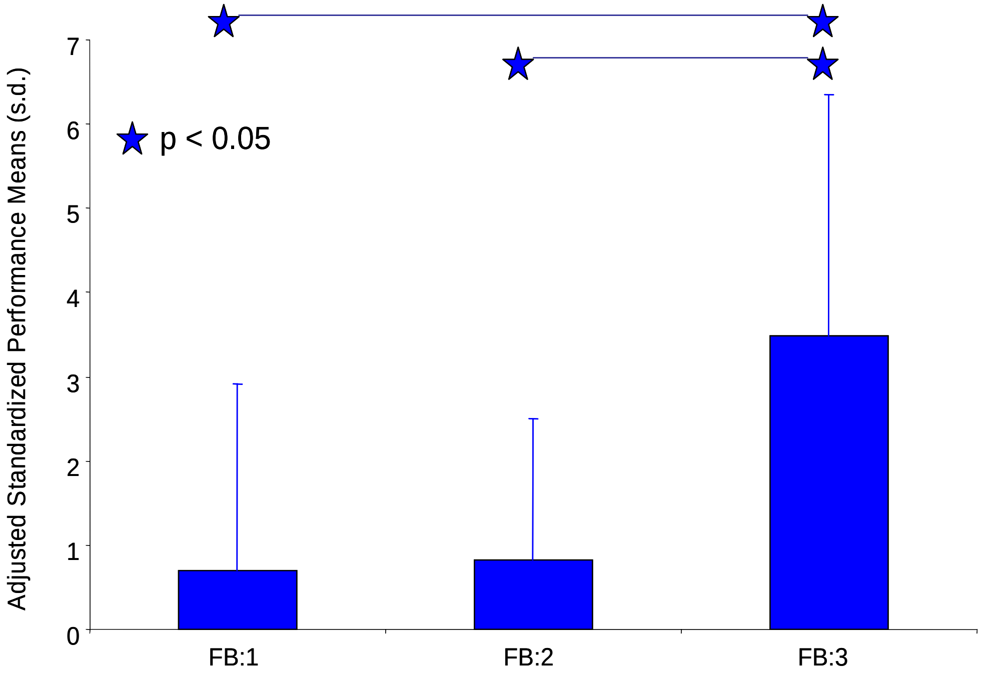


Figure 4.10. Fourth P-EX Block Performance. Adjusted standardized performance means for the fourth post-exposure block (trials 7-9) by the three feedback groups. Error bars represent one standard deviation. Standardized IDE was used as the dependent measure for the rotation groups and standardized IAE was used as the dependent measure for the gain distortion groups.

Final Level of De-adaptation

Final level of de-adaptation was calculated by averaging the last post-exposure block, P-EX trials 97-99. A 2 x 3 (distortion by feedback) ANOVA indicated a significant feedback main effect ($p < 0.05$) and a Tukey's post hoc analysis revealed that group FB1 demonstrated significantly smaller performance errors (Figure 4.11) compared to group FB3 ($p < 0.05$). Groups FB2 and FB3 failed to be significant ($p = 0.056$).

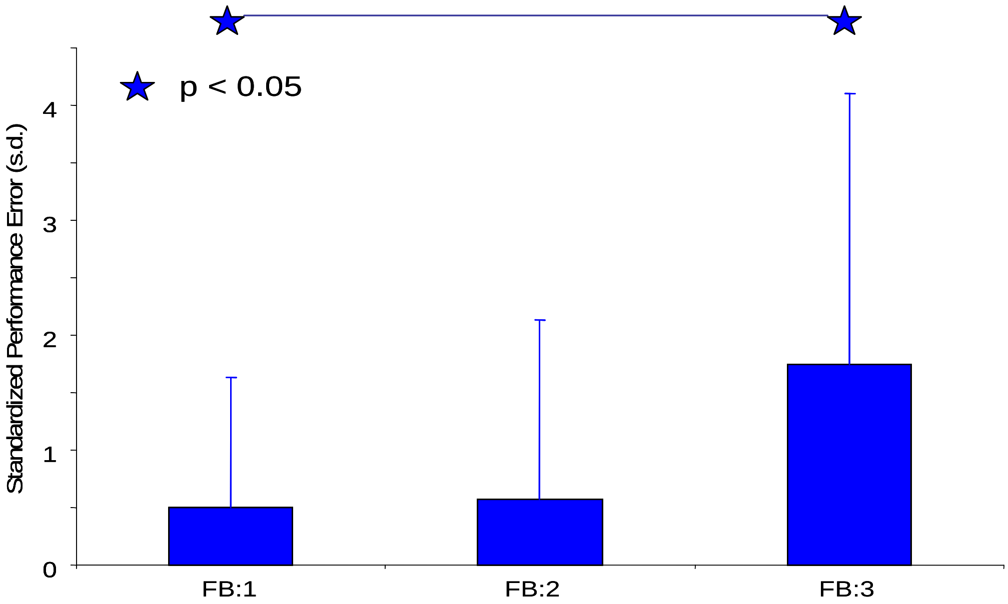


Figure 4.11: Final de-adaptation level. Standardized performance means for the final post-exposure block (trials 280-282) by the three feedback groups. Error bars represent one standard deviation. Standardized IDE was used as the dependent measure for the rotation groups and standardized IAE was used as the dependent measure for the gain distortion groups.

CHAPTER V

Discussion

Previous research has suggested that the CNS acquires an internal representation appropriate for moving in a perturbed environment following adaptation to a sensorimotor distortion (Krakauer et al., 1999; Gandolfo et al., 1996; Shadmehr & Mussa-Ivaldi, 1994). The present study demonstrated that the aftereffects resulting from an updated representation are extremely transient if visual feedback is provided to participants who performed reaching movements appropriate for the null environment in a limited number of trials. However, the rate of de-adaptation was strongly influenced by the available sensory information during post-exposure. When vision of the movement path or end point position was removed, participants failed to de-adapt at the same rate, suggesting that the CNS did not flexibly re-weight the available proprioceptive information during post-exposure of a center-out reaching task. These findings were consistent following adaptation to a visuomotor rotation or gain distortion.

Once the perturbation was removed and the updated representation was no longer reinforced, the CNS could utilize available sensory afference to execute accurate movements in the unperturbed environment. Aftereffects evident during early post-exposure were reduced within only a few trials. This rapid rate of de-adaptation was much faster compared to the rate of adaptation to a novel sensorimotor perturbation. Although this study can not compare the two processes as participants were exposed to gradually introduced distortions rather than abrupt, this result may not be fully explained by the CNS quickly returning to a previously acquired, stable representation such as that appropriate for moving in a null environment. Results from Abeele & Bock (2001) demonstrated that (de-) adaptation to a 45° rotation resulted in smaller initial errors if a 90° rotation was experienced prior to the 45° rotation as compared to participants with no prior rotation experience. Importantly, participants from both experimental groups adapted to a rotation with a change in magnitude of 45° (starting from 90° or a null field) with no prior experience in the 45° field. These data indicate that rapid de-adaptation is not specific to the null environment and the process can not be fully characterized as an abrupt 'switching' mechanism that returns to a previously acquired, stable representation. Rather, it is possible that the CNS *gradually* suppresses the new representation in order to rapidly reduce movement errors detected by sensory afference, a process much faster than the acquisition of a novel representation. This does not mean the new representation has been 'unlearned,' as participants are able to retrieve a previously acquired representation in order to execute accurate reaching movements in a distorted environment (Krakauer, Ghez, & Ghilardi, 2005; Shadmehr & Holcomb, 1997; Shadmehr & Brashers-Krug, 1997).

Gain vs. Distortion De-adaptation

It was also demonstrated that the magnitude of the standardized aftereffects and the rate of de-adaptation were identical for the two distortion conditions. Although existing research has yet to compare de-adaptation characteristics between gain and rotation distortions, results are analogous to studies that have compared the rates of adaptation. Results from Krakauer et al. (2000) indicated that the rates of adaptation for the two distortion types are identical if movements are made to only a single peripheral target, as was the case in the present study. However, if movements are made to multiple targets, the adaptation is faster and more complete during exposure to a gain distortion.

Krakauer et al. (2000) suggested that learning a novel rotated reference frame is direction-specific as movement errors to one target location can not be used to correct subsequent movements to different targets. This result is further supported by data from the same research study that demonstrated rotation adaptation to one direction does not generalize to different areas of the workspace. Conversely, gain adaptation is highly generalizeable and remains consistent regardless of the number of targets. From a neurophysiological perspective, it has been suggested that the scaling factor necessary for gain adaptation results from linear changes in the activity of a specific neuronal population. Adaptation to a visuomotor rotation requires learning a new target-specific reference frame that necessitates an entirely new neuronal activity pattern, making rotation adaptation a computationally more complex process (Krakauer et al., 2000). The present study extends this existing research in that de-adaptation to a visuomotor perturbation is identical for both types of distortions if movements are made to a single peripheral target.

Visual Feedback Manipulation

Following removal of the visuomotor perturbation, the visual feedback provided to the participants was systematically manipulated in the current study. Participants were either provided with 1) real-time, continuous feedback of the movement trajectory, 2) visual location of the movement end point relative to target position, or 3) no visual feedback. In the absence of visual feedback, existing movement errors would have to detected and corrected on subsequent trials via a mismatch between proprioceptive afference of hand position and the visually perceived target position. Previous research has investigated the relative contribution of proprioception during visuomotor adaptation paradigms, the majority of which have focused on deafferented participants. Permanently deafferented participants have demonstrated equal, or in some cases more complete, adaptation as compared to control participants (Ingram et al., 2000). However, research investigating the role of proprioception with permanently deafferented participants is often equivocal as different cognitive control strategies can be developed to better cope with the lack of proprioception. More recently, new methods have emerged to transiently degrade proprioceptive afference using a wrist vibration technique or repetitive transcranial magnetic stimulation (rTMS). Data indicate that intact proprioception can decrease the level of adaptation, suggesting that the existing visuo-proprioceptive conflict during these tasks does not trigger the adaptation process (Pipereit et al., in press; Balslev et al., 2004). Rather, the discrepancy between the distorted visual feedback and the predicted next state of the arm is most likely responsible for the feed-forward adaptive responses. Proprioceptive afference is likely down-weighted altogether in order to experience more complete adaptation, as suggested by the above research with experimentally and permanently deafferented participants.

By removing the visual feedback provided in the post-exposure phase, the role of proprioception was further investigated in the current study. Specifically, we sought to determine if proprioceptive afference is flexibly re-weighted in order to execute accurate movements in the undistorted environment in the absence of visual feedback. Results indicated that participants with no visual feedback experienced slower and less complete levels of de-adaptation compared to participants provided with visual feedback (either continuous or end-point). There are several possible explanations for this finding. One, the CNS does not flexibly re-weight available sensory information in order to reduce existing movement errors in a center-out drawing task. This explanation remains unlikely due to the high level of plasticity within the CNS. Furthermore, as will be discussed in the subsequent section, a considerable amount of existing research has demonstrated that the CNS flexibly re-weights visual and proprioceptive afference in hand localization tasks. Two, adaptation to the two distortions resulted in small linear movement errors that failed to be accurately detected by proprioception, resulting in slower and less complete de-adaptation. It has been reported that proprioception can provide the position of the elbow and shoulder angles with a precision of 0.6 to 1.1 degrees (van Beers, Sittig, & Denier van der Gon JJ, 1998). Although an error of only a single degree for the arm angles seems minimal, this can result in an end effector positional error of a few centimeters. Additional research is required to investigate the rates of de-adaptation following exposure to significantly larger perturbations. Third, in the absence of an explicit error signal, the CNS was unsure of the environment in which movements were executed. During the exposure phase, the CNS decreased the weight of the available proprioceptive afference in order to minimize the visual movement errors (Jones et al., 2001). Following the removal of the perturbation and without explicit knowledge of the environment, the CNS still considered proprioception as an unreliable sensory source and continued to down-weight its input. The present study was not designed to differentiate between these possible explanations. However, it is likely that the increased proprioceptive uncertainty resulting from the downweighting of proprioceptive feedback and the lack of an explicit error signal resulted in the slower rate of de-adaptation when visual feedback was removed in the current study.

Optimal Integration Model for De-adaptation

Prior to initiating goal-directed reaching movements, the central nervous system must have information detailing the locations of both the desired target as well as the hand. As the target is often provided by the visual system, although it could be provided in other sensory modalities such as audition, the CNS receives redundant information about hand location. An extensive amount of research has investigated the integration of vision and proprioception in order to localize the hand. Traditionally, it has been thought that vision is the dominant sensory modality, but recent research has provided evidence that the CNS flexibly re-weights visual and proprioceptive information in order to provide the most precise estimate of hand location. Robert van Beers and colleagues have investigated an optimal integration model for sensory integration. According to the model, visual and proprioceptive information are differentially weighted dependent upon the direction of localization. Visual information provides a more precise estimate of hand position in the azimuthal (left-right) direction, whereas proprioception provides a more precise estimate of hand position in the radial direction (van Beers et al., 2002a; van Beers et al., 1999). Using this model, the CNS contains knowledge about the precision of each sensory modality's estimate of hand position. The present study sought to extend the optimal integration model and determine if the CNS can differentially re-weight available proprioceptive and visual afference related to movement errors, and use this information to execute more accurate movements in subsequent trials. Since adaptation to a gain distortion results in movement errors in movement depth (radial direction) and rotation adaptation results in movement errors in the azimuthal direction, it was hypothesized that when visual feedback during post-exposure was removed, de-adaptation would be faster and more complete following gain adaptation because the CNS would up-weight available proprioceptive afference to detect movement errors existing in the radial direction.

Results from the current study indicated that gain de-adaptation was not significantly faster or more complete as compared to rotation de-adaptation, regardless of the visual feedback provided during post-exposure. The optimal integration model can not currently be extended as an optimal sensory integration mechanism used to produce more accurate reaching movements in a center-out reaching task. However, these data do not discount the optimal integration model; rather, it currently can not be applied to direction-specific integration of existing movement errors for this particular task. There are several possible explanations for this finding. One, the task used in the current study forced the CNS to significantly down-weight proprioception throughout the exposure phase in order to adapt to the visual perturbation. A task that would increase the relative contribution of proprioceptive afference could produce different results. For example, it has been demonstrated that removal of the on-line movement trajectory during the exposure phase results in greater re-calibration of proprioception (Bernier et al., 2005). Rather than displaying the continuous feedback of movement path, participants adapted to the distortion when end point position of the reaching movement was displayed relative to target position. A second explanation for the results is that adaptation produced relatively small movement errors that could not be accurately detected by proprioceptive afference. Rather, visual feedback was necessary in order to rapidly de-adapt.

In summary, the current study has demonstrated that the rate and final level of de-adaptation are nearly identical following exposure to a visuomotor rotation and gain distortion. However, these characteristics of de-adaptation are strongly influenced by the visual feedback provided to the participants during the post-exposure phase. If visual feedback, either on-line or end-point position, was provided, participants demonstrated faster and more complete de-adaptation. These results suggest that the CNS continued to down-weight proprioceptive feedback during post-exposure even when visual feedback was removed. Future research studies should extend the current paradigm to tasks that require more complete calibration of proprioceptive afference, such as proprioceptive matching tasks. Additional future research should be directed towards potential developmental implications of the current findings. Previous research has demonstrated age-related differences in adaptation to a visuomotor rotation in 6- to 10-year-old children (Contreras-Vidal, Bo, Boudreau, & Clark, 2005). Age-related differences in de-adaptation have yet to be investigated.

APPENDIX I

Edinburgh Handedness Inventory

Please indicate your preferences in the use of hands in the following activities *by putting + in the appropriate column.* Where the preference is so strong that you would never try to use the other hand unless absolutely forced to, *put* ++. If in any case you are really indifferent *put + in both columns.*

Some of the activities require both hands. In these cases the part of the task, or object, for which hand preference is wanted is indicated in brackets.

Please try to answer all of the questions, and only leave a blank if you have no experience at all of the object or task.

		Left	Right
1	Writing		
2	Drawing		
3	Throwing		
4	Scissors		
5	Toothbrush		
6	Knife (without fork)		
7	Spoon		
8	Broom (upper hand)		
9	Striking match (match)		
10	Opening box (lid)		
i.	Which foot do you prefer to kick with?		
ii.	Which eye do you use when using only one?		

APPENDIX II

Adult Neurological Health Questionnaire

Have you ever…(Please circle yes or no)
1) been seen by a neurologist or neurosurgeon? Yes No
if yes, please explain____________________________________
2) had a head injury involving unconsciousness? Yes No
if yes, how long?_______________________________________
3) required overnight hospitalization for a head injury? Yes No
if yes, please explain?_______________________________________
4) had any illness that caused a permanent decrease in memory or cognition? Yes No
if yes, please explain____________________________________
5) had a seizure? Yes No
if yes, please explain____________________________________
6) had any illness that caused a permanent decrease in motor ability (including speech)? Yes No
if yes, please explain____________________________________
7) had difficulty using your hands? Yes No
if yes, please explain____________________________________

APPENDIX III

Permission Form 11-for **adult** participant (persistence/stability)

CONSENT FORM

University of Maryland, Cognitive-Motor Behavior Laboratory

Identification of Project	Project Title: Development of Visuomotor Coordination and Adaptation
Statement of Age of Participant	You are an adult between the ages of 18 and 30, and are willing to participate in a research project being conducted by Dr. Jose L. Contreras-Vidal, Dr. Florian Kagerer, Dr. Jane Clark & Brad King at the Department of Kinesiology, University of Maryland, College Park.
Purpose	The purpose of the research is to investigate the way a person controls arm movements under changing movement conditions. The experiment is designed in a way that makes it possible to determine the influence of different task conditions, such as movement direction and distance, on movements.
Procedures	You will sit comfortably in a chair with your hand resting on a table and will perform point-to-point arm movement with the dominant hand using a special "computer pen". Movements between two points, in different directions, will be performed in the horizontal plane above the table. A computer will store information about the position of your hand and arm during the movement task. Participation in this experiment may require up to three visits to the laboratory over a three-day period, dependent upon random group assignment. Each data collection session will take approximately 45 minutes. During the whole experiment, you will be video recorded for “coding” purposes. You will be compensated ten dollars upon completion of your first visit to the laboratory and an additional five dollars following completion of each subsequent session.
Confidentiality	All information collected in the study is strictly confidential except as you specify on the signed permission form for video and image illustrations and your name will not be identified at any time. The data you provide will be grouped with data others provide for reporting and presentation. Data will be stored in a locked file cabinet in the Cognitive-Motor Behavior Laboratory. Only the principal-investigator and his collaborators will have access to this locked file.

Risk	As a result of your participation in this study, you may experience a modest degree of fatigue from the concentration required during the performance of the test but there are no other known risks and no long-term effects associated with participation in this study.
Benefits, Freedom to Withdraw and to ask questions	Your participation in this experiment is completely voluntary. The experiment is not designed to help you specifically, but it may have substantial impact on understanding how the brain controls visually-guided movement. You are free to ask questions and to withdraw permission for your participation at any time without penalty. You may request a signed copy of this consent form and the investigators will provide you with the results of this study. The University of Maryland does not provide any medical or hospitalization insurance coverage for participants in the research study nor will the University of Maryland provide any compensation for any injury sustained as a result of participation in this study except as required by law.
Investigators	Dr. Jose L. Contreras-Vidal (PI), Dr. Florian Kagerer (Collaborator), Dr Jane Clark (Collaborator), Brad King (graduate student) Department of Kinesiology, 2363 HHP Bldg University of Maryland, College Park, MD 20742 (301)-405-2495
Informed Consent Requirements	"You are voluntarily making a decision whether or not to participate in the research study described above. Your signature indicates that you have read the information provided above, are at least 18 years of age, have had all of your questions answered, and have decided to participate in this study. You will be given a copy of this consent form to keep"

Name of Participant: ____
Participant's Birth date: ____
Today's Date: ____

IF YOU HAVE QUESTIONS ABOUT YOUR RIGHTS AS A VOLUNTEER, OR WISH TO REPORT A RESEARCH RELATED INJURY, PLEASE CONTACT:
Institutional Review Board Office, University of Maryland
College Park, MD 20742; (email) IRB@deans.umd.edu; (phone) 301-405-0678

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