INVESTIGATING AN OPTIMAL MOTOR LEARNING PROTOCOL THAT LEADS TO BETTER SAVINGS AND LONG-TERM RETENTION OF VISUOMOTOR ADAPTATION

by

Reshma James

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ABSTRACT

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Reshma James

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Visuomotor adaptation is fundamental to everyday activities, from the simple act of reaching for a cup to complex athletic maneuvers. The concept of savings is particularly interesting as it sheds light on how motor skills are acquired, retained, and relearned over time. Savings refers to the phenomenon where motor skills that have been previously learned are reacquired or relearned more rapidly after a period of inactivity or after the individual has undergone de-adaptation. While it was initially believed that savings in motor adaptation stemmed from implicit learning mechanisms, recent research indicates that it is primarily attributed to explicit recall of strategies. However, various factors such as providing information about the perturbation, asking subjects to provide a verbal aiming report, offering specific strategies to counteract the perturbation, and manipulating the nature of perturbation introduction during visuomotor adaptation can impact the explicit components of motor adaptation. The primary goal of this dissertation is to determine the potential benefits of training protocols that vary in the involvement of explicit and implicit learning

components on short- and long-term savings following visuomotor adaptation. In addition, we aimed to investigate whether competing memories developed through opposing visuomotor perturbations consolidate differently with varying degree of explicit and implicit components. Our results from Experiment 1 and 2 suggested that introducing different levels of implicit and explicit learning components during adaptation to a 24-degree visuomotor rotation has a varied impact on immediate savings (five minutes) between the gradual-perturbation group (most implicit) and the three abrupt-perturbation groups (less implicit, more explicit, and most explicit). Moreover, incorporating varying degrees of explicitness or implicitness during learning to counteract visuomotor rotation did not lead to improved long-term savings measured at one week and one month post initial learning. In Experiment 3, we showed that consolidation of motor memories associated with visuomotor adaptation is affected by the training methods that involves varying degrees of interference rather than by those that differ in the utilization of implicit or explicit components. We anticipate that findings from this dissertation will be valuable for therapists in tailoring and personalizing rehabilitation sessions to reduce interference and improve long-term retention of motor memories.

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Chapter One: Introduction

Motor learning plays a crucial role in all phases of life as people of all ages are required to continue learning and perform fundamental, as well as specialized motor tasks (Ehsani et al. 2015). It is profoundly clear from the motor learning literature that the highly intricate neural mechanisms in the brain enable human beings to perform a variety of skillful movements with ease and make the interactions with complicated environments effortless. Motor learning involves some cognitive processes that enable us to adapt the motor behavior to changes in the environment and retain the learned behavior in our memory system through the process of motor memory consolidation (Shadmehr and Holocomb, 1997, Kumar et al. 2018). Understanding the neural mechanisms of motor learning and motor memory interactions has always been of great interest for the scientists as it has implications for movement rehabilitation. One way to assess an individual's capacity to adapt their motor behaviors to environmental changes is to investigate the pattern of visuomotor adaptation (VMA), a form of sensorimotor learning in which individuals learn to counteract the external perturbations by reducing kinematic errors (Lackner and Dizio 1994, Kawato 1999; Shadmehr et al. 1994). However, regarding motor adaptation, previous studies have indicated that various processes like internal model representation (Kawato 1999, Smith et al. 2006, Shadmehr and Mussa-Ivaldi 1994), explicit strategies (Taylor et al. 2014, Heuer and Hegele, 2008) and operant learning mechanisms (Huang et al. 2011, Lei et al. 2017) involved during initial learning of the adaptation task and during the retrieval of motor memories associated with the task. Since the ability to move efficiently without any restrictions in every aspect of our lives is crucial for optimal motor performance, it is imperative to understand the learning processes that underlie the formation of motor memories, as well as the evolving nature of motor memories over time. Further

insights into these cognitive and/or neural processes that can influence the design of rehabilitation interventions after neurological injuries or movement disorders.

Visuomotor adaptation is a form of motor learning in which the nervous system reduces the movement errors in response to altered external perturbations (Cassady k et al. 2018). During visuomotor adaptation, the nervous system must adjust the sensorimotor mappings in response to the changes in sensory inputs, environmental characteristics, and task requirements (Cassady et al. 2018, Krakauer et al. 1999, Kawato 1999, Wang & Sainburg 2003, Shadmehr et al. 2010). In a typical laboratory setup, an adaptation task is conducted by asking the subjects to perform center out reaching movements towards the visual targets that are projected horizontally on the screen. While they perform the reaching movements, environmental perturbations are imposed with the help of a virtual reality system (Wang & Sainburg 2003, 2004, Krakauer et al., 2005, McDougle et al., 2015), an external forcefield (Shadmehr & Mussa-Ivaldi, 1994, Miall & Wolpert, 1996, Kawato, 1999 Smith, et al.,2006), or prism goggles (Gaveau, et al., 2014, Block & Bastian, 2012). After performing reaching movements under a rotated visual display condition, the hand-paths of the individuals that are highly curved during initial trials become relatively straight by the end of the training session (Wang & Sainburg 2003, 2004; Krakauer et al., 2005). Error reduction in the subsequent trials is generally thought to occur by incrementally updating the neural representation of the novel visuomotor condition called an internal model (Kawato, 1999, Smith et al. 2006, Thoroughman and Shadmehr, 2000).

Regarding motor adaptation, young adults have demonstrated within-trial, feedback-dependent corrections during the initial exposure to a perturbation that is gradually eliminated with continuous exposure (Shadmehr and Mussa-Ivaldi, 1994). Numerous studies have reported that subjects exhibit smaller errors and faster learning rates when they encounter the same perturbation

even after a time delay. This faster relearning, termed savings, has been observed one day (Seidler et al. 2016), one month (Della Maggiore and McIntosh, 2005) and even one year (Landi et al. 2011) after initial training, suggesting the remarkable capability of the nervous system to retain learned behavior. It has been thought previously that savings is a result of model-based learning that occurs solely due to the updating of an internal model (Shadmehr and Mussa-Ivaldi, 1994, Seidler and Noll, 2008, Kawato, 1999). However, recent studies have suggested the involvement of model-free (operant) learning mechanisms such as use-dependent and reinforcement learning (Huang et al. 2011, Izawa and Shadmehr, 2011, Lei et al. 2017). In addition to these learning models, current evidence suggests that savings involves an interaction between explicit and implicit learning components where the former is related to the awareness and the latter to the unawareness of what is being learned (Haith et al. 2015, Morehead et al. 2015, Huberdeau et al. 2017, Ruitenberg et al. 2018). In the first part of my dissertation, we will conduct experiments to determine the potential benefits of various training protocols that vary in the involvement of explicit and implicit components on initial learning, short-term, and long-term visuomotor adaptation savings in younger adults. Furthermore, it remains uncertain whether competing memories developed through two opposing visuomotor perturbations consolidate differently with explicit and implicit training. Hence, the latter segment of my dissertation will involve an experiment to determine the effects of training methods with varying degrees of explicitness and interference on memory consolidation following two opposing visuomotor adaptations.

Explicit and Implicit Learning Mechanisms in Visuomotor Adaptation Savings

Visuomotor adaptation (VMA) and motor memory retention were once explained with a model-based learning mechanism that involved updating an internal model (Kawato, 1999, Smith et al. 2006, Thoroughman and Shadmehr, 2000). Later, many researchers challenged the

aforementioned view by arguing that VMA also involves model-free mechanisms like use-dependent learning (Huang et al. 2011), reinforcement learning (Butefisch et al. 2000, Diedrichsen et al. 2010) and instance-reliance learning (Wang et al. 2015). In addition, it has been suggested that VMA and savings involves an interaction between explicit and implicit learning components (Mazzoni and Krakauer, 2006, Heuer et al. 2011). This school of thought argues that implicit components are mainly related to the development of an internal model as a result of motor learning (i.e., a sensorimotor transformation associated with a newly learned condition) (Shadmehr et al. 2010), whereas explicit components are related to cognitive strategies that are employed while trying to improve motor performance. In their studies, Taylor et al. (2014) differentiated explicit and implicit learning in a visuomotor adaptation paradigm by asking subjects to verbally report aiming direction while adapting to a visuomotor rotation. The authors observed that the explicit and implicit components had distinct time courses and were completely dissociable. Recent studies have also demonstrated that explicit processes play an important role in VMA by showing overlapping activation in the right dorsolateral prefrontal cortex and bilateral inferior parietal lobule during the initial acquisition phase of VMA and during a spatial working memory task (Anguera et al. 2010, Mc Dougle et al. 2015, Seidler et al. 2017). In another study (Werner et al. 2019), a group of researchers investigated whether awareness play a role in interlimb transfer of VMA (i.e., generalization or transfer of learning from one effector to the other) by employing a 'process dissociation procedure' method. The findings from the above study suggested that the awareness of the rotation was strongly correlated with a sudden adaptation to large perturbation compared to gradual perturbation of the same rotation magnitude, thus concluding that interlimb transfer can also be influenced explicitly. However, there is a wide concern regarding the methods employed to measure the contribution of explicit and implicit components in savings. It has been

suggested that these methods overestimate the explicit and implicit learning components in motor adaptation and further suggest that savings in visuomotor adaptation involves the complex interaction between explicit and implicit learning components (Leow et al. 2017, de Brower et al. 2018, Wang et al. 2019).

Likewise, savings has also been suggested to be linked with the explicit recall of adaptation strategies in younger adults (Haith et al. 2015, Morehead et al. 2015, Huberdeau et al. 2017). In one of the studies, Morehead et al. (2015) performed a series of experiments where they observed subjects developing explicit strategies during the adaptation session with larger rotation sizes (greater than 45 degree), as evidenced by their deviation in the reported aiming direction from the direction of the target. Moreover, the researchers also observed faster readaptation in the visuomotor rotation solely due to the recall of an aiming strategy. However, similar results were not observed with rotation magnitudes less than 45 degrees. Consequently, the authors concluded that error-based implicit adaptation does not play a significant role in visuomotor adaptation, as savings were not evident with extremely small perturbation magnitudes, given the subject's inability to develop aiming strategies.

According to the model-based learning theory, visuomotor adaptation and savings (short-term, long-term) are considered error-based cerebellum-dependent learning, in which the central nervous system (CNS) updates the forward model based on sensory prediction errors. A state space model was then widely used to explain the internal model processes of sensorimotor adaptation. As researchers observed that the learning pattern for savings during re-exposure of the dynamic (force-field) perturbation perfectly matched with the stimulated learning pattern from the state space model, they concluded savings in VMA could be modelled by a state space model (Smith et al. 2006). However, this view was challenged by Zarahn et al. (2008), who conducted a study in

which subjects unlearned the initial learning either by doing washout trials or counter perturbation trials. Even though a state space model could adequately explain the savings associated with the counter perturbation paradigm, the model failed completely in explaining savings generated with paradigms involving washout trials. Therefore, the researchers argued that in addition to linear time-invariant state space dynamics, there could be other learning mechanisms that might play a role in different phases of visuomotor adaptation.

One critical piece of evidence that supports error-based learning comes from the role of the cerebellum in visuomotor adaptation. Studies have proven that the size of the error correlates with the neural activity in the cerebellum, thereby implicating the role of the subcortical structure for error correction (Seidler et al. 2004, Ogawa et al. 2006). Impairments in the cerebellum were thus associated with recalibration issues in cerebellar ataxia patients even though the patients were allowed to make error corrections within the trials (Hashimoto et al. 2015, Tseng et al. 2007, Mazzoni and Krakauer, 2006). However, recent findings do not support the idea that the cerebellum is the structure dedicated exclusively for implicit learning. Cerebellar patients were equally compromised while learning to counteract the perturbation introduced both gradually (more implicit) and abruptly (more explicit) (Butcher et al. 2017). In their studies, Butcher et al. (2017) showed that cerebellar impairments were accompanied with not only reduced aftereffects but also with reduced strategic control. This recent evidence points to a complicated relationship between implicit and explicit learning, thereby challenging the traditional view that the cerebellum is the core structure dedicated to implicit learning.

Recently, there has been a growing interest in exploring the factors that influence sensorimotor adaptation. Research suggests that the structure of the task can significantly influence the learning of the motor task and its memory consolidation. The introduction of a perturbation

has a differential effect on adaptation and savings. It has been suggested that subjects learning to counteract a perturbation gradually in small increments have stronger aftereffects and better learning rates compared to the abrupt introduction of a perturbation (Kagerer and Vidal, 1997). Likewise, adaptation to a gradual perturbation is associated with a lower reaction time and better adaptation recalibration since introducing the rotation in small increments is thought to involve less explicit awareness. However, the same researchers (Kagerer and Vidal, 1997) observed an increase in reaction time when the online cursor feedback for the gradual perturbation was eliminated. The authors suggested that the observed reaction time hike could be attributed to an extra cognitive load imposed by the no-feedback condition on the gradual perturbation. Similarly, the size of the rotation is thought to have a differential effect on the aftereffects developed after sensorimotor perturbation. For example, when the perturbation size was reduced to 30 degrees, the disparity in aftereffects between gradual and abrupt introductions became less pronounced (Kagerer and Vidal, 1997).

The role of explicit awareness in visuomotor adaptation and savings is still a controversial debate. Even though there are a few studies that support the significant role of explicit learning in VMA and savings, there are several other studies that suggest explicit awareness can influence the initial adaptation rate, but not short- or long-term savings (Benson et al. 2011, Yin and Wei, 2020). In a recent study, researchers Yin and Wei investigated whether formation of an explicit strategy is a prerequisite for savings in VMA (Yin and Wei, 2020). The findings from the study indicated robust savings for the group that implicitly learned the rotation from sensory prediction errors. The results also indicated that savings in the explicit group were not due to the quick recall of the explicit strategies but were instead due to the enhanced implicit learning. Therefore, these findings

suggest that the formation of savings in VMA is independent of forming or remembering explicit aiming strategies.

Although understanding how movements are modified and learned in response to changing environmental requirements is crucial, it is equally important to investigate how learned motor memories are retained for long-term retrieval. Savings following visuomotor adaptation has been observed immediately, 24 hours later, and even after one year (Della-Maggiore and McIntosh, 2005 Krakauer et al. 2005, Landi et al. 2011)**.** Retention following a mirror tracing task have been observed even after 5 years of initial training (Rodrigue et al. 2005). Healthy young adults were able to maintain the performance measures like speed and accuracy during the readaptation session performed even after 5 years (Rodrigue et al. 2005). However, long-term savings in VMA remains to be further investigated. Previous work has suggested that individuals exhibit long-term savings after training for one week with a complex optical rotation adaptation task (Landi et al. 2011). Furthermore, one week of intensive training induced changes in the neural network connections between the anterior cerebellum, the contralateral PPC and the M1 (Landi et al. 2011, Della-Maggiore and McIntosh, 2005). One week of training with the same visuomotor adaptation paradigm also produced enlargement in the gray matter volume along with changes in the white matter functional anisotropy corresponding to the hand area of the contralateral M1. Moreover, the volume of gray matter measured immediately after one week of training predicted faster adaptation than what was observed in the subjects one year after initial training (Landi et al. 2011). Clearly, the evidence from the above studies suggests how well motor training paradigms can affect long-term behavior by producing functional and structural changes in the brain.

Supporting evidence regarding the role of implicit learning for long-term retention comes from the field of aging studies (Heuer and Hegele, 2008, Rodrigue et al. 2005). As suggested by

numerous studies, aging is accompanied by a lower rate of initial adaptation learning due to poor explicit control. However, the consolidation of motor memories after motor skill learning has been reported to be intact in older populations. In a five-year follow up study done by Rodrigue et al. **(**2005**),** older adults were able to retain a learned behavior for a mirror tracing task**.** However, the same study reported that the magnitude of long-term savings was significantly smaller in older populations than young adults. Additional studies on aging (Seidler, 2006, Bock et al., 2001) provide further evidence that long-term savings is associated with implicit learning.

Accordingly, whether or not to involve cognitive strategies (explicit control) can be determined by the training environment, nature of the task and awareness of the perturbation. No study has explored whether altering the degree of explicitness in an adaptation paradigm involving a smaller rotation size affects learning rates and retention (both short-term and long-term), despite the majority of previous research focusing on tasks with larger visuomotor rotations (45 degrees or more), manipulation of visual feedback, and short-term memory retention experiments. Regarding the role of explicit components in motor adaptation, these components can be affected by various factors that differ in terms of their explicitness levels. These factors include offering details about the perturbation, requesting verbal aiming reports from participants, presenting a particular strategy to address the perturbation, and adjusting the method of introducing the perturbation (whether gradually or abruptly) during visuomotor adaptation.

Interference between competing motor memories of VMA

Newly formed motor memories are unstable and susceptible to interference (Thoroughman and Shadmehr, 2000, Caithness et al. 2004, Miall et al. 2004). We can better understand the role of conscious and unconscious learning components in motor memory consolidation by investigating how motor memories consolidate differently across VMA training protocols with varying degrees

of explicitness. Interference occurs when subjects adapt to two opposing force-field or visuomotor perturbations (task A, task B) in close succession. It is believed that when subjects learn a conflicting motor task, regardless of the hand used, the motor memories compete for the same neural resources (Thoroughman and Shadmehr, 2000, Caithness et al. 2004, Miall et al. 2004). Most studies on interference have typically investigated the memory of task A, 24 hours after initial learning. If the learning rate during readaptation is faster or produces smaller errors during the first few trials, it is suggested that task B did not interfere with the memory of A. However, if the initial readaptation trials produce larger or similar errors with either a decreased or the same learning rate, it can be concluded that task B interfered with the motor memory of A. A few studies have suggested that interference due to conflicting memories can be prevented if both motor tasks are associated with distinct movement contexts (Cothros et al. 2009, Howard et al. 2013, Nozaki et al. 2006).

Interference can be either anterograde or retrograde for sensorimotor adaptation. The interference is thought to be anterograde if either task A interferes with the learning of task B or task B interferes with the relearning of task A (Miall et al. 2004, Shadmehr and Mussa-Ivaldi, 1994). Conversely, retrograde interference occurs if task B interferes with the initial learning of task A (Smith et al. 2006). Interference with visuomotor or dynamic adaptation is thought to be retrograde in nature (Krakauer et al. 2005, Krakauer, 2009, Kumar et al. 2018, Caithness et al. 2004, Shadmehr and Mussa-Ivaldi, 1994). According to Shadmehr and Mussa-Ivaldi (1997), learning an opposing force-field rotation after adapting to the first rotatory viscous force field imposed an interference that disturbed the relearning of the first force field. However, leaving a time gap of five-and-a half hours between the learning of two tasks eliminated the interference and consolidated the motor memory efficiently. Subsequent studies have suggested that

interference also occurs for visuomotor adaptation if a conflicting motor task is learned after the initial training (Krakauer et al. 2005). In contrast to a force field perturbation, the second task interfered with the relearning of the first task even after leaving a 24-hour time interval between the two tasks. The authors observed a resistance to interference when washout trials (i.e., turning of perturbation) were inserted before the learning of the second task that removed the anterograde effects. Furthermore, doubling the number of trials for the first motor task facilitated faster relearning even with a small-time gap of five minutes between the two conflicting tasks (Krakauer et al. 2005). Therefore, the authors concluded that increasing the initial training trials and time intervals between the conflicting tasks can lead to a resistance to retrograde effects that will eventually contribute to better memory retrieval.

Recently, the interference paradigm was employed to examine the stability of motor memories learned with different arms (Kumar et al. 2018). In that study, subjects learned a clockwise (CW) cursor rotation with their right hand, followed by washout trials and learning the opposing perturbation with their left hand. The authors not only observed an interference when the conflicting task was learned with different arms, but they also noticed that the washout trials (left arm) failed to eliminate interference. However, the passage of time between the two conflicting tasks, together with the washout trials, eliminated the interference to the consolidation of motor memories. Such a time-dependent pattern confirmed that interference between memories developed with the two arms is indeed retrograde in nature. It is clear from the above studies that the interference posed to the motor memory developed with individual or both arms in VMA exhibits retrograde characteristics.

Numerous studies have suggested that the consolidation of initially acquired memory can resist interference from the motor memory associated with an opposing perturbation by allowing

some passage of time between the two opposing perturbations (Krakauer et al. 2005, Kumar et al. 2018). However, it remains uncertain whether memory stabilization and interference occurs differently depending on the nature of training protocols that involve varying degrees of implicit and explicit components.

Motor memory Consolidation and Interference in Rehabilitation

The motor learning literature has consistently reported that various factors can unmask the interference posed on motor memory consolidation when two opposing perturbations are learned in close succession. Understanding the neural mechanisms of motor learning and motor memory interactions has always been of great interest as it has implications for movement rehabilitation. While memory consolidation and interference effects are relevant in psychotherapy treatments, we are uncertain about whether these interference effects can trigger any issues when patients receive multiple rehabilitation services (e.g... occupational therapy, physical therapy, speech language pathology). Since each of these rehabilitation services involves the creation and modification of memory traces associated with specific task performance (Dimyan and Cohen, 2011), it is crucial to identify the factors that can lead to minimum interference effects and thereby, enhance consolidation between the rehabilitation sessions. As the motor learning literature stresses the importance of goal-oriented or task-specific training in rehabilitation sessions, it is equally important that therapists need to be aware of the interference effects that can occur when these sessions are done in successive sessions. Understanding the interference effects can help therapists to schedule therapy sessions and organize the therapy content that can lead to minimum interference to memory traces. It is well known that explicit and implicit training methods are employed in rehabilitation session post stroke (Johnson et al. 2014, Kleynen et al. 2019). For stroke patients suffering with cognitive impairments, explicit training methods might not be always

efficient as it requires them to process a large amount of verbal information. However, in some cases, clinicians may have to use a mixture of implicit and explicit training methods while subjects recover from stroke-related impairments. Therefore, it is crucial that therapists tailor rehabilitation sessions by incorporating explicit and implicit training methods based on several factors such as impairment level, time after stroke, type of stroke and other individual needs.

To the best of our knowledge, there is no study that has compared the effects of different training methods involving various amounts of explicit and implicit learning components on motor adaptation as well on motor memory retention. The knowledge gained from my dissertation will elaborate our understanding of whether competing memories developed through opposing tasks consolidate differently between explicit and implicit training methods. This is important as it will help us determine the patterns of memory stabilization and interference across varying degrees of implicit and explicit training methods.

Summary

In this chapter, we reviewed the explicit and implicit learning mechanisms in VMA, especially in relation to savings and motor memory interference. As discussed in this chapter, identifying the factors that can lead to more stable motor memories will provide deeper insights into the neural processes underlying long-term motor memory retention. Although factors such as providing information about the perturbation, presenting a specific strategy to counteract it, and adjusting the introduction of the perturbation (whether gradually or abruptly) have been examined individually in some prior studies (Taylor et al., 2014; Herzfeld et al., 2014; Krakauer et al., 2005), their collective impact on savings and long-term retention after visuomotor adaptation has not been thoroughly investigated within a single study. It also remains to be studied how the motor memories obtained following visuomotor adaptation that involves these different factors are

consolidated and how they can resist an interference when competing motor memories exist. Gaining a better understanding of the contributions of implicit vs. explicit components to motor memory consolidation, as well as interference, may prove valuable not only for motor learning researchers, but also for rehabilitation professionals who must deal with scheduling and designing consecutive therapy sessions regularly for persons with neuromotor impairments.

Statement of Purpose

The long-term goal of our research is to identify an optimal training method that can maximize savings and retention following motor learning in both healthy young and older adults. Furthermore, it holds practical significance as the findings from this study could prove valuable for developing optimal rehabilitation interventions for clinical populations particularly stroke patients. The objective of this dissertation proposal is to determine the potential benefits and resilient effects of training protocols that vary in the involvement of explicit and implicit components on initial learning, savings and long-term retention in younger adults. As the involvement of explicit and/or implicit components during initial adaptation can impact the rate of learning and motor memory consolidation differently, the need for identifying an optimal protocol is critical. However, the effects of these learning components on visuomotor adaptation have not been systematically investigated. Although recent evidence from the literature emphasizes the crucial role of explicit components for savings and faster adaptation rates, the role of implicit components (i.e., unconscious learning) for long-term retention cannot be neglected. Also, it is uncertain whether competing memories developed through opposing visuomotor perturbations consolidate differently between explicit and implicit training methods. Determining whether or not the resilience of motor memories depends on the level of implicit and explicit components involved in visuomotor adaptation has significant implications for neuromotor rehabilitation.

Aim 1: To determine the beneficial effects of training methods with varying degrees of explicitness on short-term savings following visuomotor adaptation.

Working Hypothesis: According to the notion that explicit learning is associated with savings (Morehead et al. 2015, Huberdeau et al. 2017), we hypothesize that the involvement of more explicit components during visuomotor adaptation will evoke greater short-term savings (i.e., immediately following initial training).

Aim 2: To determine the beneficial effects of training methods with varying degrees of explicitness on long-term savings following visuomotor adaptation.

Working Hypothesis: According to the notion that implicit learning is associated with long-term motor memory consolidation (Rodrique et al. 2005, Landi et al. 2011), we hypothesize that the involvement of more implicit components during visuomotor adaptation will lead to greater long-term savings (i.e., one week and one-month post training).

Aim 3: To determine the effects of training methods with varying degrees of explicitness and interference on memory consolidation following two opposing visuomotor adaptations.

Working Hypothesis: If interference to motor memory consolidation depends on the nature of the training method, we propose that short- and long-term savings following adaptations to two opposing visuomotor perturbations will vary as a function of explicitness or implicitness of the task employed during training. More specifically, we hypothesize that adapting to two opposing visuomotor perturbations will produce higher short-term savings when the training method involves less interference (24-hour time gap and washout) compared to the training method that involves more interference (counter rotation

immediately after initial adaptation, without washout). We also hypothesize that the amount of long-term savings will be greater than that of short-term savings, based on the notion that memories associated with motor learning become stronger as anterograde interference effects are weakened with the passage of time (Shadmehr and Mussa-Ivaldi, 1994).

The remainder of this dissertation is outlined as follows: Chapters 2 and 3 describe Experiments 1 and 2 that were conducted to achieve Aims 1 and 2, respectively. Chapter 4 describes Experiment 3 that was conducted to achieve Aim 3. Finally, Chapter 5 describes the summaries and conclusions.

Delimitations of the Study

1. The proposed study has been designed based on a notion that visuomotor adaptation and savings involve the interaction of implicit and explicit components.

2. Data will be collected on healthy young adults. Thus, any generalization of the findings from this study will be limited to such populations.

Assumptions of the Study

1. Participants do not have any neurological damage and are right-handed.

2. Participants will honestly follow all instructions regarding the experimental procedures.

Significance of the Study

The involvement of explicit and implicit components in visuomotor adaptation has been investigated by numerous researchers previously, although it has not been evaluated systematically whether, or how, the two types of components contribute differently to savings. The proposed research is significant as it is the first step toward determining the effects of different training methods that are systematically varied in terms of the involvement of implicit and explicit components during visuomotor adaptation on short- and long-term savings. Also, our study aims to probe the resilient effects of explicit and implicit training methods on motor memory consolidation. The impact of my dissertation projects will be that findings from the proposed work will advance our understanding of the potential benefits of different training conditions that involve varying degrees of implicit and explicit components related to a given motor task and their potential effects on long-term retention of motor memory in healthy young adults. Such knowledge may prove valuable for designing optimal training protocols in rehabilitation settings, as well as in sports settings.

Chapter 2: The effects of training methods with varying degrees of explicitness on short-term savings following visuomotor adaptation

In Chapter 1, I have reviewed the explicit and implicit learning mechanisms and motor memory interference in visuomotor adaptation. In this chapter, I will describe the first experiment that was conducted to determine the beneficial effects of training methods with varying degrees of explicitness on short-term savings following visuomotor adaptation. The results from the above study will help us understand the potential impact of various training protocols on short-term retention of motor memories.

Introduction

Visuomotor adaptation (VMA) is a form of motor learning in which the nervous system adjusts the sensorimotor mapping in response to sensory inputs or environmental perturbations (Cassady k et al. 2018). It is widely known that the motor system counteracts the imposed perturbations with a large direction error upon initial exposure and gradually adjusts the motor behavior to reflect adaptation to the imposed manipulations (Krakauer et al. 2005, Shadmehr et al. 1997). VMA results in savings defined as faster learning of the perturbed movement when participants experience the same perturbation for the second time after being forgotten (Krakauer, 2009). Savings following visuomotor adaptation have been observed to occur immediately, as well as persisting up to 24 hours later**,** and even after the course of one year (Della et al. 2005, Krakauer et al. 2005, Landi et al. 2011)**.** Even though there is overwhelming support regarding the existence of savings and motor memory retention in young adults, the mechanisms that are responsible for these phenomena are still unclear.

Various learning models have been proposed to explain the learning and retention observed in visuomotor adaptation. Earlier, researchers used a state space model to explain how

the control policy gets updated during VMA. Using the formula of state space model, the internal model hypothesis can predict motor responses to novel imposed perturbations (Scheidt et al. 2001; Donchin et al. 2003, Baddeley et al. 2003). According to the state space model (Baddeley et al. 2003, Donchin et al. 2003), the learning rate parameter determines trial-to-trial movement error corrections whereas the retention parameter defines the learning performed throughout the trials. However, variations of the state space model have been suggested since the model could not account for long-term savings (Diedrichsen et al. 2010, Seidler et al. 2017) and the model failed completely in explaining savings generated with paradigms involving washout trials (Zarahn et al. 2008). According to recent studies, visuomotor adaptation involves multiple learning processes with distinct time scales (Huang VS et al. 2011, Diedrichsen et al., 2010). In particular, a few studies have suggested that visuomotor adaptation incorporates an interplay between explicit and implicit learning components, where the former involves the awareness of the given perturbation, and the latter relates to the unawareness of the perturbation (Mazzoni et al. 2006, Heuer et al. 2011). According to this idea, the implicit learning components in VMA are mainly related to the development of an internal model that progressively adjusts motor commands by comparing the predicted sensory sequence with the actual motor output (Shadmehr et al. 2010). On the other hand, explicit components refer to the strategic corrections intentionally employed to change the movement characteristics (Taylor et al. 2012).

Recently, savings in VMA have been linked to the_explicit recall of both adaptation strategies and awareness (Haith et al. 2015, Morehead et al. 2015, Huberdeau D.M. et al., 2017, Ruitenberg et al. 2018). Morehead et al. (2015) conducted various experiments in which the participants were tested if an aiming strategy was evoked when the visuomotor rotation was reencountered. Savings were tested by a color-cued task or by employing a rotation differing in

terms of magnitude and direction from the originally exposed rotation. The authors reported that in both experiments, savings were generated when participants recalled the aiming strategy, and they concluded that savings generated after visuomotor adaptation were due to action selection evoked from remembering and using the aiming strategies developed during initial training. In addition, Huberdeau et al. (2017) proposed that extended practice is not essential to evoke long-term memory of learning because participants could generate faster relearning after just two trials of visuomotor adaptation. Taken together, these studies suggest that the phenomenon of savings is due to the recall of explicit strategies, or the rapid retrieval of explicit strategies learned during the initial adaptation trials (Huberdeau D.M. et al., 2017, Morehead et al. 2015, Ruitenberg et al. 2018). It has been reported that early stages of adaptation and second day memory retention activates the dorsolateral prefrontal cortex and bilateral inferior parietal lobe (IPL) that is important for cognitive control. The same region was also found to be involved during the performance of a spatial working memory task (Seidler et al. 2017). These neuroanatomical findings also suggest the role of cognitive processes (which may or may not be explicit in nature) involved during the early learning stages of adaptation important for generating savings.

Besides the crucial role of explicit cognitive strategies in visuomotor adaptation savings, these studies have failed to demonstrate savings with small size perturbations. For example, Morehead and colleagues conducted an experiment to investigate whether savings differs across variable perturbation sizes (15°, 30°, 45°, 60°). The results from the study suggested an absence of savings for perturbation size of 30 degrees and 15 degrees. Since an extremely small size of perturbation couldn't evoke savings as the subjects were unable to develop aiming strategies, researchers concluded that savings in visuomotor adaptation is driven mainly if not solely by recalling of aiming strategies. However, the study from our lab have demonstrated savings in

younger adults who learned to counteract 30-degree counterclockwise rotation (James et al. 2022). In one of the studies, we examined whether the amount of savings would be different if subjects performed a washout session with different arms. The subjects performed the adaptation and readaptation session with their left arm but used either their right or left arm to perform the washout session. In the above study we hypothesized that if cognitive strategies are heavily involved in savings, then the pattern of savings would be similar even if we use different arms for a washout session. However, we observed that the amount of savings was larger when the subjects performed the washout session with their right arm compared to their left. Therefore, we concluded that the recall or retrieval of explicit cognitive strategies was not the single component that contributed to savings, but effector specific model free learning mechanisms can also play a crucial role in savings.

It should be noted that the explicit components of learning can be reinforced by several factors such as color cues, providing instruction or strategy, verbal aiming reports, or the introduction of a perturbation during the adaptation training. For example, when young adults were exposed to a gradual introduction of 90-degree visuomotor rotation (10 step increments), their learning rate became faster with fewer spatial errors and stronger aftereffects compared to an abrupt introduction of a perturbation with the same magnitude (Kagerer and Vidal, 1997). In another study **(**Heuer et al. 2008)**,** the participants were made aware of the presence/ absence of a perturbation by employing color cues (i.e., cursor turned red for the presence of rotation). The researchers observed a stronger explicit adaptive shift for the group that was explicitly aware of the presence or absence of the perturbation as compared to the group with no explicit knowledge. Similarly, verbally reporting the aiming directions during the perturbation trials produced a faster change in the heading angle than was estimated as an enhancement in the explicit learning

components (Taylor et al. 2014). Collectively, the evidence from these studies suggests that reinforcing or adding explicit components during visuomotor adaptation learning may have a significant impact on the learning rate and trial-by-trial error reduction.

Many previous studies have examined the effects of various factors on visuomotor adaptation, such as the degree of visuomotor rotation (Morehead et al. 2015), the nature of perturbation introduction (e.g., gradual vs. abrupt) (Kagerer and Vidal, 1997), and the presence of an instruction (Benson et al. 2011) that can result in the use of a cognitive strategy. To our knowledge, however, it has not been investigated how training methods of varying degrees of explicit vs. implicit components by combining these different factors will influence short-term savings following visuomotor adaptation. Thus, the objective of the first aim is to determine the beneficial effects of training methods with varying degrees of explicitness on short-term savings following visuomotor adaptation. This will be achieved by comparing four subject groups that vary in terms of their training protocol: 1) gradual perturbation (i.e., most implicit), 2) abrupt perturbation, 3) abrupt + instruction, and 4) abrupt + instruction + strategy (i.e., most explicit). Based on the belief that explicit learning is thought to be associated with savings (Morehead et al. 2015, Huberdeau et al. 2017), we hypothesize that the involvement of more explicit components during visuomotor adaptation will evoke greater short-term savings measured after five minutes following initial training.

Experiment 1

Materials and Methods

Participants

Forty neurologically intact right handed young adults (18-35 years old) participated in the study. The power analyses from our previous studies (Wang & Lei 2015, Lei et al. 2019) indicated the

effect sizes of 1.4 to 2.2, respectively, which then indicated the sample size of 4 to 7 per group, respectively (for the power of .8 and the alpha of .05). Informed consent was obtained from each subject prior to participation, using a form approved by the Institutional Review Board of the University of Wisconsin-Milwaukee (Appendix A). Handedness of the participants was ensured with the 10-item version of Edinburgh inventory (Oldfield, 1971; Appendix B) in which laterality quotient of -100 indicates fully left-handed and +100 fully right-handed. All our participants scored +100. An awareness questionnaire was also used to assess the subject's awareness of the visuomotor rotation condition (Benson et al. 2011, Appendix C). The participants were recruited on the campus of University of Wisconsin Milwaukee through word of mouth or posted flyers (Appendix D). The Inclusion criteria were: the subject (a) is right handed; (b) falls in the age range of 18-35; (c) has no severe psychiatric diagnoses; (d) has no peripheral movement restrictions from neuropathy or orthopedic injuries; (e) no neurological sensory or motor dysfunction; and (f) has normal or corrected-to-normal vision. Exclusion criteria were: the subject (a) is unable to complete assessment due to a low level of consciousness, developmental delay, low literacy, or inability to understand English; (b) has a history of neurological disease; (c) is taking psychoactive medication; (d) has a history of substance abuse; (e) has a vision impairment including color blindness; and (f) has certain conditions that may restrict their arm movements (e.g., nerve compression syndromes, arthritis, lupus, infection, or in general any bone ,muscle, tendon or joint problems. People with other conditions that do not affect their arm movements substantially (e.g., diabetes, high cholestrol) will not be excluded from the study.

Apparatus

A bilateral robotic exoskeleton device called KINARM (BKIN Technologies Ltd, Kingston, ON, Canada) was used to collect movement data (Fig. 2.1). Participants were seated on a chair with

both arms placed on the exoskeleton, which provided support against gravity. The KINARM was incorporated with a simple virtual reality system in which the participants looked directly into the mirror placed above the arms, to which the visual targets were projected (i.e., the horizontal display). This setup created an illusion that the visual targets appeared in the same horizontal plane as the arm. Direct vision of the arms was blocked by the horizontal display. A cursor representing the location of the index fingertip was provided to guide the subject's reaching movement. The 2-D position of the index fingertip was sampled at 1,000 Hz, low-pass filtered, and differentiated to yield movement velocity. Data was processed and analyzed using Matlab (MathWorks, Natick, MA).

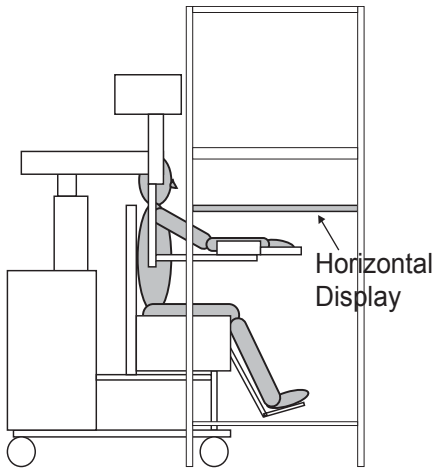

Fig 2.1: Experimental Setup: KINARM Exoskeleton robot was used for data aquisition

Experimental Protocol

In general, participants performed rapid reaching movements from a start circle to one of four targets (10 cm away from the starting circle) repeatedly with the right arm (Fig 2.2A). They were instructed to move the cursor to each target rapidly and as straight as possible in response to the appearance of the target and then bring the cursor slowly back to the starting circle. The

experiment consisted of four sessions (Fig 2.2C): baseline (40 trials), adaptation (160 trials), washout (40 trials), and readaptation (160 trials). The *baseline* session had 10 cycles of reaching movements where each cycle contained four consecutive trials corresponding to the four targets that are placed radially around the starting circle. Veridical feedback of the index fingertip location was provided to the subject by a cursor displayed on the screen, so that the participants could familiarize with the general reaching task without visuomotor perturbation (Fig 2.2A).

The *adaptation* session had 40 cycles with different types of training conditions depending on the experimental protocol. Participants were randomly assigned to four different groups in which the training conditions varied based on the involvement of explicit and implicit components. Participants in the gradual perturbation group (GP; most implicit) adapted to a 24-degree counterclockwise (CCW) rotation condition in which the degree of rotation was zero from cycles one to nine. Then, the CCW rotation was gradually increased at a rate of one degree per cycle up to 24 degrees from cycles 10 to 33. After that, the 24-degree CCW rotation was maintained until the end of the adaptation session. Participants in the abrupt perturbation group (AP; more implicit) adapted to a 24-degree CCW rotation condition in which the cursor was rotated 24 degrees from the very first trial. Before they performed reaching movements in this session, the participants in the GP and AP groups received the following instruction: "A target will appear on the screen. Your task is to hit the target as accurately and straight as possible." Participants in the abrupt perturbation + instruction group (AP+I; more explicit) adapted to the 24-degree CCW rotation condition in which the cursor was rotated 24 degrees from the first trial. Before they performed reaching movements in this session, the participants were provided with the following instructions: "A target will appear on the screen. The cursor will be rotated 24 degrees CCW relative to the location of your index fingertip. Your task is to hit the target as accurately and straight as possible."

Participants in the abrupt perturbation + instruction + strategy group (AP+I+S; most explicit) adapted to the 24-degree CCW rotation condition in which the cursor was rotated 24 degrees from the first trial. Before they performed reaching movements in this session, the participants were provided with the following instructions along with the picture in Fig 2.2B.: "A target will appear on the screen. The cursor will be rotated 24 degrees CCW relative to the location of your index fingertip. Your task is to hit the target as accurately and straight as possible. You can counteract the rotation by aiming in the direction that is rotated 24 degrees clockwise (CW) relative to the target location." The baseline and adaptation session were separated by five-minutes. During the five-minute time gap, the participants in AP+I+S group were given the above instruction with the help of the picture in Fig 2.2B. Participants in the remaining three groups (GP, AP, AP+I) were also provided with specific instructions based on their assigned groups during the five-minute interval between the baseline and adaptation session. This ensured uniformity in the time gap between baseline and adaptation across all the four groups.

Following that, all participants performed reaching movements with veridical feedback and without visuomotor rotation in the *washout* session. In the *readaptation* session, which took place five minutes after the washout session (called, 'readaptation at 5 minutes'), all participants adapted to the 24-degree CCW rotation condition in which the cursor was rotated 24 degrees from the first trial, with the following instruction: "A target will appear on the screen. Your task is to hit the target as accurately and straight as possible."

After the task was completed, participants in all four groups were polled for strategy use or explicit awareness by using the awareness questionnaire (Appendix C). In the questionnaire, all the participants that followed the bold arrow suggests no awareness of perturbation and all of them that followed the gray arrows indicating least awareness of the perturbation. All the participants

that followed the black dotted lines indicates the subjects were aware of the perturbation and strategies were being used.

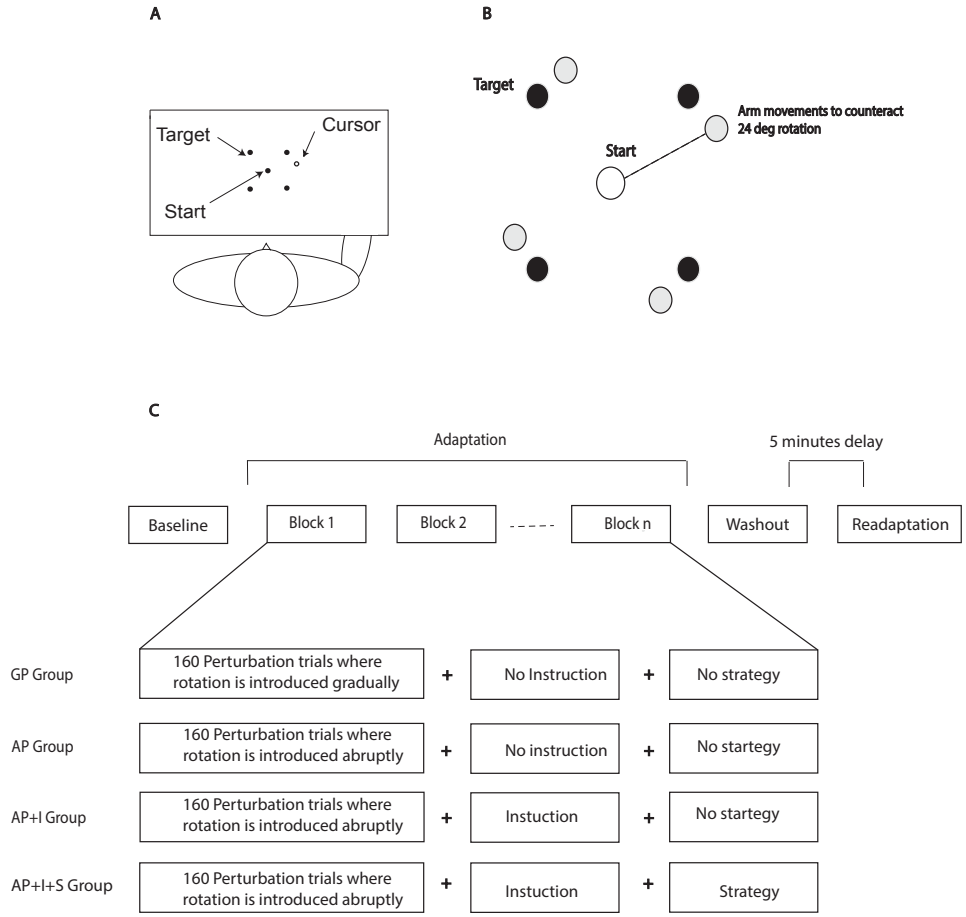

Fig 2.2: A) Visual display of target, cursor and start circle: Target was randomly displayed at one of the four locations. During the experiment, participants moved their arm straight from the start circle to the target. Direct vision of the hand was blocked by horizontal display. The visual feedback was provided as a cursor indicating the mouse position. B) Setup for adaptation session: During adaptation, the participants moved their arm in the desired direction. The position of cursor was rotated 24^{o} CCW about the position of index fingertip, so the subject will have to reach toward the direction that is 24^{o} CW about the target (gray circles). C) Experimental Protocol: Participants

performed a baseline followed by an adaptation session. The adaptation session had 160 trials, and each subject performed adaptation session differently depending on the subject groups. The adaptation session was followed by a washout session. Participants in all the four groups performed a readaptation session five minutes after the washout session.

Data Analysis

Direction Error (DE) was calculated as the measure of performance. DE is defined as the angular difference between a vector from the starting circle to a target and another vector from the hand position at movement start to that at peak arm velocity. The *rate of learning* in the adaptation and readaptation sessions was calculated by fitting DE values from every single subject within each group to an exponential function:

$$DE(n) = A*\exp(-R*n) + B;$$

where A is a constant, n is the trial number, and R is the estimated value of the learning rate.

For statistical analysis, separate analyses were done in the following ways. The DE data was subjected to a repeated-measures ANOVA with group (GP, AP, AP+I, AP+I+S) as a between-subject factor and cycle (First cycle of adaptation, washout, and readaptation session at 5 minutes) as a within-subject factor. Then, the learning rate from readaptation session at 5 minutes was subjected to a one-way ANOVA, with group (GP, AP, AP+I, AP+I+S) as a between-subject factor. For significant effects, post hoc comparisons were done (Tukey's tests for between-group comparisons, Fisher's LSD tests for within-group comparisons). The alpha level was set at 0.05 for all comparisons. In addition to the statistical tests, we also collected the awareness information for each subject using the awareness questionnaire provided in Appendix C.

Results

The changes in performance across the cycles during the adaptation, washout and the readaptation session at 5 minutes for each group are shown in Figure 2.3. All the four groups in our study were different in terms of the involvement of explicit and implicit components in the adaptation session. GP group (most implicit) adapted to a 24-degree counterclockwise (CCW) rotation condition in which the degree of rotation was gradually increased one degree per cycle whereas AP group (more implicit) adapted to a 24-degree CCW rotation condition in which the cursor was rotated 24 degrees from the very first trial. Similarly, AP+I (more explicit) adapted to a 24-degree CCW rotation that was introduced from the very first trial soon after they were given instructions that made them aware about the cursor rotation. On the other hand, AP+I+S group (most explicit) were given the instruction regarding the presence of perturbation along with the strategies requires to counteract the abruptly introduced 24-degree CCCW rotation. The three subject groups who experienced the abrupt rotation condition (AP, AP+I, AP+I+S) adapted to the 24-degree CCW rotation by reducing the direction errors trial by trial (Fig 2.3). The difference in DEs in the adaptation session for the GP group is expected as they were imposed with a rotation that was introduced gradually. DEs in the washout session shows a stronger aftereffect for the GP group as compared with the other three groups (AP, AP+I, AP+I+S). It can also be seen in Fig 2.3 that the three groups (AP, AP+I, AP+I+S) showed faster learning with less initial errors during the readaptation session performed five minutes post washout session as compared with the most implicit group (GP).

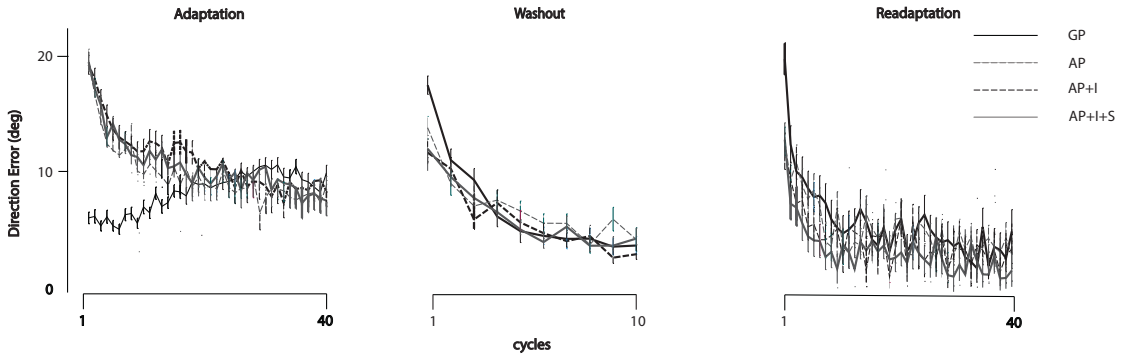

Fig 2.3: The change in Direction Error (DE) across the cycles for Adaptation, Washout and Readaptation session. Every data point on the x axis represents the mean value of one cycle across the participants in each group.

The repeated-measures ANOVA with the DE data from the adaptation, washout, and readaptation sessions at five minutes indicated a significant interaction effect between cycle and session ($p<.001$) indicating that the pattern of performance changes across the cycles varied among the four groups (Fig 2.4A). Post hoc analyses using the DE data from the washout session (1st cycle) indicated a significant difference between group GP vs group AP+I ($p=.019$) and group GP vs group AP+I+S ($p=.003$), which indicates the aftereffects were different between GP group and the other two groups. With regards to DEs from the readaptation session at five minutes (Fig 2.4A), there was a significant difference between group GP and the other three groups (Group GP vs group AP: $p<.001$, Group GP vs Group AP+I: $p<.001$, Group GP vs group AP+I+S: $p<.001$).

The responses from the awareness questionnaire that was used to assess the awareness of the rotation condition is shown in in Appendix E under Experiment 1 and 2. The responses from the participants indicated that the most implicit group (GP) who followed the bold black arrow (Appendix C) did not notice any change in the direction of the cursor. Similarly, the participants in the more implicit group (AP) pushed left when they felt the cursor was not moving in the

intended direction (Gray lines in Appendix C). The responses clearly indicates that the participants in GP and AP group were unaware of the perturbation and therefore, they did not use any strategy to counteract the rotation. On the other hand, it is clear from the responses as shown in Appendix E that the participants in AP+I was aware of the 24-degree CCW rotation and most of them pushed left to land on the target. It can be also seen from the responses that the participants in AP+I+S were completely aware of the rotation and used a strategy (i.e., moving the cursor 24 degree clockwise with respect to target location) to counteract the rotation in the adaptation session. The data from one of the participants in the AP group was not included in the analysis as the participant informed the experimenter that he/she was aware of the rotation in the adaptation condition. To clarify, if the removal of subject caused any change to overall results of the study, we did the data analysis by including the same subject's data. We found no difference in our overall results by including his data.

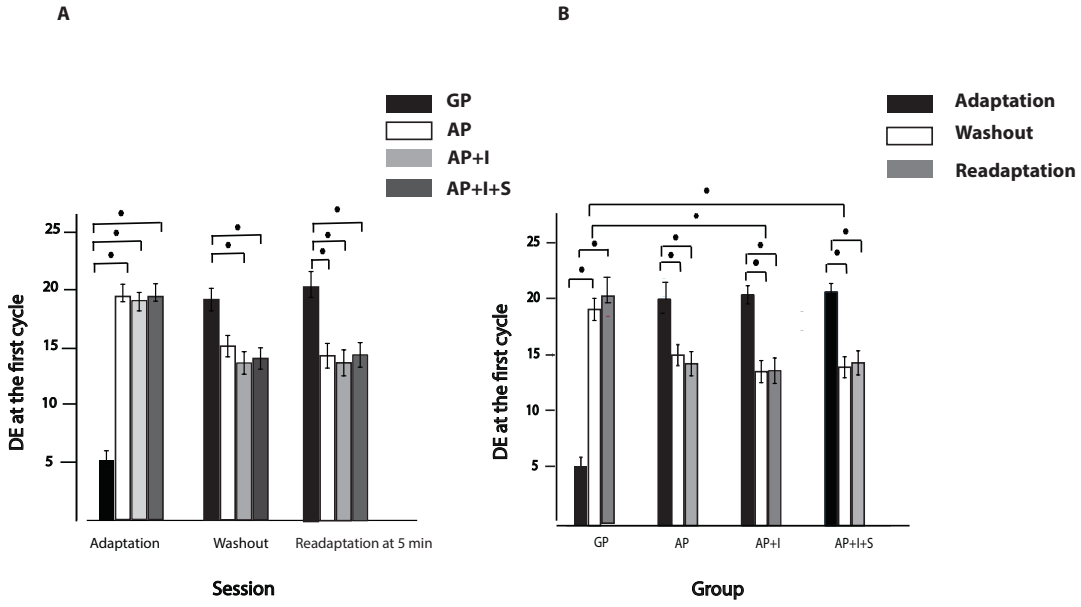

Fig 2.4: A, The change in DE at the first cycle for each group across the sessions (Adaptation, washout, readaptation-5 min). B, The change in DE at the first cycle for each session across the four different groups (GP, AP, AP+I, AP+I+S).

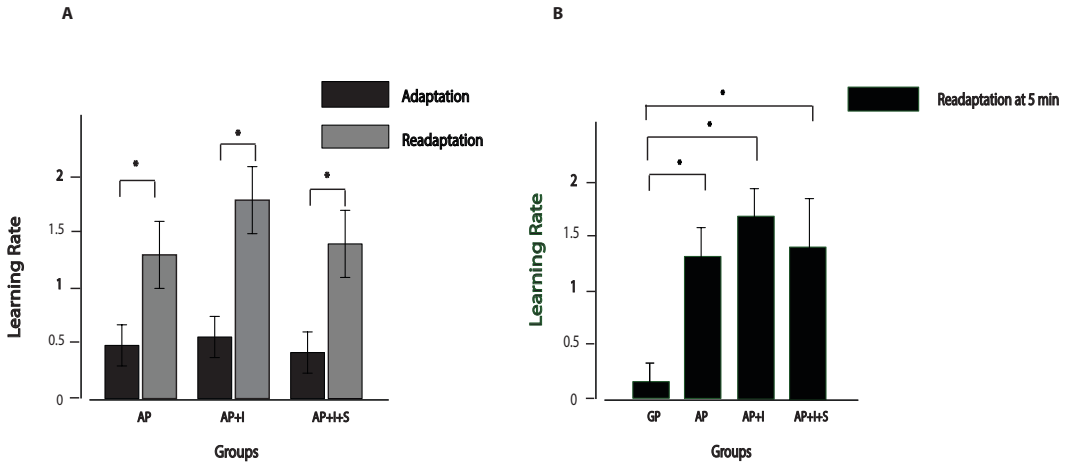

Fig 2.5: A, Rate of learning during adaptation and readaptation for the groups (AP, AP+I, AP+I+S). B, Difference in savings for all the four groups (GP, AP, AP+I, AP+I+S).

Furthermore, the results from the one-way ANOVA for learning rate revealed a significant difference between the groups (p=.003). Post hoc analysis revealed that the learning rate measured at 5 min were significantly different between the groups (GP vs AP, GP vs AP+I, GP vs AP+I+S) (p=.042, p=.002, p=.024) as shown in Fig 2.5B. These results from DE and learning rate analyses indicate that all the groups (AP, AP+I, AP+I+S) except the GP group exhibited savings. (Fig 2.4B, 2.5A). As shown in 2.5B and 2.4A, the introduction of perturbation (gradually vs abruptly) was the main factor that influenced the difference in the learning rate for the readaptation session at five minutes. The subjects in the GP group that learned to counteract the rotation gradually (i.e. rotation was introduced 1 degree per cycle) did not have savings at five minutes compared to the other three groups (AP, AP+I, AP+I+S) that learned to counteract the rotation that was introduced abruptly from the very first trial. It can be also observed from the savings data that awareness of perturbation (AP+I) or incorporating a strategy to counteract the perturbation (AP+I+S) did not

make a significant difference in five minutes savings. Therefore, our results suggest that incorporating strategies or being aware of the rotation does not have a beneficial effect on five minutes savings if the size of the perturbation is extremely small or less than 30 degrees (i.e., in our case 24 degree).

Discussion

Previous studies have shown that the involvement of explicit components during a visuomotor adaptation task results in better savings (Morehead et al. 2015, Huberdeau et al. 2017). In this study, our aim was to investigate how different training methods incorporating varying degrees of explicit vs. implicit learning components could influence short-term savings (i.e., 5 min after washout) following visuomotor adaptation. This was done by comparing the learning rates and DEs of four subject groups that varied in terms of their adaptation protocol: 1) gradual perturbation (i.e., most implicit), 2) abrupt perturbation, 3) abrupt + instruction, and 4) abrupt + instruction + strategy (i.e., most explicit). The experiment consisted of four sessions: baseline, adaptation, washout, and readaptation. After the experiment was complete, all the participants were surveyed regarding the usage of cognitive strategy and awareness with the help of an awareness questionnaire (Appendix C). The responses from each participant have been shown in Appendix E under Experiment 1 and 2. The responses from the participants suggested that the most implicit group (GP) and more implicit group (AP) were completely unaware of the rotation, whereas the data from the more explicit group (AP+I) and most explicit group (AP+I+S) indicated that the participants were completely aware of the 24-degree CCW rotation, and they used strategies to counteract it. Therefore, the surveyed responses obtained from the awareness questionnaire indicates that the participants in the four groups differed in terms of incorporating the implicit and explicit components during the adaptation session.

The results for both learning rates and DEs have shown that incorporating varying levels of implicit and explicit learning components in visuomotor adaptation have a differential effect on immediate savings (five minutes) between the gradual perturbation group and the three abrupt-perturbation groups. These results are partially in agreement with our initial hypothesis that the involvement of more explicit components during visuomotor adaptation would evoke greater short-term savings measured immediately following initial training. Even though there was an advantage for two explicit groups (AP+I, AP+I+S) in terms of savings (DE, lr) compared with the GP group, the differences between them, or among all three abrupt-perturbation groups, failed to reach a significance level. Given that most of our subjects in the AP group were unaware of the rotation condition, our findings suggest that increasing the degree of explicitness regarding the visuomotor rotation condition does not necessarily lead to greater short-term savings.

According to the explicit strategy account, faster adaptation observed during relearning of the rotation, is thought to be merely due to the recalling of an aiming strategy (Morehead et al. 2015, Taylor et al. 2014). In a study conducted by Morehead et al. (2015), participants underwent readaptation session immediately to examine whether they employed an aiming strategy upon encountering the visuomotor rotation again. The researchers concluded that the savings observed following visuomotor adaptation were a result of action selection prompted by the recollection and utilization of the aiming strategies acquired during the initial training phase. Even though our results demonstrated that savings were increasingly higher for groups that involved more explicit learning components compared to the most implicit group (GP), it should be taken into consideration that the rotation size incorporated in our study was only 24 degrees. According to the explicit strategy account, forming an aiming strategy requires larger perturbation (>30 degrees) and therefore larger salient errors (Morehead et al. 2015, Taylor et al. 2014). Morehead et al.

(2015) investigated whether participants exhibited savings with perturbations of varying magnitudes and reported that savings were dependent on size of the perturbation with most savings for the group that learned to counteract the perturbation magnitude of 60 degrees and less savings for smaller magnitude perturbations (i.e. 15 degrees and 30 degrees). In their study, the participants failed to show savings for perturbation of 30 degrees and less. However, several studies (Krakauer et al. 2005, Huberdeau et al. 2015; Herzfeld et al. 2014; Haith et al. 2015, James et al. 2022, James and Wang, 2023) have reported significant savings even for smaller, less noticeable perturbation sizes (i.e., 30-degree perturbation). Also, our current results demonstrated that participants in the AP group who learned to counteract a 24-degree counter-clockwise rotation exhibited similar savings as compared with the other groups that involved more explicit components during initial learning. In fact, the questionnaire outcomes also indicate that these subjects were not aware of the rotation condition and provides further support that explicit strategies were not used by AP group. Since we observed savings in the AP group (more implicit), it is reasonable to argue that there are mechanisms other than explicit aiming strategies that underlie savings associated with visuomotor adaptation.

The results from experiment 1 indicated no savings for the gradual perturbation group in which participants learned to counteract the rotation that was gradually increased during the adaptation session. In other words, the mean DE at cycle one for adaptation session was not significantly different from the mean DE at cycle one for readaptation session at five minutes. This is in accordance with previous studies that failed to demonstrate savings for similar gradual perturbation protocols when examining immediate savings (Herzfeld et al. 2014, Yin et al. 2020). The absence of savings for the gradual group where the rotation was introduced gradually can be explained with the two popular accounts of savings: namely the error sensitivity account and the

explicit strategy account. According to the error sensitivity account, exposure to salient errors during multiple trials in the adaptation session is crucial for faster relearning or savings (Huang et al. 2011; Braun et al. 2009; Herzfeld et al. 2014; Kobak et al. 2012). Since gradually introducing perturbations of smaller magnitude doesn't allow the participants to detect any large errors to learn from, the gradual group is expected to not show savings. On the other hand, the absence of savings in the gradual group can also be explained with the explicit strategy account. Experiencing extremely small errors while counteracting gradual rotations does not require, or cause, participants to incorporate any explicit aiming strategies, and thus cannot produce savings (Morehead et al. 2015, Taylor et al. 2014). Both theories offer partial explanations for our findings across all four groups; however, neither theory fully accounts for our results. For example, if savings in VMA is solely due to the sensitivity towards the history of errors made during adaptation, the AP group should have demonstrated larger savings than the other two groups (AP+I, AP+I+S). But all the three groups (AP, AP+I, AP+I+S) had similar savings at five minutes both in terms of DE and learning rate. Similarly, if forming and recalling the explicit strategies determines the amount of savings, then the AP+I and AP+I+S groups should have performed better than the implicit groups (GP, AP). That was also not the case in our study.

It is possible that the participants in the explicit groups (AP+I, AP+I+S) might not have used strategies while learning to counteract the perturbation. However, the data from the awareness questionnaire suggest otherwise. The responses from the participants in the groups AP+I and AP+I+S suggested that they were aware of the 24-degree counter-clockwise (CCW) rotation and they used strategies while moving the cursor towards the target (Appendix E). Moreover, the participants in the AP+I+S group responded that they used the strategy provided by the experimenter that was to aim in the direction that is rotated 24 degrees clockwise (CW) relative to

the target location. Furthermore, the results from the washout session in our study also supports the claim that the subjects have used explicit learning components while learning to counteract the perturbation. When one first adapts to a novel visuomotor condition and then performs reaching movements with no cursor rotation, the subject's arm moves in the direction opposite to the direction in which their arm moved upon initial exposure to the novel condition. This phenomenon, termed as "aftereffects", is observed as larger errors in the washout session. The presence of larger aftereffects indicates the formation of an internal model and is generally considered as a measure of implicit adaptation. As observed from the aftereffects in the washout session, a significant difference in the aftereffects has been observed between GP group vs AP+I group, as well as GP group vs AP+I+S group, with larger aftereffects for GP group (most implicit). The smaller aftereffects observed in the groups AP+I and AP+I+S must be due to the involvement of strategies or awareness in the explicit groups (Fig. 2.3). In fact, the awareness questionnaire outcomes corroborate this point, indicating that all the participants in the explicit group were aware of the perturbation present in the adaptation session. Collectively, these findings regarding aftereffects and results from awareness questionnaire indicate that the participants in the explicit groups employed instructions and cognitive strategies to counteract the cursor rotation, potentially interfering with the recalibration process, and consequently, demonstrated minor aftereffects.

The role of explicit awareness in visuomotor adaptation savings is still a controversial debate. Even though there are a few studies that support the significant role of explicit learning in VMA and savings (Taylor et al. 2014, Morehead et al. 2015, Huberdeau et al. 2017), several other studies suggest that explicit awareness can influence the initial adaptation rate (Benson et al. 2011; Yin et al. 2020**)** but neither short-term nor long-term savings. In a recent study, Yin and colleagues investigated whether formation of an explicit strategy is a prerequisite for savings in VMA. The

findings from the study indicated robust savings for the group that implicitly learned the rotation from sensory prediction errors. Therefore, the researchers concluded that savings in VMA is due to the interaction between explicit and implicit learning components that is based on the available feedback and initial adaptation protocols. However, it should be taken into consideration that in their study (Yin et al. 2020), the participants in the gradual perturbation group were asked to report their aiming direction before making the actual movement. This instruction could potentially increase participants' awareness of the perturbation, challenging the assertion that the gradual rotation condition exclusively involved implicit learning components. Nevertheless, Yin and colleagues quantified the contribution of explicit and implicit learning components in the gradual report group using verbal reports of aiming, as described by Taylor et al. (2014). In Taylor et al.'s studies, explicit and implicit learning in a visuomotor adaptation paradigm were differentiated by asking participants to verbally report their aiming direction while adapting to a visuomotor rotation. The authors observed distinct time courses for explicit and implicit components, which were completely dissociable. Using verbal reports of aiming, Yin et al. (2020) demonstrated that the increased savings observed in the gradual report group in their study were primarily attributable to contributions from implicit learning components, even when participants were instructed to report the aiming direction, which typically evokes explicit learning components.

However, there has been a wide concern regarding the verbal report of aiming task used by Taylor and colleagues (Taylor et al. 2014, Morehead et al. 2015). Several studies have raised the concern that the verbal reporting method may overestimate the explicit learning component in VMA. In one study, de Brower and colleagues (2018) observed eye fixation before every reaching movement and compared these results to the verbal aiming report. They found that the reported aiming directions closely matched the eye fixation for most of the reaching movements. However,

the verbal reporting results enabled the participants to fixate their eyes toward the re-aiming direction at a faster pace which led to a better adaptation rate (de Brower et al. 2018). Similarly, Leow et al. 2017 have also suggested that reporting the aiming direction (Taylor et al. 2014) while counteracting a 30-degree rotation increases the explicit learning component thereby suppressing the extent or persistence of implicit learning. Therefore, the evidence from these studies suggests that the aiming report method overestimates explicit learning during VMA. Therefore, it is not a reliable method to quantify explicit and implicit learning components in VMA. Unlike the results from our study, other studies have reported faster adaptation rate when participants use strategies to counteract the perturbation (Benson et al. 2020, Yin et al, 2020). However, incorporating strategies was not beneficial in increasing the adaptation rate in the AP+I and AP+I+S groups in our study. The discrepancy in our findings might be due to the difference in the experimental setup in other labs, or due to the nature of instruction provided to the participants. Apart from these factors, the small rotation size employed in our study might have also contributed to the lack of faster adaptation in the explicit groups. It has been suggested that participants may initially use strategies to compensate for salient (most noticeable) perturbations in sensorimotor adaptation tasks (Taylor 2014, Wei and Kording 2009). Therefore, it is possible that the small rotation size employed in our study was not sufficient to produce a faster adaptation by using an aiming strategy.

In recent times, there has been an increasing focus on exploring the dynamic interaction between implicit and explicit learning during visuomotor Adaptation. A pivotal aspect supporting this concept stems from investigations into the role of the cerebellum in visuomotor adaptation. Research has revealed that the degree of rotation error correlates with neural activity in the cerebellum, suggesting its involvement in error correction processes (Seidler et al., 2004; Ogawa et al., 2006). Dysfunction in the cerebellum has been linked to challenges in recalibration among

individuals with cerebellar ataxia, despite their ability to make error corrections within trials (Hashimoto et al. 2015; Tseng et al. 2007; Mazzoni et al. 2006). However, recent findings do not support the idea that the cerebellum is the structure exclusively for implicit learning. In their study, Butcher et al. (2017) illustrated that cerebellar impairments were not only associated with diminished aftereffects but also with a decrease in strategic control. This recent evidence highlights a complex interplay between implicit and explicit learning, challenging the conventional notion that the cerebellum is the central structure dedicated solely to implicit learning.

While we agree with the conclusions from other studies that the interaction between explicit and implicit learning components are crucial for visuomotor adaptation (Butcher te al 2017, Yin et al. 2020, Gibo et al. 2013), these interactions alone could not provide a clear explanation regarding the phenomenon of short-term savings associated with visuomotor adaptation. Certainly, besides explicit and implicit learning components, there are additional motor learning mechanisms such as reinforcement learning and use dependent learning that contribute significantly to the retrieval of motor memory over time ((Diedrichsen et al., 2010, Bu¨ tefisch et al., 2000, Wang et al. 2015, James et al. 2022, Huang et al. 2011). Huang et al. (2011) demonstrated that savings are elicited when the imposed rotation direction required an adapted solution aligning with a previously successful hand movement direction. This underscores the crucial role of reinforcement learning in facilitating savings. Several studies have also reported the involvement of use dependent learning in visuomotor adaptation savings. For example, in one of the studies, Diedrichsen and colleagues demonstrated that the direction of the reaching movements was biased towards the direction in which the force channel was shifted. This bias in the movement persisted even after the removal of the force channel. Therefore, researchers suggested that since no visual feedback, such as reward or punishment, was available during this condition, it was use-dependent,

rather than reinforcement, learning that influenced the behavioral output during subsequent movements. However, our data from GP and AP group can be explained by the concept of reinforcement learning. According to this idea of reinforcement learning, it is expected not to observe savings for a gradual perturbation. This is expected as it does not give the participants a chance to reinforce the successful actions with learning because of the extremely small size perturbation (1 degree per cycle) as well as due to the variable rotation size in each cycle. Similarly, the same idea of reinforcement learning can be used to explain our findings where we observed savings in the AP group that learned to counteract 24-degree CCW rotation with no explicit instruction or strategies. By introducing the perturbation abruptly from the very first trial (24 deg CCW rotation), the participants might have mapped the behavioral output to a successful hand movement direction. In this light, we would like to extend our thoughts that savings in visuomotor adaptation cannot be explained solely with explicit/or implicit learning components. In fact, there are additional mechanisms that are associated with a memory of successful action /or repetition of movement that give rise to retention of motor memories in short-term.

In summary, we have demonstrated that involvement of explicit components during a visuomotor adaptation task does not produce better short-term savings. Our results suggest that incorporating varying levels of implicit and explicit learning components while learning to counteract a 24-degree visuomotor rotation has a differential effect on immediate (5 min.) savings between the gradual-perturbation (i.e., most implicit) group and the three abrupt-perturbation (i.e., less implicit, more explicit and most explicit) groups, but with no significant difference among the three abrupt-perturbation groups. Even though there was an advantage for explicit groups (AP+I, AP+I+S) in terms of savings (DE, lr) compared with GP group, the differences between them, or among all three abrupt-perturbation groups, failed to reach a significance level. Based on the

responses from the questionnaire, most of our subjects in the AP group were unaware of the rotation condition and they were still able to generate savings. Our findings suggest that increasing the degree of explicitness regarding the visuomotor rotation condition does not necessarily lead to greater short-term savings. Collectively, our findings suggest that increasing the level of explicitness while learning to counteract a smaller size perturbation (i.e., 24 deg) does not lead to better short-term savings. However, introduction of perturbation (i.e., gradual vs abrupt) has a differential effect on savings associated with VMA. Although, we agree that using strategies and instructions are definitely advantageous for short-term retention of adaptation memories (Morehead et al.2015), it should be taken into consideration that the interaction between the implicit as well as explicit components during initial learning/ or relearning can vary based on several factors like adaptation protocol, available feedback, and size of the perturbation. As we are currently in short of a paradigm that can measure these components directly, we cannot clearly define the intriguing relationship between explicit and implicit learning component in VMA. Based on the results from our study and other studies (Morehead et al. 2015, Taylor et al. 2014), it can be concluded that participants require salient perturbation (perturbation size >= 30) to make use of strategies efficiently and contribute to better savings during relearning trials. Therefore, we would like to extend the idea by other researchers that there are additional model free learning mechanisms that can lead to increased relearning/ or savings in visuomotor adaptation tasks that involves perturbations of extremely small sizes. As much as we understand the crucial role of explicit/implicit interaction for adaptation, our results suggest that distinct learning mechanisms (explicit/or implicit learning, reinforcement learning and use dependent learning) are lumped together and make significant interactions between each other that eventually contributes to short-term retention of visuomotor memories. The amount with which these components interact with

each other depends on various factors like perturbations size, nature of the instruction, experimental setup etc.

Chapter 3: The effects of training methods with varying degrees of explicitness on long-term savings following visuomotor adaptation

There is no study to date, that has investigated whether the retention of long-term motor memories in visuomotor adaptation learning varies as a function of explicit or implicit components incorporated during initial training. In this chapter, I have conducted a study to determine the beneficial effects of training methods with varying degrees of explicitness on long-term savings following visuomotor adaptation. The results from the above study will help us understand the potential impact of various training protocols on long-term retention of motor memories.

Introduction

In 1900, psychologists Georg Elias Muller and Alfons Pelzecker proposed that memories can initially be in a pliable state and slowly adapt into a more stable state with time (Muller and Plizecker 1990, Lechner et al. 1999). According to the motor learning literature, motor memory consolidation refers to a behavioral marker for stabilized motor representations that leads to an automatic motor behavior resistant to interference. Typically, the consolidation process involves two different phases: a short-term consolidation processes, which operate over a period of seconds to hours after the initial learning of the motor skill and a long-term consolidation process that is mediated over a period of days to months after initially learning the motor skill. The former involves the local cellular mechanisms that drives long term potentiation (LTP) whereas the latter one is driven by neural reorganization (Goedert & Willingham 2002, McGaugh 2000, Dudai 2002) Understanding the factors that lead to stable motor memories can provide deeper insights into the neural mechanisms responsible for long-term motor memory retention. Despite the scarcity of research specifically addressing the long-term retention of motor skills, a few studies have observed the sustained preservation of motor memory for as long as eight years (Draganski et al.

2004, Hill, 1934, Park 2014, Swift, 1910, Rodrigue et al. 2005). In Rodrigue et al.'s study (2005), the researchers showed the retention linked with a mirror tracing task even after a five-year gap from the initial training (Rodrigue et al., 2005). Healthy young adults exhibited the ability to maintain their performance in terms of speed and accuracy during a readaptation session conducted five years after their initial learning (Rodrigue et al., 2005).

Although visuomotor adaptation (VMA) was previously considered to be mostly implicit (Izawa et al. 2012, Mazzoni et al. 2006, also see Wang et al. 2019), recent findings emphasize the potential role of explicit cognitive processes in VMA and savings. For example, adaptation occurred faster with a reduction in initial errors when participants were explicitly instructed about the visual rotation (Benson et al. 2011). Similarly, evidence from other studies suggest that action selection evoked from remembering and using the aiming strategies developed during the initial training contributed to faster relearning as well as savings in VMA (Morehead et al. 2015, Haith et al. 2015). Haith and colleagues demonstrated there were no savings when participants were forced to start the reaching movements rapidly. The researchers concluded that a smaller preparation time prevented the subjects from using explicit cognitive strategies and therefore contributed to lack of savings. The results from the above studies support the view that re-aiming strategies are driven by cognitive processes, and therefore, savings in motor adaptation are driven solely by the recall and retrieval of explicit strategies. It has been reported that early stages of adaptation and second day memory retention activate dorsolateral prefrontal cortex and bilateral Inferior Parietal lobe (IPL). These areas are crucial for cognitive control. Collectively, these findings suggest cognitive processes (which may or may not be explicit in nature) activated during the early learning stages of adaptation are important for generating short-term savings. However,

it is still unknown whether similar explicit contributions play an equivalent role in long-term savings.

A few studies have examined long-term savings of motor memory with sensorimotor learning paradigms (Seidler et al. 2017, Della Maggiore and McIntosh 2005, Landi S et al. 2011). These studies have consistently reported significant motor memory retention when participants were tested one day (Seidler et al. 2017), one month (Della Maggiore and McIntosh 2005) and even after one year (Landi S et al. 2011) of initial training. Previous work has suggested that participants exhibited long-term savings after training for one week with a complex optical rotation adaptation task (Landi et al. 2011). Furthermore, one week of intensive training induced changes in the neural network connections between the anterior cerebellum, the contralateral posterior parietal cortex (PPC) and the Primary Motor Cortex (M1) (Landi et al. 2011, Della- Maggiore and McIntosh 2005). One week of training with the same visuomotor adaptation paradigm also produced enlargement in the gray matter volume along with changes in the white matter functional anisotropy corresponding to the hand area of the contralateral M1. Moreover, an increase in the volume of gray matter measured immediately after one-week of training predicted there would be faster adaptation that was observed in the participants one year after initial training (Landi et al. 2011). Clearly, the evidence from the above studies suggest how well motor training paradigms can impact long-term behavior by producing functional and structural changes in the brain that are important for cognitive control.

While recent evidence from the literature emphasizes the crucial role that the cognitive components play in long-term retention of motor memories, the role of unconscious learning cannot be neglected. Supporting evidence regarding the role of implicit learning for long-term retention comes from the field of aging research (Heur et al. 2011, Rodrique et al. 2005). As

suggested by numerous studies, aging is accompanied by lower initial adaptation rates due to poor explicit control. However, the consolidation of motor memories after motor skill acquisition has been reported to be intact in older populations. In a 5-year follow-up study done by Rodrigue et al. (2005)**,** older adults were able to retain a learned behavior for a mirror tracing task. However, the same study reported that the magnitude of long-term savings was significantly lower in older populations than their younger counterparts. Additional studies on aging (Seidler, 2007, Bock and Schneider, 2001) provide further evidence that long-term savings are associated with implicit learning. However, it is still unknown whether varying the level of implicit and explicit learning components in a visuomotor adaptation can have a beneficial effect on learning rate, savings, or long-term memory retention.

Accordingly, whether or not to involve the cognitive strategies (explicit control) can be determined by the training environment, nature of the task and awareness of the perturbation. As described in the previous chapter, the level of explicitness in a motor task can be reinforced by several factors such as color cues, providing instructions, verbal aiming reports, and the nature of perturbation introduction (i.e., gradual, abrupt) during motor adaptation. The participants learned faster and had stronger aftereffects when the rotation was introduced abruptly compared to gradually learning the rotation in small increments (Kager and Vidal, 1997). Similarly, manipulating the visual feedback with color cues and increasing the awareness of perturbation during initial learning had a beneficial effect on savings (Vandervoorde, K. et al., 2019, Morehead et al. 2015). It has also been suggested that size of the perturbation has a differential effect on visuomotor adaptation saving, with more savings for larger perturbation sizes (Morehead et al. 2015). In conclusion, the evidence from these studies suggests that reinforcing or adding explicit components during visuomotor adaptation learning can differentially influence the initial learning

and savings. Most of the previous work has focused on tasks with visuomotor rotations of larger magnitudes (45-degrees or more), manipulating the visual feedback, short-term memory retention, and dual tasks. To our knowledge, none of the studies have investigated whether varying the degree of the explicitness in the adaptation training incorporating smaller rotation magnitudes has a differential effect on the long-term retention of motor memories (one week, one month).

Thus, the objective of the second aim was to determine the beneficial effects of training methods with varying degrees of explicitness on long-term savings following visuomotor adaptation. This was achieved by comparing four subject groups that varied in terms of their training protocols: gradual perturbation (most implicit), abrupt perturbation, abrupt + instruction, and abrupt + instruction + strategy (most explicit). The learning rates and savings (one week and one month after initial adaptation) were evaluated in all the subject groups. All participants who participated in Aim 1 experiment also participated in the Aim 2 experiment. Based on the belief that implicit learning is thought to be associated with long-term savings (Willingham et al. 1997), we hypothesize that the involvement of more implicit components during visuomotor adaptation will evoke greater long-term savings measured one week and one month after initial training.

Experiment 2

Materials and Methods

Participants

A total of 40 (10 participants per group) neurologically intact right-handed individuals participated in Experiment 2. The participants tested in Aim I served as the participants in Aim II.

Apparatus

The data acquisition system used for Aim I was used for collecting data for Aim II (Fig 3.1).

Experimental Protocol

In general, the four groups of participants tested in Aim I was retested to assess long-term savings following initial visuomotor adaptation. The participants were asked to return to the lab at two different time points: 1) one week after the initial training; 2) One month after the initial training. Same as in Aim I, the participants performed rapid reaching movements with the right arm from a starting circle to one of four targets (10 cm away from the start circle). They were instructed to move the cursor to each target rapidly and as straight as possible in response to the appearance of the target, and then bring the cursor slowly back to the starting circle (Fig 3.1).

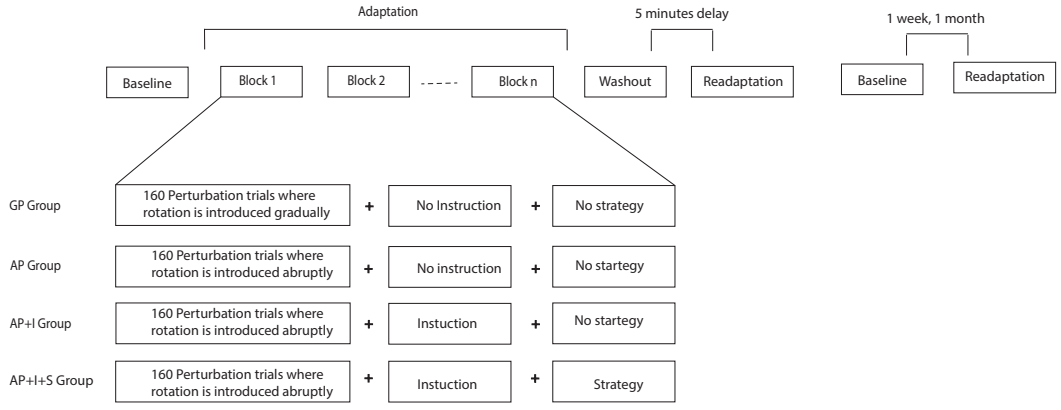

Fig 3.1: Experimental Protocol: The adaptation session had forty cycles and each participant performed the adaptation session differently depending on the groups assigned. During the second (i.e., 1 week) and third visits (i.e.,1 month), all the participants performed a baseline session (10 cycles) followed by a readaptation session where the rotation was introduced abruptly for the entire session (40 cycles).

During each of the two visits, all the participants performed two sessions: baseline (40 trials) and readaptation (160 trials). The *baseline* session had 10 cycles of reaching movements where each cycle consisted of four consecutive trials corresponding to the four targets that were

placed radially around the starting circle. Veridical position of the index fingertip was provided to the participants by a cursor displayed on the screen, so that the participants could familiarize with the general reaching task without visuomotor perturbation. In the *readaptation* session, all the participants were assigned to the same group they were assigned in Aim I (GP; AP; AP+I; AP+I+S). All participants adapted to the 24-degree CCW rotation condition in which the cursor was rotated 24 degrees from the first trial, with the following instruction: "A target will appear on the screen. Your task is to hit the target as accurately and straight as possible."

Data Analysis

Direction Error (DE) was calculated as the measure of performance. DE is defined as the angular difference between a vector from the starting circle to a target and another vector from the hand position at movement start to that at peak arm velocity. The *rate of learning* in the adaptation and readaptation sessions (5 min, 1 week and 1 month) was calculated by fitting DE values from every single subject within each group to an exponential function:

$$DE(n) = A*\exp(-R*n) + B;$$

where A is a constant, n is the trial number, and R is the estimated value of the learning rate.

For statistical analysis, separate analyses were done in the following ways. The DE data was subjected to a repeated-measures ANOVA with group as a between-subject factor and cycle (First cycle of adaptation, washout, readaptation session at 5 min, readaptation session at 1 week, readaptation session at 1 month) as a within-subject factor (Huberdeau 2015a, Huberdeau 2015b, Yin eta l. 2020, Haith 2015). To compare the learning rates for all the four groups during the three-readaptation sessions (5 min, 1 week, 1 month), the learning rate data was subjected to a repeated-measures ANOVA, with groups (GP, AP, AP+I, AP+I+S) as a between-subject factor and session

(readaptation at 5 min, readaptation at one week and readaptation at one month) as a within-subject factor. For significant effects, post hoc comparisons were done (Tukey's tests for between-group comparisons, Fisher's LSD tests for within-group comparisons). The alpha level was set at 0.05 for all comparisons. In addition to the statistical tests, we also collected the awareness information for each subject using the awareness questionnaire provided in Appendix C. The details regarding the awareness questionnaire have been explained in Chapter 2.

Results

The changes in performance across the cycles during the adaptation, washout and all the three readaptation sessions (5 minutes, 1 week, 1 month) for each group are shown in the Figure 3.2. All the four groups in our study were different in terms of the involvement of explicit and implicit components in the adaptation session. GP group (most implicit) adapted to a 24-degree counterclockwise (CCW) rotation condition in which the degree of rotation was gradually increased one degree per cycle whereas AP group (more implicit) adapted to a 24-degree CCW rotation condition in which the cursor was rotated 24 degrees from the very first trial. Similarly, AP+I (more explicit) adapted to 24-degree CCW rotation that was introduced from the very first trial soon after they were given instructions that made them aware about the cursor rotation. On the other hand, AP+I+S group (most explicit) were given the instruction regarding the presence of perturbation along with the strategies requires to counteract the abruptly introduced 24-degree CCW rotation. All the groups performed in a similar manner during the readaptation session at one week and one month with no difference among savings between the groups (Fig 3.2). The savings at five minutes was better than savings at one week and one month for the groups who experienced the abrupt condition (AP, AP+I, AP+I+S) but not for the GP group that adapted to a gradual rotation.

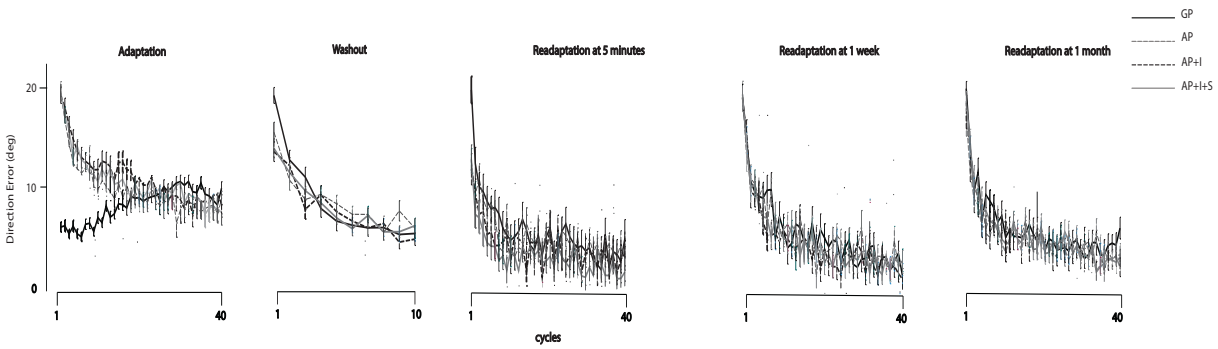

Fig 3.2: The change in Direction Error (DE) across the cycles for Adaptation, Washout and Readaptation sessions (5 min, 1 week, 1 month). Every data point on the x axis represents the mean value of one cycle across the participants in each group.

The repeated-measures ANOVA with the data for the DE (First cycle) from the adaptation, washout and all three readaptation sessions (5 min, 1 week, 1 month) indicated a significant interaction effect between cycle and session ($p<.001$) which suggest that the pattern of performance changes across the cycles varied among the four groups (Fig 3.3). With regards to the DE for readaptation session at 5 min (Fig 3.3A), there was a significant difference between group GP and the other three groups (GP vs AP: $p=.002$, Group GP vs Group AP+I: $p<.001$, Group GP vs group AP+I+S: $p<.001$). The results from the washout session (1st cycle) indicated a significant difference between group GP vs group AP+I and group GP vs group AP+I+S which indicates the aftereffects were different between GP group and the other two groups. However, the DE from the first cycle of readaptation sessions at one week and one month were not different across the four groups. Therefore, the results from DE data in our study indicate that varying the level of implicit and explicit components during adaptation session do not have a differential effect on long-term savings at 1 week or 1 month post initial training.

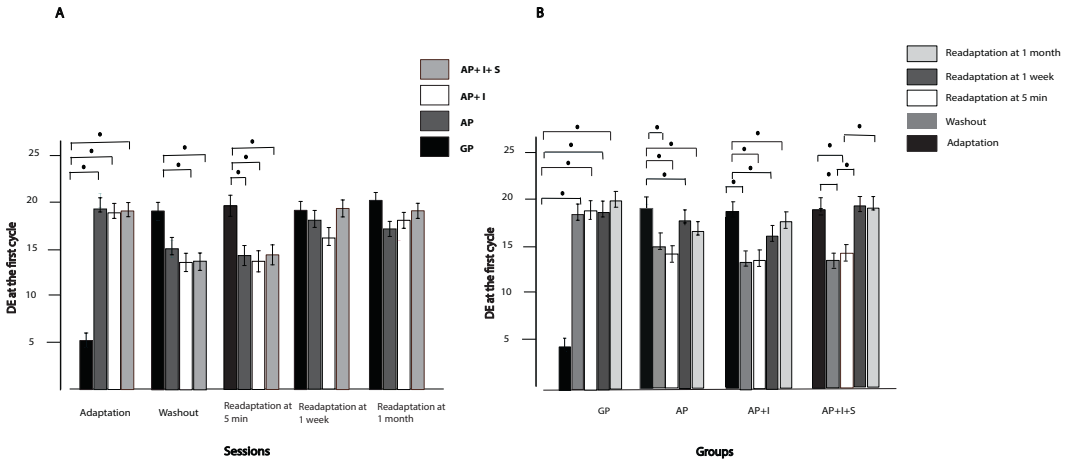

Fig 3.3: A, The change in DE at the first cycle for each group across the sessions (Adaptation, washout, readaptation at 5 min, readaptation at 1 week, readaptation at 1 month). B, The change in DE at the first cycle for each session across the four different groups (GP, AP, AP+I, AP+I+S).

The repeated measures ANOVA for the learning rate were similar with the DE data with a significant interaction effect between learning rate and groups (P=.021). The savings in terms of learning at 5 min were significantly different between group GP and other three groups (Group GP vs Group AP: p=.009, Group GP vs Group AP+I: p<.001, Group GP vs Group AP+I+S: p=.005) which was like the results from the DE data (Fig 3.4B). The results from the repeated-measures ANOVA also suggested a significant difference in savings at 1 week in terms of learning rates for group GP vs group AP+I+S (p=.048) and group AP+I vs group AP+I+S (p=.014). The group that incorporated more explicit components (AP+I+S) performed better in relearning the rotation at 1 week compared with Groups GP and AP+I (Fig 3.4B). The post hoc also revealed that savings measured at 5 min and 1 week were different for the groups AP and AP+I (P=.009, P<.001) (Fig 3.4A). Similarly, post hoc also revealed that the savings at five minutes and one month were different for AP+I (P=.002) further suggesting that relearning rate five minutes post initial adaptation was higher than the relearning rate 1 week and 1 month (Fig 3.4A).

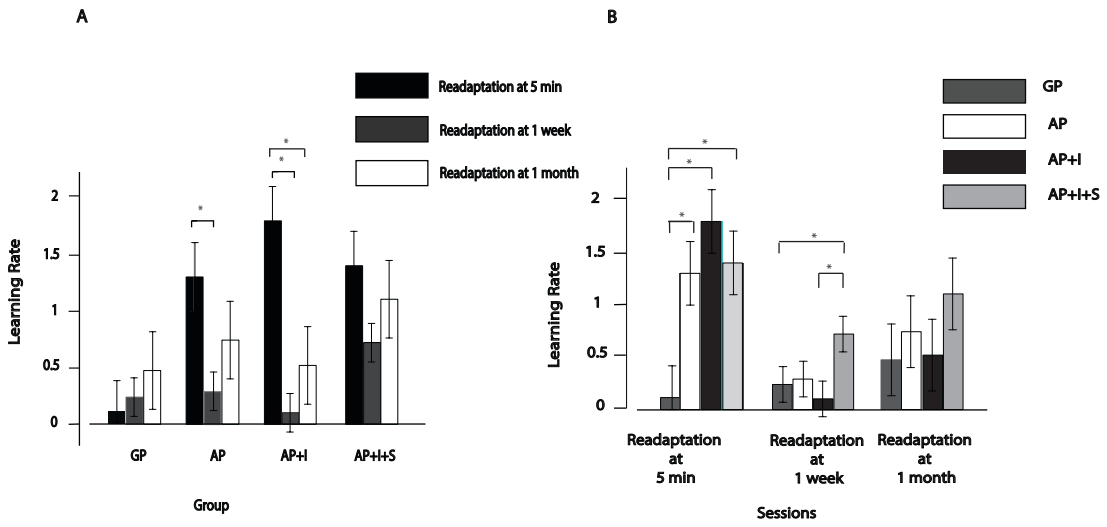

Fig 3.4: A, Rate of learning during adaptation and readaptation for the groups (AP, AP+I, AP+I+S). B, Difference in savings for all the four groups (GP, AP, AP+I, AP+I+S).

The responses from the awareness questionnaire that was used to assess the awareness of the rotation condition is shown under Experiments 1 and 2 in Appendix E. The details of the responses have been provided in Chapter 2. In general, the responses from participants in the implicit groups (GP, AP) were unaware of the perturbation whereas the explicit group (AP+I, AP+I+S) participants indicated an awareness of the perturbation. The people in AP+I+S group also suggested that they used the strategy that was provided to them by the experimenter.

Discussion

Understanding how our brain learns new movements and store the memory of the learned movement for long-term retrieval is crucial for us. Recent studies have indicated the interaction of explicit and implicit learning components when subjects learn and relearn the same rotation after few minutes of initial learning (i.e., savings). However, the emphasis on the involvement of explicit components during savings were limited to immediate savings in most of the studies

(Morehead et al 2015, Huberdeau et al. 2017). While immediate saving is considered as an indicator of long-term retrieval of motor memories, we are yet to determine whether similar savings from explicit learning components exists long-term (1 week or more) for visuomotor adaptation. To determine the beneficial effects of training methods with varying degrees of explicitness on long-term savings following visuomotor adaptation, we compared the visuomotor adaptation savings in terms of DE and learning rate. For conducting this experiment, all the participants who participated in the first experiment (Aim 1) came back twice for their follow up visits (i.e., 1 week and 1 month after their first visit). During both the visits, every participant performed two sessions: baseline, and readaptation. As described in the discussion section of Chapter 2, we polled the participants regarding the usage of strategies and awareness with the help of an awareness questionnaire. The detailed responses collected from the participants in our study can be found in Appendix E. We have detailed the summary of responses from Appendix E in discussion section of Chapter 2. In summary, the data from the awareness questionnaire suggest that all the participants in our implicit groups (GP, AP) were unaware of the perturbation. The subjects in the explicit groups (AP+I, AP+I+S) demonstrated that they incorporated strategies to counteract the rotation in addition to being aware of the 24 deg CCW perturbation.

Our study provides supporting evidence that training methods incorporating varying degrees of explicitness has a differential effect on savings in terms of learning rate measured one week following visuomotor adaptation with no difference between the groups one month post training. The results from experiment 2 have indicated that the rate of relearning (i.e., learning rate) at one week was higher for the group (AP+I+S) that incorporated most explicit components compared with the other two groups (GP, AP+I). However, the results from the learning rate data suggest that the relearning benefits of the AP+I+S group was not better than the relearning rate of

the same group at five minutes after adaptation. This further indicate that the memories are weakened over time (Fig. 3.4A). It can be observed that all the groups (AP, AP+I, AP+I+S) who counteracted the perturbation abruptly had better savings at five minutes compared to their savings at one week and one month after initial learning. Therefore, our findings further suggest that the motor memories associated with visuomotor adaptation can be consolidated in a short term, but the memories start to decay with time (Fig. 3.4B). In fact, the DE for all the three groups (AP, AP+I, AP+I+S) during the readaptations session at one month became same as their DE during initial adaptation session (Fig. 3.3A). In conclusion, when people adapt and readapt to 24-degree CCW rotation, they failed to demonstrate savings associated with VMA in the long term (1 week, 1 month). Even though, incorporating more explicit components during initial training can help the participants to relearn the cursor rotation faster than the adaptation session (i.e., savings at 5 minutes), the results from our study suggest that those learning benefits on immediate savings may not lead to better savings in the long-term.

The results (learning rate) from our long-term retention data suggest that the group that incorporated most explicit components (AP+I+S) exhibited faster relearning during their one-week visit, with no difference among the four groups (GP, AP, AP+I, AP+I+S) during their one-month visit. Moreover, the long-term savings measured at one week and one month were not better than their immediate savings at 5 minutes for all the three groups that learned to counteract the rotation abruptly (AP, AP+I, AP+I+S). Therefore, our study demonstrates that either varying the level of explicitness or implicitness while learning to counteract a smaller size perturbation (i.e. 24-degree CCW) or the manner in which the perturbation is introduced (gradual vs abrupt) leads to enhanced savings in the long-term. Apparently, long-term savings in VMA has not been extensively investigated. Previous work by Landi and colleagues has suggested that one week of training with

a complex optical rotation adaptation task produced changes in the neural network connections between the anterior cerebellum, the contralateral PPC and the M1, eventually leading to a long-term retention of the same task (Landi et al. 2011, Della- Maggiore et al. 2004). Moreover, the same one-week training also produced enlargement in the gray matter volume along with changes in the white matter functional anisotropy corresponding to the hand area of the contralateral M1. However, we did not observe similar long-term retention when the participants relearned the rotation one week or one month after their initial training with a VMA task**.** The discrepancy between our findings and those reported by others (Landi et al. 2011, Della- Maggiore et al. 2005) can be attributed to the difference in the frequency and intensity of the learning sessions incorporated in those studies. Landi et al. (2011) observed long-term savings of a complex optical rotation adaptation task after training the participants for one week with the same task. Similarly, Della Maggiore and colleagues trained the participants on a visuomotor tracing task spanning seven days, followed by long-term savings assessments conducted one month after the initial training session. The cumulative findings from these studies in the motor learning literature underscore the significance of prolonged practice sessions characterized by heightened intensity and frequency to sustain memory retention over the long term, spanning weeks, months, or even years. However, further investigation is warranted to explore whether manipulating the degree of explicitness during extended training periods may yield divergent outcomes. For instance, it remains to be seen if the most explicit training condition, conducted over a seven-day learning period, might exhibit the greatest degree of savings when reassessed one month later.

Even though our results indicate a difference in the readaptation (learning rate) measured at one week between the groups GP vs. AP+I+S ($p=.048$) and groups AP+I vs. AP+I+S ($p=.014$), the rate at which participants relearned the perturbation was not better than how they relearned the

rotation at five minutes. Therefore, there is no beneficial effect of incorporating explicit or implicit components during initial training that can lead to better retention of motor memories in the long term. Lately, savings have been suggested to be linked to the_explicit recall of both adaptation strategies and awareness by many researchers (Haith et al. 2015, Morehead et al. 2015, Huberdeau D.M. et al., 2017). Huberdeau et al. (2017) proposed that extended practice is not required to evoke savings since participants could generate faster relearning after just two adaptation trials. Similarly, in their study Haith and colleagues (2015) demonstrated that longer movement preparation time is essential for the expression of savings. In addition, Morehead et al. (2015) performed various experiments in which the participants were tested if an aiming strategy was evoked when the visuomotor rotation was reencountered. The researchers concluded that the savings generated after visuomotor adaptation training was due to an action selection evoked from remembering and using the aiming strategies developed during the first exposure to a perturbation. However, our data demonstrates that the above results may be true for short-term savings (i.e., measured immediately or in a day) after one learn to counteract the rotation initially. Therefore, these conclusions may not be generalized for the long-term retention of motor memories associated with visuomotor adaptation.

Aftereffects observed in the washout session after learning to counteract a visuomotor perturbation indicate the formation of an internal model. The results from the washout session in our study suggest small aftereffects` for the explicit groups (AP+I, AP+I+S) compared to the implicit group (GP) in which participants adapted to the 24-degree CCW rotation gradually. It can be observed from our results that there was a significant difference in the aftereffects between the GP group and AP + I group as well between GP group and AP+I+S group. This clearly suggests that the training incorporating more implicit components had a substantial influence on the

formation of internal model. The appearance of smaller aftereffects in the explicit groups (AP+I, AP+I+S) further supports our claim that the participants in the explicit groups in fact used explicit cognitive strategies to counteract rotation and recalibrated less than the implicit participants (Fig. 3.2). In fact, the awareness questionnaire outcomes corroborate this point, indicating that all the participants in the explicit group were aware of the perturbation present in the adaptation session. Collectively, these findings regarding aftereffects indicate that the participants in the explicit groups used instructions and cognitive strategies to counteract the cursor rotation that might have interfered in the recalibration process and therefore, demonstrated fewer aftereffects.

A possible explanation for the disparity between our results and those documented in other studies concerning aftereffects (e.g., Kagerer et al., 1997, Benson et al., 2011) among GP and AP groups could be attributed to the varying magnitudes of rotation utilized in the respective studies. While our study employed a 24-degree rotation, the studies mentioned above implemented a larger 90-degree rotation. The size of the rotation is thought to have a differential effect on the aftereffects developed after sensorimotor perturbation. The difference in reported aftereffects after undergoing training with gradual and abrupt 90-degree perturbations shrinked as the perturbation size became smaller (i.e. 30 degrees) (Heuer and Hegele, 2008) Individuals may not be aware of the nature of the perturbation when it is less than 30 degrees (Wang et al. 2011). However, an increase in perturbation size can increase the awareness of the rotation along with an elevated contribution from explicit learning components while learning to counteract the cursor rotation. In their study (Neville and Cressman 2018), investigated whether different sizes of rotational perturbations have a differential effect on visuomotor adaptation. The result from the study indicates that even though the implicit contributions to the learning did not vary with the rotation sizes, the awareness of perturbation for larger rotation sizes clearly influenced the contribution of explicit processes

during adaptation (i.e. higher explicit adaptation for larger size perturbations). Therefore, it can be concluded that the smaller rotation size incorporated in our study (i.e. 24-degree CCW rotation) might have caused the participants to be less aware of the perturbation during AP training trials. This could have further reduced the explicit contributions during adaptation trials and thereby eliminated the difference in the aftereffects between the AP and GP groups.

As observed in previous studies, we expected a higher long-term savings for the implicit group since long-term memory consolidation is associated with implicit nature of motor tasks (Huer et al. 2008, Kagerer et al. 1997). In contradiction to our hypothesis, the group that involved the most explicit components during initial learning had the higher readaptation rate one week post learning. Maksimovic et al. (2016) investigated whether the passage of time influenced implicit adaptation by measuring aftereffects after participants learned to counteract a 30-degree rotation. The researchers demonstrated that the aftereffects decayed from 24 degrees to seven degrees after a 24-hour delay period. Similarly, Neville and Cressman employed PDP procedure to differentiate explicit and implicit learning components in VMA (Werner et al. 2019, Neville and Cressman 2018) and suggested a decay of implicit adaptation in five minutes after learning to counteract the rotation (Werner et al. 2019, Nevil and Cressman 2018). Therefore, based on the above results, it may be possible that implicit adaptation is not as stable as explicit adaptation, which might have contributed to the lack of long-term savings in the GP group (most implicit group).

While numerous studies have documented immediate savings linked to visuomotor adaptation, it's noteworthy that not a single study has explored the influence of implicit or explicit components on long-term savings (e.g., one week or one month) in VMA. One of the reasons that we couldn’t find any advantage of using explicit strategies or instruction on long-term savings can be attributed to the size of the perturbation, lack of extended training sessions, and the use of

specific motor learning protocol. Typically, in visuomotor adaptation experiments, participants become more aware of the perturbation when the perturbations are larger. Incorporating larger perturbations enable the participants to notice the perturbations and use explicitly evoked strategies to counteract the rotation. It has been suggested that savings reflect the memory of the explicitly evoked adaptation (Morehead et al. 205, Haith et al. 2015, Huberdeau et al. 2017). In one of the studies, Neville and colleagues demonstrated that involving explicit learning components (i.e strategies) does not have any beneficial effect on adaptation when the cursor rotation is 20 degrees (Neville and Cressman 2018). However, the same study reported a significant difference in the adaptation rate between the groups using starategy and not using strategy when the cursor rotations were large (i.e. 40 deg., 60 deg.). Collectively, the evidence from these studies suggests icorporating smaller size perturbation (i.e. 24 deg. in our case) might not be beneficial to produce retention of visuomotor adaptation memories due to limited awareness and less involvement of explicit learning components. With regards to the intensity and frequency of training protocol, all the studies that has demonstrated long-term savings of VMA, had their participants undergo minimum seven days of training with the motor task (Landi et al. 2011, Della- Maggiore et al. 2005). The absence of long-term retention of VMA in our study might be also due to the lack of extended training session (i.e. weeks or months) before testing the participants again for savings. Similarly, it is hard to generalize the results from other motor learning protocols to our results as different training protocols (e.g. visuomotor tracking task, visuomotor adaptation, motor sequence learning) incorporate distinct neural mechanisms to learn and retain the motor memory in a long-term. In particular, learning and performing a sequence relies on Supplementary motor (SMA) and Basal Ganglia (BG) (Willingham 1997, Grafton et al. 1998) whereas learning kinematic transformation involving motor and perceptual information involves Posterior Parietal Cortex

(PPC), Primary motor Cortex (M1) and cerebellum (Landi et al. 2011, Ghilardi et al. 2000, Donchin et al. 2012, Karabanov et al. 2012). Therefore, demonstrating long-term savings in one training protocol might not be necessarily informative regarding a different one as each one involves unique brain structures while learning and retaining the task in formation.

In this study, we did an experiment to investigate the effects of varying the explicit and implicit learning components on long-term savings of visuomotor adaptation. Our results show that incorporating varying degrees of explicitness or implicitness while learning to counteract a small size perturbation (i.e., 24-degree counter rotation) doesn't have a beneficial effect on long-term savings of visuomotor adaptation that was measured one week and one month post initial learning. Although, the explicit group (AP+I+S) demonstrated faster relearning (i.e., learning rate) in the readaptation session at one week compared to the other two groups (GP, AP+I), their relearning rate at one week was not better than the relearning at five minutes**.** More specifically the learning rate for one month visit became similar to the learning rate at initial adaptation session for all the groups that learned to counteract the rotation abruptly (AP, AP+I, AP+I+S). Therefore, our results suggest that the motor memories decay over time and the beneficial effects of explicit or implicit learning components on short-term savings does not translate into long-term retention of motor memories. Although several studies support the role of explicit cognitive strategies and awareness on visuomotor adaptation savings, our results indicate that it cannot lead to long term retention of motor memories associated with extremely small size perturbations (24 deg. in our case). The inconsistencies in our results for not observing a beneficial effect of aiming strategies might be due to the perturbation size, the intensity of motor training protocol and complex interactions between explicit and implicit learning components. Few studies in the past have demonstrated that long term retention of motor tasks is associated with implicit nature of task.

However, we couldn't observe long-term savings for the groups that adapted to the perturbation implicitly without being aware of the 24-degree perturbation. Although, this may appear to be contradictory, recent studies have reported a decay in implicit adaptation within 5 minutes of learning to counteract the rotation (Werner et al 2019, Neville and Cressman 2018). As we are currently in short of a paradigm that can measure the contribution of explicit and implicit learning components in motor adaptation and savings, we cannot clearly define how these learning components make interactions based on the task requirements. In summary, our results, suggest that incorporating varying levels of explicit and implicit learning components while learning to counteract a 24-degree perturbation does not have a beneficial effect on long-term savings. Disparities in our findings compared to other studies in the literature can be attributed to the perturbation size, frequency of training protocol and specific motor learning protocol used in our study. Therefore, future studies should consider the above factors when they evaluate long-term savings associated with VMA.

Chapter 4: The effects of *training methods with varying degrees of explicitness and interference on memory consolidation following two opposing visuomotor adaptations*

It remains uncertain whether memory stabilization and interference occurs differently for training protocols involving varying degrees of implicit and explicit components. In this chapter, we sought to examine how the training methods with different combinations of explicitness and interference conditions would influence memory consolidation associated with visuomotor adaptation against anterograde and retrograde interference.

Introduction

Sensorimotor adaptation serves as a fundamental learning mechanism that enables humans to compensate for the disturbances in the environment (Cassady k et al. 2018). Like all other types of motor learning, the newly formed motor memories acquired via motor adaptation are susceptible to facilitation or interference depending on the congruency of learning (Krakauer, 2009). Facilitation of motor learning (i.e., savings) refers to a process of faster learning when exposed to a previously experienced perturbation. On the other hand, interference causes disruption of motor memories, which leads to impairment in future task performance. Interference normally occurs when two opposing visuomotor or force perturbations are learned in close succession (Krakauer et al., 1999, Miall et al.,2004). Interference can be either anterograde or retrograde. In a typical visuomotor research paradigm (A1-B-A2) in which individuals experience task A (A1) first (e.g., counterclockwise (CCW) rotation), then task B (e.g., clockwise (CW) rotation) soon after, the memory of task A (A2) is probed a few hours after the initial learning of both tasks. The interference is thought to be anterograde if initial learning of A (A1) interferes with the subsequent learning of B or if B interferes with relearning of A (A2) (Miall et al. 2004, Shadmehr et al. 1997, Sing and Smith, 2010). Conversely, retrograde interference occurs if B interferes with the memory

of A (i.e., measured during A2). It is to be noted that both anterograde and retrograde interference affects the performance in relearning of A (Sing and Smith, 2010).

The interference that occurs to the motor memories learned through motor adaptation can be either retrograde or anterograde as stated above (Krakauer et al. 2005, Shadmehr et al. 1997). Krakauer and colleagues (2005) performed a few experiments to investigate whether the interference between motor memories associated with conflicting visuomotor adaptation tasks were anterograde or retrograde in nature. The researchers observed that even after leaving a 24-hour time interval between the two tasks (i.e., A, B), interference persisted during the relearning session that was performed one week after initial learning of task A. To eliminate the observed interference to motor memory consolidation, the researchers performed another experiment in which two blocks of baseline trials as a washout session were inserted before every relearning session. It was evident from the results that the washout (unlearning) session masked the interference and successfully improved relearning (A2), one week after initial learning of A1. In addition to the above results, increasing the initial learning cycles from 33 to 66 cycles prevented the interference from B on relearning of task A (A2) even when B was learned five minutes after learning A1. Since the anterograde effects of B on relearning of A (A2) was removed by incorporating null trials before A2 and leaving a time interval between tasks B and task A (24 hours), researchers concluded that consolidation defined as a resistance to retrograde interference can occur for visuomotor adaptation.

Additionally, a recent study examined the time dependency of anterograde interference by employing empirical and model-based methods. (Lerner et al. 2020). In this experiment, the researchers investigated whether varying the time interval between adaptation to two opposing rotations (A vs. B) can influence the performance of B. The impact of prior learning of A on B

was examined by evaluating the initial level of performance and the rate of learning with the time interval of five minutes through 24 hours between A and B. The results indicated that the learning parameters (initial level of performance; learning rate) were expressed differently as a function of time interval. The learning of A impacted the initial level performance of B even after leaving a time gap of 24 hours between the two tasks. Conversely, the rate of learning with B was reduced only when the time interval was five minutes or one hour. The researchers attributed these reductions in learning rates to decreased error sensitivity. Furthermore, the results from the study also indicated that the same error sensitivity was recovered as the time interval between them increased (i.e., > six hours). Therefore, the researchers concluded that anterograde interference is predominantly due to reduction in error sensitivity, which can recover over time.

Another study examined whether opposing perturbations learned with different limbs would cause interference in a similar manner as those learned with the same limb. Kumar et al. (2018) proposed that interference between the motor memories learned with different limbs is retrograde in nature. In their experiment, subjects adapted to the clockwise (CW) rotation (A1) with their right arm, followed by washout trials with the left arm, and left-hand learning of the opposing perturbation (B). After 24 hours, the subjects performed washout trials with the right arm, followed by relearning of the CW rotation (A2) with the right arm. The results indicated a retrograde interference to the consolidation of motor memories since anterograde effects were already removed with washout trials. However, increasing the duration between initial CW rotation (A1) and counter-clockwise (CCW) rotation (B) conditions to 24 hours made the task A-associated motor memory (A1) resistant to the interference caused by the competing task B-associated memory (B). This in turn allowed faster relearning of task A (A2) on the next day. The

results from the above study confirmed that the interference between the memories developed with two arms is also retrograde in nature.

In summary, the motor learning literature has consistently reported that various factors can unmask the interference posed on motor memory consolidation when two opposing perturbations are learned in close succession. Evidence from motor adaptation studies suggests that the motor memory associated with one perturbation can resist the interference caused by the competing memory associated with an opposing perturbation when a time interval (24 hours) is provided between the exposure to two perturbations (Shadmehr and Holcomb. 1997, Krakauer et al. 1999, Kumar et al. 2018). The removal of anterograde effects by making the subjects return to baseline performance by inserting washout trials have also proven to be a key factor that promotes memory consolidation (Krakauer et al. 2005, Kumar et al. 2018, Shadmehr et al. 1997). The beneficial effect of prolonged training (Krakauer et al. 2005, Krakauer et al. 2005, Kumar et al. 2018) on consolidation has been also suggested to limit motor adaptation interference. Among these factors, especially the graded effect of time interval and washout are considered to be the most crucial components that could eliminate the hindrance on consolidation of motor memories.

It is well known that multiple learning mechanisms operating at different time scales play a vital role when subjects learn to counteract a novel environmental perturbation (Diedrichsen et al. 2010, Butefisch et al. 2000), as well as during relearning of the same perturbation (Morehead et al. 2015, James et al. 2022, Huberdeau et al. 2019). These learning mechanisms vary from more strategic or explicit processes contributing to the performance gains during the initial stages of adaptation (Morehead et al. 2015) to more implicit learning components leading to gradual/slower changes in behavior (Mazzoni et al. 2006). However, it remains uncertain whether memory stabilization and interference occurs differently for training protocols involving varying degrees

of implicit and explicit components. Identifying the factors that prevent the retrieval of consolidated memory is critical in understanding how humans can form short- and long-term, context-dependent motor memory.

Thus, the objective of the third aim was to determine how the training methods with different combinations of explicitness (of visuomotor perturbations) and interference conditions would influence memory consolidation associated with visuomotor adaptation against anterograde and retrograde interference. This was achieved by combining two explicitness conditions (more implicit vs. more explicit) with two interference conditions (more interference vs. less interference). The more implicit condition involved adapting to a novel visuomotor rotation condition without any instructions provided, and the more explicit condition involved adapting to the same condition with specific information about the rotation condition, as well as a strategy to deal with the condition (see Chapter 2). The more interference condition involved learning B immediately after learning A, without a washout session in between A and B, and the less interference condition involved learning B 24 hours after learning A, with a washout session in between A and B. The interference occurs when a counter-rotation, equal and opposite in magnitude to the initial rotation, is learned shortly after the initial rotation without any washout blocks (Wigmore et al. 2002; Krakauer et al. 1999; Krakauer et al. 2005). However, introducing a time gap between learning the two rotations (e.g., 24 hours) along with a washout session has been successful in minimizing interference and promoting savings (Krakauer et al. 2005; Kumar et al. 2018). Short-term (five min.) and long-term (one week, one month) savings were evaluated in each subject group.

While the traditional view proposes savings in visuomotor adaptation as a cerebellum-dependent, implicit and error-based learning process, recent studies have suggested that savings

are solely driven by the recall of explicit cognitive aiming strategies (Haith et al. 2015, Morehead et al. 2015, Tylor et al. 2014). This idea leads us to predict that the ability to consolidate motor memories in a short- and long-term period would therefore differ between the implicit and explicit conditions. If the interference effects were larger for the explicit condition, such a finding would indicate that cognitive processes that mainly involve explicit components of visuomotor adaptation are inherent to the interference effects caused by the combination of time intervals and washout. If the effects were larger for the implicit condition, such a finding would indicate that the neural processes that mainly involve implicit components are inherent to the interference effects. In addition, we hypothesized that adapting to two opposing visuomotor perturbations would produce greater short-term savings when the training method involved less interference (24-hour time gap and washout) than more interference (counter-rotation immediately after initial adaptation, without washout). It has been suggested that adapting to opposing rotations 24 hours apart would limit the interference on the retention of first rotation (Shadmehr and Basheer-Krug, 1997, Krakauer et al. 2005). In addition, previous studies have indicated the importance of performing washout trials before learning the opposing rotation to remove the anterograde effects from previous learning (Krakauer et al. 2005, Kumar et al. 2018). We also hypothesized that savings would be greater in the less-interference condition, especially in terms of long-term savings, as memories associated with motor learning become stronger as anterograde interference effects are weakened with the passage of time (Shadmehr et al. 1997).

Experiment 3

Materials and Methods

Participants

A total of 40 neurologically intact right-handed inviduals participated in this study. Subjects were randomly assigned to a particular group for the experiment (Table 4.1). There were four subject groups with ten subjects per group. The subjects who were tested in Aims I and II were not tested in this experiment. According to our previous studies, the sample size of 40 subjects (10 per group) were large enough to meet the most stringent statistical requirements and allows room for possible attrition. The cretiria of inclusion and exclusion were the same as in *Aim I*.

Apparatus

The data acquisition system used for Aim I was used for collecting data in Aim III

Experimental protocol

In general, subjects performed rapid reaching movements with the right arm from a start circle to one of four targets (10 cm away from the start circle) repeatedly (Fig 4.1B). They were instructed to move the cursor to each target rapidly and as straight as possible in response to the appearance of the target, stop without correcting their movement, and bring the cursor slowly back to the start circle. The experiment consisted of four sessions: baseline (40 trials), adaptation (160 trials), counter rotation (160 trials), and readaptation (160 trials). The *baseline* session had 10 cycles of reaching movements where each cycle had four consecutive trials corresponding to the four targets that were placed radially around the start circle (Table 4.1). Veridical feedback of the index fingertip location was provided to the subject by a cursor displayed on the screen, so that the subjects could familiarize with the general reaching task without a visuomotor perturbation.

All subjects performed 40 cycles of reaching movements in the *adaptation* session with the cursor rotated 24 degrees CCW about the start circle (Table 4.1). The subjects were randomly assigned to four different groups that varied in terms of the training condition (i.e., explicit vs.

implicit) and the magnitude of interference effects (more vs. less interference). With regard to the training condition, the subjects were separated into two following groups: more implicit (i.e., abrupt perturbation, which is identical to group AP in Aims I and II) and more explicit (i.e., abrupt perturbation + instruction + strategy group, identical to group AP+I+S in Aims I and II). (See chapter 3 for the rationale for these two conditions.) Here, the abrupt perturbation condition was employed as the more implicit condition instead of the gradual perturbation condition, so that the perturbation method would be comparable between the adaptation and counter-rotation sessions. The subjects in the more implicit groups (ABA (Imp.), AWBA (Imp.)) adapted to a 24-degree CCW rotation introduced abruptly from the very first trial. The subjects in the above two groups reached toward the visual targets following the instruction: "A target will appear on the screen. Your task is to hit the target as accurately and straight as possible." Those in the more explicit groups (ABA (Exp.), AWBA (Exp.)) adapted to the same 24-degree CCW rotation condition, in which the cursor was rotated 24 degrees from first trial and was provided with the following instruction: "A target will appear on the screen. The cursor will be rotated 24 degrees CCW relative to the location of your index fingertip. Your task is to hit the target as accurately and straight as possible. You can counteract the rotation by aiming in the direction that is rotated 24 degrees CW relative to the target location." (Fig 4.1B).

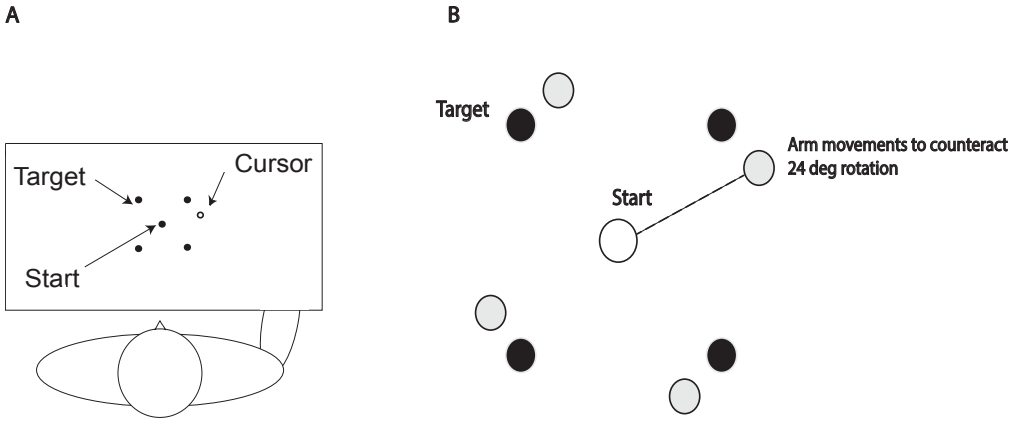

Fig 4.1: A) Visual display of target, cursor and start circle: Target was randomly displayed at one of the four locations. During the experiment, participants moved their arm straight from the start circle to the target. Direct vision of the hand was blocked by horizontal display. The visual feedback was provided as a cursor indicating the mouse position. B) Setup for adaptation session: During adaptation, the participants moved their arm in the desired direction. The position of cursor was rotated 24º CCW about the position of index fingertip, so the subject will have to reach toward the direction that is 24º CW about the target (gray circles).

Groups	**Explicitness of visuomotor perturbation (24° rotation)**	**Adaptation (A1)**	**Interference**		**Counter-rotation (CR)**	**Readaptation**		
			Wash out (W)	**Time Gap btwn A1 & CR**		**A2 (5 min)**	**A2 (1 wk)**	**A2 (1 mo)**
ABA (Imp.)	Implicit ((No instruction)	CCW rotation (160 trials)	No	Immediate	CW Rotation (160 trials)	CCW Rotation (160 trials)	CCW Rotation (160 trials)	CCW Rotation (160 trials)
ABA (Exp.)	Explicit (I+S)	CCW rotation (160 trials)	No	Immediate	CW Rotation (160 trials)	CCW Rotation (160 trials)	CCW Rotation (160 trials)	CCW Rotation (160 trials)

AWBA (Imp.)	Implicit (No instruction)	CCW rotation (160 trials)	Yes	24 hrs	CW Rotation (160 trials)	CCW Rotation (160 trials)	CCW Rotation (160 trials)	CCW Rotation (160 trials)
AWBA (Exp.)	Explicit (I+S)	CCW rotation (160 trials)	Yes	24 hrs	CW Rotation (160 trials)	CCW Rotation (160 trials)	CCW Rotation (160 trials)	CCW Rotation (160 trials)

Table 4.1: Description of the training conditions for the four different groups. CW:Clockwise rotation, CCW: Counter-clockwise Rotation

With regard to the interference effect, the subjects were divided further into the two following conditions: more interference (ABA (Imp.), ABA (Exp.)) and less interference (AWBA (Imp.), AWBA (Exp.)) (Fig 4.2). As stated above, strong interference has been observed in conditions in which two opposing perturbations are learned in close succession (Shadmehr et al. 1997, Kumar et al. 2018, Caithness et al. 2004). Such interference is reduced substantially with a 24-hour time interval between learning two opposing conditions, especially when accompanied with washout trials (Kumar et al. 2018, Krakauer et al. 2005, Caithness et al. 2004). Thus, those in the more interference condition experienced the abrupt counter rotation session (24-degree CW rotation) immediately after the adaptation session with no washout trials in between the adaptation and counter-rotation sessions (Fig 4.2A, 4.2B); and those in the less interference condition experienced the counter rotation 24 hours after the initial adaptation session (Fig 4.2C, Fig 4.2D). The subjects in the less interference condition (AWBA (Imp.), AWBA (Exp.)) also performed 40

washout trials (veridical feedback provided with no visuomotor rotation) in between the adaptation and counter-rotation sessions (Fig 4.2C, 4.2D). These two conditions are thought to cause a larger and smaller amount of interference, respectively, when learning two opposing tasks (Krakauer et al. 2006, Kumar et al. 2018, Krakauer et al. 2005). Both the less interference and more interference groups were given the following instruction for the readaptation session: "A target will appear on the screen. Your task is to hit the target as accurately and straight as possible."

Five minutes past the counter-rotation session, all subjects irrespective of their groups performed a baseline session (40 trials) and a readaptation session (160 trials; abrupt 24-CCW rotation) to assess short-term savings of visuomotor adaptation (Fig 4.2). The participants were asked to return to the lab at two different time points after their first visit to assess long-term savings: 1) one week after the initial training; 2) One month after the initial training. During both visits, all participants performed a baseline session (40 trials) and a readaptation session (160 trials; abrupt 24-CCW rotation).

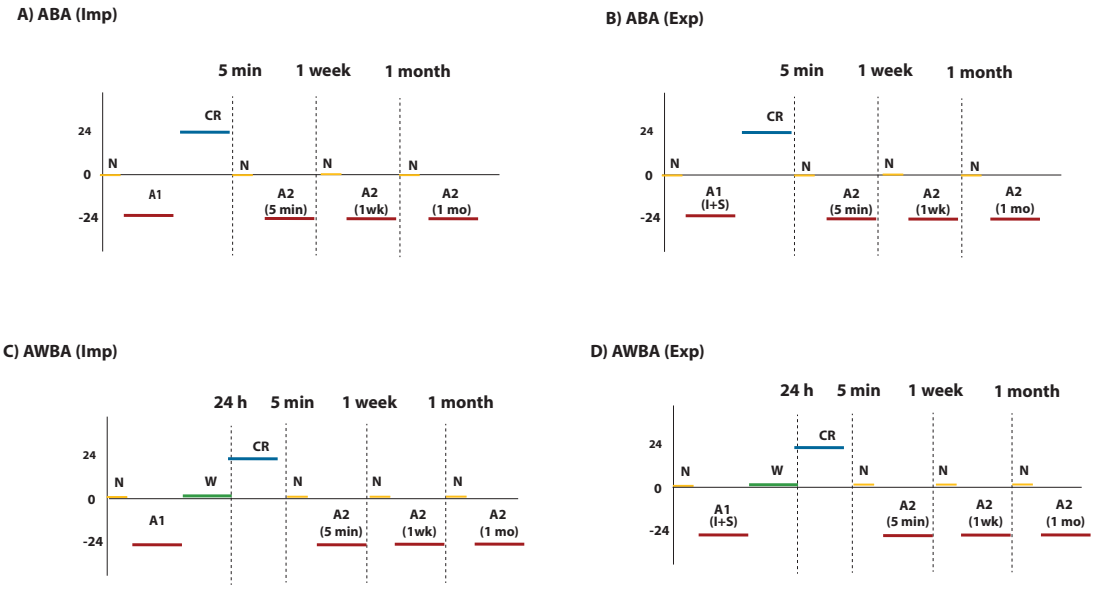

Fig 4.2: Experimental Protocol: A, B) Subjects in group ABA(Imp.) and ABA (Exp.) (top left, top right) first performed baseline session (N, yellow) and then adapted to a 24° abrupt counterclockwise rotation (A1, red) followed by adaptation to a clockwise rotation (CR, blue). The group ABA (Imp) performed the adaptation session (A1) with no instructions or strategies whereas the ABA (Exp) were provided with instruction and strategies during adaptation session. Both groups were then required to perform baseline session (N) followed by a readaptation session (A2, red) in five minutes after adapting to CR to assess short-term savings. To assess long-term savings, the same subjects also performed two readaptation sessions (A2, red) in 1 week and (A2, red) in 1 month. C, D) Subjects in group AWBA(Imp.), AWBA (Exp.) (bottom left, bottom right) first performed a baseline session (N, yellow) and then adapted to a 24° abrupt counterclockwise rotation (A1, red) followed by a washout session (W, green). AWBA (Imp.) ABA (Imp.) group performed the adaptation (A1) implicitly without using any instructions or strategies whereas AWBA (Exp.) utilized the instructions and strategies provided for them during the adaptation session. This was followed by an adaptation to a clockwise rotation (CR, blue) 24 hours after A1. They were then required to perform a baseline session (N) followed by a readaptation session (A2, red) five minutes after learning CR to assess short-term savings. To assess long-term savings, the same subjects also performed two readaptation sessions (A2, red) in 1 week and (A2, red) in 1 month.

After the task was completed, participants in all four groups were polled for strategy use and explicit awareness of the perturbation by using an awareness questionnaire (Benson et al. 2011) (Appendix F). In the questionnaire, all participants who followed the bold arrow indicated no awareness of perturbation whereas all participants who followed the black dotted lines indicated that they were aware of the perturbation and used strategies.

Data Analysis

We used initial directional error (DE) as the main measure of rotation adaptation. DE is defined as the angular difference between a vector from the starting circle to a target and another vector from the hand position at movement start to that at peak arm velocity. In addition to DE, we calculated the rate of learning, because the time course of error reduction during visuomotor adaptation typically shows a rapid change in the first few cycles, followed by a slower decline (Krakauer et al., 1999, 2005, Ghilardi et al., 2000, Yin et al. 2020). The rate of learning in the adaptation and three readaptation sessions (5 min, 1 week, 1 month) was calculated by fitting DE values from every single subject within each group to an exponential function.

To capture the extent of initial learning, we computed the DE at the first cycle of each session and then performed (1) a repeated-measures ANOVA with session (adaptation, readaptation at 5 min, readaptation at 1 week, readaptation at 1 month) as a within-subject factor and explicitness (more explicit, more implicit) as well as interference (more interference, less interference) as between-subject factors. We also performed (2) a separate repeated-measures ANOVA for the DE at the first and last cycle of the counter rotation session with cycle as a within-subject factor and explicitness and interference as two between-subject factors. To compare learning rates between initial learning (adaptation) and relearning (at 5 min, at 1 week, at 1 month), the learning rate data were subjected to (3) another repeated-measures ANOVA with explicitness (more explicit, more implicit) as well as interference (more interference, less interference) as between-subject factors and session (adaptation, readaptation at 5 min, readaptation 1 week, readaptation at 1 month) as a within-subject factor. For significant effects, post hoc comparisons were done (Tukey's tests for between-group comparisons, Fisher's LSD tests for within-group comparisons). The alpha level was set at 0.05 for all comparisons.

Results

The changes in performance across the cycles during the baseline, adaptation, washout, and readaptation sessions for each group are shown in Fig 4.3A. Direction errors (DE) in the adaptation session were initially large for all the four groups, which then gradually reduced over the cycles (Fig 4.3A). Relearning the rotation one week and one month later (readaptation at 1 week, readaptation at 1 month) was more rapid and the initial DEs (i.e., errors in the first few cycles) in the readaptation sessions appeared to be smaller than those in the adaptation session, especially for groups AWBA (Imp.) and AWBA (Exp.) in which participants experienced less interference, than those in groups ABA (Imp.) and ABA (Exp) that did experienced more interference. Compared with the adaptation session, the relearning at one week and one month also appeared faster for the subjects in groups AWBA (Imp.) and AWBA (Exp.). than those in groups ABA (Imp.) and ABA (Exp.).

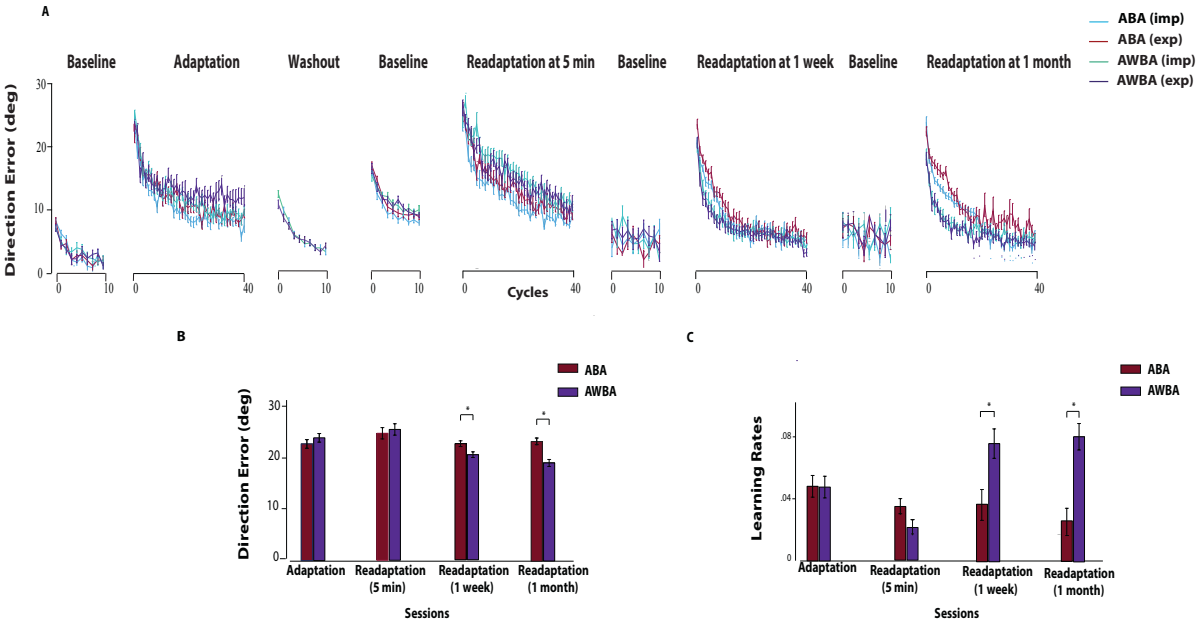

Fig 4.3. A, The change in Direction Error (DE) across the cycles for the sessions: Baseline, Adaptation, Washout, Baseline, Readaptation at 5 min, Baseline, Readaptation at 1 week, Baseline

and readaptation at 1 month for each group. Every data point on the x axis represents the mean value of one cycle across the participants in each group. **B. Interference, Changes in DEs (1st cycle) for more interference (ABA) and less interference (AWBA) groups:** DE's for all the sessions (Adaptation, readaptation-5 min, 1 week, 1 month) are shown. The savings were higher for the less interference groups both at 1 week and 1 month compared with the more interference groups. **C. Interference**, **Changes in learning rates for more interference groups (ABA) and less interference (AWBA) groups:** Learning rates for all the sessions (Adaptation, readaptation-5 min, 1 week, 1 month) are shown. The less interference groups showed higher learning rate during the readaptation session at 1 week and 1 month compared with more interference groups. * Indicates significant difference at $p<.05$.

The repeated-measures ANOVA with the DE data from the adaptation and three readaptation sessions (5 min, 1 week, 1 month) indicated a significant 2-way interaction effect between interference and session ($p=.004$). Post hoc analyses from the adaptation session revealed that all four groups performed in a similar way during the adaptation session with no significant difference between the groups. During the readaptation sessions, none of the four groups showed any five minutes savings irrespective of the training condition. However, savings at one week were significantly different between the more-interference and less-interference groups ($P=.010$), and the difference between these groups became more obvious after 1 month ($p<.001$) (Fig 4.3B). The results also indicated a significant difference between the readaptation at five min. vs. readaptation at one week ($p<.001$) as well as between readaptation at five min. vs readaptation at one month ($p<.001$) for groups AWBA (Imp.) and AWBA (Exp.). These results indicate that the groups that had less interference from the counterrotation performed better, in terms of DEs, during the

readaptation sessions at one week and one month than the groups that had more interference. No effect involving the factor of explicitness was statistically significant.

The repeated-measures ANOVA for the learning rates indicated a significant two-way interaction effect of session (adaptation, readaptation at 5 min., readaptation at 1 week, readaptation at 1 month) and interference (more vs. less interference) ($p<.001$). Post hoc analyses indicated a significant difference in one week savings between the more- and less-interference groups again ($P<.001$); that was also the case in savings at one month ($P<.001$) (Fig 4.3B). Post hoc analyses also indicated significantly higher learning rates in the readaptation at one week ($P=.021$) and at one month sessions ($P=.005$) compared to the readaptation at five minutes for groups AWBA (Imp.) and AWBA (Exp.). No difference was observed between savings at one week and at one month (>.05). These results indicate that the long-term (1 week, 1 month), but not short-term (5 min.) savings were different between the more and less interference groups. No effect involving the factor of explicitness was statistically significant.

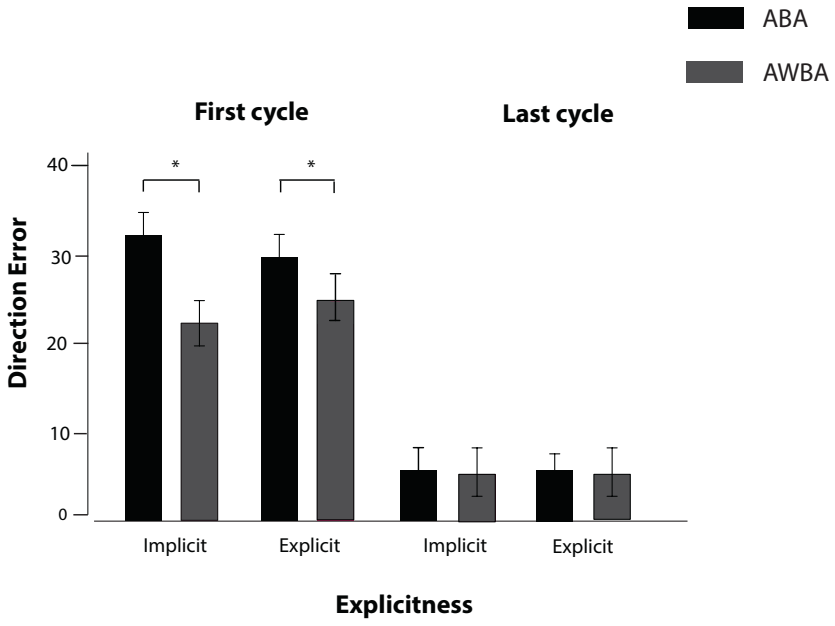

Fig 4.4: Washout: Change in DE for first and last cycle of counter-rotation session for less interference (AWBA) and more interference (ABA) groups. The initial DE during the counter-

rotation session was significantly different between the explicit groups (ABA (Exp.) and AWBA (Exp.) and also between the implicit groups (ABA (Imp.) and AWBA (Imp.). No difference was observed between the groups for the last cycle of the counter-rotation session.

The results from the separate repeated-measures ANOVA with the DE's from the first and last cycle for the counter-rotation session revealed a significant three way interaction effect between cycle, interference, and explicitness ($p=.05$) as well as a two way interaction effect between cycle and interference ($p<.001$). Post hoc results indicated that at the first cycle, a significant difference was observed between ABA(Exp.) and AWBA(Exp.) ($p<.001$), and also between ABA(Imp.) and AWBA(Imp.) ($p=.027$) (Fig 4.4). At the last cycle, no difference was observed across the four groups ($p>.05$). The significant differences were expected as ABA (Imp.) and ABA (Exp.) learned the counter rotation (CW rotation) immediately after learning the adaptation session (CCW rotation) without a washout session or a 24-hr delay. Therefore, the large errors in the counter rotation session for the above groups were due to the anterograde interference from CCW rotation (task A) on CW rotation (task B). Significantly smaller errors observed in the AWBA (Imp.) and AWBA (Exp.), then, can be attributed to the reduced anterograde interference following the washout session and the 24-hr delay.

The results from the awareness questionnaire(Under Experiment 3 in Appendix E), which was used to assess the awareness of the visuomotor rotation condition, indicated that all participants in the more implicit group (ABA (Imp.), AWBA(Imp.)) pushed left when they felt the cursor was not moving in the intended direction (Gray lines in Appendix E) and they were unaware of the perturbation. They also reported not using any strategies during the adaptation session. However, the participants in the more explicit groups (ABA (Exp.), AWBA (Exp.)) reported that

they were completely aware of the rotation and used strategies provided by the experimenter to counteract the rotation.

Discussion

The main objective of this study was to determine how competing motor memories associated with two opposing visuomotor adaptations would be consolidated against anterograde and retrograde interference differently. To investigate that question, we incorporated training methods with varying combinations of explicitness of the visuomotor perturbation (more explicit vs. more implicit) and interference (more vs. less). We evaluated short-term (five min.) and long-term (one week, one month) savings separately for each of the four groups: ABA (Imp.), ABA (Exp.), AWBA (Imp.), and AWBA (Exp.). While the traditional view supports that savings in visuomotor adaptation mainly involves an implicit error-based learning mechanism (Herzfeld et al. 2014, Leow et al. 2016), recent evidence suggests explicit cognitive strategies as the crucial contributor to generate savings (Morehead et al. 2015, Huberdeau et al. 2019). This idea led us to the prediction that the ability to consolidate motor memories in a short- and/or long-term period would also differ between the implicit and explicit conditions. However, we did not observe any significant differences in the amount of short-term as well as long-term savings between the more implicit and more explicit conditions. These findings suggest that visuomotor adaptation may undergo similar motor memory consolidation processes regardless of whether it mainly involves explicit (i.e., AP+I+S) or implicit (i.e., AP) components. Our current findings are also in agreement with the results from chapters 2 and 3, which indicated that involving varying levels of explicit or implicit components during initial adaptation does not lead to improved short-term (i.e., five minutes) or long-term savings (i.e., one week, one month).

In contrast, the long-term savings data (both learning rates and DEs) indicated a significant effect of the interference level (more vs. less). Groups AWBA (Imp.) and AWBA (Exp.), who underwent the training conditions with a washout session and a 24-hour delay, exhibited greater savings at one week and one month compared to the other two groups. Additionally, long-term savings at one week and one month were significantly greater than short-term savings at five minutes for groups AWBA (Imp.) and AWBA (Exp.) (Fig. 4.3B, C). These results validate that the training methods involving different levels of interference conditions impact memory consolidation following visuomotor adaptation against anterograde and retrograde interference in distinct ways. This is in line with previous findings reported by Krakauer and colleagues (2005), who demonstrated that it is crucial to incorporate a washout session in the training protocol in addition to the critical time interval (≥ six hours) for minimizing the interference effects.

It should be noted here that the savings examined during the readaptation sessions in our study would have been influenced by the anterograde, as well as the retrograde interference effect of the counter-rotation adaptation (Miall et al. 2004, Shadmehr et al. 1997, Sing and Smith, 2010). This leads to the question of whether the greater savings observed in the less-interference groups was either due to the reduced anterograde or retrograde effects of the counter-rotation adaptation. With regards to the anterograde effect of the counter-rotation adaptation on the readaptations, our data showed no difference across the four groups in terms of DEs at the last cycle of the counter-rotation session. This indicates the same effect of the counter-rotation adaptation for all subject groups at the beginning of the readaptation. Therefore, the greater savings observed in the less-interference groups in the readaptation sessions cannot be attributed to the anterograde interference effects of the counter-rotation adaptation on the readaptations (i.e., it is not a learning issue).

Then, would the savings observed during the readaptations have more to do with the retrieval of motor memories obtained following the initial adaptation? It is likely that the counter-rotation adaptation had retrograde interference effects on the motor memories obtained following the initial adaptation. One thing to consider at this point is that the manipulations done in this study (i.e., less vs. more interference) were provided before the counter-rotation adaptation session. Thus, the manipulations with the level of interference first influenced the extent to which the motor memories associated with the initial adaptation were consolidated, in such a way that the memories were consolidated significantly better in the less-interference groups. This resulted in reduced anterograde interference effects of the initial adaptation on the counter-rotation adaptation in the less-interference groups, as indicated by the smaller DEs at the first cycle of the counter-rotation session in these groups (Fig. 4.4). This would have also resulted in reduced retrograde interference effects of the counter-rotation adaptation on the original adaptation (i.e., less conflicts between two competing memories) in the less-interference groups, which in turn, would interfere less with the retrieval of memories obtained following the initial adaptation. These findings seem to be in agreement with a notion that it is not consolidation, but rather retrieval, of motor memories associated with an initially learned task that is negatively influenced by an opposing task learned in close succession. (Brashers-Krug et al., 1996; Krakauer et al., 2005, Overduin et al., 2006). Our findings may also expand that notion by demonstrating that motor memories that were consolidated to a greater extent are less susceptible to conflicting motor memories, thus resulting in a better retrieval of the original memories later (i.e., greater savings).

In the present study, we observed the lack of short-term (five min.) savings, which may be due to the competitions for common neural substrates during visuomotor adaptations. For example, learning of one perturbation can negatively affect the prior memory of the other perturbation

because motor memories may compete for the same neural resources during adaptation (Overduin et al. 2006). Furthermore, a few visuomotor adaptation studies have suggested that the cerebellum shares an extensive network connection with the prefrontal cortex and the posterior parietal cortex during a sensorimotor adaptation task (Della Maggiore et al. 2017; Tanaka et al. 2009). The results from the study done by Della-Maggiore and colleagues (Della- Maggiore et al. 2017) suggest a dynamic interplay of the cerebellum in the cerebellar-thalamic-cortical network that influences the initial adaptation and retention of the same motor memories. This idea has also gained support from other studies on motor memory interferences, which proposed an involvement of a shared lateralized neural substrate while performing conflicting motor adaptation tasks in close succession (Krakauer et al. 2006, Brasher-kurg 1996). Our current research also aligns with the findings reported by Krakauer et al. (2006), who failed to observe savings in five minutes, but reported enhanced learning 24 hours after initial learning. Similar observations have also been made for consolidation of motor memories associated with use-dependent learning, particularly those associated with passive movement training (Tays et al. 2020). These findings collectively suggest that the competitions for common neural substrates during visuomotor adaptations may lessen as motor memories are consolidated further with the passage of time, which in turn may impact the amount of savings as well.

The role of explicit learning components in visuomotor adaptation and savings is still a controversial debate. There are a few studies that support the significant role of explicit learning in VMA and savings (Taylor et al. 2014, Bond and Taylor 2015, Haith et al. 2015, Morehead et al. 2015, Huberdeau et al. 2017), although other studies also suggest that savings can be generated without involving explicit cognitive strategies (Yin et al. 2020, James et al. 2022, also see Wang et al. 2011,). The involvement of explicit components may be influenced by factors such as training

environments, specific demands of a task, and the level of awareness regarding a perturbation (Ying et al. 2020, Javidalsaadi et al. 2021, Werner et al. 2015). In our current study, we manipulated the awareness of the perturbation by employing two different training conditions: abrupt adaptation with no information regarding the perturbation (more implicit), and abrupt adaptation with specific information regarding the perturbation, as well as a specific strategy to deal with the perturbation (more explicit). Our questionnaire outcomes indicate that the subjects performed appropriately depending on the conditions to which they were assigned. For example, those in the more implicit condition did not use any specific strategies or instructions to counteract the rotation while those in the more explicit condition did counteract the rotation using specific strategies provided and were completely aware of the perturbation. Despite that, our results show that there was no difference between the two conditions in terms of the amount of savings observed during the readaptation sessions, regardless of whether the time gap between adaptation and readaptation were five minutes, one week, or one month.

The current findings are consistent with the observations reported by Yin et al. (2020), who demonstrated that savings in VMA is independent of forming or remembering explicit aiming strategies. The findings from the above study indicated robust savings for the group that implicitly learned the rotation from sensory prediction errors. In addition, the same study also indicated that savings in the explicit group were not due to the quick recall of the explicit strategies but were instead due to the enhanced implicit learning. These findings are also in agreement with the findings reported in our previous study (James et al. 2022), in which we investigated how using different arms during a washout session would influence savings in visuomotor adaptation. In that study, participants first adapted to a visuomotor rotation with the left arm, underwent a washout session with either the left or right arm, and then readapted to the same rotation with the left arm.

The results indicated a significant difference in savings based on the arm used during the washout session. According to the notion that savings mainly occurs based on the recall of explicit strategies, there was no reason to think that the amount of savings would differ depending on the arm used during the washout session. Thus, these results, along with our current findings, suggest that the explicit recall of strategies cannot be the only source for savings, and further that the role of explicit components in the generation of savings may not be as large as currently thought.

The subjects' awareness of a perturbation, and thereby the contributions from explicit processes during visuomotor adaptation, can vary with the size of the visuomotor rotation (Neville & Cressman 2018; Morehead et al. 2015, Huer & Hegele 2008, Taylor et al. 2014, Wang et al. 2019). Increasing the size of a rotation can cause more awareness of the given perturbation, which in turn can lead to a more involvement of explicit learning components during visuomotor adaptation (Werner et al. 2015; Neville & Cressman 2018). Interestingly, in our current study, we observed that no difference in savings was observed between the more explicit groups and the more implicit groups, even though the subjects in the explicit groups reported awareness of the perturbation and the use of strategies. It is possible that the relatively small rotation size employed in our study (i.e., 24°) might have limited the effectiveness of explicitness (i.e., awareness of the perturbation, use of specific strategies) in our study. Indeed, a study conducted by Neville and Cressman (2018) have demonstrated that the involvement of implicit vs. explicit components could be influenced by the size of a visuomotor rotation. In their study, a no-strategy group was compared to a strategy group that employed specific cognitive strategies to counteract a given visuomotor rotation. In the no-strategy group, the magnitude of implicit adaptation remained consistent when subjects were required to adapt to varying rotation sizes (20°, 40°, 60°), whereas manipulating the rotation sizes influenced the contribution of explicit components in the strategy group. A

visuomotor perturbation of 20° has also been shown to produce no awareness, even after providing instructions in advance, in some studies (Werner et al. 2015, Neville & Cressman 2018). Therefore, the lack of differences in savings between the explicit and implicit groups in the present study may be related to the size of the rotation employed.

In conclusion, the present study has demonstrated that consolidation of motor memories following visuomotor adaptations is influenced substantially based on the training methods that involve different levels of interference, although not based on those that differ in terms of the involvement of explicit or implicit components. Furthermore, our study suggests that the motor memories that have been more efficiently consolidated are less prone to interference from conflicting motor memories, leading to improved retrieval of the original memories later and thus yielding greater savings. (i.e., at one week and one month). Our findings indicate that the variations in long-term savings between the groups that experienced less vs. more interference stemmed from the reduced impact of retrograde interference caused by the counter-rotation on retrieving the memory of the original adaptation rather than from a reduction in the anterograde interference effects of the counter-rotation on relearning the original rotation. Our study revealed a lack of immediate savings (five minutes), possibly due to the competition between neural resources during the acquisition of conflicting visuomotor mappings. However, our results for long-term savings (i.e. one week and one month) also indicate that this competition might diminish with sufficient time for memory consolidation, further enhancing savings. The persistence of long-term savings associated with visuomotor rotation irrespective of the training condition (more implicit vs. more explicit) support the idea that explicit recall of strategies may not account for all savings observed. This further indicates that the contribution of explicit components to generating savings can vary based on the specifics of the learning protocol and the measurement of explicit processes/or awareness.

Additional experiments are warranted to better differentiate the conditions that can lead to greater savings in short-term vs. long-term based on the level of individual's awareness in adaptation protocols. Given the existing inconsistencies across studies in terms of their experimental paradigms aimed at distinguishing between explicit and implicit learning components, we highlight the significance of developing a novel task design that can effectively account for the influence of various factors on explicit processes and awareness.

Chapter 5

Summaries and Conclusions

Savings occurs when people relearn faster when they encounter something similar to what they have learned before (Ebbinghaus 1913). This phenomenon has since been demonstrated in different domains including visuomotor adaptation where individuals showed faster readaptation as they encountered similar cursor rotations a second time after being forgotten (James et al. 2021, Krakauer et al, 2005, Seidler et al. 2017). This faster-relearning effect associated with motor adaptation paradigms were observed on the same day, overnight, or even after a year. (Della-Maggiore and McIntosh 2005; Krakauer et al. 2005; Seidler et al. 2017, Landi et al. 2011). Traditionally, researchers explained savings in visuomotor adaptation as an ability of individuals to recall a previously consolidated motor memory (Landi et al. 2011, Caithness et al. 2004). Later, many researchers then challenged the view that savings in VMA involve model-free mechanisms like use-dependent learning (Huang et al. 2011), reinforcement learning (Butefisch et al. 2000, Diedrichsen et al. 2010) and instance-reliance learning (Wang et al. 2015). Recent evidence suggest that savings associated with visuomotor adaptation involves an interaction between explicit and implicit learning components (Mazzoni et al. 2006; Heuer et al. 2011) where few researchers proposed that savings results from the recall of an explicit strategies with no contributions from implicit learning components. In our study, our objective was to determine the potential benefits and effects of various training protocols that vary in the involvement of explicit and implicit components on short-term and long-term saving in younger adults. Additionally, we also investigated the impact of training methods incorporating various combinations of explicitness and interference conditions on memory consolidation associated with visuomotor

adaptation, against both anterograde and retrograde interference. In this dissertation we conducted three experiments to achieve the objectives of our study.

Summaries from Experiments 1, 2 and 3

In experiment 1 and 2, we investigated the beneficial effects of training methods with varying degrees of explicitness on short-term and long-term savings following visuomotor adaptation. Our findings from experiment 1 indicated that introducing different levels of implicit and explicit learning components during adaptation to a 24-degree visuomotor rotation have a varied impact on immediate savings (measured at 5 minutes) between the gradual-perturbation group (most implicit) and the three abrupt-perturbation groups (less implicit, more explicit, and most explicit). However, there was no significant difference observed among the three abrupt-perturbation groups themselves. Moreover, incorporating varying degrees of explicitness or implicitness during learning to counteract visuomotor rotation did not improve long-term savings measured neither at one week nor at one month post initial learning. While the explicit groups showed faster relearning at one week compared to the other groups, their relearning rate did not surpass their initial learning rate measured during the adaptation session. Hence, our findings indicate that motor memories decay over time. While explicit or implicit learning components may benefit short-term savings, they do not result in long-term retention of motor memories. Despite previous studies supporting the role of explicit cognitive strategies and awareness in visuomotor adaptation savings, our results suggest that these factors do not facilitate long-term retention, particularly with smaller perturbations such as the 24-degree rotation studied here. Our findings align with previous studies indicating that savings in visuomotor adaptation occurs independently of the formation or recollection of explicit cognitive strategies. This supports the idea that savings in visuomotor adaptation involves intricate interactions between explicit and implicit learning

components. These interactions can vary depending on factors such as perturbation magnitude, the presence of visual feedback, and the measurement of explicit processes or awareness.

In experiment 3, we investigated whether the training methods with different combinations of explicitness and interference conditions would influence memory consolidation associated with visuomotor adaptation against anterograde and retrograde interference. We found that the consolidation of motor memories after visuomotor adaptation is significantly influenced by training methods that incorporate varying levels of interference, rather than those that differ in the involvement of explicit or implicit components. Moreover, our findings suggest that visuomotor adaptation memories can be protected from retrograde interference that can lead to higher savings in the long-term compared to short-term. In conclusion, our results support the idea that the retrieval of the memory associated with the initially learned task was temporarily blocked by the counter-rotation task learned shortly thereafter.

The contribution of explicit and implicit learning components in visuomotor adaptation savings

Savings in visuomotor adaptation has garnered significant attention from numerous researchers, as it serves as a vital biomarker for understanding how the nervous system retains motor memories related to learning to compensate for an unexpected change in the environment (Della et al. 2005; Krakauer et al. 2005; Landi et al. 2011). However, there has been a longstanding debate in the literature regarding which mechanistic processes contribute to savings (Herzfeld et al. 2014, Huang et al. 78 2011, Morehead et al. 2015, Orban de Xivry and Lefevre 2015, James et al. 2021). While savings was previously believed to be solely attributed to model-based learning, involving the updating of an internal model (Shadmehr et al., 1994; Seidler et al., 2008; Kawato, 1999), a few studies have suggested the involvement of model-free (operant) learning mechanisms

such as use-dependent and reinforcement learning (Huang et al., 2011; Izawa et al., 2011; Lei et al., 2017). Recently, it has been suggested that savings is generated due to the enhanced contribution from strategic reaiming or using explicit cognitive strategies during adaptation session (Morehead et al., 2015, Huberdeau et al. 2019, Werner et al. 2019). This body of literature proposes that explicit strategies are the main if not the sole contributor to savings in visuomotor adaptation. In our previous research form our lab, we argued that explicit and implicit learning components interact in a complimentary manner during a visuomotor adaptation task, and the explicit recall of strategies cannot be the only source for savings (James et al. 2022, Wang et al. 2011; Javidialsaadi et al. 2021).In this study, we discovered that motor memories deteriorate over time, and the advantageous effects of explicit or implicit learning components on short-term savings do not extend to long-term retention of motor memories. In this light, we would like to extend the idea by other researchers that explicit recall of strategies may not fully account for all observed savings. Implicit learning, grounded in salient sensory prediction error and model-free mechanisms like use-dependent learning and reinforcement learning, can indeed contribute to generating both short- and long-term savings associated with visuomotor adaptation.

Role of motor memory consolidation and retrieval in Rehabilitation

Motor learning and memory consolidation are critical concepts in rehabilitation settings. The goal of rehabilitation is to retrain the brain to regain lost abilities by forming new motor memories, which requires an understanding of how different rehabilitation services may affect memory consolidation and potential interference effects (Bisaz et al., 2014, Maier et al., 2019). During the rehabilitation process, patients may re-learn motor skills through repetitive practice, which helps to reinforce and strengthen motor memories. Interference occurs when learning one task disrupts the retrieval of a previously learned task, especially when two tasks learned in

succession involve similar or opposing actions. This can be critical when patients engage in various rehabilitation therapies, as the overlapping or conflicting demands of different tasks could affect the consolidation of motor memories (Silva & Soares, 2018). After events like strokes or injuries that affect motor function, understanding how motor memories interact can help clinicians design more effective rehabilitation programs that avoid interference and maximize recovery.

Some patients respond better to implicit learning techniques, while others benefit more from explicit instruction (Maier et al., 2019, Kleynen et al. 2019). For example, stroke patients with cognitive impairments may find it challenging to process verbal information. Therefore, implementing strategies or following complex instructions may not be advantageous for them. Implicit learning, which occurs without conscious knowledge, often through task repetition, may be more accessible for such patients. Our study has furnished evidence demonstrating that motor memories associated with sensorimotor adaptation can be effectively consolidated and retrieved even after a prolonged period, regardless of the training conditions involving either more implicit or more explicit methods, provided they are less prone to interference from conflicting motor memories. Since each patient is unique in terms of their cognitive abilities, goals, and preferences it is very crucial that we need to understand the neural mechanisms behind motor memory consolidation and interference (Hatem et al. 2016). This can help therapists design and individualize rehabilitation sessions that minimize interference, such as alternating between motor tasks that use different parts of the body or different cognitive processes and ensuring there are adequate breaks between sessions that involve similar task demands.

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APPENDIX A: Informed Consent Form

UNIVERSITY OF WISCONSIN-MILWAUKEE

CONSENT TO PARTICIPATE IN RESEARCH

Study title	*Investigating an optimal motor learning protocol that leads to better savings and long-term retention of visuomotor adaptation*
Researcher[s]	• Jinsung Wang, PhD, Kinesiology Department, College of Health Science, UWM • Reshma James, PhD Candidate, Kinesiology Department, College of Health Science, UWM

We're inviting you to participate in a research study. Participation is completely voluntary. If you agree to participate now, you can always change your mind later. There are no negative consequences, whatever you decide.

What is the purpose of this study?

The objective of our study is to

1. Determine the effects of different training methods that are systematically varied in terms of the involvement of implicit and explicit components during visuomotor adaptation on short- and long-term savings.
2. To probe the resilient effects of explicit and implicit training methods on motor memory consolidation.

What will I do?

1. Qualified participants will come to the lab, fill out handedness questionnaire. After that RA explains about the study and they will be asked to sign the consent form.
2. The subjects have to visit our laboratory three times. During those visits, they will perform reaching movements while playing a computer game-like task. The biomechanical features of their arm movements will be recorded using a non-invasive, 2-dimensional movement data acquisition system called KINARM throughout the experiment.

3. The subjects will be randomly assigned to different experimental conditions across which motor learning protocols vary.
4. The subjects will be required to visit the lab three times. The length of the lab visit will be approximately one hour during the first visit, and it will be around 30 minutes during their second and third visit.

Risks

Possible risks	How we're minimizing these risks
• Minimal risk: Data collection and consenting process • Minimal Risk: Breach of confidentiality (your data being seen by someone who shouldn't have access to it)	• If the participant gets upset, RA will stop the consenting process. • If the participant gets upset during the experiment, RA will remind him/her that he/she may request to stop the experiment. The KINARM system is non-invasive and has two safety measures: an emergency stop button for the operator, and mechanical stops to prevent the robot arms from moving outside of the subject's range of motion. The KINARM chair is not connected to its horizontal display, thus it does not look very intimidating (no one who has ever seen or been tested in this system has mentioned that it is intimidating); and claustrophobia has never been a concern for any subject we have tested previously. • It is possible that the participants feel tired or muscle soreness by moving the arm repeatedly. Also, subjects will be allowed to take short rest periods frequently during the experiment, although they will not be allowed to remove themselves from the KINARM because that will require recalibration of the system (which will lengthen the total duration of the experiment). • All identifying information will be removed and will be replaced with a study ID. • All the electronic data will be saved on a password-protected, encrypted computer. • All the paper data will be stored in a locked filing cabinet in a locked office. Only the PI and his lab personnel will have access. • After the study is complete, movement data will be kept in the PI's password-protected computer for up to six years; it will be destroyed afterwards

Other Study Information

Possible benefits	• There is no direct benefit to you. • If you like, we will share the result of the study with you. • Findings from this study will be added to the body of literature in various fields of research including neurorehabilitation, motor learning, motor-memory retention and robotics.
Estimated number of participants	160 young adults within the age range of 18-35 years.
How long will it take?	2 years.
Costs	Costs for parking if you drive to our lab.
Compensation	In return for your participation, you can choose to receive $25 in cash or class extra credit. You will receive $5 after your first visit, $5 after your second visit, and $15 after your third and final visit. Class extra credit will be offered to students of the PI (1% point out of 100% point scale toward the final grade) or the instructors who encourage their students to participate in any faculty research and offer an extra credit for doing that (the amount of credit up to the instructors). Due to UWM policy and IRS regulations, we may have to collect your name, address, social security / tax ID number, and signature to give you this compensation.
Future research	Your data won't be used or shared for any future research studies.
Removal from the study	The subjects will not be removed from the study after they consent to be a participant in the study.
Funding source	College of Health Sciences student research award

Confidentiality and Data Security

We'll collect the following identifying information for the research (your name, phone number, and email address). This information is necessary to remind you to come to the three sessions. Also, we will contact you to share the results of the study with you.

Where will data be stored?	• Electronic data password-protected, encrypted computer. • We'll store all paper data in a locked filing cabinet in a locked office.
How long will it be kept?	• After the study is complete, movement data will be kept in the PI's password-protected computer for up to six years; it will be destroyed afterwards

Who can see my data?	**Why?**	**Type of data**
The researchers	To conduct the study and analyze the data	• Coded data (names, age, gender). These coded data are collected and stored separately from study data, but

		a unique number id exists to link data to identifiable information • Quantitative data (your scores and results collected from the study)
The IRB (Institutional Review Board) at UWM The Office for Human Research Protections (OHRP) or other federal agencies	To ensure we're following laws and ethical guidelines	• Coded data (names, age, gender). These coded data are collected and stored separately from study data, but a unique number id exists to link data to identifiable information • Quantitative data (your scores and results collected from the study)

Contact information:

For questions about the research	• Dr. Jinsung Wang • Reshma James	• wang34@uwm.edu • Reshma@uwm.edu
For questions about your rights as a research participant	IRB (Institutional Review Board; provides ethics oversight)	414-662-3544 / irbinfo@uwm.edu
For complaints or problems	• Dr. Jinsung Wang • Reshma James	• wang34@uwm.edu • Reshma@uwm.edu
	IRB	414-662-3544 / irbinfo@uwm.edu

Signatures

If you have had all your questions answered and would like to participate in this study, sign on the lines below. Remember, your participation is completely voluntary, and you're free to withdraw from the study at any time.

_____

Name of Participant (print)

_____ _____

_____

Signature of Participant

Date

Signature of Parent, Guardian or Legally Authorized Representative

Date

Name of Researcher obtaining consent (print)

Signature of Researcher obtaining consent Date

APPENDIX B: Handedness Questionnaire

Age: Height: Weight:

This questionnaire is designed to thoroughly evaluate one's degree of handedness. Please place a check mark in the appropriate box for each task. If you use both hands, check both, but indicate the one used more often or that you feel is more controlled. If you have any questions, do not hesitate to ask.

	R	L		R	L
Signing			Throwing		
Writing			Broom (upper hand)		
Drawing			Striking Match		
Scissors			Opening Box		
Toothbrush			Foot to kick with		
Knife			Bat (swing)		
Spoon					

1. Do you consider yourself:

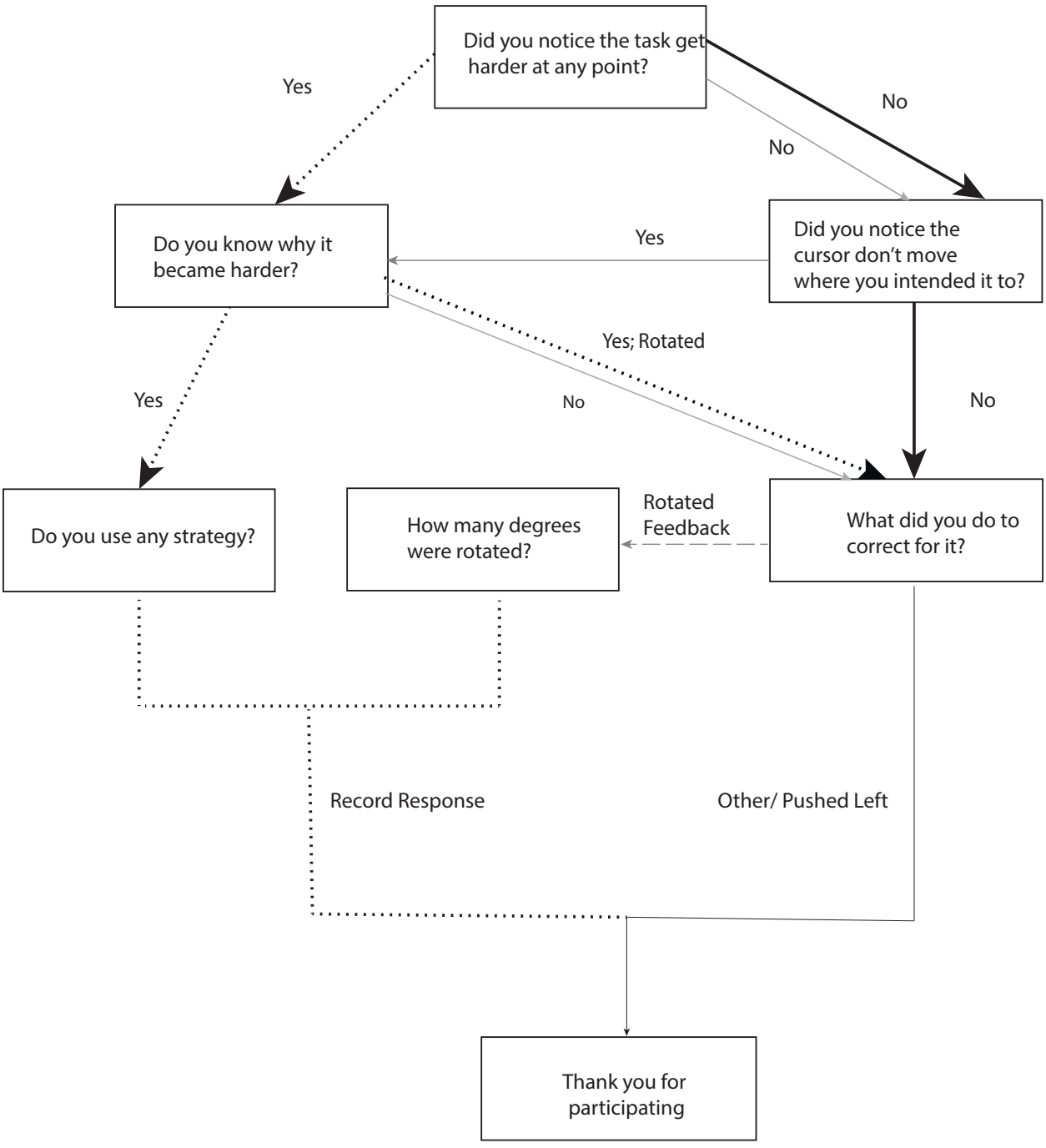
   Right-Handed Left-Handed Ambidextrous (Both Hands)

2. Is there anyone in your family who is Left-handed? Yes or No
   If yes, then who _____

3. Did you ever change handedness? Yes or No
   If yes, please explain _____

4. Is there any activity not in this list that you do consistently with your Left Hand?
   If yes, please explain _____

APPENDIX C: Awareness Questionnaire



APPENDIX D: Recruitment Flyer

Research Participants Needed

The Neuromechanics Laboratories (Dept. of Kinesiology) at UWM are seeking subjects for research to study how memory is retained following motor learning.

Eligible Participants:

- 18 to 35 years of age
- Right hand dominant
- No neurological disease or peripheral disorders (e.g., peripheral neuropathy) affecting sensation or movement of arms
- Normal or corrected normal vision
- No color blindness

Study Information:

If you participate in this study, you will be asked to perform a number of reaching movements while playing a computer game-like task. The process is non-invasive, and you are required to visit the lab 3 times (first visit, 1 week and 1 month after first visit). The length of the lab visit will be approximately an hour during the first visit, and it will be around 30 minutes during the second and third visit.

Location:

Neuromechanics Laboratories (END 136)

Compensation:

You may receive monetary compensation (25$ cash) or extra credit (please confirm with your course instructor(s)) for participating in this research.

Please Contact for more information or to schedule a time:

Reshma James: Reshma@uwm.edu

APPENDIX E: Responses from awareness questionnaire

Experiment 1 and Experiment 2

Subject id	Group	Sex	Response
1	GP	F	No, I did not find the task harder
2	GP	M	No, I did not find the task harder
3	GP	M	The cursor was moving to the target
4	GP	F	I did not find any difference in the cursor direction
5	GP	F	Task was not harder
6	GP	F	Cursor landed on the target
7	GP	F	The cursor was moving to the target
8	GP	M	No difference in the cursor direction
9	GP	F	Cursor landed on the target accurately
10	GP	F	No difference in the cursor direction
11	AP	F	Cursor did not go where I wanted, So I pushed left
12	AP	M	Pushed left
13	AP	F	Sometimes the cursor was going differently, pushed left
14	AP	F	Pushed left
15	AP	F	I pushed left to land on the target
16	AP	F	Felt something wrong with the cursor, so pushed left
17	AP	M	Pushed left
18	AP	M	Pushed left
19	AP	M	Cursor went differently, pushed left
20	AP	M	Something was off with the cursor, pushed left
21	AP+I	M	Yes, cursor was rotated 24 deg, Pushed left
22	AP+I	F	Cursor was rotated and pushed toward the target
23	AP+I	M	Feedback was rotated
24	AP+I	M	Pushed left, cursor rotated to 24 degrees
25	AP+I	F	Yes, rotated cursor. Pushed towards the target
26	AP+I	M	Cursor rotated
27	AP+I	M	Rotated feedback
28	AP+I	M	Cursor rotated to 24 deg
29	AP+I	M	Pushed left, Cursor was rotated.
30	AP+I	F	Rotated feedback
31	AP+I+S	M	Cursor rotated. Pushed 24 degree clockwise to reach target
32	AP+I+S	M	Rotated feedback. Used the strategy being told
33	AP+I+S	M	Pushed 24 degree clockwise to land on target
34	AP+I+S	F	Rotated cursor. Used the strategy to land on the target

35	AP+I+S	F	Cursor rotated 24 degrees. Pushed in a clockwise direction to reach the target
36	AP+I+S	F	Rotated feedback. Used the strategy being told
37	AP+I+S	M	Rotated feedback. Used the strategy being told
38	AP+I+S	M	Moved in 24-degree clockwise direction to reach the target
39	AP+I+S	F	Rotated cursor, 24-degree rotation, pushed 24-degree clockwise direction to land on the target
40	AP+I+S	F	Pushed 24 degree clockwise to land on target

Experiment 3

Subject id	Group	Sex	Response
1	ABA (imp)	M	Pushed left
2	ABA (imp)	F	Pushed left to land on target
3	ABA (imp)	M	Something was wrong, pushed left
4	ABA (imp)	M	Pushed left
5	ABA (imp)	F	Cursor went in a different direction pushed left
6	ABA (imp)	F	Pushed left
7	ABA (imp)	M	Cursor was going weird, So pushed left
8	ABA (imp)	F	Pushed left
9	ABA (imp)	M	Cursor did not go in the intended direction, pushed left
10	ABA (imp)	M	Pushed left
11	ABA (exp)	F	Cursor rotated 24 degrees. Pushed in a clockwise direction to reach the target
12	ABA (exp)	F	Rotated cursor, 24-degree rotation, pushed 24-degree clockwise direction to land on the target
13	ABA (exp)	F	I moved in 24-degree clockwise direction to reach the target
14	ABA (exp)	M	I was aware of the rotated feedback and used the strategy being told
15	ABA (exp)	M	I pushed 24 degrees clockwise to land on target
16	ABA (exp)	F	The feedback was rotated. Used the strategy being told
17	ABA (exp)	F	Rotated cursor, 24-degree rotation, pushed 24-degree clockwise direction to land on the target
18	ABA (exp)	M	Aware of the rotated feedback and made use of the strategies
19	ABA (exp)	M	Moved in 24-degree clockwise direction to reach the target without error.
20	ABA (exp)	F	Cursor was rotated and therefore used strategies
21	AWBA (imp)	F	Cursor was weird, Pushed left

22	AWBA (imp)	M	Something was off. So pushed left to reach the target
23	AWBA (imp)	M	Pushed left
24	AWBA (imp)	F	Pushed left
25	AWBA (imp)	M	I had to push left to land on the target
26	AWBA (imp)	M	Cursor was off. So pushed left
27	AWBA (imp)	F	Moved my index finger to the left to land on the target
28	AWBA (imp)	F	Pushed left
29	AWBA (imp)	M	Cursor went in a different direction. Had to push left to land on the target
30	AWBA (imp)	M	Something was weird with the cursor. Pushed left
31	AWBA (exp)	M	Cursor was rotated 24 degrees. So, I pushed in a clockwise direction to reach the target
32	AWBA (exp)	M	Used the strategy being told since the cursor was rotated.
33	AWBA (exp)	M	Rotated feedback, Used the strategy being told
34	AWBA (exp)	M	Rotated cursor. I used the strategy being told
35	AWBA (exp)	F	I had to push 24-degree clockwise direction to land on the target.
36	AWBA (exp)	F	Cursor was rotated. Yes, I used the strategy told by the experimenter.
37	AWBA (exp)	F	Rotated feedback. Used the strategy being told
38	AWBA (exp)	F	I knew the feedback was rotated. So I used the strategy to land on the target
39	AWBA (exp)	M	Cursor was rotated 24-degree anticlockwise. So, I had to push in the opposite direction to land on the target
40	AWBA (exp)	M	Rotated feedback, Used the strategy being told