# Bimanual transfer and retention of visuomotor adaptation is driven by explicit processes

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Thesis submitted in partial fulfillment of the requirements for a degree of Master of Science in Human Kinetics

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## Statement of Contributors

I hereby declare that I am the sole author of this Master of Science thesis. My contributions include: A review of literature in the area of interest, participant recruitment, participant testing, data collection, data compilation, statistical analyses, and the write-up of this thesis document. All of these duties were performed under the guidance and mentorship of my research supervisor, Dr. Erin K. Cressman.

The experiment in this thesis was performed in collaboration with my research supervisor, Dr. Erin K. Cressman, who provided editorial corrections and feedback, and is the co-author of the article presented in this thesis.

## Acknowledgements

These last two and a half years have been some of the most difficult and challenging years of my life, but they have also helped me grow not only as a researcher, but as a person.

First and foremost, I would like to thank my supervisor, Dr. Erin Cressman. I cannot thank you enough for your patience, guidance, encouragement and advice throughout my degree. You always made yourself available to address my concerns and questions, and always took the time to reassure me of my doubts. I am incredibly grateful for your commitment to my success and well-being. I could not have asked for a better guide throughout my academic career.

Next, I would also like to thank my committee members Dr. Anthony Carlsen and Dr. Diane Ste-Marie. Your time, knowledge, and guidance has helped me improve my critical thinking skills, my understanding for statistics, and gain a greater appreciation for research.

I also want to take the opportunity to thank the wonderful people I have had the pleasure of getting to know and work with in the sensorimotor control lab (past and present). Know that your support, help and encouragement was immensely appreciated, and I could not have asked for better lab mates.

And finally, I want to thank my family and friends, but most importantly, my wife-to-be. Words cannot describe how much appreciation and admiration I have for you. You helped me persevere through the many obstacles I have faced during my academic career and kept me sane throughout this journey. I am truly blessed to have your ongoing support for the rest of my life.

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## Abstract

Reaching with altered visual feedback of the hand's position in a virtual environment leads to reach adaptation in the trained hand, and also in the untrained hand (Wang & Sainburg, 2002). In the current study, we asked if reach adaptation in the untrained (right) hand is due to transfer of explicit (i.e., EA; conscious strategy) and/or implicit Adaptation (i.e., IA; unconscious) from the left (trained) hand, and if the transfer of EA and IA changes depending on how one is made aware of the visuomotor distortion. We further asked if EA and IA are retained in the trained and untrained hand for 24 hours. Participants (n=60) were evenly divided into 3 groups (Strategy, No-Strategy, and Control). All participants reached to visual targets while seeing a cursor on the screen that was rotated 40° clockwise relative to their hand motion. Participants in the Strategy group were instructed on how to counteract the visuomotor distortion. The No-Strategy group was not told of the upcoming visuomotor distortion but was later asked to reach while engaging in any strategy they had learned in order to assess EA. Participants in the Control group were also not told of the upcoming visuomotor distortion and were never instructed to engage in any strategy when reaching. EA and IA were assessed in both the trained and untrained hands immediately following rotated reach training, and 24 hours later by having participants reach without the cursor when instructed to: (1) aim so that your hand lands on the target (to assess IA) and (2) use what was learned during training so that the cursor lands on the target (to assess EA + IA; exception of Control group). Results revealed that the groups differed with respect to the extent of reach adaptation achieved when initially training with the rotated cursor, such that the Strategy group had greater EA and less IA compared to the No-Strategy group in the trained hand. Unexpectedly, the Control group also showed less IA compared to the No-Strategy group, but was similar to the Strategy group. For both the Strategy and No-Strategy groups, EA was transferred between hands and was retained over time. While the extent of IA varied between groups in the trained (left) hand immediately following reach training trials, significant transfer of IA was not found in any of the three groups. Retention of IA was observed in the trained hand but decayed over testing days. Together, these results suggest that while initial EA and IA in the trained hand is dependent on how one is made aware of the visuomotor distortion, transfer and retention of visuomotor adaptation is driven almost exclusively by EA, regardless of instructions provided.

# Chapter I: Literature Review

## 1. General introduction

Our environment is continually changing. Thus, movements must be adapted in order to interact with objects in a meaningful way. Motor adaptation is defined as the reduction of systemic errors introduced by altered conditions (e.g., environmental change(s)), enabling one to return to a former level of performance (Krakauer, 2009). Motor adaptation has been assessed within a laboratory setting for many years (Harris, 1963; Francis & Wonham, 1976; Wolpert & Kawato, 1998; Krakauer et al., 1999). Recently, in order to examine visuomotor adaptation, researchers have had participants reach in a virtual environment with misaligned visual feedback of their hand position in the form of a cursor on a screen (Wolpert & Kawato, 1998; Krakauer et al., 1999; 2000; 2009, Caithness et al., 2004; Mazzoni & Krakauer, 2006; Taylor et al., 2014). In general, participants adapt their movements in response to the visuomotor distortion. Moreover, following removal of the visuomotor distortion, participants continue to reach with their newly acquired visuomotor mapping, thus providing evidence of persistent motor adaptation through aftereffects (Ghahramani et al., 1996; van Beers et al., 2002; Heuer & Hegele, 2008; Cressman & Henriques, 2009; Wang & Lei, 2015). These aftereffects have been shown to transfer from the trained to untrained hand (Taylor et al., 2011; Mostafa et al., 2015; Poh et al., 2016), and be retained for a long period of time (e.g., from 24 hours up to a year following initial visuomotor adaptation; Yamamoto et al., 2006; Nourouzpour et al., 2015; Maksimovic & Cressman, 2018).

Visuomotor adaptation has been suggested to involve two distinct processes. Traditionally, these two processes have been referred to as: (1) Strategic perceptual-motor control, which leads to a quick reduction in reaching errors when the visuomotor distortion is first introduced and (2) adaptive spatial alignment, which arises unconsciously and contributes to a reduction of reaching errors over time (Redding & Wallace, 1993; 1996). More current research refers to these processes as explicit and implicit visuomotor adaptation, respectively (Taylor & Ivry, 2014; McDougle et al., 2015; Poh et al., 2016; Neville & Cressman, 2018). Presently, the contribution of explicit and implicit adaptation to bimanual transfer, as well as retention of visuomotor adaptation in the trained and untrained hand, is unclear. The purpose of the current study was twofold. First, we looked to establish the role of explicit and implicit processes in intermanual transfer of visuomotor adaptation when awareness of the visuomotor distortion was manipulated. Secondly, we set out to determine their contributions to the retention of visuomotor adaptation in both hands.

This review of literature will first outline the mechanisms underlying goal-directed actions and the adaptation of these movements to meet changing environmental demands. Next, the role of explicit and implicit processes in visuomotor adaptation will be discussed, as well as how their contributions to visuomotor adaptation can be assessed. This will be followed by an examination of the transfer of visuomotor adaptation between hands (i.e., from the trained to untrained hand). Retention of aftereffects in the form of recall seen in the trained hand will then be discussed in greater detail. Finally, the literature review will conclude with the rationale for the proposed experiment and outline the hypotheses regarding the expected results.

## 2. Goal-directed movements

Goal-directed movements require complex sensorimotor transformations, engaging many levels of the central nervous system (CNS). For example, when reaching to a visual target, the CNS uses vision of the limb and target position, as well as proprioceptive information regarding the reaching hand to correctly plan and execute the required movement (Jeannerod et al., 1988). It has been suggested that within the CNS there is an internal representation of the sensorimotor system, termed an internal model, that model that facilitates the transformation of incoming sensory information to appropriate motor commands (Francis & Wonham, 1976; Wolpert et al., 1995; Shadmehr et al., 2010). The internal model is comprised of an inverse model and a forward model. The inverse model makes use of incoming sensory information (e.g., visual and proprioceptive information related to target and hand positions) to determine the motor commands required for the hand to get to the target. The forward model uses a predicted state estimate, including predicted sensory information, as a baseline with which to compare incoming sensory information (Wolpert & Ghahramani, 2000). In the case where a sensory discrepancy arises between the predicted and actual limb states, the internal model utilizes the predicted errors (i.e., distinction between the predicted and true limb position) to update (i.e., adapt) motor commands as needed in order to accurately perform a goal-directed movement (i.e., land on the target; Wolpert & Kawato, 1998).

### 3. Motor adaptation

Practice and experience performing a novel motor task can give rise to the formation of a new motor pattern (i.e., internal model), that is stored and recalled at a later time when needed (Bastian, 2008). The acquisition of a novel motor task is just one form of motor learning. Motor adaptation can also be considered a form of motor learning (Bastian, 2008), as it requires a new internal model (i.e., updating of a previous one), and demonstrates an improvement in motor performance of a well-learned movement through practice or experience to meet changing environmental demands (Krakauer, 2009). Motor adaptation, specifically visuomotor adaptation, has been extensively examined in the laboratory by modifying the visual environment in which participants perform goal-directed movements. The visual environment is modified by having participants reach while wearing laterally displacing prism goggles, or by having them reach in a virtual reality environment in which a cursor on a screen misrepresents where their hand is in space (Harris et al., 1963; Kagerer et al., 1997; Rossetti et al., 1998; Krakauer et al., 1999; 2000;

Fernández-Ruiz et al., 2000; Hwang et al., 2006; Cressman & Henriques, 2010; Taylor et al., 2011).

When participants initially reach within these novel visual environments, they generally have large reaching errors. For example, if a cursor's trajectory on the screen is rotated clockwise (CW) relative to actual hand motion, participants initially reach so that the cursor lands to the right of the target. However, over trials, participants adapt their movements so that the cursor accurately lands on the target. In other words, participants adapt their motor commands after experiencing reaching errors in which their "seen" hand (i.e., the cursor) does not land on the target by reaching to the left of the target (Wolpert & Kawato, 1998; Krakauer et al., 1999; Wolpert et al., 2001). Moreover, if the rotated visual feedback is then removed (i.e., participants no longer reach with the visuomotor distortion), participants continue to reach left of the target, as if they were still influenced by the visual distortion (Baraduc & Wolpert, 1998; van Beers et al., 2002; Buch et al., 2003; Cressman & Henriques, 2010; Bond & Taylor, 2015). These changes in movements are referred to as aftereffects and are taken as evidence that the internal model has been updated.

In general, visuomotor adaptation is studied within paradigms involving three phases of testing: a baseline phase, a learning or training phase, and a post-test phase. The baseline phase, or pre-test, assesses how participants reach prior to the introduction of the environmental change. Within the learning, or testing phase, participants are introduced to the visual distortion. Thus, in order to accurately reach to the target within this phase, participants must adapt their movements to counteract the visual distortion. The post-test is performed in similar conditions as the pre-test, such that reaches are completed in the absence of visual feedback (Ghahramani et al., 1996; Baraduc & Wolpert, 2002; Krakauer, 2009; Cressman & Henriques, 2010; Bond & Taylor, 2015), or with visual feedback that is aligned with their hand position (Buch et al., 2003; Heuer & Hegele, 2008; Benson et al., 2011; Wang & Lei, 2015). If visuomotor adaptation has occurred, reaching errors in the baseline and post-test will differ (Redding & Wallace, 1996; Wolpert & Kawato, 1998).

## 4. Mechanisms underlying visuomotor adaptation

Traditionally, visuomotor adaptation has been proposed to arise implicitly (i.e., unconsciously) due to sensory prediction error-based learning, modeled as changes to the internal model. Recently, other non-model processes have been suggested to contribute to visuomotor adaptation. These processes include use-dependent learning, operant reinforcement and strategic processes. Use-dependent learning leads to changes in movement trajectories through the repetition of a movement (i.e., repetition induced bias) to a specific area of the workspace in the absence of reaching errors (Classen et al., 1998; Diedrichsen et al., 2010). Operant reinforcement is suggested to contribute to visuomotor adaptation by associating successful target attainment with a change in movement trajectory (Huang et al., 2011; van der Kooij & Overvliet, 2016). Strategic processes contribute to visuomotor adaptation when participants utilize a deliberate, cognitive strategy (engaged in on the participant's own initiative or provided by the researcher) to minimize errors in response to an environmental change (e.g., visuomotor distortion) (Mazzoni & Krakauer, 2006; Benson et al., 2011; Taylor et al., 2011; 2014, Seidler et al., 2012). In general, strategic processes can be thought of as explicit processes (Taylor et al., 2014; Bond & Taylor, 2015; McDougle et al., 2015, Werner et al., 2015, Neville & Cressman, 2018), a term used in models of visuomotor adaptation outline below, and throughout this thesis.

The notion that explicit processes contribute to visuomotor adaptation was put forth by Redding and Wallace to explain their results from prism adaptation experiments (Redding &

Wallace, 1988; 1993; 1996). They proposed that changes in movements first arise when participants put on laterally displacing prism goggles due to strategic perceptual-motor control, defined as conscious strategic processes that coordinate action and perception. For example, following reaches in which one receives visual feedback indicating that their reach was incorrect (i.e., their hand did not land on the target), participants strategically alter their trajectory to accurately complete the movement (Redding & Wallace, 1996). Following large initial changes in reaching, accuracy continues to gradually improve over the course of further reach training trials until performance returns to baseline levels. Redding and Wallace (1996) suggested that this later visuomotor adaptation was due to the combination of strategic and implicit processes. Specifically, they proposed that implicit adaptation arises gradually and reflects adaptive spatial realignment, where visual and proprioceptive maps are realigned to reduce reaching errors (Redding & Wallace, 1996).

More recently, Taylor, Krakauer, and Ivry (2014) have also suggested that explicit and implicit processes contribute to visuomotor adaptation during reach training trials. While they do not use the same terminology as put forth by Redding and Wallace (1996), their model incorporates similar processes, with a similar time-course. Specifically, Taylor and colleagues (2014) propose that conscious, explicit processes initially give rise to visuomotor adaptation through the reduction of large systematic errors (i.e., the difference between target and visual feedback locations), experienced when first introduced to a visuomotor distortion. In contrast, unconscious implicit processes are driven by sensory-prediction error signals (i.e., the difference between aiming direction and predicted feedback locations). While these implicit processes are also engaged when first introduced to the visuomotor distortion, they have been shown to increase in magnitude over the course of training (Taylor et al., 2014). The sum of explicit and implicit processes is assumed to reflect the extent of visuomotor adaptation observed.

The notion of two processes following different time scales is also present in the two-state model put forth by Smith and colleagues in 2006 to explain how reaching dynamics are adapted when reaching in a velocity-dependent force-field. Specifically, Smith and colleagues proposed that a fast process initially contributes to motor adaptation by immediately reducing movement errors during the first few reach training trials when exposed to a perturbation. This fast process is suggested to have poor retention. At the same time, a slow process is engaged, which responds slowly to reaching errors throughout reach training trials. The slow process is better retained compared to the fast process. More recently, Taylor and colleagues (McDougle et al., 2015), have suggested that the fast and slow processes within Smith and colleagues' (2006) two-state model can be mapped onto their explicit and implicit processes, respectively. The fast explicit process is responsible for rapid decreases in systematic errors by exploring proper reaching strategies when a visual distortion is first introduced during reach training trials, while the slow implicit process is responsible for continual small reach adjustments to reduce sensory-prediction errors (Taylor et al., 2014).

Collectively, all of the models outlined above describe a similar time-course for the engagement of explicit and implicit visuomotor adaptation processes. Moreover, they suggest an independent relationship between the two processes. Previous accounts had indicated that the implicit process either (1) replaced the explicit process, (2) emerged from the explicit process, or (3) operated independently (Willingham, 1998; 1999; Sulzenbruck & Heuer, 2009). Work by Sulzenbruck and Heuer (2009) support the "independence hypothesis," where explicit and implicit processes operate independently of each other. In accordance with these findings, the models described above regard explicit and implicit contributions to visuomotor adaptation as independent processes, which amount to the extent of visuomotor adaptation achieved (Sulzenbruck & Heuer, 2009; Taylor et al., 2011; 2014; Bond & Taylor, 2015; Poh et al., 2016; Neville & Cressman, 2018).

## 5. Manipulations of explicit and implicit processes during motor adaptation

The magnitude of explicit and implicit contributions to visuomotor adaptation has been shown to change with experimental manipulations. For example, being aware of a visuomotor distortion or environmental change has been shown to limit implicit visuomotor adaptation (Kagerer et al., 1997; Hwang et al., 2006; Anguera et al., 2010, Benson et al., 2011; Werner et al., 2015; Neville et al., 2018). Awareness of the visuomotor distortion has been manipulated indirectly, by changing the size of the initial error signal experienced by participants (i.e., by introducing the visuomotor distortion abruptly compared to increasing its size gradually throughout training, or introducing a large versus small visuomotor distortion), or directly, by the experimenter providing insight into the visual distortion and/or how to counteract it. Kagerer and colleagues (1997) found that participants who were introduced to an abrupt 90° cursor rotation reported being aware that the environment had changed, while other participants, who were introduced to the 90° cursor rotation gradually over the course of 540 trials, remained unaware of the change in the environment. Participants reaching with the abruptly introduced cursor rotation showed large reaching errors in the first few reach training trials, but quickly reduced their errors over trials to accurately reach the target. In comparison, participants reaching with the gradual rotation showed small reaching errors throughout reach training, such that reaching accuracy was similar to trials completed prior to the introduction of the visuomotor distortion. While performance across both groups was similar towards the end of training with the visuomotor distortion, those reaching with the gradual rotation showed greater aftereffects in the post-test compared to those who reached with the abrupt visual distortion. These aftereffects have been proposed to reflect implicit visuomotor adaptation (Kagerer et al., 1997). Other studies manipulating how the visual distortion was introduced (i.e., abruptly versus gradually) have reported similar findings with respect to aftereffects (e.g., Michel et al., 2007, Saijo & Gomi, 2010), leading to the conclusion that implicit processes have a greater contribution to visuomotor adaptation when participants are unaware of the visual distortion.

Varying the size of the visuomotor distortion has also been shown to lead to participants becoming aware or remaining unaware of the distortion, and hence influencing the contribution of implicit processes to visuomotor adaptation as measured through aftereffects. For example, Werner and colleagues (2015) had participants adapt to visuomotor distortions of various sizes (i.e., cursor rotations of 20°, 40° and 60°). They found greater aftereffects following training with the 20° rotation in comparison to both the 40° and 60° rotations, when aftereffects were expressed as a percentage of the visuomotor distortion size experienced during reach training trials. Similar to the results observed when participants were introduced to a gradual versus abrupt cursor rotation, these results suggest that smaller errors experienced during the initial portion of reach training (i.e., associated with participants being unaware of the visual distortion) lead to greater implicit adaptation. Similarly, Bond & Taylor (2015) found that training with smaller cursor distortions (i.e., 15° or 30° compared to 60° or 90°) resulted in greater implicit adaptation, when aftereffects were expressed relative to the size of the cursor rotation, compared to when training with larger cursor distortions. Interestingly, they found that the magnitude of the aftereffects was similar across all rotation sizes (8° to 15°), while the magnitude of explicit adaptation scaled with rotation size. Taken together, these studies indicate that when experiencing a small visuomotor distortion (i.e., less than 20°), participants tend to remain unaware of the visual distortion, leading to more implicit visuomotor adaptation and less explicit visuomotor adaptation. Moreover, the magnitude of implicit visuomotor adaptation seems to be limited in extent.

A number of studies have also manipulated awareness of the visual distortion directly by informing participants that the reaching environment will change and instructing them on how to counteract the upcoming visuomotor distortion (i.e., providing an explicit strategy; Mazzoni & Krakauer, 2006; Taylor et al., 2011; Benson et al., 2011; Werner et al., 2007; 2015; Neville et al., 2018). Mazzoni & Krakauer (2006) found that when participants were told that the cursor representing their hand would be rotated 45° counter-clockwise (CCW) relative to their hand motion and hence they should aim 45° CW of the target, they immediately reached correctly so that the cursor went straight to the target. Benson and colleagues (2011) also provided participants with a strategy demonstrating how to counteract the visual distortion using a modified clock face (see Appendix D). Similar to Mazzoni and Krakauer (2006), they found that participants who had been instructed on how to counteract the visuomotor distortion nearly eliminated all reaching errors within the first few reach training trials. However, the same participants had greater trial-to-trial reaching variability within the first half of reach training trials and smaller aftereffects following training. Interestingly, Neville and Cressman (2018) found that implicit adaptation, as assessed through aftereffects, was less in participants who were made aware of the cursor rotation directly compared to participants who become aware of the visuomotor distortion on their own. To summarize, awareness of a visuomotor distortion leads to benefits early on in reach training, but decreases the contribution of implicit processes overall, as seen by smaller aftereffects. Moreover, how participants are made aware of the visuomotor distortion (directly vs. indirectly), also seems to modulate the amount of implicit adaptation observed. Specifically, less implicit adaptation is observed when participants are made aware of the distortion directly compared to participants who become aware indirectly.

## 6. Assessing explicit and implicit contributions to motor adaptation

Implicit visuomotor adaptation has been traditionally assessed by examining reaching errors within a post-test (i.e., establishing aftereffects; Ghahramani et al., 1996; Baraduc & Wolpert, 1998; van Beers et al., 2002; Buch et al., 2003). The assessment of explicit visuomotor adaptation has proven to be more difficult. Post-examination questionnaires have been used in the past to establish if participants were aware or unaware of a visuomotor distortion (Hwang et al., 2006, Wang et al., 2011, Benson et al., 2011, Werner et al., 2015, Neville & Cressman, 2018). Typically, these questionnaires are completed at the end of the experiment and participants are asked if they noticed a change in the task/reaching environment. Following initial questions, participants are encouraged to describe the nature of this change and how they counteracted it to successfully reach to the target. If participants indicate that they used a strategy (e.g., reached to the left of the target), or were aware of the distorted visual feedback, they are classified as being aware of the visuomotor distortion. Initial attempts to quantify explicit contributions to visuomotor adaptation compared the performance of participants classified as aware to participants classified as unaware (Hwang et al., 2006; Heuer & Hegele, 2008; Benson et al., 2011). Adaptation observed in participants classified as aware was deemed to be explicit in nature, while adaptation observed in participants classified as unaware was deemed to be implicit in nature.

Recent studies have shown that categorizing visuomotor adaptation as explicit versus implicit based on participants' awareness of the visuomotor distortion is too strict. As mentioned previously, explicit and implicit contributions to visuomotor adaptation are present at the same time and are likely independent processes. Therefore, explicit and implicit processes can both contribute to visuomotor adaptation, in aware and unaware participants (Taylor et al., 2014, Werner et al., 2015, Neville & Cressman, 2018).

Recently, two methods have been put forth to simultaneously examine explicit and implicit contributions to visuomotor adaptation within the same participant (regardless of whether they are aware of the visuomotor distortion or not). The first method, developed by Taylor and colleagues (2014), has participants verbally report where they plan to aim prior to reaching in order for the rotated cursor to accurately hit the target. Specifically, during reach training trials with the visuomotor distortion, participants are shown a target which is surrounded by a circular array of numbered landmarks (i.e., a total of 63 numbers separated by 5.625° surround the target). Prior to each trial, participants indicate which landmark they intend to reach towards in order for the cursor to land on the target (Taylor et al., 2014). Reaching errors relative to the reported landmark and target are then used to calculate explicit adaptation (equal to the difference between target location and reported landmark) and implicit adaptation (equal to the difference between the reported landmark and actual hand aiming location). The magnitude of implicit adaptation measured by this verbal reporting method at the end of reach training has been shown to be similar to that measured in aftereffect trials, in which participants are made aware that the visual distortion has been removed and are instructed to aim so that their hand goes directly to the target (Taylor et al., 2014).

A second method currently used to assess the contributions of explicit and implicit processes to visuomotor adaptation is the process dissociation procedure (PDP). First used in cognitive psychology, the PDP was developed as a methodological tool to separate and measure the contributions of automatic and intentional processes to memory (Jacoby, 1991). This method was recently modified by Werner and colleagues (2015) to examine the contributions of explicit and implicit processes to visuomotor adaptation. Similar to initial PDP testing by Jacoby (1991), Werner and colleagues had participants complete trials with inclusion and exclusion instructions. On inclusion "aftereffect" trials, participants were asked to express, or to "use the strategies that you developed from what was learned during training". On exclusion "aftereffect" trials, participants were instructed to repress, or to "not use any strategies, and aim to the target as you would have during baseline". The difference in reaching errors on the inclusion compared to exclusion trials have been proposed to reflect explicit adaptation, whereas the errors on exclusion trials relative to the target reflect implicit adaptation.

Results attained using these two methods are similar. Specifically, using the PDP method, Neville & Cressman (2018) recently demonstrated that implicit processes took time to develop (i.e., they found that implicit adaptation gradually increased across sets of 30 reach training trials) and were limited in magnitude, as demonstrated by Taylor and colleagues using their verbal reporting method (Taylor et al., 2014; Bond & Taylor, 2015). Neville and Cressman (2018) further showed that explicit contributions to visuomotor adaptation were consistent over time, whereas implicit visuomotor adaptation partially decayed following a five-minute delay, using the PDP method. Morehead and colleagues (2015) have also shown that implicit visuomotor adaptation decays with time using the verbal reporting method. While the two methods give rise to similar patterns of results, the methods use different types of trials to arrive to their conclusions. Importantly, the PDP method assesses the contribution of both explicit and implicit processes to visuomotor adaptation following reach training, in the absence of online visual feedback. Hence, the PDP method allows for the assessment of persistent explicit and implicit contributions to visuomotor adaptation in the absence of trial-to-trial movement corrections. In contrast, Taylor's reporting method assesses explicit and implicit adaptation during reach training trials, in which movements can be continually modified (both online and offline) in response to error feedback. Moreover, in Taylor's method, the sum of explicit and implicit adaptation is equivalent to the amount of reach adaptation observed during reach training trials.

## 7. Intermanual transfer: potential role for explicit processes

Having established the role of explicit and implicit processes in visuomotor adaptation, and outlined methods to assess explicit and implicit processes, we next discuss transfer of visuomotor adaptation to the untrained hand. A number of studies have shown that visuomotor adaptation transfers to the untrained hand, such that performance in the untrained hand benefits from practice of the task with the trained hand (Cunningham & Welch, 1994; Imamizu & Shimojo, 1995; Sainburg & Wang, 2002; 2003; 2006; Wang et al., 2011; 2015; Taylor et al., 2011; Mostafa et al., 2015; Poh et al., 2016). While the transfer of visuomotor adaptation between hands is well established, the extent of transfer has been shown to vary widely (e.g., from 0 to 90% of visuomotor adaptation measured in the trained hand; Anguera et al., 2007; Balitsky et al., 2010; Carroll et al., 2014; Wang, Lei, & Binder, 2015). The range of intermanual transfer observed may have to do with which limb was initially trained. Specifically, it has been shown that transfer is greater when assessed in the dominant (right) hand after training the non-dominant (left) hand, compared to in the non-dominant hand after training the dominant hand (Sainburg & Wang, 2002; 2003; Taylor et al., 2011). That said, it should be noted that two studies have shown the opposite pattern of results (Balitsky et al., 2010; Mostafa et al., 2015), and two other studies found no differences in the magnitude of intermanual transfer, regardless of which hand was initially trained (Wang & Sainburg, 2006; Poh et al., 2016). In addition, potential differences in the extent of intermanual transfer observed may have to do with how intermanual transfer is assessed. Some experiments have examined intermanual transfer to the untrained hand during reach training trials in which cursor feedback is present and participants are able to adapt their movements based on errors experienced with the untrained hand (i.e., re-learn the task with the opposite hand; Sainburg & Wang, 2002; 2003; 2006; Wang et al., 2011). In contrast, other experiments have assessed intermanual transfer during aftereffect trials, in the absence of (rotated) cursor feedback (Anguera et al., 2007; Balitsky et al., 2010; Mostafa et al., 2015; Poh et al., 2016). While intermanual transfer has been shown to be present using both of these assessment methods, the extent of transfer established based on performance in aftereffect trials is typically lower than that measured during reach training trials with the untrained hand.

Preliminary experiments investigating the role of explicit and implicit processes in intermanual transfer looked to compare performance between aware and unaware participants. For example, Wang and colleagues (2011) had two groups of participants adapt to a cursor that was abruptly or gradually rotated 32° CCW relative to hand motion. Results indicated that participants had the same extent of transfer regardless of how the cursor rotation was introduced, such that performance with the untrained (right) hand was similar regardless if the cursor rotation was introduced abruptly or gradually when training with the left hand. Based on these results, the authors proposed that intermanual transfer arises due to implicit processes. While these findings suggest that intermanual transfer is independent of the initial size of the error signal experienced, they provide limited insight into the role of awareness and hence implicit and/or explicit processes in intermanual transfer, as (1) it is unclear if participants training with the abruptly or gradually introduced cursor rotations were aware (or unaware) of the visuomotor distortion, (2) explicit adaptation was not probed, and (3) intermanual transfer was assessed during reach training trials when the cursor rotation was present, providing participants with the opportunity to quickly adapt their movements with their untrained hand. Taylor and colleagues (2011) replicated the initial findings of Wang and colleagues (2011) in a paradigm that assessed intermanual transfer in the absence of visual feedback. However, they also did not probe participants' awareness of the visual distortion or look to measure the extent of explicit adaptation. Thus, from these results, it is difficult to draw conclusions regarding the role of explicit and implicit processes in intermanual transfer of visuomotor adaptation.

We are aware of only one study that has looked to assess both explicit and implicit contributions to intermanual transfer of visuomotor adaptation. In their study, Poh and colleagues (2016) had participants complete reach training trials with their right or left hand. During these trials, participants first reported which direction they planned to aim to in order to get the cursor (that was rotated 45° CW relative to their hand motion) to the target. Following an initial block of 40 reach training trials, or 20 reach training trials (for the remaining 9 blocks), participants reported the direction they intended to aim to and reached with no visual feedback of their hand position (i.e., no cursor was present). These no-cursor reaches were completed with the trained and untrained hands. As in Taylor's studies (2014; 2015), the reported reach direction was then compared to the actual reach direction and target location in order to isolate the contributions of explicit and implicit processes to intermanual transfer. Poh and colleagues (2016) found that when both hands moved in the same horizontal plane, explicit contributions to visuomotor adaptation showed complete intermanual transfer, such that approximately 22°, or 100% of explicit adaptation measured in the trained hand transferred to the untrained hand. In contrast, the transfer of implicit adaptation was incomplete (i.e., 11.5°, or 48% of implicit adaptation observed in the trained hand transferred to the untrained hand). Interestingly, these results are the first to demonstrate that both explicit and implicit processes may contribute to intermanual transfer.

## 8. Retention in the motor system: potential role for explicit processes

Recently, it has been suggested that explicit processes may also play a significant role in the retention of visuomotor adaptation. In general, the amount of visuomotor retention observed is dependent on the assessment task used and the length of time between initial training and the retention test (Yamamoto et al., 2006, Nourouzpour et al., 201; Maksimovic & Cressman, 2018). Retention of visuomotor adaptation in the form of recall is assessed by having participants perform a second post-test, in which reaches are performed without cursor feedback some time after the first post-test (where reaches were also completed without cursor feedback). In contrast, retention in the form of savings is assessed by reintroducing a previously encountered visuomotor distortion and having participants re-learn how to counteract it (Caithness et al., 2004; Klassen et al., 2005; Krakauer et al., 2005). With respect to the recall of visuomotor adaptation, Maksimovic and Cressman (2018) showed that aftereffects were still present four days following initial training with a 30° cursor rotation, though they were smaller in magnitude compared to following initial training (7° on the $5^{th}$ day vs 24° on the $1^{st}$ day). Yamamoto and colleagues (2006) have further shown that aftereffects can last up to a year following initial training with a joystick, which required participants to grasp a manipulandum and move their wrist in order to produce movements of the cursor on the screen. In particular, they showed recall of aftereffects ranging in magnitude from 59% to 91% of those observed following initial training, on a retention test approximately one year following initial training (384-418 days later).

Evidence of retention via savings (i.e., faster re-learning upon re-exposure to a previously encountered visuomotor distortion) has also been shown 24 hours, 48 hours and up to one week after the initial training period (Klassen et al., 2005; Caithness et al., 2004; Krakauer et al., 2005). For example, Klassen et al., (2005) had participants reach with a 30° CCW visuomotor distortion that was introduced either gradually or abruptly. Following a 24-hour period, participants returned and trained with the same visuomotor distortion. For all participants, performance during the second session of testing showed a faster rate of learning (i.e., directional errors decreased faster) compared to the initial testing session. Similarly, Caithness et al., (2004) found that participants showed evidence of savings following re-exposure to a 30° CCW visuomotor distortion 48 hours after initial training. With respect to long-term savings, Krakauer et al., (2005) found evidence of savings seven days following initial training. In fact, the week-long break between the first and subsequent training sessions led to greater savings than that seen with a break of only 24, or 48 hours (i.e., reaches were adapted approximately 24% faster following a seven day break vs. 17% and 21% faster following a one and two day break respectively, compared to an initial learning rate).

Recently, Morehead and colleagues (2015) have attributed retention, particularly in the form of savings, to the recall of aiming strategies (explicit adaptation), rather than retention of an updated internal model (implicit adaptation). Specifically, they only observed faster re-learning for participants who adapted to large visuomotor perturbations (45° and 60° vs. 15°), and these savings were accompanied by recall of an explicit aiming strategy (as established via Taylor's verbal reporting method). In contrast, Morehead and colleagues (2015) did not find evidence of savings with respect to implicit adaptation.

## 9. Purpose and research questions

Previous work has implicated explicit processes in both intermanual transfer and retention of visuomotor adaptation. These conclusions have been drawn from changes in verbal reports indicating where participants plan to reach to (Taylor et al., 2014; McDougle et al., 2015; Poh et al., 2016). As outlined above, this method of assessing explicit and implicit contributions to visuomotor adaptation allows participants to make trial-to-trial adjustments in their reaching movements (and hence reported aiming direction), as visual feedback of their hand is typically provided in the form of a rotated cursor on the screen during the reach training trials. In the current research, we look to extend these preliminary findings and establish the role of explicit and implicit contributions to intermanual transfer and retention of visuomotor adaptation using Werner and colleagues' (2015) PDP method, in which participants reach in the absence of visual feedback, and consequently are not able to adjust their reaches over trials. Moreover, we look to determine if the contributions of explicit and implicit adaptation to intermanual transfer and retention of visuomotor adaptation are dependent on how participants are made aware of the visuomotor distortion.

The current research questions are: (1) Do explicit and implicit processes contribute to intermanual transfer of visuomotor adaptation?, (2) Is the contribution of explicit and implicit processes to intermanual transfer of visuomotor adaptation dependent on how participants are made aware of the visual distortion?, and (3) Are explicit and implicit contributions to visuomotor adaptation retained in the trained and untrained hand for 24 hours following initial training? To address these questions, explicit and implicit contributions to visuomotor adaptation were assessed in the trained and untrained hands using the PDP method of Werner and colleagues (2015) on 2 consecutive testing days. The PDP procedure was chosen as it allows for the assessment of explicit and implicit visuomotor adaptation after reach training has occurred, when explicit and implicit contributions to visuomotor adaptation are assumed to have stabilized. Three groups of participants were recruited. Instructions to the groups regarding the visuomotor distortion differed in order to manipulate how awareness of the visual distortion was achieved. One group (i.e., the Strategy group) was provided with a strategy describing the nature of the upcoming visual distortion and how to counteract it. A second group (i.e., the No-Strategy group) was not informed that a cursor rotation would be introduced nor told how to counteract it. However, similar to the Strategy group, they were asked to use any aiming strategy that they had developed throughout reach training during the PDP trials. The last group, the Control group of participants, were not informed of the rotation, nor were they asked to use any aiming strategy during the PDP trials. Instead, in all "PDP" trials, they were instructed to reach so that their hand went directly to the target. This group of participants was included as we questioned if merely providing instructions indicating that participants should engage in a strategy alters their awareness of the visuomotor distortion and hence the contributions of explicit and implicit processes to intermanual transfer and retention of visuomotor adaptation.

Based on previous literature, we hypothesized that all groups of participants would adapt to the visuomotor distortion such that they would reduce their reaching errors with the trained hand when reaching with the rotated cursor to return to near baseline performance levels on the initial day of testing (Krakauer et al., 1999). Furthermore, the Strategy group was expected to demonstrate the greatest explicit adaptation in the trained hand (Anguera et al., 2010; Benson et al., 2011; Neville & Cressman, 2018). Participants in the No-Strategy and Control groups were expected to demonstrate greater implicit adaptation in the trained hand compared to the Strategy group. In the two groups where explicit contributions to visuomotor adaptation were assessed (i.e., the Strategy and No-Strategy groups), explicit visuomotor adaptation was hypothesized to transfer between hands and be retained on the second day of testing. In contrast, implicit visuomotor adaptation was expected to decay across days (Neville & Cressman, 2018). With regards to the manipulation of awareness and its influence on intermanaul transfer, it was expected that the Strategy group would transfer the greatest explicit contributions from the trained to the untrained hand (Poh et al., 2016). The greatest transfer of implicit visuomotor adaptation was expected in the Control group, which was not given a strategy nor asked to use a strategy at any time when reaching. Together, these results would indicate that while explicit and implicit processes contribute to intermanual transfer and retention of visuomotor adaptation, their contributions are dependent on how one is made aware of the visuomotor distortion. Moreover, these results would suggest that merely asking participants to engage in strategic reaching alters the contribution of explicit and implicit processes to visuomotor adaptation.

## Chapter II: Research Article

Bimanual transfer and retention of visuomotor adaptation is driven by explicit processes

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Keywords:
Visuomotor Adaptation
Bimanual Transfer
Retention
Implicit
Explicit

## 1. Introduction

Reaching with altered visual feedback of the hand's position in a virtual reality environment leads to reach adaptation in the trained hand, and also in the untrained hand (Cunningham & Welch, 1994; Sainburg & Wang, 2002; Anguera et al., 2007; Carroll et al., 2014). The phenomenon of intermanual transfer of visuomotor adaptation has been studied by having participants reach to visual targets with a single hand while seeing a cursor on a screen that is misplaced relative to their actual hand position (e.g., the cursor's trajectory is rotated relative to actual hand motion). Following these reach training trials with the trained hand, participants are asked to reach to targets with the opposite (untrained) hand in the presence (Sainburg & Wang, 2002; 2003; 2006; Wang et al., 2011) or absence of the visuomotor distortion (Anguera et al., 2007; Balitsky et al., 2010; Taylor et al., 2011; Mostafa et al., 2015).

Initial work suggested that intermanual transfer of visuomotor adaptation arises because the underlying processes are effector independent (Taylor & Heilman, 1980). In other words, both hands have shared access to a sensorimotor map (Taylor & Heilman, 1980), that has been adapted through error-based motor learning, where motor commands are adapted to minimize the difference between predicated and actual sensory feedback experienced (Wolpert et al., 1995). This explanation for intermanual transfer of visuomotor adaptation has recently been called into question given that the extent of transfer has been shown to vary depending on experimental design. Specifically, the method of assessment (i.e., cursor present vs. absent; Sainburg & Wang, 2002; Anguera et al., 2007; Taylor et al., 2011) influences the extent of intermanual transfer observed, with the extent of transfer established in the absence of the visuomotor distortion is typically lower than that measured in the presence of the visuomotor distortion. The extent of transfer has also been shown to be dependent on which hand is trained first (Sainburg & Wang, 2002; Balitsky et al., 2010; Mostafa et al., 2015), and the location of the targets in the workspace

(Sainburg & Wang, 2006). Together, these results suggest that the two hands do not have the same access to the new sensorimotor mapping and/or that different non model-based learning processes may contribute to visuomotor adaptation in the trained hand, which are or are not accessible to the untrained hand.

In accordance with this latter suggestion, it has recently been suggested that explicit processes play a role in visuomotor adaptation (Mazzoni & Krakauer 2006; Benson et al., 2010; Seidler et al., 2012; Taylor et al., 2014; Neville & Cressman, 2018), retention of visuomotor adaptation (Morehead et al., 2015) and intermanual transfer of visuomotor adaptation (Poh et al., 2016). Explicit processes refer to cognitive strategies, provided by the researcher or engaged in on the participant's own initiative, that lead to a rapid reduction in errors following an environmental change (i.e., introduction of a visuomotor distortion; Taylor & Ivry, 2011). In contrast to implicit processes, that are driven by error-based motor adaptation as described previously, explicit processes are proposed to lead to large changes in reach trajectories when one initially reaches with a visuomotor distortion and experiences large reaching errors (i.e., a large difference is observed between the positions of the target and the on-screen cursor; Taylor et al., 2014). The magnitude of explicit adaptation in the trained hand has been shown to scale with the size of the visuomotor distortion, whereas implicit adaptation appears to reach a maximum of 8° to 15°, regardless of rotation size (Bond & Taylor, 2015; Neville & Cressman, 2018). Explicit processes have also been implicated in the retention of visuomotor adaptation observed in the trained hand through the recall of aiming strategies (Morehead et al., 2015; Haith et al., 2015; Huberdeau et al., 2015).

To establish the role of explicit processes in intermanual transfer, preliminary research assessed explicit contributions indirectly, by manipulating participants' awareness of the visuomotor distortion. Specifically, participants either reached with a cursor rotation that was introduced gradually (i.e., cursor rotation increased by small increments over trials, presumably leaving participants unaware of the perturbation) or abruptly (presumably leading to participants becoming aware of the perturbation). Using this methodology, Wang and colleagues (2011) found that the extent of intermanual transfer was similar across participants in both the gradual and abrupt cursor rotation groups. Similar findings were also shown by Taylor and colleagues (2011). Based on these results, the authors concluded that intermanual transfer is not influenced by awareness (i.e., explicit processes requiring the engagement of cognitive strategies). Instead, it was suggested that implicit processes underlie intermanual transfer of visuomotor adaptation. Critically, however, it is possible that both explicit and implicit processes may have contributed to visuomotor adaptation in the trained and untrained hands in these previous studies, regardless of how the rotation was introduced and hence participant's awareness. In support of this criticism, more recent work suggested that both explicit and implicit processes contributed to visuomotor adaptation in the trained hand simultaneously, even when adapting to small visuomotor distortions (Bond & Taylor, 2015; Neville & Cressman, 2018).

As well, recent work by Poh and colleagues (2016) established that explicit and implicit processes contribute to intermanual transfer of visuomotor adaptation within the same participants. In their study, Taylor and colleague's (2014) verbal reporting method to simultaneously establish explicit and implicit contributions to intermanual transfer. Within the reporting trials, participants had to indicate when a rotating arrow was pointing in the same direction to which they planned to reach to in order to get the cursor to the target. Following their reports, the arrow promptly disappeared, and participants reached to the target. These reporting trials were completed with both the trained and untrained hands after performing reach training trials with the trained hand in which a cursor was rotated 45° relative to hand motion. The difference between the reported direction and target was used to establish explicit adaptation, while the difference in actual hand aiming direction and reported direction was used to establish implicit adaptation. Poh et al. (2016) found that when both the trained and untrained hands moved in the same horizontal plane, explicit contributions to visuomotor adaptation showed complete transfer between hands, such that approximately 22°, or 100% of the explicit contributions measured in the trained hand transferred to the untrained hand. In contrast, transfer of implicit adaptation was incomplete across hands, with only 11.5°, or 48% of implicit contributions in the trained hand, transferring to the untrained hand.

In the current research, we looked to extend these findings by asking if the contributions of explicit and implicit adaptation to intermanual transfer changes depending on how participants were made aware of the visuomotor distortion. We have recently shown that the contributions of explicit and implicit processes to visuomotor adaptation in the trained hand are modified depending on whether participants were made aware of the visuomotor distortion directly by the experimenter or become aware of the distortion indirectly when reaching in the new visuomotor environment (Neville & Cressman, 2018). In order to probe the role of awareness instructions on intermanual transfer of explicit and implicit visuomotor adaptation, the process dissociation procedure (PDP) used by Werner and colleagues (2015) was adopted. The PDP was first used in cognitive psychology to measure the contributions of two different sources of memory processing (i.e., familiarity and recollection; Jacoby, 1991). It was then modified by Werner and colleagues (2015) to examine the contributions of explicit and implicit processes to visuomotor adaptation in the trained hand by having participants reach with specific instructions following reach training trials with a visuomotor distortion. Participants completed inclusion trials, in which they were asked to express, or to use any strategy that they learned during training (to assess explicit plus implicit adaptation). During exclusion trials, participants were instead instructed to repress, or to not use any strategies, and aim to the target as they would have during baseline (to assess implicit adaptation). The difference in reaching errors on the inclusion compared to exclusion trials was considered to reflect explicit visuomotor adaptation, whereas the error on exclusion trials relative to the target was considered to reflect implicit visuomotor adaptation. In contrast to Taylor and colleagues' (2014; 2016) verbal reporting method, using the PDP method allows one to manipulate the instructions provided to participants regarding the introduction of the visuomotor distortion, and hence how participants are made aware of the visual distortion. This is not possible with Taylor and colleagues' reporting method. In fact, the researchers make it clear that participants should not be made directly aware of the visuomotor distortion when their paradigm is used (Taylor et al., 2014), presumably because participants would continue to report the same number/aiming strategy.

In addition to establishing whether the contributions of explicit and implicit processes to intermanual transfer of visuomotor adaptation are dependent on how participants are made aware of the visuomotor distortion, we looked to determine if these contributions are retained in the trained and untrained hand for 24 hours following initial training. To address these questions, explicit and implicit contributions to visuomotor adaptation were assessed in the trained and untrained hands using the PDP framework over two consecutive testing days. Specifically, participants reached with the visuomotor distortion on a first day of testing with their (trained) left hand and one day later on a second day of testing with their (untrained) right hand. Explicit and implicit adaptation in both the trained (left) and untrained (right) hands were assessed within sets of trials with no visual feedback of cursor position before and after reach training blocks on both days of testing. Participants were either assigned to a Strategy group, a No-Strategy group, or a Control group, which differed with respect to instructions provided in order to manipulate how awareness of the visual distortion was achieved. Specifically, participants in the Strategy group were provided with a strategy describing the nature of the visuomotor distortion and how to counteract it. Participants in the Strategy and No-Strategy groups completed both inclusion and exclusion trials as in Werner et al. (2015). Participants in the Control group were instructed to reach so that their hand went directly to the target in all ‘PDP trials’ (i.e., all PDP trials were exclusion trials), and hence aiming strategies were never probed. All participants completed a post-experiment questionnaire to assess awareness of the rotation when reaching with either hand at the end of the experimental testing session on the second day.

We had hypothesized that the Strategy group would demonstrate the greatest explicit contribution to visuomotor adaptation in the trained hand (Anguera et al., 2010; Benson et al., 2011; Neville & Cressman, 2018). For the Strategy and No-Strategy groups, where explicit contributions to visuomotor adaptation were assessed, explicit visuomotor adaptation was hypothesized to transfer between hands and be retained on the second day of testing. In contrast, implicit visuomotor adaptation was expected to decay over time (Neville & Cressman, 2018). With respect to the manipulation of awareness and its influence on intermanual transfer, we had expected that participants who were made aware of the distortion directly (i.e., provided with a strategy), would transfer the greatest explicit contributions from the trained to the untrained hand. The greatest transfer of implicit visuomotor adaptation was expected in the Control group, who was not given a strategy or asked to use a strategy when reaching. Together, these results would indicate that explicit and implicit processes contribute to the intermanual transfer and retention of visuomotor adaptation, but that their contributions were dependent on how one is made aware of the visuomotor distortion.

## 2. Methods

### *2.1 Participants*

Sixty participants, aged 19-30 years (M = 22 years, SD = 2.5), from the University of Ottawa community were recruited to participate in this study. All participants were naïve to the purpose of the study and had never participated in a visuomotor adaptation study involving reaching to targets with misaligned visual feedback of their hand position. In addition, participants self-reported having normal or corrected-to-normal vision, and no neurological, sensory or motor dysfunction. All participants provided written informed consent and the experiment was approved by the University of Ottawa Research Ethics Board.

Prior to starting the experiment, participants completed the modified version of the Edinburgh Handedness scale to ensure that they were right-hand dominant (M = 80, SD = 16.8) (Appendix C: Oldfield, 1976). Participants then completed testing over 2 consecutive days. The first session lasted approximately 40 minutes, while the second session (taking place approximately 24 hours later) lasted 25 minutes. Participants were assigned to one of three groups: i) a Strategy group (n=20), ii) a No-Strategy group (n=20), or iii) a Control group (n=20). To note, pilot testing was conducted on the Strategy group (n=12). The remaining participants were randomly assigned. One participant from the Strategy group was removed from the analyses and results reported below due to their reaching errors falling 3 standard deviations above the group's mean.

### *2.2 Experimental apparatus and set-up*

Participants were seated comfortably in a height-adjustable chair located in front of the experimental apparatus. They were asked to grasp the handle of a two-joint robot manipulandum (KINARM; Kingston, Canada) that moved in a 70 cm by 36 cm work area. Visual targets were projected from a downward facing monitor (EzSign model 47LD452B; refresh rate 60 Hz; LG Seoul, South Korea), located 20.5 cm above a reflective surface that was located 20.5 cm above the robot handle. Thus, visual stimuli appeared to lie in the same plane as the reaching hands (Figure 1A). Participants' view of their limbs was obstructed by a black cloth draped between participants' shoulders and the apparatus. The lights in the room were turned off once participants were comfortably seated and ready to begin testing.

During testing, the location of the reaching hand (left or right) holding the robot manipulandum was displayed as a white circular cursor (1 cm in diameter) on the reflective surface. At the beginning of a trial, the robot brought the hand to the home position (1 cm in diameter), which was located along body midline, approximately 20 cm in front of a participant's chest. Participants then reached to one of three potential visual targets, which were represented by green circles (1 cm in diameter) and located 15 cm away from the home position. Specifically, the center target was straight-ahead, aligned with body midline, and the remaining two targets were positioned either 52° CW or CCW with respect to straight-ahead. The targets were presented randomly, such that each target was displayed an equal number of times throughout the testing block.

### *2.3 Experimental procedure*

Upon receiving confirmation that participants were ready to begin, the experimenter provided a brief explanation of the tasks detailed below and participants were made aware of the testing procedure.

All participants completed 4 testing blocks on the first testing day, and 3 testing blocks on the second testing day (see Figure 2). Specifically, testing Blocks 1 and 3 on Day 1 were completed with the left non-dominant hand, Block 2 on Day 2 with the right dominant hand, and all remaining blocks were performed with both hands. The hand used to begin these remaining blocks was counterbalanced across participants. Within Block 1, participants completed 39 reaches with the left hand; 36 trials were reach training trials with aligned visual feedback of the hand, such that the position of the cursor on the screen accurately depicted the position of the participant's hand. The remaining 3 trials were catch trials, in which no visual feedback was provided (i.e., the cursor was absent). The catch trials were randomly interspersed throughout the 36 trials, such that 1 catch trial occurred every 12 trials. These trials were included as a means of measuring baseline levels of performance during aligned reach training and were compared to catch trials within rotated reach training blocks to confirm that participants adapted their movements to the visuomotor distortion. Block 2 consisted of 36 PDP trials, which were divided into 18 trials per hand. Following the PDP trials, participants performed 120 reach training trials with rotated visual feedback of their left hand in Block 3, such that the cursor's trajectory was rotated 40° clockwise (CW) relative to participants' hand motion. 10 additional catch trials were interspersed randomly within the rotated reach training trials (1 every 12 trials), for a total of 130 trials. Testing on Day 1 concluded with one final block of 36 PDP trials, 18 trials per hand (Block 4).

On the second day of testing, participants completed another block of 36 PDP trials (18 trials per hand; Block 1). Following this, participants performed 72 reach training trials in Block 2 with the same rotated visual feedback experienced on the first day of testing (i.e., the cursor's trajectory was rotated 40° CW relative to a participant's hand trajectory), but this time the trials were completed with the right (dominant) hand. Six catch trials were included in the block. The final block on Day 2 consisted of 36 PDP trials (18 trials per hand; Block 3). Once all reaches were completed, participants answered a series of questions to assess their awareness of the cursor rotation on both testing days. The questions were given in accordance with the questionnaire of Benson and colleagues (2011; see Appendix E).

*2.4.1 Reach training trials*

To perform a reach training trial, participants were instructed to reach to the target as quickly and accurately as possible in such a way that the white cursor landed on the target. To begin these trials, participants firmly grasped the robot manipulandum. The robot then moved the participant's hand so that their hand and cursor were at the home position. The hand was held at the home position for 500 ms. After this time, the home position and cursor disappeared, and one of the three green targets appeared. This was the cue for participants to start their movement. Once participants had moved 7 cm away from the starting position, they saw the white cursor again, representing their current hand position. This position corresponded to the location at which peak velocity was typically achieved, hence limiting participants' ability to make corrections early in the movement in response to online visual feedback (Kuang & Gail, 2015).

As indicated above, the first testing block required participants to perform reaches with aligned visual feedback of their hand position, such that the white cursor accurately represented where the hand was located in the work area (Figure 1B). During Block 3 on Day 1 and Block 2 on Day 2, participants reached to targets with misaligned visual feedback of their hand position. Specifically, the trajectory of the cursor was rotated 40° CW from a participant's hand trajectory. Thus, participants had to reach 40° CCW, or in a leftward direction from the target, to have the cursor accurately land on the intended target (Figure 1C).

Once the cursor stopped on the green target (i.e., the center of the cursor and the center of the target were within 0.5 cm), the target disappeared, and the trial was considered complete. The participant's hand was held at the final position for 500 ms. Following this delay, the robot passively returned the hand to the starting position (movement time = 1000 ms in duration). The robot handle followed a linear grooved path from the target position to the home position and no visual feedback was provided. If participants attempted to move outside of the linear path, a resistance force (proportional to the depth of penetration with a stiffness of 2 N/mm and a viscous dampening of 5 N/mm) perpendicular to the grooved path was produced. The position of the KINARM robot was recorded at a sampling rate of 1000 Hz, with a spatial accuracy of 0.1 mm.

Randomly interspersed catch trials were included in the reach training trials. These catch trials were similar to reach training trials, such that participants began their reach at the home position and reached to one of the three visual targets. However, no visual feedback regarding the hand position was provided at any time during the reach trajectory (Figure 1D). A trial was considered complete once velocity decreased below 0.01m/s and participants held their final hand position for 500 ms. Once completed, the visual target disappeared and the participant's hand was moved back to the home position following a linear grooved path, as described above.

*2.4.2 Process dissociation procedure (PDP)*

Participants assigned to the Strategy and No-Strategy experimental groups performed 36 total trials in each PDP block. 18 of these trials were performed with the right hand and the other 18 with the left hand. The 18 trials for each hand were further divided into 9 exclusion trials and 9 inclusion trials (3 to each target). The order in which participants completed the exclusion and inclusion trials, as well as the hand that participants used first (i.e., left or right hand), were counterbalanced across participants. Participants performed all 18 trials of a certain type (exclusion or inclusion), 9 with each hand, before performing the second type of trials (inclusion or exclusion). In the exclusion PDP trials, participants were asked to "refrain from using a strategy or anything you have learned during reach training trials, when reaching to the targets, and reach so that your *hand* lands on the target." In the inclusion trials, participants were instructed to "use any strategy you have developed or use anything you have learned during reach training trials, to reach to the targets, so that your *cursor* lands on the target." Blocks of PDP trials were performed prior to the introduction of the rotation (Day 1, Block 2 and Day 2, Block 1), as well as after rotated reach training on both days of testing (Day 1, Block 4 and Day 2, Block 3), for a total of 4 blocks of PDP trials across both testing sessions (Figure 2).

Similar to the catch trials, participants began these PDP trials by grasping the robot handle and holding the handle at the home position for 500 ms. A visual target then appeared at one of the three designated locations and the home position disappeared, cuing participants to start their movements. Participants reached with no visual feedback of their hand position. A trial was considered complete once participants had stopped moving (i.e., velocity decreased below 0.01 m/s and a final hand position was held for 500 ms). At that time, the robot passively moved the hand back to the home position following a linear grooved path.

Participants assigned to the Control group also completed 36 trials within each PDP Block, separated into 2 sets of 18 trials (i.e., 2 x (9 trials with the left hand + 9 trials with the right hand)). These participants did not receive the instructions indicated above. Instead, they only received the second part of the exclusion trial instruction on all trials, "reach so that your *hand* lands on the target". This particular group was included as we hypothesized that giving participants in the other two groups inclusion instructions during assessment would promote the engagement of explicit processes, hence decrease the contributions of implicit processes (Leow et al., 2017; de Brouwer et al., 2018).

#### *2.4.3 Groups of participants: Explicit strategy (Appendix D)*

Immediately following the first block of PDP trials on Day 1 (Block 2, Figure 2), participants assigned to the Strategy group were informed of the upcoming rotation and instructed on how to counteract it. Specifically, these participants were shown a modified clock face, similar to that used by Benson et al. (2011; Appendix D), and told where they needed to aim in order to get the cursor to the target. For example, in order to accurately reach the intended target, they would be required to aim two numbers to the left of the target to compensate for the 40˚ CW rotation. To ensure that participants understood the nature of the rotation and the strategy provided to them, they were asked to draw an arrow towards where they needed to reach to counteract the visuomotor distortion for one of the three targets. Once a participant demonstrated that they understood the strategy and verbally confirmed that they understood, they were instructed to use the strategy when reaching to all three of the targets. Following this, testing resumed. Participants were reminded to use the strategy that they were provided with at the midway point of the rotated reach training trials on Day 1 of testing (i.e., after 65 trials). They were not reminded of the strategy on Day 2. Participants in the No-Strategy and Control groups were not provided with a strategy, nor told that a visuomotor distortion would be introduced. Instead, they sat quietly for approximately 5 minutes after Block 1 on Day 1, before testing resumed.

#### *2.4.4 Post-experimental questionnaire (Appendix E)*

After having completed testing on Day 2, all participants were asked a series of questions to assess their awareness of the visuomotor distortion introduced during the reach training trials. The questions asked were the same as those used by Benson et al. (2011; Appendix E). Specifically, the post-experimental questionnaire began by asking participants if they noticed the task change or get harder during testing on Day 1 with the left hand. If participants answered yes, they were asked if they knew how the task changed or became harder. If a response related to rotated feedback or a rightwards cursor was given, they were asked by how many degrees they thought the cursor/trajectory was deviated and which direction they pushed to counteract it. Participants were only classified as being aware of the visual distortion if they reported using a strategy (e.g., reaching to the left of the target), or noticed a change in how they had to reach to get the cursor to the intended targets (i.e., the cursor did not go where they intended it to). Participants were then asked the same questions regarding testing with the right hand on Day 2. If participants answered no to the first question (i.e., indicated that they did not notice the task change in any way), or provided no indication of being aware that a cursor rotation/distortion was present, they were classified as unaware. Once the questionnaire was completed, participants were debriefed on the purpose of the study, as well as how it related to the testing procedure, and its practical significance.

### *2.5 Data analyses*

All reaching trials (reach training and PDP trials) were visually screened and analyzed using custom written MATLAB programs. The start and end points of each trial were selected based on a velocity criterion, such that the start and end points were defined as when velocity first increased above or decreased below 0.01m/s for a minimum of 50 ms, respectively. For each trial, reaction time (RT), movement time (MT), and angular error at peak-velocity (PV) were determined, such that the angular error was defined as the difference between a vector joining the home position to the desired target, and a vector joining the home position to the hand’s location at peak velocity.

We first looked to establish if participants adapted to the 40° cursor rotation on Day 1 with the left hand. To do this, PV angular errors were averaged over 6 consecutive reach training trials with the aligned or rotated cursors. From these average errors, initial and final PV angular errors when reaching with an aligned cursor (Block 1) and rotated cursor (Block 3) were compared using a 3 Group (Strategy vs. No-Strategy vs. Control) x 2 Cursor (aligned vs. rotated) x 2 Time (mean of first bin of 6 trials vs. last bin of 6 trials) mixed analysis of variance (ANOVA), with repeated measures (RM) on the last two factors. In addition, catch trials were used to confirm reach adaptation. Given the limited number of catch trials, PV angular errors on catch trials were averaged over 2 no cursor trials rather than 6. PV angular errors in the catch trials were then compared using a 3 Group (Strategy vs. No-Strategy vs. Control) x 3 Time (mean of first bin of 2 aligned catch trials vs. mean of first bin of 2 rotated catch trials vs. mean of last bin of 2 rotated catch trials) mixed ANOVA, with RM on the last factor.

Following this, we established if participants adapted to the 40° cursor rotation on Day 2 with the right hand. Similar to Day 1, PV angular errors were averaged over 6 consecutive reach training trials with a rotated cursor. From these average errors, initial (first bin of 6 trials) and final (last bin of 6 trials) PV angular errors when reaching with a rotated cursor (Block 2) were compared using a 3 Group (Strategy vs. No-Strategy vs. Control) x 2 Time (mean of first bin of 6 trials vs. mean of last bin of 6 trials) mixed ANOVA with RM on the last factor. In addition, catch trials were used to confirm adaptation by averaging over 2 consecutive catch trials and comparing errors in a 3 Group (Strategy vs. No-Strategy vs. Control) x 2 Time (mean of first bin of 2 rotated catch trials vs. mean of last bin of 2 rotated catch trials) mixed ANOVA with RM on the last factor.

Next, explicit and implicit contributions to visuomotor adaptation in the trained and untrained hand were established using the same PDP trials. PV angular errors were averaged across targets within each PDP block of inclusion and exclusion trials completed with the left or right hand. These average errors for each hand within each block were used to establish explicit and implicit indices according to the following formulas:

Explicit index (EI) = $M_{Inclusion} - M_{Exclusion}$

Implicit index (II) = $M_{Exclusion}$

To determine potential explicit contributions to visuomotor adaptation in both hands and how they changed over time, explicit indices were analyzed using a 2 Group (Strategy vs. No-Strategy) x 2 Hand x 4 Time mixed ANOVA, with RM on the last two factors. Since the Control group did not perform inclusion trials, the group was excluded from this analysis. Implicit indices were compared across all groups of participants using a 3 Group (Strategy vs. No-Strategy vs. Control) x 2 Hand x 4 Time mixed ANOVA, with RM on the last two factors. For the Control group, only data from 18 PDP reaching trials were included in the analysis (corresponding to the 18 exclusion trials performed by the other 2 groups of participants). For half of the participants in the Control group, these 18 PDP trials corresponded to the first set of 18 PDP trials completed. For the other Control participants, the second set of 18 PDP trials were used.

The significance value for all statistical tests was set at $p < .05$, and Bonferonni post-hoc tests corrected for multiple comparisons were used to find the locus of significant effects for all pre-planned comparisons. Partial eta squared ($\eta_p^2$) are reported as measures of effect size. All analyses were performed using the statistical software package SPSS 25 for Windows 10.

## 3. Results

### *3.1 Post-experiment questionnaire*

Participants were classified as being aware of the visual distortion if they reported i) being aware of the distortion (i.e., noted that the cursor did not go where they intended it to go), or ii) claimed to have used a strategy (i.e., “pushed” their hand left in order to successfully land the cursor on the target). Results from the post-experiment questionnaire revealed that all participants in all 3 groups were classified as aware of the visuomotor distortion when training with the trained (left) hand on Day 1 and with the untrained (right) hand on Day 2.

### *3.2 Reach performance in reach training trials*

At the end of aligned reach training, all groups reached fairly accurately such that the Strategy group reached with an average cursor PV angular error of 1.72° (*SD* = 2.16°) to the right of the target, compared to errors of 0.96° (*SD* = 1.97°) and 1.16° (*SD* = 2.75°) to the right of the target for the No-Strategy and Control groups, respectively. Figure 3A presents mean cursor PV angular errors relative to the target over reach training trials with the 40° visuomotor distortion for participants in the Strategy group (dashed line), No-Strategy group (dotted line), and Control group (solid line) with the left hand on Day 1. From this Figure, it is evident that participants adapted their reaches to the visuomotor distortion but that the extent of their adaptation was dependent on the group they were assigned to. Participants in the No-Strategy and Control groups initially showed large rightward reaching errors. In contrast, the Strategy group had smaller initial reaching errors, as they started aiming to the left of the target immediately, as instructed. Differences in performance relative to errors observed when reaching with an aligned cursor in Block 1 (i.e., Day 1) showed that participants in the Strategy group were initially reaching with an average cursor PV angular error of 0.72° (*SD* = 10.34°) left of the target compared to 26.47° (*SD* = 8.66°) and 25.86° (*SD* = 4.58°) right of the target for the No-Strategy and Control groups, respectively. By the end of rotated reach training, the Strategy group showed an average cursor PV angular error of 4.22° (*SD* = 6.39°) compared to 10.21° (*SD* = 5.62°) and 8.55° (*SD* = 6.46°) to the right of the target for the No-Strategy and Control groups. In accordance with these observations, ANOVA revealed a Group x Cursor x Time interaction [$F(2,56) = 30.916$, $p < 0.001$, $\eta_p^2 = 0.525$]. Post hoc analyses indicated that the Strategy group showed greater reach adaptation than the No-Strategy group when first introduced to the visuomotor distortion ($p < 0.001$), and at the end of the reach training trials ($p = 0.023$). Similarly, the Strategy group showed greater reach adaptation than the Control group at the start of rotated reach training ($p < 0.001$). At the end of training, the Control group did not differ significantly from the Strategy ($p = 0.153$) or No-Strategy groups ($p = 1.0$). Analyses of catch trials showed similar findings; Group x Time interaction [$F(4,112) = 6.70$, $p < 0.001$, $\eta_p^2 = 0.193$]. All groups had similar errors during the catch trials in the aligned reach training block (all $p > 0.058$). The Strategy group reached similarly in both bins of catch trials performed during rotated reach training ($p = 0.376$), but the No-Strategy and Control groups showed a significant decrease in cursor PV angular error over the course of the reach training trials (both $p < 0.004$).

Right hand reach training performance on Day 2 with the rotated cursor is shown in Figure 3B. Initial cursor PV angular errors were 5.27° (*SD* = 7.47°), 19.07° (*SD* = 12.16°), and 14.43° (*SD* = 8.62°) to the right of the target for the Strategy, No-Strategy and Control groups, respectively. Contrary to Day 1, the Strategy group was not reminded of the reaching strategy. However, as revealed by a Group x Time interaction [$F(2,56) = 5.024$, $p = 0.010$, $\eta_p^2 = 0.152$], the Strategy group showed smaller initial (i.e., 1st bin) cursor PV angular errors compared to the No-Strategy and Control groups (both $p < 0.014$). This trend was also seen at the end of rotated reach training (i.e., last bin) for the Strategy group (*M* = 1.92°, *SD* = 4.84°) compared to the No-Strategy group (*M* = 9.29°, *SD* = 7.22°; $p = 0.003$) and Control group (*M* = 8.07°, *SD* = 7.53°; $p = 0.017$), who did not differ from each other at the start or end of reach training (both $p > 0.404$). Catch trial analyses further revealed a significant main effect of Group [$F(2,56) = 5.549$, $p = 0.006$, $\eta_p^2 = 0.165$], indicating that the Strategy group reached with less error at PV compared to the No-Strategy group ($p = 0.005$). PV angular errors in the Control group did not differ statistically from either group (both $p > 0.269$). Together, these results indicate that the Strategy group adapted their reaches earlier and to a greater extent during the rotated reach training trials compared to the No-Strategy and Control groups when reaching with both the left (trained) and right (untrained) hands.

### *3.3 PDP trials: Explicit and implicit adaptation*

The magnitudes of explicit and implicit adaptation relative to baseline (i.e., PDP Time 1) are shown in Figure 4. As seen in the figure, the magnitude of explicit adaptation consistently differed across groups in PDP Blocks 2, 3 and 4. Analysis of EIs revealed a significant Group x Time interaction [$F(3,111) = 22.345$, $p < 0.001$, $\eta_p^2 = 0.377$]. Both the Strategy and No-Strategy groups showed similar EIs at PDP Time 1 (M = 0.83°, SD = 3.52°; p = 0.731), and significant changes in EIs at PDP Times 2, 3, and 4 compared to PDP Time 1 across the left and right hands (all $p < 0.024$). However, the Strategy group had greater explicit adaptation than the No-Strategy group at PDP Times 2, 3 and 4 when reaching with both the left and right hands (all $p < 0.001$). ANOVA also revealed a Time x Hand interaction [$F(3,111) = 4.814$, $p = 0.003$, $\eta_p^2 = 0.115$]. Post hoc analyses indicated that explicit adaptation was maintained at a similar magnitude when reaching with the left hand across PDP Blocks for both the Strategy (*M* = 36.61°, *SD* = 10.28°; all $p > 0.886$) and No-Strategy groups (*M* = 10.30°, *SD* = 18.13°; all $p > 0.072$). Explicit adaptation was similar when reaching with the right hand at the corresponding PDP Blocks for both groups except for PDP Block 3, where both groups showed greater explicit adaptation in the right hand compared to the left hand (Strategy group: left hand: *M* = 38.30°, *SD* = 11.36°; right hand: *M* = 41.07°, *SD* = 12.66°; No-Strategy group: left hand: *M* = 8.08°, *SD* = 18.43°; right hand: *M* = 13.10°, *SD* = 19.41°; both $p < 0.039$).

In comparison to explicit adaptation, and as shown in Figure 4, changes in the magnitude of IIs relative to PDP Time 1 were fairly small (range = 5° – 11° across all groups). Analysis of

IIs revealed a significant Group x Time x Hand interaction [$F(6, 168) = 3.269$, $p = 0.005$, $\eta_p^2 = 0.105$]. Performance between the groups at PDP Time 1 was similar for both the left and right hands (all $p = 1.0$). All groups showed significant changes in IIs when reaching with the left (trained) hand at PDP Time 2, compared to baseline (all $p < 0.002$). Post-hoc analyses revealed that the No-Strategy group ($M = 11.34°$, $SD = 6.97°$) had greater implicit adaptation when reaching with the left (trained) hand at PDP Time 2, compared to the Strategy ($M = 5.35°$, $SD = 3.86°$) and Control groups ($M = 6.32°$, $SD = 6.74°$; both $p < 0.034$), which did not differ from each other ($p = 1.0$).While the extent of implicit adaptation at PDP Times 3 and 4 in the left hand did not differ between groups (all $p = 1.0$), retention of implicit adaptation on Day 2 was only significant (i.e., different from PDP Time 1) in the Strategy and No-Strategy groups (i.e., Strategy and No-Strategy groups: PDP Times 3 and 4 vs PDP Time 1, all $p < 0.022$; Control group: PDP Times 3 and 4 vs PDP Time 1, both $p > 0.133$).

With respect to transfer of implicit adaptation to the right hand, we found that none of the groups showed significant implicit adaptation when reaching with the right hand at PDP Time 2, after training with the left hand (all $p > 0.168$). All groups only showed significant implicit adaptation when reaching with the right hand at PDP Time 4 (all $p < 0.022$), after completing the rotated reach training trials with their right hand. The magnitude of implicit adaptation was similar between groups at PDP Time 4 ($M = 5.49°$, $SD = 5.77°$; all $p > 0.516$).

Together, these results indicate that while explicit adaptation is similar in magnitude across the left and right hands, it differs in magnitude depending on how participants are made aware of the visuomotor distortion. Explicit adaptation is retained across time (i.e., for at least for 24 hours) and is the primary contributor to reach adaptation observed (at least in the Strategy group). Similarly, initial implicit adaptation differs in magnitude in the trained hand depending on how one becomes aware of the visuomotor distortion. Importantly, for our questions of interest, we did not observe significant transfer of implicit adaptation to the untrained hand, and the retention of implicit adaptation was minimal in the trained hand. Significant implicit adaptation was only seen in the right hand following rotated reach training with the right hand.

## 4. Discussion

The main objectives of the current study were to determine whether intermanual transfer of explicit and implicit adaptation are dependent on how participants are made aware of the visuomotor distortion and to establish if these contributions are retained in both the trained and untrained hands for 24 hours following initial training. Participants were assigned to a Strategy, No-Strategy, or Control group, and were required to reach with their left hand on Day 1, and their right hand on Day 2, while seeing a cursor that was rotated 40° CW relative to their hand motion. Explicit and implicit adaptation were assessed in both hands by having participants perform reaches without visual feedback of their hand within the process dissociation procedure (PDP), before and after rotated reach training at 4 time points across 2 days of testing. Using the PDP, we looked to determine group differences in the transfer and retention of explicit and implicit adaptation.

### *4.1 Visuomotor adaptation achieved during rotated reach training*

We found evidence of visuomotor adaptation in the left hand during rotated reach training trials across all groups. Interestingly, our results revealed that the extent of reach adaptation achieved during reach training trials differed between participants depending on the instructions. Participants in the Strategy group, who were made aware of the visuomotor distortion directly, demonstrated the greatest reach adaptation. It was expected that this group would have lower errors when first reaching with the visuomotor distortion compared to the No-Strategy and Control groups, as they had been given a strategy on how to counteract the distortion, and correctly get the cursor to the target (Mazzoni & Krakauer, 2006; Benson et al., 2011; Taylor et al., 2011; Neville & Cressman, 2018). What was surprising was that the participants in the Strategy group continued to reach with lower errors compared to the No-Strategy and Control groups, even at the end of the 120 rotated reach training trials. This is contradictory to previous literature, as similar performance by the end of reach training has typically been shown between Strategy and No-Strategy groups (Benson et al., 2011, Bond & Taylor., 2015; McDougle et al., 2015). In fact, work from our own laboratory found similar errors between participants provided with a strategy and those not who were not. This was observed within 30 to 60 reach training trials when participants reached with their right (dominant) hand while seeing a cursor that was rotated 40° CW relative to hand motion (Neville & Cressman, 2018).

We also found that reaching errors differed between the Strategy group and the two other groups on Day 2, when all groups completed additional reach training trials with their right hand, with no further instructions. Finally, the No-Strategy and Control groups demonstrated less reach adaptation compared to the Strategy group, even at the end of the 72 rotated reach training trials. The consistent differences observed among groups in the current study suggest that the left hand does not return to a baseline level of reaching performance when adapting to a cursor rotation when no strategy is provided. Moreover, trends in reaching errors seem to carry over to the opposite untrained (right) hand.

We chose to have participants initially reach with their non-dominant (left) hand, as work from Wang and Sainburg (2002; 2003; 2006), as well as Anguera and colleagues (2007), has shown asymmetric intermanual transfer across limbs. According to the dynamic dominance hypothesis put forth by Sainburg (2002), each brain hemisphere is specialized for stabilizing different aspects of task performance. Specifically, the hypothesis suggests that the dominant hemisphere specializes in stabilizing the initial direction of a movement and its trajectory, while the non-dominant hemisphere is specialized for stabilizing final position control. Thus, the dynamic dominance hypothesis would suggest that initially training the non-dominant hand leads to a greater transfer of initial movement direction to the dominant hand, while initially training the dominant hand leads to greater final position accuracy in the non-dominant hand. Evidence in support of the dynamic dominance hypothesis predictions regarding intermanual transfer of visuomotor adaptation has come from work by Wang & Sainburg (2002; 2003; 2006).

Given our interest in examining changes in movement planning (i.e., errors at peak velocity), we chose to initially train the non-dominant (left) hand before online corrections took place. Our results for the non-dominant (left) hand are in agreement with the dynamic dominance hypothesis, in that our participants never fully compensated for the 40° cursor rotation. Even at the end of the rotated reach training trials, participants in the No-Strategy and Control groups continued to reach with PV errors ranging between 8° and 11°, suggesting poor stabilization of initial movement direction. These errors were then corrected online so that participants landed on the target by the end of the movement. Additional research is required to determine why participants continued to reach in a similar manner on Day 2, when training the dominant (right) hand.

There has been limited research investigating differences in the extent of visuomotor adaptation across hands. Data reported by the Henriques lab tend to show smaller aftereffects in the left (non-dominant) versus right (dominant) hand (though the differences are not significant; e.g., Salomonczyk et al., 2012; Mostafa et al., 2015), while others demonstrate similar aftereffects in both hands (Sainburg, 2002; Balitsky et al., 2010; Poh et al., 2016). It remains to be determined why initially training the left hand would lead to greater reaching errors at peak velocity in comparison to initially training the right hand (e.g., as shown by Neville and Cressman, 2018).

### *4.2 Explicit and implicit adaptation during PDP trials: Trained (left) hand*

Previous literature has, for the most part, indirectly assessed explicit and implicit contributions to visuomotor adaptation. In particular, participants were categorized as either aware or unaware of the visuomotor distortion, and their resulting reach performance regarded as being either explicit or implicit in nature, respectively (Heuer & Hegele, 2008; Benson et al., 2011; Wang et al., 2011; Taylor et al., 2011). Using a similar questionnaire to that used by Benson and colleagues (2011), we found that all of our participants, regardless of the group, reported being aware of the cursor rotation when reaching with their left and right hands (i.e., on Days 1 and 2 respectively). Despite being aware of the distortion, most of our participants showed evidence of both explicit and implicit adaptation in the trained hand, suggesting that defining reach adaptation as being driven by either explicit or implicit processes based on awareness is too strict.

The PDP (Werner at al., 2015) and Taylor and colleagues' (2014) verbal report framework enable researchers to simultaneously assess explicit and implicit adaptation, independent of participants' level of awareness of the visuomotor distortion. In the current study, we established explicit and implicit adaptation in the trained (left) hand following rotated reach training using the PDP framework across most participants. However, the magnitudes of explicit and implicit adaptation differed between groups, revealing that how participants were made aware of the visuomotor distortion influenced the contribution of explicit and implicit processes.

In accordance with previous findings (Benson et al., 2011; Neville & Cressman, 2018), we found that the Strategy group showed greater explicit adaptation, when expressed in terms of magnitude or as a percentage of reach adaptation achieved, compared to the No-Strategy group (36° vs. 9°, respectively). As well, we found that the No-Strategy group showed greater magnitude of implicit adaptation (M = 11°), than the Strategy group (M = 5°), which is also shown by Benson and colleagues (2011), and Neville and Cressman (2018). Surprisingly, we found that the No-Strategy group showed greater implicit adaptation compared to the Control group (M = 6°), which is similar to that observed in the Strategy group. The Control group was included in the current experiment because we hypothesized that simply asking participants to engage in explicit processes during the assessment trials may lead to increased awareness of the visuomotor distortion, therefore promoting and/or magnifying explicit adaptation at the expense of implicit adaptation (as suggested by Leow et al., 2017; de Brouwer et al., 2018).

Given that the Control group's mean implicit adaptation was similar to the Strategy group, our hypothesis was not supported. That said, further examination of our data reveals that implicit adaptation was more similar across participants in the Control and No-Strategy groups compared to the Control and Strategy groups. Mean implicit adaptation varied greatly for participants in the Control group (range: -2.09° to 22.80°) and No-Strategy group (range: 0.03° to 32.32°). In contrast, implicit adaptation was more consistent across participants in the Strategy group (range: -0.12° to 11.35°). Five participants (or 20% of participants) in both the Control and No-Strategy groups demonstrated greater implicit adaptation than the maximum implicit adaptation achieved by participants in the Strategy group. This data suggests that not being provided with a strategy directly tends to promote implicit adaptation. Our results would further suggest that implicit adaptation is not affected by having to engage in explicit processes during assessment trials.

Although implicit adaptation was greatest in the No-Strategy group, it only achieved approximately 11°. Limited implicit adaptation has been shown by Bond and Taylor (2015), Neville and Cressman (2018), and Modchalingam and colleagues (2019), who have collectively suggested that implicit adaptation reaches a ceiling level of approximately 15°, regardless of the visuomotor rotation size that participants train with, and hence their awareness. While we did not manipulate the size of our rotation, the current experiment once again demonstrates that implicit adaptation is limited in extent and supplements previous findings by showing that this limit is present even when training the left (non-dominant) hand. Based on our findings, it seems that implicit adaptation is quite rigid (as stated by Bond & Taylor, 2015), while explicit adaptation is more flexible, and changes based on how participants become aware of the visuomotor distortion.

### *4.3 Transfer of explicit and implicit adaptation to the untrained (right) hand*

Initial literature showed that intermanual transfer was independent of whether a small (e.g., 20 to 30°) visuomotor rotation was introduced gradually or abruptly (Wang et al., 2011; Taylor et al., 2011). Based on these findings, it was assumed that intermanual transfer was driven by implicit processes, as opposed to explicit processes. However, Poh and colleagues (2016) showed that both explicit and implicit adaptation contributed to intermanual transfer when participants adapted to a larger visuomotor distortion (i.e., 45°). The authors modified Taylor and colleagues’ (2014) reporting method, such that participants indicated when a rotating arrow was pointing in the same direction as where they planned to aim before reaching. They found that participants showed transfer of explicit adaptation to the untrained hand (left or right), and that in fact, explicit adaptation transferred to a greater extent than implicit adaptation. Similar to Poh and colleagues (2016), we also found complete transfer of explicit adaptation between hands, within our Strategy and No-Strategy groups. Based on our results and those of Poh and colleagues (2016), it is evident that both hands are able to effectively utilize a learned strategy, regardless of the hand that was initially trained. In addition, explicit adaptation seems to be primarily responsible for intermanual transfer, at least when participants adapt to a large cursor rotation (i.e., at or above 40°).

In contrast to the significant transfer of explicit adaptation, we did not find significant transfer of implicit adaptation to the right hand, across any of our groups (M = 3°). In fact, significant implicit adaptation in the right hand was only observed after participants had completed reach training trials with the right hand on Day 2 of testing. Once again, we observed an upper limit to implicit adaptation of approximately 7°, which remains within the range previously shown by our lab (Neville & Cressman, 2018).

This lack of transfer of implicit adaptation to the right hand is in contrast to Poh and colleagues' (2016) recent findings, who observed that 50% of implicit adaptation transferred to the untrained hand (i.e., 11.5° of the 23° implicit adaptation observed in the trained hand transferred to the untrained hand). The magnitude of implicit adaptation Poh and colleagues (2016) observed in the trained hand is considerably larger than that observed within the current study and falls outside the maximum magnitude of implicit adaptation previously reported (e.g., Bond & Taylor, 2015; Neville & Cressman, 2018). Important methodological differences between the current study and that of Poh and colleagues (2016), as well as the placement of assessment trials within the experiments, might be responsible for the different patterns in results.

Poh and colleagues (2016) intermixed trials with the trained and untrained hand, such that visuomotor adaptation was assessed repeatedly (9x) in the untrained hand, following every 20 rotated reach training trials. Participants were also required to report their aiming direction during each assessment trial (i.e., use an arrow to indicate the direction in which they intended to reach). Contrary to Poh's (2016) design, our study used a block design, where visuomotor adaptation in the untrained limb was only assessed following a single block of 120 rotated reach training trials, and participants were never required to indicate where they intended to reach prior to the movement. Using a similar block design to the current study, early work by Taylor and colleagues (2011) also showed minimal transfer of aftereffects (reflecting implicit adaptation). Specifically, they observed that the untrained hand reached with errors of approximately 3°, following reach training trials with a cursor that was rotated 22.5°. Taken together, these findings suggest that implicit adaptation does not appear to significantly transfer between hands, regardless of the trained rotation size (e.g., smaller as in the study by Taylor et al. (2011), or larger as in the current study) when using a block design. Instead, in order for implicit adaptation to significantly contribute to intermanual transfer, the untrained hand needs to be engaged early in training. It is possible that the extent of implicit adaptation transferred to the untrained hand increases with its repeated use, as previous literature has shown that implicit adaptation gradually increases across training trials (Taylor et al., 2014; Poh et al., 2016). In contrast, explicit adaptation can be transferred to the opposite limb, regardless of experimental design (i.e., blocked versus intermixed trials), and hence whether or not the opposite (untrained) hand is engaged early on during reach training trials.

### *4.4 Retention of explicit and implicit visuomotor adaptation*

In addition to assessing explicit and implicit contributions to intermanual transfer, we looked to establish the stability of these processes in the trained and untrained hands over time (i.e., 24 hour period). Recent work by Morehead et al (2015) suggests that retention of visuomotor adaptation is driven by recall of a cognitive strategy specific to action selection, such that participants engage their adopted aiming strategy when immediately reintroduced to a large perturbation. Within their paradigm, participants were told that the cursor would occasionally change colour, indicating that "something" would change. Colour cues during rotated reach training trials were used to indicate whether or not a visuomotor distortion was present (i.e., red = distortion, white = no distortion). They found that participants who trained with a small cursor rotation (i.e., 15° CW visuomotor distortion) primarily engaged implicit processes, while participants who trained with larger rotations (i.e., visuomotor distortions greater than 45°) showed evidence of both explicit and implicit adaptation. Following a washout period, in which participants reached with an aligned cursor, participants performed a second session of rotated reach training trials without being informed that the cursor would be rotated. They observed that on the first trial, the 45° group showed immediate recall (approximately 22°) when cued, while the 15° group did not (only 2°). Thus, those who adapted their movements explicitly during initial training recalled what they had learned, while those who had adapted their movements implicitly did not. Our results support and extend these findings, such that explicit adaptation was retained across a 24 hour period. In fact, we found that 100% of the initial (i.e., PDP Time 2) explicit adaptation observed in the trained (hand) hand was retained 24 hours later. A similar amount of retention was seen in the right (untrained) hand, suggesting that explicit adaptation is also accessible to both hands 24 hours following initial training.

Similar to Morehead and colleagues (2015), and previous studies from our laboratory (e.g., Maksimovic and Cressman, 2018), we observed decay of implicit adaptation. Maksimovic and Cressman (2018) showed that initial aftereffects after training with a 30° CW visuomotor distortion decayed by 71% across a 24 hour period (i.e., from 24° to 7°). Similar results were also reported by Nourouzpour and colleagues (2015). As well, using the PDP framework, Neville and Cressman (2018) observed evidence of implicit decay within just 5 minutes. Based on these results, it seems that implicit adaptation is much less stable than explicit adaptation, further supporting the proposal that explicit processes drive the (long-term) retention of visuomotor adaptation.

## 5. Summary

Using the PDP framework, we established that intermanual transfer of visuomotor adaptation is primarily driven by explicit adaptation, regardless of whether participants are provided with a strategy or not to counteract the visuomotor rotation. Explicit adaptation observed initially in the trained hand was transferred almost 100% to the untrained (right) hand. In contrast, implicit contributions to visuomotor adaptation did not significantly transfer between hands. Explicit adaptation was also retained in both hands over testing days, while implicit adaptation decayed. Together, these findings further support that explicit and implicit processes are independent, but most importantly, they suggest that explicit processes are primarily responsible for intermanual transfer and the retention of visuomotor adaptation in both hands.

## 6. Supplemental Materials

### *6.1. PDP trials: reaction and movement time*

RT and MT during PDP exclusion trials were both assessed using a 3 Group (Strategy vs. No-Strategy vs. Control) x 2 Hand (trained (left) vs untrained (right)) x 4 Time (PDP Time 1 (Day 1, Block 2) vs. PDP Time 2 (Day 1, Block 4) vs. PDP Time 3 (Day 2, Block 1) vs. PDP Time 4 (Day 2, Block 3)) mixed ANOVA, with RM on the last two factors. As was described in the explicit and implicit analyses section (see data analysis section), only 18 PDP reaching trials for the Control group were included in the analysis (either the first 18, or the last 18 trials).

RT and MT during PDP inclusion trials were assessed using a 2 Group (Strategy vs. No-Strategy) x 2 Hand x 4 Time mixed ANOVA, with RM on the last two factors. The Control group was excluded from this analysis, as those assigned to this group did not perform inclusion trials. These variables were analyzed to establish whether instructions (i.e., engagement of cognitive processes) were linked to changes in the time required to prepare or execute a movement (Fernandez-Ruiz, 2011; Leow et al., 2017). RT and MT variability during inclusion and exclusion trials were analyzed in a similar manner. Finally, paired samples T-tests were used to determine whether mean RT and/or MT differed between inclusion and exclusion trials, for the Strategy and No-Strategy groups. Mean and variability data for RT and MT is displayed in Table S1 and S2.

Overall, RT was 402.78 ms across all exclusion trials. Analysis of RT on exclusion trials revealed an effect of Hand [$F(1,56) = 5.753$, $p = 0.020$, $\eta_p^2 = 0.093$], such that RT was longer when reaching with the right hand (*M* = 410.64 ms, *SD* = 101.13 ms) compared to the left hand (*M* = 394.92 ms, S*D* = 82.12 ms). Otherwise, RT did not vary significantly across Group or Time (both $p > 0.138$). RT variability was on average 88.86 ms (*SD* = 71.62 ms), and did not differ significantly across Group, Hand or Time (all $p > 0.293$).

RT for inclusion trials tended to be longer than exclusion trials, such that it was 441.92 ms on average across all PDP inclusion trials. In support of this observation, T-tests revealed that average RT on inclusion PDP trials across PDP Times 2, 3, and 4, with the left hand, was significantly slower for the Strategy and No-Strategy groups compared to average RT during exclusion PDP trials across the same PDP trials (both $p < 0.001$). Moreover, RT was longer for right hand inclusion trials compared to right hand exclusion trials in the Strategy group ($p < 0.001$). There was no difference in RT between the right hand inclusion and exclusion trials completed by the No-Strategy group ($p = 0.102$). Comparing RT on inclusion trials across groups, ANOVA revealed a significant Group x Time interaction [$F(3,111) = 7.027$, $p < 0.001$, $\eta_p^2 = 0.160$]. There was no difference between the 2 groups at PDP Time 1, following aligned reach training (*M* = 392.93 ms, *SD* = 78.67 ms; $p = 0.563$). However, the Strategy group had significantly slower RT on inclusion trials completed at PDP Times 2, 3 and 4 compared to PDP Time 1 (all $p < 0.001$), and RT at PDP Times 2, 3 and 4 did not differ from each other ($M$ = 496.74 ms, $SD$ = 89.64 ms; all $p = 1.0$). Moreover, the Strategy group had significantly slower RT on inclusion trials compared to the No-Strategy group at PDP Times 3 and 4 ($M$ = 407.80 ms, $SD$ = 97.18 ms; both $p < 0.007$), and there was a trend for slower RT at PDP Time 2 ($M$ = 449.43 ms, $SD$ = 112.11 ms; $p = 0.083$). Analyses of RT variability also revealed a significant Group x Time interaction [$F(3,111) = 3.322$, $p = 0.022$, $\eta_p^2 = 0.082$]. RT variability for the No-Strategy group remained consistent across all PDP Times ($M$ = 97.93 ms, $SD$ = 67.90 ms; all $p > 0.181$), but the Strategy group showed greater RT variability at PDP Times 3 and 4 on Day 2 of testing ($M$ = 111.67 ms, $SD$ = 60.39 ms) compared to PDP Time 1 ($M$ = 71.75 ms, $SD$ = 34.68 ms; both $p < 0.022$). In addition, the Strategy group demonstrated greater RT variability than the No-Strategy group at PDP Time 3 ($p = 0.038$).

MT was on average 943.39 ms during exclusion trials. MT did not significantly differ across Group or Time, but ANOVA revealed a main effect of Hand [$F(1,56) = 9.853$, $p = 0.003$, $\eta_p^2 = 0.150$], such that reaches with the trained (left) hand ($M$ = 958.34 ms, $SD$ = 262.81 ms) had a slower MT than reaches with the untrained (right) hand ($M$ = 928.45 ms, $SD$ = 263.09 ms). With respect to analysis of MT variability during exclusion PDP trials, ANOVA revealed a Group x Time x Hand interaction [$F(6,168) = 2.471$, $p = 0.026$, $\eta_p^2 = 0.081$] and post hoc analyses indicated that the Strategy group showed greater MT variability when reaching with the left hand during PDP Trials at Time 2 compared to the No-Strategy and Control groups (both $p < 0.047$). In contrast, no other differences were found between the groups at any other time when using the left hand (all $p > 0.912$). The No-Strategy group also showed greater MT variability when reaching with the right hand during PDP Times 1 and 2 compared to the Control group (both $p < 0.029$), but the groups showed similar MT variability at all other PDP Times (all $p > 0.133$).

MT for inclusion trials was longer, such that is was 1019.30 ms on average across all Groups, Hands and Time. As expected, T-tests revealed that MT for both hands for the Strategy and No-Strategy groups was slower in the inclusion PDP trials compared to exclusion PDP trials (all $p < 0.018$). Compared to exclusion trials, ANOVA revealed no significant changes in MT during inclusion trials across Group, Hand or Time (all $p > 0.085$). MT variability during inclusion trials was on average 152.32 ms, which also did not differ significantly across Group, Hand or Time (all $p > 0.057$).

Together, these RT and MT results indicate that, in general, all groups performed with a similar RT and MT on exclusion trials. Participants in the Strategy and No-Strategy groups then increased their preparation time (i.e., RT) and the time it took to execute a movement (i.e., MT) when reaching with both hands on inclusion trials compared to exclusion trials. Furthermore, participants in the Strategy group increased their preparation time even more on inclusion trials compared to participants in the No-Strategy group after training with a rotated cursor.

### *6.2. Explicit + implicit adaptation in PDP trials expressed as a percentage of reach adaptation*

We compared overall explicit + implicit adaptation expressed as a percentage of reach adaptation observed in the corresponding reach training blocks between the Strategy and No-Strategy groups in a 2 Group x 2 Hand x 3 Time (PDP Time 2 (Day 1, Block 4) vs. PDP Time 3 (Day 2, Block 1) vs. PDP Time 4 (Day, Block 3)) mixed ANOVA, with RM on the last two factors. The data was log transformed to ensure a normal distribution. Explicit and implicit adaptation were defined in PDP Blocks 2, 3 and 4 by subtracting the EI or II at PDP Time 1, respectively. The extent of reach adaptation corresponding to PDP Blocks 2 and 3 was considered to be the mean PV angular error of the last 6 rotated reach training trials with the left hand on Day 1 (i.e., Block 3, Day 1) minus the mean PV angular error of the last 6 aligned reach training trials with the left hand on Day 1 (i.e., Block 1, Day 1), while the extent of reach adaptation corresponding to PDP Block 4 was considered to be the mean PV angular error of the last 6 rotated reach training trials with the right hand on Day 2 (i.e., Block 2, Day 2) minus the mean PV angular error at PDP Time 1 when reaching with the right hand (i.e., Block 2, Day 1). The Control group was excluded from these analyses as they did not perform inclusion trials. Mean and variability data for explicit and implicit percentages are displayed in Table S3 and S4.

The sums of explicit + implicit adaptation achieved during PDP trials as a percentage of reach adaptation are shown in Figure S1, with implicit adaptation in the Control group expressed as a percentage of reach adaptation included as well. A Group x Hand x Time interaction [$F(2,60) = 7.526$, $p < 0.001$, $\eta_p^2 = 0.201$], revealed that explicit + implicit adaptation in the Strategy group during PDP trials was similar to the extent of reach adaptation observed in both hands when reaching with the cursor during rotated reach training trials (*M* = 118.93%, *SD* = 24.56%). This percentage of reach adaptation accounted for by explicit + implicit adaptation did not differ across Hand or Time for the Strategy group (all $p > 0.428$). In contrast, the percentage of reach adaptation accounted for by explicit + implicit adaptation in the No-Strategy group was less than the Strategy group at all PDP times in both hands (all $p < 0.004$). Moreover, greater reach adaptation in the No-Strategy group was accounted for by explicit + implicit adaptation in the trained (left) hand at PDP Time 2 (*M* = 65.22%, *SD* = 38.80%) compared to PDP Time 3 (*M* = 41.64%, *SD* = 50.21%) and PDP Time 4 (*M* = 45.85%, *SD* = 58.93%; both $p < 0.008$), suggesting that significant decay occurred across testing days. Explicit + implicit adaptation for the No-Strategy group in the right hand did not differ significantly between PDP Time 2 (*M* =

37.24%, *SD* = 47.82%) and PDP Time 3 (*M* = 34.72%, *SD* = 60.14%; %; $p = 0.335$), but significantly increased following rotated reach training with the same (right) hand (i.e., PDP Time 4; *M* = 47.20%, *SD* = 69.56%; $p < 0.018$). Together these results indicate that explicit and implicit adaptation accounted for a greater percentage of reach adaptation in the Strategy group compared to the No-Strategy group. Moreover, explicit and implicit adaptation account for greater amount of reach adaptation following training of a given hand.

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## Figures & Tables

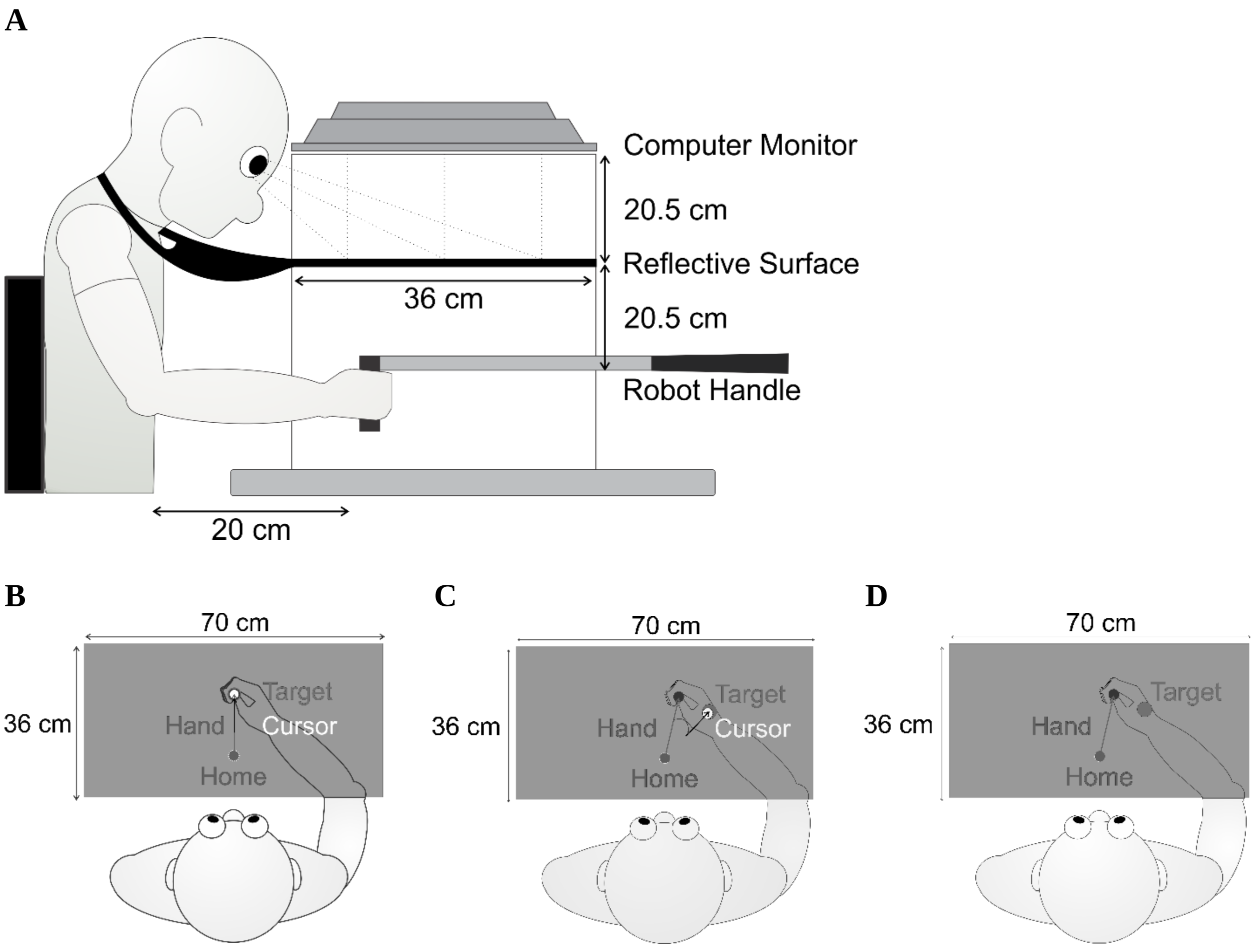


**Figure 1. Experimental apparatus and reach conditions**

(A): Side-view of the experimental apparatus. Participants were instructed to grasp the robot handle with either the left or right hand. (B): Top view of the experimental apparatus and visual feedback displayed during reach training trials with an aligned cursor. (C): Visual feedback displayed during reach training trials with a rotated cursor. (D). Example of a PDP trial. For (B – D), the target was displayed as a green circle (shown here as a black circle), and the cursor as a white circle. Thin black arrows and grey lines represent the trajectory of the cursor movement and actual hand movement respectively (not seen during testing).

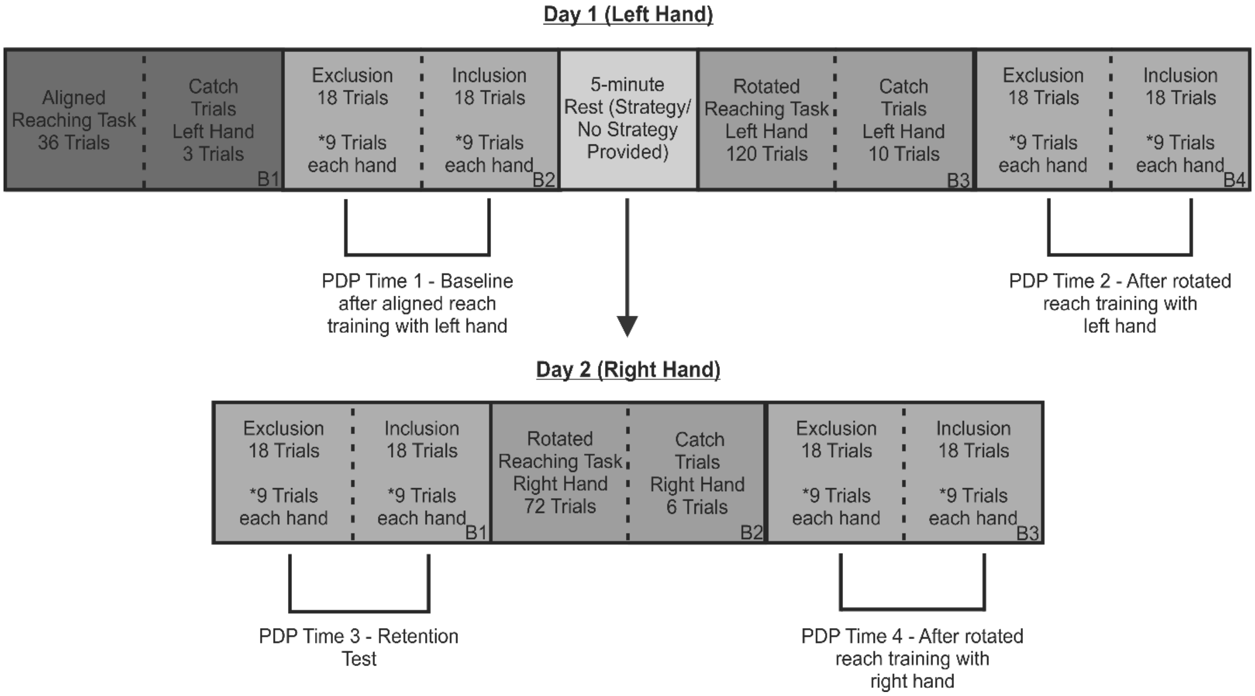


**Figure 2. Experimental Design**

Outline of testing Blocks completed by all participants. All Blocks are outlined by solid black lines and the Block number is indicated in the bottom right corner. Dotted lines represent Block division by type of trial completed. The top portion demonstrates blocks completed on the first day of testing, while the lower portion represents blocks completed on the second testing day (24 hours later). During PDP Blocks, the order of exclusion and inclusion trials, and hand that participants initially reached with (left vs. right hand), were counterbalanced across participants. Participants assigned to the Control group only received the second part of the exclusion trial instruction, which was to "reach so that your hand lands on the target."

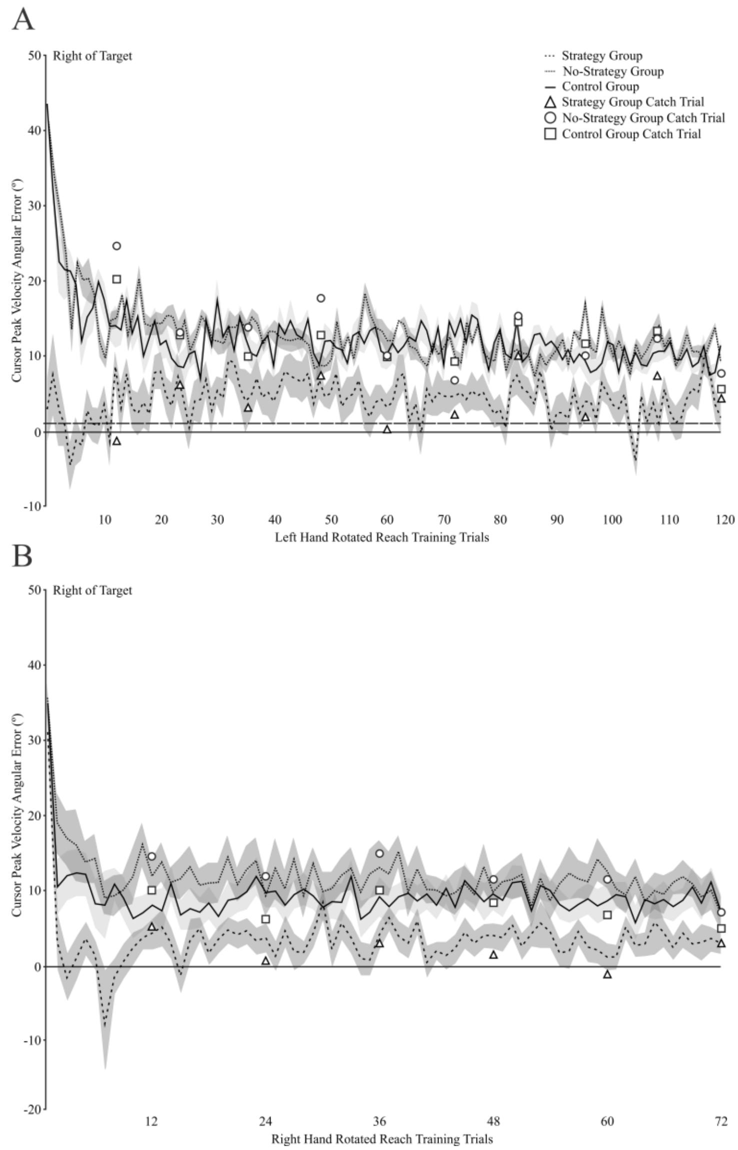


**Figure 3. Average reaching errors across rotated reach training trials with the (A) left (trained) and (B) right (untrained) hands**

Average cursor directional errors when reaching with the left (A: Block 3, Day 1) and right (B: Block 2, Day 2) hands during rotated reach training. The dashed, dotted, and solid lines represent average reach direction for the Strategy, No-Strategy, and Control groups over rotated reach training trials, respectively. For all groups, the shaded region surrounding each line represents the standard error of the group mean. The triangle, circle, and square symbols represent average errors on catch trials, when no cursor was displayed for the Strategy, No-Strategy and Control groups, respectively. In (A), the dashed straight line represents the average cursor directional error during aligned reach training trials across all participants. Positive cursor PV angular errors indicate the cursor position was to the right of the target, while negative cursor PV angular errors indicate the cursor position was to the left of the target.

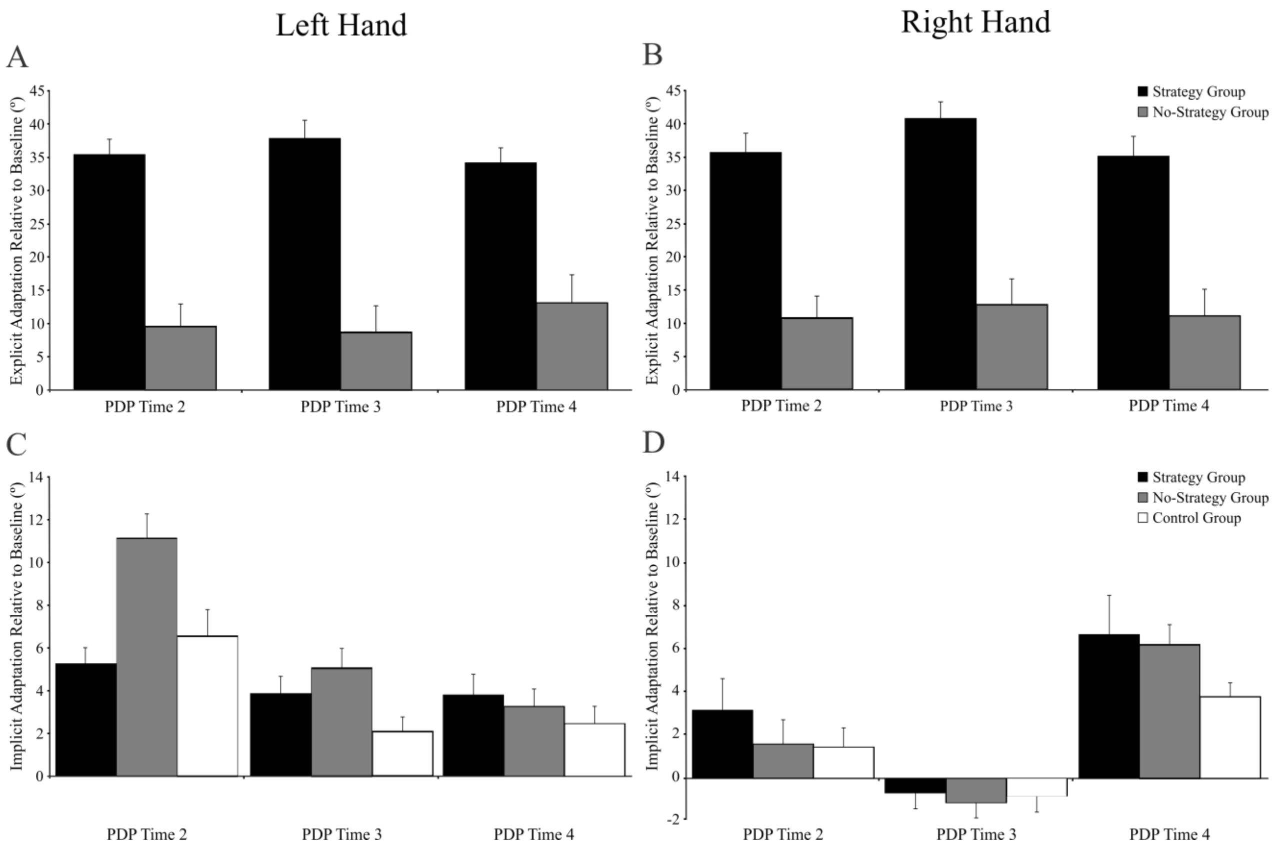


**Figure 4. Magnitude of explicit and implicit adaptation during PDP trials**

(A-B): Magnitude of explicit adaptation achieved in the left (A) and right (B) hands at PDP Time 2, PDP Time 3, and PDP Time 4 relative to baseline (i.e., PDP Time 1). Black and grey bars represent the magnitude of explicit adaptation for the Strategy and No-Strategy groups, respectively. (C-D): Magnitude of implicit adaptation achieved in the left (C) and right (D) hands at PDP Time 2, PDP Time 3, and PDP Time 4 relative to baseline (i.e., PDP Time 1). Black, grey, and white bars represent the magnitude of implicit adaptation for the Strategy, No-Strategy, and Control groups, respectively. Error bars reflect standard error of the mean.

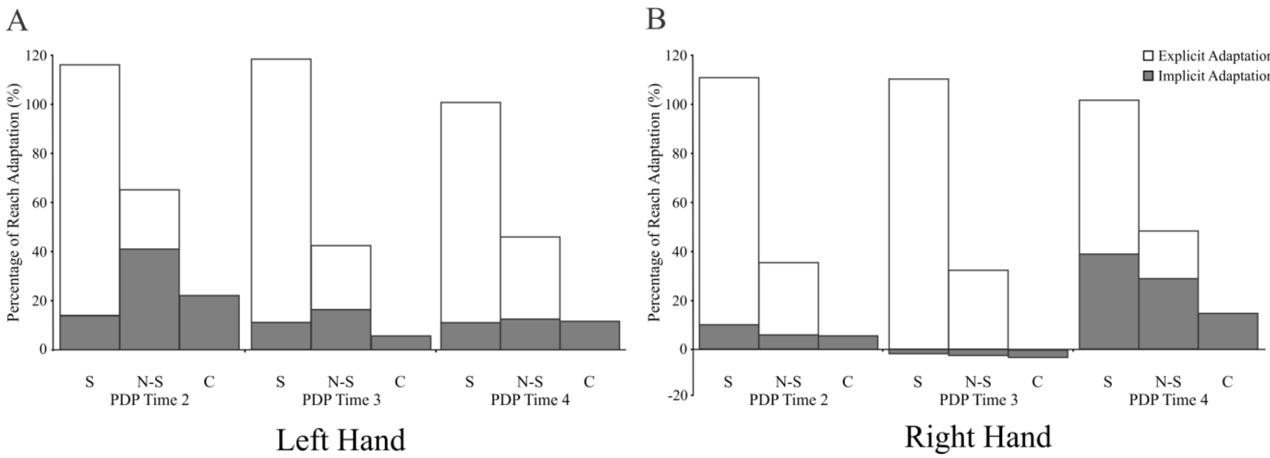


**Figure S1. Percentage of Explicit + implicit adaptation relative to reach adaptation**

(A-B): Explicit adaptation (white bars) + implicit adaptation (grey bars) in the left (A) and right (B) hands at PDP Time 2, PDP Time 3, and PDP Time 4 expressed relative to the magnitude of reach adaptation achieved in the left or right hands during rotated reach training trials for the Strategy (S), No-Strategy (N-S), and Control (C) groups. Only implicit adaptation, expressed as a percentage of reach adaptation, is shown for the Control group.

**Table S1.** Mean and standard deviation (in brackets) for kinematic variables in the Strategy, No-Strategy, and Control group. Reaction time, reaction time variability, movement time, movement time variability is presented for exclusion trials in both hands at all PDP times.

| Measure | | Left Hand | | | | Right Hand | | | |
|---|---|---|---|---|---|---|---|---|---|
| Variable | Group | Time 1 | Time 2 | Time 3 | Time 4 | Time 1 | Time 2 | Time 3 | Time 4 |
| RT (ms) | Strategy | 379.97 (56.61) | 418.24 (47.27) | 453.86 (117.12) | 409.18 (58.87) | 403.39 (127.10) | 431.60 (72.19) | 452.91 (98.57) | 429.99 (75.50) |
| | No-Strategy | 376.51 (100.15) | 390.13 (85.45) | 375.76 (84.98) | 372.85 (76.85) | 415.37 (196.59) | 407.51 (72.27) | 412.26 (99.31) | 384.99 (74.87) |
| | Control | 397.18 (80.05) | 390.67 (83.82) | 398.89 (77.92) | 379.86 (77.48) | 411.51 (101.99) | 401.11 (81.26) | 403.17 (72.79) | 377.69 (72.88) |
| RT Variability (ms) | Strategy | 78.11 (32.43) | 97.68 (41.71) | 142.54 (242.32) | 77.64 (33.86) | 95.42 (111.74) | 101.08 (69.98) | 101.13 (75.41) | 86.37 (68.52) |
| | No-Strategy | 89.94 (67.93) | 81.07 (38.18) | 75.65 (33.40) | 83.60 (29.43) | 102.45 (78.77) | 105.02 (80.63) | 83.02 (66.53) | 85.12 (29.03) |
| | Control | 71.98 (28.44) | 80.85 (25.97) | 74.53 (27.18) | 78.67 (36.77) | 81.69 (49.79) | 85.99 (22.51) | 77.92 (39.03) | 79.35 (38.54) |
| MT (ms) | Strategy | 961.12 (300.68) | 955.81 (202.16) | 995.58 (280.70) | 977.01 (235.24) | 933.99 (242.74) | 937.29 (206.94) | 929.50 (228.35) | 935.46 (254.13) |
| | No-Strategy | 967.50 (317.63) | 992.92 (289.36) | 993.84 (278.46) | 1004.68 (306.35) | 951.47 (302.35) | 973.09 (333.24) | 964.48 (325.24) | 978.46 (234.57) |
| | Control | 928.87 (246.88) | 921.21 (216.49) | 929.23 (267.74) | 875.09 (223.74) | 874.98 (290.19) | 870.01 (220.08) | 909.29 (290.87) | 884.53 (229.54) |
| MT variability (ms) | Strategy | 145.83 (90.76) | 107.98 (29.50) | 144.33 (56.50) | 137.42 (44.38) | 135.26 (59.85) | 132.61 (76.65) | 137.86 (52.12) | 140.38 (84.49) |
| | No-Strategy | 164.26 (80.44) | 159.41 (65.60) | 134.93 (43.67) | 128.25 (66.22) | 179.55 (96.34) | 162.7 (46.53) | 133.69 (53.08) | 148.69 (71.88) |
| | Control | 181.60 (140.88) | 151.60 (60.35) | 129.64 (50.58) | 127.81 (39.66) | 104.73 (25.19) | 116.04 (34.37) | 134.76 (50.57) | 124.18 (46.41) |

**Table S2.** Mean and standard deviation (in brackets) for kinematic variables in the Strategy, No-Strategy, and Control group. Reaction time, reaction time variability, movement time, movement time variability is presented for inclusion trials in both hands at all PDP times.

| Measure | | Left Hand | | | | Right Hand | | | |
|---|---|---|---|---|---|---|---|---|---|
| Variable | Group | Time 1 | Time 2 | Time 3 | Time 4 | Time 1 | Time 2 | Time 3 | Time 4 |
| RT (ms) | Strategy | 385.91 (68.36) | 489.04 (74.92) | 507.23 (92.80) | 486.23 (99.80) | 386.69 (64.08) | 515.04 (78.70) | 495.99 (105.08) | 486.91 (90.95) |
| | No-Strategy | 393.90 (89.94) | 443.93 (107.61) | 394.09 (96.22) | 399.43 (92.22) | 404.56 (91.88) | 454.92 (118.96) | 434.51 (114.79) | 403.18 (85.36) |
| RT Variability (ms) | Strategy | 73.03 (30.56) | 103.71 (28.01) | 118.43 (50.40) | 105.59 (61.40) | 70.48 (39.17) | 123.62 (39.17) | 116.23 (75.63) | 106.41 (55.01) |
| | No-Strategy | 103.74 (61.21) | 99.87 (35.51) | 79.48 (26.88) | 89.64 (40.46) | 86.23 (49.16) | 136.88 (139.85) | 95.86 (62.15) | 91.75 (55.94) |
| MT (ms) | Strategy | 967.46 (242.27) | 1044.82 (243.74) | 1045.73 (300.48) | 1019.32 (288.92) | 943.04 (279.29) | 990.23 (235.51) | 1044.93 (326.22) | 1004.27 (321.57) |
| | No-Strategy | 1033.09 (334.45) | 997.27 (326.05) | 1053.47 (320.82) | 1071.95 (339.45) | 982.02 (340.86) | 1024.24 (301.31) | 1051.17 (343.27) | 1031.12 (348.18) |
| MT variability (ms) | Strategy | 139.81 (57.38) | 169.20 (86.38) | 131.34 (39.68) | 137.58 (73.14) | 143.90 (79.43) | 131.88 (55.79) | 145.75 (55.13) | 136.21 (61.43) |
| | No-Strategy | 150.70 (50.59) | 166.21 (80.27) | 182.64 (126.45) | 181.32 (64.41) | 155.78 (63.99) | 182.98 (102.78) | 160.54 (74.02) | 157.49 (72.59) |

**Table S3.** Mean and standard deviation (in brackets) for explicit adaptation in PDP trials expressed as a percentage of reach adaptation for the Strategy and No-Strategy groups. Explicit percentages are presented in both hands at all PDP times.

| Measure | | Left Hand | | | Right Hand | | |
|---|---|---|---|---|---|---|---|
| Variable | Group | Time 2 | Time 3 | Time 4 | Time 2 | Time 3 | Time 4 |
| Explicit Adaptation (%) | Strategy | 103.59 (25.07) | 109.37 (33.60) | 90.20 (23.98) | 102.86 (39.13) | 115.59 (37.05) | 86.95 (32.28) |
| | No-Strategy | 24.89 (50.90) | 23.12 (57.12) | 30.76 (79.17) | 32.10 (52.26) | 40.01 (58.88) | 26.62 (67.35) |

**Table S4.** Mean and standard deviation (in brackets) for implicit adaptation in PDP trials expressed as a percentage of reach adaptation for the Strategy, No-Strategy, and Control groups. Implicit percentages are presented in both hands at all PDP times.

| Measure | | Left Hand | | | Right Hand | | |
|---|---|---|---|---|---|---|---|
| Variable | Group | Time 2 | Time 3 | Time 4 | Time 2 | Time 3 | Time 4 |
| Implicit (%) | Strategy | 15.34 (11.93) | 11.46 (11.72) | 10.70 (13.77) | 9.60 (19.93) | -3.11 (13.69) | 18.32 (20.18) |
| | No-Strategy | 40.33 (26.74) | 18.52 (18.85) | 15.08 (27.91) | 5.14 (26.71) | -5.29 (24.55) | 20.58 (25.42) |
| | Control | 20.85 (23.99) | 7.99 (15.99) | 9.22 (28.28) | 5.05 (19.04) | -4.21 (15.65) | 13.73 (14.31) |

# Chapter III: General Discussion

Reaching with altered visual feedback of the hand's position, introduced by way of a cursor on a screen in a virtual environment, leads to visuomotor adaptation in the trained hand, and also in the untrained hand (Wang and Sainburg, 2002; Poh et al., 2016). Visuomotor adaptation has been suggested to reflect both explicit (i.e., conscious and strategic) and implicit (i.e., unconscious) processes (Sulzenbruck & Heuer, 2009; Taylor et al., 2011; 2014; Bond & Taylor, 2015; Neville & Cressman, 2018). We sought to establish the role of explicit and/or implicit adaptation in intermanual transfer using the PDP framework when instructions regarding the visuomotor distortion were manipulated. We also looked to determine whether explicit and/or implicit contributions to visuomotor adaptation are retained in both the trained and untrained hands.

We revealed that explicit and implicit contributions to visuomotor adaptation within the trained (left) hand differed between those who were provided with a strategy regarding how to counteract the cursor rotation, and those who were not. Specifically, participants in the Strategy group showed greater explicit adaptation and smaller implicit adaptation, compared to the No-Strategy group, who showed the opposite trend. These findings are consistent with previous work from our lab (Neville & Cressman, 2018) and suggest that being instructed on how to counteract a visuomotor distortion minimizes the contribution of implicit processes. Unexpectedly, the Control group also showed less implicit adaptation than the No-Strategy group. However, the extent of implicit adaptation observed across groups (5° to 12°), was similar to results reported in the literature in which implicit adaptation reaches a ceiling at of approximately 15°, regardless of the rotation size or how participants become aware of the visuomotor perturbation (Bond & Taylor, 2015; Neville & Cressman, 2018; Modchalingam et al., 2019). Our current findings extend this proposal and establish that this ceiling is not limited to reaches performed with the dominant hand, but extends to the non-dominant hand, as we observed that all groups showed a similar extent of implicit adaptation following training with either hand.

We also established that explicit adaptation transfers from the trained to the untrained hand, while implicit adaptation does not, regardless of how one becomes aware of the cursor rotation. This result is contrary to previous literature which assumed a minimal role for explicit adaptation in intermanual transfer by assessing explicit and implicit adaptation indirectly (i.e., by comparing performance across participants who adapted to an abruptly versus gradually introduced visuomotor distortion). Consistent with findings from Poh and colleagues (2016), directly assessing explicit and implicit adaptation reveals that explicit processes are primarily responsible for intermanual transfer.

We further found that explicit adaptation is retained in the trained and untrained hands over time, while implicit adaptation decays considerably across testing days. As suggested by Morehead and colleagues (2015), retention of visuomotor adaptation could be due to the recall of a previously learned strategy, as implicit adaptation has been shown to decay within minutes following training (Neville & Cressman, 2018). Our results show that a learned strategy can also be accurately recalled by the untrained hand at a later time.

**Assessing explicit and implicit contributions to visuomotor adaptation**

It is only recently that researchers have developed paradigms to directly assess both explicit and implicit contributions to visuomotor adaptation simultaneously, within the same participant (Taylor et al., 2014; Bond & Taylor, 2015; Werner et al., 2015; Neville & Cressman, 2018). The verbal reporting method, developed by Taylor and colleagues (2014), asks participants to report where they intend to aim to prior to performing the movement. Specifically, participants begin a trial by verbally indicating a number from a ring of numbers surrounding the target. The number reported reflects explicit adaptation. Participants are then cued to reach to the target, and the difference between where they actually reach to and the number reported is considered to reflect their implicit adaptation. The second method to assess explicit and implicit contributions to visuomotor adaptation within the same participant is the process dissociation procedure (PDP), put forward by Werner and colleagues (2015). Within this procedure, participants are given specific reaching instructions; (1) “use what was learned during training” (to assess explicit + implicit adaptation) or (2) “refrain from using what was learned during training” (to assess implicit adaptation only). While both paradigms measure the contributions of explicit and implicit processes to visuomotor adaptation, there are important methodological differences between the paradigms. In particular, the verbal reporting method typically assesses explicit and implicit adaptation during rotated reach training trials, when participants are provided with visual feedback of the on-screen cursor. As well, it has been indicated that participants cannot be made aware of the visuomotor distortion directly or instructed on how to counteract it (Taylor et al., 2014), as they would presumably continue to report the same number. In contrast, the PDP assesses explicit and implicit adaptation after rotated reach training trials, when participants are reaching with no visual feedback of the cursor (i.e., these trials are similar to aftereffect trials and do not have the same potential for trial-to-trial changes in movements as in Taylor’s verbal reporting method).

Recently, the verbal report framework was used to assess the contributions of explicit and implicit adaptation to intermanual transfer (Poh et al., 2016). Poh and colleagues (2016) modified Taylor’s (2014) protocol slightly, in that the visual landmarks were removed, and participants were to use a pointer to indicate where they intended to reach to (which promptly disappeared before participants reached to the target). As well, unlike Taylor’s early work, participants reached when no visual cursor was present. Results indicated that both explicit and implicit adaptation transferred to the untrained hand, with greater explicit adaptation transferring than implicit adaptation (i.e., 100% explicit adaptation transferred vs. 48% implicit adaptation). Interestingly, the magnitude of implicit adaptation in the trained hand (24° when adapting to a 45° cursor rotation), was much greater than that previously reported using the verbal reporting method (Bond & Taylor, 2015) or PDP (Neville & Cressman, 2018; Modchalingam et al., 2019). The larger magnitude of initial implicit adaptation, or the placement of assessment trials within the experimental design (as discussed in the Discussion of Chapter 2), could be factors contributing to the significant transfer of implicit adaptation in Poh's previous work compared to the current study.

Given that the PDP and verbal report framework for assessing explicit and implicit adaptation are relatively new, there are a limited number of studies that have used them, and no study to date has compared results arising from the two paradigms directly (i.e., determined if they are assessing similar explicit and implicit adaptation). There are important methodological differences between the paradigms. The PDP asks participants to use or refrain from using a strategy following reach training, while Taylor's verbal report framework has participants verbally report the direction in which they intend to reach during reach training. These methods could be engaging different visuomotor systems, as the PDP is a more action oriented task, while the verbal report framework could be considered more perceptually oriented (Milner & Goodale, 1992). As it is currently unknown whether these two methodologies are measuring similar explicit and implicit processes, further research is required to directly compare these two methodologies.

## The role of explicit processes in motor learning

As suggested by Krakauer (2019), motor learning encompasses two important mechanisms: (1) skill acquisition (i.e., acquiring the ability to identify an appropriate movement goal, select the correct action, and execute the movement with accuracy) and (2) skill maintenance (i.e., ability to maintain performance within changing conditions). Fitts and Posner (1967) proposed that, when first learning a new skill, the learner uses explicit or cognitive processes, such that movements are controlled consciously. For example, when first learning to ride a bicycle, we consciously attempt to balance ourselves to simply stay upright. With time and practice, the skill becomes automatic (implicit) and we no longer rely on explicit processes. Recently, motor adaptation research has shown a similar progression, such that explicit processes are primarily engaged when initially learning to counteract a visuomotor distortion (Krakauer et al., 2006; Taylor et al., 2011; 2014; McDougle et al., 2015; Poh et al., 2016; Neville & Cressman, 2018). In fact, these explicit processes enhance the rate of learning by immediately decreasing directional errors, improving accuracy when participants are first introduced to a visuomotor distortion. However, as training continues, the contribution of explicit processes decreases as we rely less on developed strategies, and the movement is driven more implicitly (Taylor et al., 2014). Moreover, if we are reintroduced to the movement again, or asked to recall what we learned, explicit processes again appear to play a dominant role, as we once again rely on a learned strategy (as shown in the current study by the retention of explicit adaptation, and by Morehead et al., 2015).

## Limitations

In the current study, all participants initially trained with their left (non-dominant) hand. We found that the extent of reach adaptation during reach training trials varied between the Strategy and No-Strategy groups. It is unknown whether these results arose because of which hand was initially trained. Based on previous literature, we expected to observe differences between the Strategy and No-Strategy groups during the initial portion of training, but similar performance by the end of training (Benson et al., 2011, Bond & Taylor., 2015; McDougle et al., 2015; Neville & Cressman, 2018). Furthermore, it is unclear if the choice of hand influenced how participants developed/employed a strategy during the rotated reach training trials. These differences could be further explored by examining the interaction between how explicit and implicit processes develop over the course of reach training trials in both hands, possibly revealing important hemispherical specializations, as suggested by the Dynamic Dominance Hypothesis discussed in the Discussion of Chapter 2.

**Rehabilitative applications**

Understanding the role of explicit and implicit adaptation in motor performance with the trained and untrained hands is important to further improve how we apply rehabilitative techniques. Consider individuals suffering from unilateral spatial neglect (i.e., patients who neglect the left side of space due to right brain damage; Rode et al., 2003; Michel et al., 2003; Aimola et al., 2012). Visuomotor adaptation after wearing prism goggles that shift their field of view to the right (i.e., the left neglected visual field is shifted to the right visual field) has been shown to benefit their overall motor performance, as patients interact with stimuli in the left visual field which they had previously neglected (Rossetti et al., 1998). Interestingly, current research suggests that motor performance deficits in unilateral neglect are due to impairment in strategic (explicit) processes, rather than spatial realignment (implicit) processes (Aimola et al., 2012). Perhaps then, promoting awareness, through explicit adaptation, could be beneficial for these patients. According to recent visuomotor adaptation research and our current results, explicit adaptation can be promoted by providing participants with a strategy prior to training, or by having participants train with a larger distortion size (40° vs 20°; Bond & Taylor, 2015;

Neville & Cressman, 2018). In addition, the current study also shows that participants who engage explicit processes with the trained hand can transfer these processes to the untrained hand. Thus, engaging the trained hand in explicit adaptation in neglect patients may further improve their motor performance, such that they begin to interact with objects with their untrained hand. Using the PDP could provide insight into the benefit of explicit adaptation to changes in motor performance in neglect patients and should be considered when moving forward with this area of research.

## Conclusion

By directly assessing explicit and implicit contributions to visuomotor adaptation, we found that explicit processes play a prominent role in how the untrained hand performs following visuomotor adaptation, regardless of how one is made aware of the distortion (i.e., directly or indirectly). Specifically, explicit adaptation observed in the trained hand is transferred to the untrained hand, indicating either effector can engage a learned strategy. Moreover, either hand can recall a strategy at a later time. In comparison, implicit adaptation is limited to the trained hand (at least when one is aware of the distortion) and decays considerably over time. Taken together, our results suggest that regardless of how participants become aware of a visuomotor distortion, transfer and retention is driven almost exclusively by explicit processes.

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# Appendix A

File Number: H12-13-09 Date (mm/dd/yyyy): 03/15/2018

Université d'Ottawa University of Ottawa
Bureau d'éthique et d'intégrité de la recherche Office of Research Ethics and Integrity

## Ethics Approval Notice

### Health Sciences and Science REB

**Principal Investigator / Supervisor / Co-investigator(s) / Student(s)**

| First Name | Last Name | Affiliation | Role |
|---|---|---|---|
| Erin K. | Cressman | Health Sciences / Human Kinetics | Supervisor |
| Jean-Michel | Bouchard | Health Sciences / Human Kinetics | Student Researcher |
| Eadan | Farber | Health Sciences / Human Kinetics | Student Researcher |
| Michael | Vered | Health Sciences / Human Kinetics | Student Researcher |
| Darrin | Wijeyaratnam | Health Sciences / Human Kinetics | Student Researcher |

**File Number:** H12-13-09

**Type of Project:** 4th year

**Title:** Motor Adaption and sensory recalibration

| Renewal Date (mm/dd/yyyy) | Expiry Date (mm/dd/yyyy) | Approval Type |
|---|---|---|
| 03/12/2018 | 03/11/2019 | Renewal |

**Special Conditions / Comments:**
N/A

1

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**File Number:** H12-13-09 **Date (mm/dd/yyyy):** 02/15/2018

Université d'Ottawa
Bureau d'éthique et d'intégrité de la recherche

University of Ottawa
Office of Research Ethics and Integrity

This is to confirm that the University of Ottawa Research Ethics Board identified above, which operates in accordance with the Tri-Council Policy Statement (2010) and other applicable laws and regulations in Ontario, has examined and approved the ethics application for the above named research project. Ethics approval is valid for the period indicated above and subject to the conditions listed in the section entitled "Special Conditions / Comments".

During the course of the project, the protocol may not be modified without prior written approval from the REB except when necessary to remove participants from immediate endangerment or when the modification(s) pertain to only administrative or logistical components of the project (e.g., change of telephone number). Investigators must also promptly alert the REB of any changes which increase the risk to participant(s), any changes which considerably affect the conduct of the project, all unanticipated and harmful events that occur, and new information that may negatively affect the conduct of the project and safety of the participant(s). Modifications to the project, including consent and recruitment documentation, should be submitted to the Ethics Office for approval using the "Modification to research project" form available at: https://research.uottawa.ca/ethics/forms.

Please submit an annual report to the Ethics Office four weeks before the above-referenced expiry date to request a renewal of this ethics approval. To close the file, a final report must be submitted. These documents can be found at: https://research.uottawa.ca/ethics/forms.

If you have any questions, please do not hesitate to contact the Ethics Office at extension 5387 or by e-mail at: ethics@uOttawa.ca.

**Appendix B**

**Background information and consent form**

# Motor Adaptation and Sensory Recalibration

**Supervisor:** Dr. Erin Cressman,
Assistant Professor,
Montpetit Hall, Room 360
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**Principal Investigator(s):**

Darrin Wijeyaratnam, M.Sc. Student
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**Funding:** National Science and Engineering Research Council (NSERC)

**Background**

Most of us perform goal directed actions – i.e. reaching for a cup of coffee – without thought or effort. It is only after something goes wrong (i.e. damage to part of the brain), that we begin to appreciate how complex a job the brain has in transforming sensory signals (e.g. visual input) into appropriate action plans. The overall goal of the research being undertaken in my laboratory is to understand how the brain transforms sensory input into motor output in the "healthy" brain. This research has important implications for people suffering from neurological disorders, as it is only after we gain a fundamental understanding of the normal mechanisms underlying goal directed action that we can begin to design effective rehabilitation programs, targeted at individuals with damage to certain areas of the brain.

**Purpose**

The purpose of this research is to determine how the brain combines multiple sources of sensory information so that it can plan an appropriate movement and form a coherent estimate of where the limb is in space. In particular, we are looking at the integration of visual and proprioceptive information in the brain, where proprioceptive input arises from sensory receptors inside the body that enable us to localize various parts of the body in relation to each other (e.g. proprioception is the sense that allows you to touch your index finger to your nose when your eyes are closed).

**Subject Profile**

To be a participant you must be a right-handed, healthy (no history of neurological, and/or motor dysfunction) adult with normal or corrected-to-normal visual function, aged between 16 and 40 years.

**Study Procedures**

In order to examine how visual and proprioceptive inputs are integrated in the brain you will be asked to point to targets (i.e. a visual dot) with your right/left hand as fast and as accurate as possible. You may also be asked to indicate where your hand is relative to a target (i.e. left or right of the target). In order to record your hand movement, you will hold onto a robot handle (KINARM, Kingston, ON, Canada). We do not need to do any preparation of the skin. It is important to note that this robot system only captures the position of the handle (it does not capture your image (i.e. personal features) in any form).

**Experimental Session**

The entire experiment will be completed in Room 403 in Montpetit Hall. Each participant will complete testing on 1 or up to 5 consecutive days, with each testing session lasting up to 2 hours. Upon completion of the testing session(s) the experimenter will provide additional details on the visual information displayed and the hypothesized results.

**Risks and discomforts**

The risks involved in participating in this experiment are minimal. That is, the risks are no greater than the risks experienced in everyday life. However, you might experience slight fatigue, as you will be asked to maintain focused attention throughout the experiment and perform multiple reaching movements. In attempt to ensure that you do not become fatigued, we have scheduled 5 minute breaks approximately every 15 minutes. As well, please let us know if you require longer or more frequent periods of rest.

**Benefits**

Thank you for taking the time to participate in this study. While there are no direct benefits to you from participating in this study, this research has important implications for people suffering from neurological disorders. It is only after we gain a fundamental understanding of the normal mechanisms underlying sensory guided action that we can begin to design effective rehabilitation programs, targeted at individuals with damage to certain areas of the brain.

**Anonymity and Confidentiality**

All information and data collected are coded to maintain confidentiality. Specifically, raw data will be stored using an alphanumeric coding system so that no one will be able to identify you as your name will not appear on these files. The data will be analyzed on password protected computers that only the researchers directly involved in this study will have access to. Once analyzed the data will be kept in Room 403, Montpetit Hall, in locked filing cabinets and only the researchers directly involved in this study will have access to your data.

No records bearing your name will leave the institution. You are encouraged to request and discuss the results of the experimental trials at any time.

The data collected in this study may be published in scientific journals, as well as in a University of Ottawa MSc thesis. The data will be kept for a period of 10 years post-publication and will subsequently be destroyed by the physical resources service of the University of Ottawa.

**Voluntary Participation**

For the entire duration of the study, it is fully understood that you may refuse to participate or withdraw from the study at any time, without question.  As well, you can ask the researcher any questions about any part of the research being conducted at any time. Data of participants who withdraw from the study will be destroyed immediately.

**INFORMED CONSENT OF PARTICIPANT**

Research involving human subject require written consent of the participants.

I, ___________________________, hereby volunteer to participate as a subject in the study entitled **"Motor Adaptation and Sensory Recalibration"**. I have read the information presented in the above background information and I had the opportunity to ask questions to the investigators. I understand that my participation in this study, or indeed any research, may involve risks that are currently unforeseen.

I recognize that there will be no direct benefit to me from my participation in this study.

I understand that if I have any questions regarding the study, I may contact Dr. Erin Cressman. If I have any questions or complaints with regards to the ethical conduct of this study, I may contact the Protocol Officer for Ethics in Research, University of Ottawa, Tabaret Hall, 550 Cumberland Street, Room 154, Ottawa, ON K1N 6N5, tel.: 613-562-5387, email: ethics@uottawa.ca .

I have been given a copy of this Background Letter and Consent Form for me to keep.

Signature of participant: _________________________ Date: ___________________

Signature of Researcher: _________________________ Date: ___________________

**Research Summary/Debriefing Text**

The overall goals of this research are to examine the ability of the sensory and motor systems to learn, transfer, retain, and recall information over time, while manipulating the degree of explicit awareness.

The goal of this experiment was to investigate the ability of the sensory and motor systems to transfer and recall a strategy used to learn a novel goal-directed movement in one limb to the other limb. To examine this, we had you reach to targets when provided with false visual feedback of the hand (e.g. reaching to a target while seeing a cursor that was rotated with respect to the hand's actual location). We then had you reach to targets without any feedback to assess motor learning/adaptation in both the dominant and non-dominant limbs. The study was 2 consecutive days in order to determine if you learned faster on the second day and recalled what you learned on the first day, allowing us to establish whether awareness contributed to the transfer of savings (i.e. faster re-learning of a movement upon a later exposure) and retention in the sensorimotor system.

Your results from the motor tasks will be compared in order to determine the influence of awareness on the recall of motor memories in the opposite limb.

After having been briefed on the purpose of this research, do you consent to have your data included in this study?

Signature of participant: ________________________ Date: __________________

Signature of Researcher: ________________________ Date: __________________

## Appendix C

Edinburgh Handedness Inventory (Oldfield, 1979)

Your participant ID:______________

Please indicate with a one (1) your preference in using your left or right hand in the following tasks.

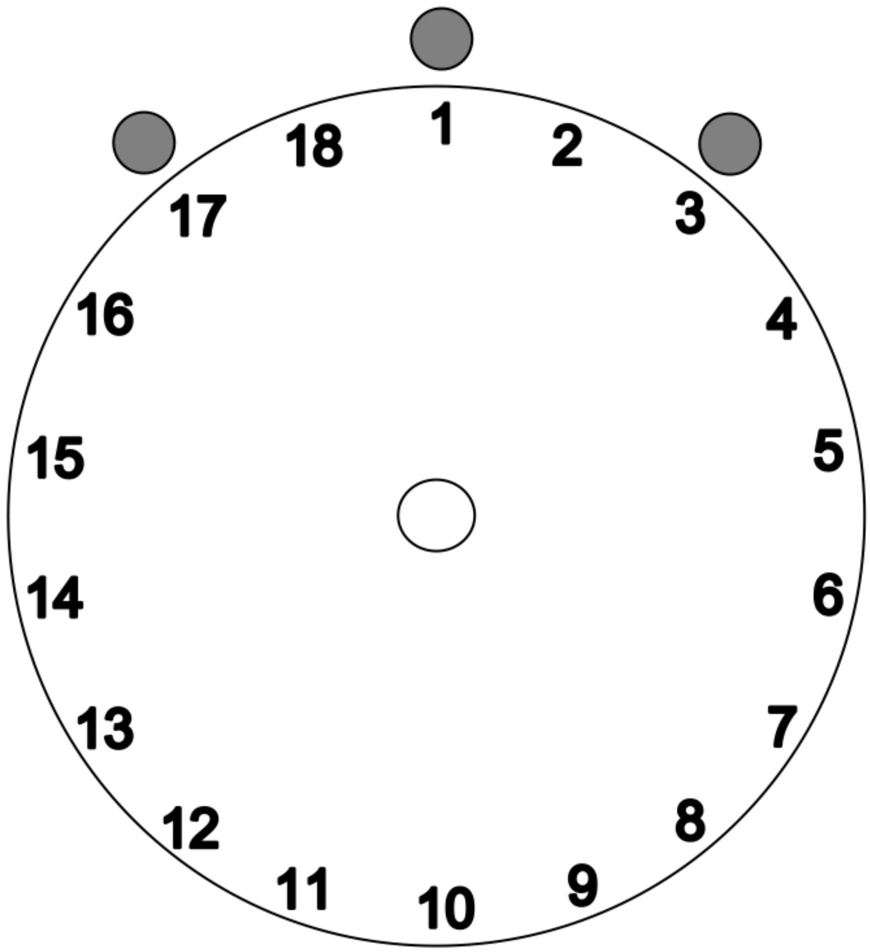
Where the preference is so strong you would never use the other hand, unless absolutely forced to, put a two (2).

If you are indifferent, put a one in each column (1 | 1).

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

| Task / Object | Left Hand | Right Hand |
|---|---|---|
| 1. Writing | | |
| 2. Drawing | | |
| 3. Throwing | | |
| 4. Scissors | | |
| 5. Toothbrush | | |
| 6. Knife (without fork) | | |
| 7. Spoon | | |
| 8. Broom (upper hand) | | |
| 9. Striking a Match (match) | | |
| 10. Opening a Box (lid) | | |
| Total checks: | LH = | RH = |
| Cumulative Total | CT = LH + RH = | |
| Difference | D = RH – LH = | |
| Result | R = (D / CT) × 100 = | |
| Interpretation:<br>(Left Handed: R < -40)<br>(Ambidextrous: -40 ≤ R ≤ +40)<br>(Right Handed: R > +40) | | |

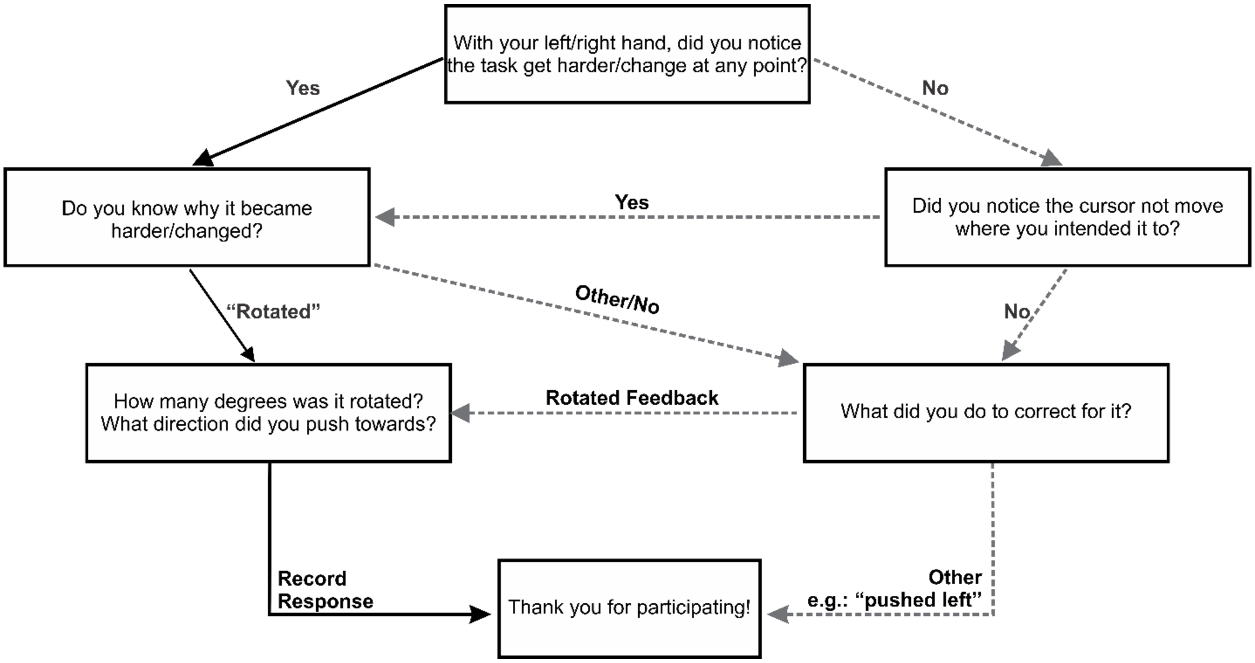
**Appendix D**




**Modified Clock face**

The modified clock face that was used to explain the nature of the 40° rotation to the Strategy group and how participants were to counteract it. Between testing blocks 2 and 3 on Day 1, participants assigned to the Strategy group were shown an image of the modified clock face and instructed on how to accurately reach to the targets in the presence of the rotation. Specifically, they were told that the cursor representing their hand motion would be rotated clockwise relative to their actual hand motion. Thus, in order to have the cursor land on the target, they needed to aim to the number that was 2 over in the counter-clockwise (i.e., leftwards) direction. The yellow center circle represents the home position, while the grey circles represent the potential target locations. To confirm participants understood the nature of the rotation and the strategy provided, participants were asked to draw an arrow towards where they needed to reach to counteract the visuomotor distortion for one of the three targets. Following this, they were instructed to use the strategy when reaching to all three of the targets.

## Appendix E




### Post-Experiment Questionnaire

Questionnaire adapted from Benson et al. (2011) that was provided to all participants upon completion of our study (i.e., following all reaching trials on Day 2). The researcher asked a series of questions as outlined above. Depending on how participants responded, participants were then classified as being aware or unaware of the visuomotor distortion. If participants reported using a strategy to counteract the distortion or noticed a difference in how they had to reach in order to get the cursor to the intended target they were classified as aware. Those reporting otherwise were classified as unaware of the distortion. The questionnaire was completed twice for each participant, once focusing on movements completed with the left hand on Day 1 and the second time focusing on movements made with the right hand on Day 2.