# INVESTIGATING THE INFLUENCE OF PROPRIOCEPTIVE TRAINING ON VISUOMOTOR ADAPTATION

By

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# Statement of Contributors

I hereby declare that I am the sole author of this Master's 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 Cressman.

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

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# Abstract

Visuomotor adaptation arises when reaching in an altered visual environment, where one's seen hand position does not match their felt (i.e., proprioceptive) hand position in space. Here, we investigated if proprioceptive training (PT) benefits visuomotor adaptation, and if these benefits arise due to implicit (unconscious) or explicit (conscious strategy) processes. A total of 72 participants were divided equally into 3 groups: Proprioceptive training with feedback (PTWF), Proprioceptive training no feedback (PTNF), and Control (CTRL). The PTWF and PTNF groups completed proprioceptive training (PT), where a participant's hand was passively moved to an unknown reference location and they judged the felt position of their unseen hand relative to their body midline on every trial. The PTWF group received verbal feedback with respect to their response accuracy on the middle 60% of trials. The CTRL group did not complete PT and instead sat quietly during this time. Following PT or time delay, all three groups reached when seeing a cursor that was rotated 30° clockwise relative to their hand motion, followed by a series of no-cursor reaches to assess implicit and explicit adaptation. Results indicated that the PTWF group improved their sense of felt hand position following PT. However, this improved proprioceptive acuity did not benefit visuomotor adaptation, as all three groups showed similar visuomotor adaptation across rotated reach training trials. Visuomotor adaptation arose implicitly, with minimal explicit contribution for all three groups. Thus, these results suggest that passive proprioceptive training with feedback does not benefit, nor hinder, implicit visuomotor adaptation.

# Chapter I: Literature Review

## Introduction

The goal of this research is to better understand the role of proprioception (i.e., sense of felt body position in space) in visuomotor adaptation. In order to situate this research within the context of current findings, this review of literature will first discuss goal-directed reaches and motor adaptation. This discussion will then be followed by the mechanisms underlying motor adaptation, focussing on the contribution of implicit (i.e., unconscious) processes arising from different error signals. We will then discuss the role of proprioception, specifically proprioceptive recalibration following visuomotor adaptation and the benefit of proprioceptive training on motor learning and motor adaptation. Finally, the literature review will conclude with the proposed research question and the expected outcomes.

## Goal-Directed Reaching

Throughout our daily life, we continually perform goal-directed reaching movements. Consider the task of working at a computer, for example. When using a personal computer, one is able to execute comfortable and coordinated reaches with the keyboard and mouse, such that they are able to press the desired keys and control the cursor on the screen with relative ease. However, if one were to switch to a friend's computer, initial errors in reaching may be experienced. For example, the size and placement of the keys may be different, and the responsivity of the mouse may also be altered. Thus, in order to press the appropriate keys and accurately guide the cursor on the screen, one must adjust the way they interact with these items. This process of adjusting one's movements is known as motor adaptation.

## Motor Adaptation

Motor adaptation is a form of motor learning, and is defined as the ability to systematically reduce movement errors created by altered environments, in order to return to a former level of performance (Bastian, 2008; Krakauer, 2009). In other words, performance errors are once again

similar to what is observed when moving (e.g., reaching) in a typical, known, environment. A form of motor adaptation typically studied in the laboratory is visuomotor adaptation, where participants are tasked with making goal-directed reaches. In these visuomotor adaptation studies, the visual representation of the target and/or reaching limb is typically manipulated, creating a conflict between visual and felt (i.e., proprioceptive) information related to hand position (Held, 1965; Jeannerod, 1988; Krakauer, Ghilardi & Ghez, 1999; Cressman & Henriques, 2009). It is then possible to examine the way the motor system adapts to this conflict.

Early research looked to manipulate visual information by using laterally displacing prism goggles (Harris, 1963; Held, 1965; Redding & Wallace, 1978; Welch, Bridgeman, Anand & Browman, 1993), which shifted the seen position of the target and reaching limb laterally, to the left or to the right. Today, most research studying visuomotor adaptation in the laboratory has participants reach in virtual reality environments, where a cursor on the screen misrepresents where their hand is in space (Ghahramani, Wolpert & Jordan, 1996; Krakauer, Ghilardi & Ghez, 1999; Krakauer, Pine, Ghilardi & Ghez, 2000; Cressman & Henriques, 2009). For both visual distortions (i.e., created via prism goggles or manipulations of cursor feedback on the screen), testing typically includes three phases: a pre-test, an adaptation phase, and a post-test (Redding & Wallace, 1993; Ghahramani, Wolpert & Jordan, 1996; Cressman & Henriques, 2009; Werner et al., 2015).

During the pre-test (also known as the baseline phase), participants reach in a normal environment, where visual and proprioceptive information related to hand position are aligned. Little-to-no reaching errors are experienced during this phase because no distortion has been presented. The pre-test is then followed by the adaptation phase, where a visuomotor distortion is introduced, altering the reaching environment by creating a mismatch between seen and felt hand

positions. Initial reaching errors are expected during this phase because if a participant completes a reach to the seen target position as they did in the pre-test, the seen representation of their hand (i.e., cursor on the screen) will head away from the target. For example, if the cursor's path is rotated 30° clockwise (CW) relative to hand motion, as the hand moves directly to the target, the cursor will be seen to fall 30° to the right of the target. Previous research has shown that the motor system adapts quickly to the visuomotor distortion. In fact, participants begin aiming to the left of the target after just a few trials, achieving baseline levels of performance, such that the cursor once again lands on the target as seen in the pre-test phase in as little as 20 to 30 trials (Krakauer, Ghilardi & Ghez, 1999; Krakauer, Pine, Ghilardi & Ghez, 2000; Maksimovic & Cressman, 2018).

Following the adaptation phase, the distortion is removed and participants complete another series of reaches, known as a post-test. In this phase, participants reach in a similar environment as in the pre-test, where the seen and felt hand positions are once again aligned (Buch, Young & Contreras-Vidal, 2003; Heuer & Hegele, 2008; Wang & Lei, 2015), or when no cursor is presented (Ghahramani, Wolpert & Jordan, 1996; Cressman & Henriques, 2009; Werner et al., 2015). Interestingly, results indicate that participants continue to reach as they did in the adaptation phase, aiming to the left of the target, even if they are instructed to aim directly to the target (Heuer & Hegele, 2008; Cressman & Henriques, 2009; Wang & Lei, 2015). These reaching errors are referred to as after-effects, and are taken as evidence that the motor system has adapted to the visual distortion introduced in the adaptation phase (Jeannerod, 1988; Redding & Wallace, 1993; Ong & Hodges, 2010; Wang & Lei, 2015).

In addition to adapting one's reaches in response to a visual distortion, similar trends with respect to motor adaptation are observed following the introduction of a dynamic (i.e., forcefield) distortion during reaching. Unlike visuomotor adaptation studies, forcefield adaptation paradigms

manipulate hand motion while maintaining accurate sensory feedback (i.e., the visual environment is not manipulated and there is no conflict between visual and proprioceptive information related to hand position). Typically, forcefield distortions are velocity-dependent, such that as participants reach out to a target, an external force is applied to their hand, pushing the hand away from the desired trajectory in the CW or counter clockwise (CCW) direction (Lackner & Dizio, 1994; Shadmehr & Mussa-Ivaldi, 1994). The applied force increases (or decreases) with increases (or decreases) in one's hand velocity (Lackner & Dizio, 1994; Shadmehr & Mussa-Ivaldi, 1994). As seen in visuomotor adaptation studies, participants soon begin to adapt their movements such that they aim (i.e., push their hand) in the opposite direction of the forcefield. This pushing motion leads to trajectories becoming less curved over the course of the adaptation phase, such that more linear trajectories are observed as seen in the baseline phase. During the post-test, curved movements in the opposite direction of the forcefield are observed, as participants reach as they did in the adaptation phase (Scheidt, Dingwell & Mussa-Ivaldi, 2001; Donchin, Francis & Shadmehr, 2003; Ostry et al., 2010).

## Mechanisms Underlying Motor Adaptation

Traditionally, it has been suggested that *implicit* processes underlie motor adaptation. Implicit processes are described as unconscious changes in one's movement that arise in the absence of awareness or intention (Taylor, Krakauer & Ivry, 2014; Bond & Taylor, 2015). In visuomotor adaptation studies, (implicit) adaptation has been suggested to be driven in part due to a sensory prediction error signal (Wolpert, Ghahramani & Jordan, 1995), and a cross-sensory error signal (Cressman & Henriques, 2009; Salomonczyk, Henriques & Cressman, 2013; Maksimovic, Neville & Cressman, 2020). In contrast, adaptation to a velocity-dependent forcefield has been suggested to be driven implicitly in response to a sensory prediction error signal only (Tseng et al., 2007; Sarlegna & Bernier, 2010).

In visuomotor and forcefield adaptation paradigms the sensory prediction error signal is resolved by updating of the internal model. Specifically, when reaching to a target, the central nervous system is said to create an internal representation of the movement, known as the internal model (Francis & Wonham, 1976; Wolpert, Ghahramani & Jordan, 1995; Krakauer, Ghilardi & Ghez, 1999). The internal model consists of two parts: the inverse model and the forward model. The inverse model uses sensory input from the environment (i.e., visual and proprioceptive information) regarding body and target position information to select the appropriate motor command, whereas the forward model predicts the sensory consequences of the selected movement (Wolpert, Ghahramani & Jordan, 1995). Incoming sensory information is then compared to the predicted sensory outcome of the movement, and if they do not match, a sensory prediction error signal is generated (Tseng et al., 2007; Shadmehr, Smith & Krakauer, 2010). The motor plan (i.e., inverse model) and the predicted sensory consequences (i.e., forward model) are then updated unconsciously in response to this error signal, in order to enable the movement to be performed correctly and to reduce future movement errors (Wolpert, Ghahramani & Jordan, 1995; Shadmehr, Smith & Krakauer, 2010). This sensory prediction error has been suggested to contribute to implicit adaptation, as there is a conflict between predicted sensory information (e.g., seen position of the hand landing on the target) and actual sensory feedback experienced (e.g., seen position of the hand veers away from the target; Wolpert, Ghahramani & Jordan, 1995).

Implicit adaptation in visuomotor adaptation paradigms is also proposed to arise in part due to a cross-sensory error signal (i.e., a visual-proprioceptive conflict regarding hand position; Cressman & Henriques, 2009; Salomonczyk, Henriques & Cressman, 2013; Maksimovic, Neville & Cressman, 2020). When reaching to a target, visual information related to one's hand position is distorted such that it no longer matches one's felt hand position in space. A potential method for

resolving this sensory conflict is for one of the two senses to be recalibrated so that the sensory signals are once again aligned. Previous research by Cressman and colleagues (Cressman & Henriques, 2009, 2010; Salomonczyk et al., 2011, 2012, 2013; Mostafa et al., 2014), has demonstrated that proprioception is typically recalibrated in visuomotor adaptation paradigms, such that one's sense of felt hand position is shifted in the direction of the distorted visual feedback. This proprioceptive recalibration has been shown to contribute to visuomotor adaptation and will be discussed in further detail in the following section. In contrast to visuomotor adaptation paradigms, proprioceptive recalibration is not suggested to play a role in motor adaptation to a velocity-dependent forcefield, as there is no cross-sensory error signal experienced (i.e., visual and proprioceptive signals related to hand position remain aligned).

Before discussing proprioceptive recalibration in detail below, it should be noted that, recently, explicit processes have also been suggested to play a role in visuomotor adaptation, depending on the size of the cursor distortion introduced (Werner et al., 2015; Neville & Cressman, 2018; Modchalingam, Vachon, 't Hart & Henriques, 2019). Explicit processes refer to the strategic changes in reaches that arise due to the conscious awareness of the visuomotor distortion and/or knowledge of how to move in the novel visuomotor environment (Benson, Anguera & Seidler, 2011; Taylor, Krakauer & Ivry, 2014; Werner et al., 2015). Work from our laboratory (Neville and Cressman, 2018), as well as Henriques' laboratory (Modchalingam, Vachon, 't Hart & Henriques, 2019; Vachon et al., 2020) has demonstrated that the contribution of explicit processes to visuomotor adaptation are negligible when the visuomotor distortion is 30° or less. In fact, it is only when the visuomotor distortion is 40° or larger, that explicit process have been shown to contribute significantly to visuomotor adaptation (Werner et al. 2015; Neville and Cressman, 2018).

The contribution of explicit processes to visuomotor adaptation has been demonstrated using the Process Dissociation Procedure (PDP). The PDP was first introduced by Jacoby (1991) to measure the contributions of automatic and intentional memory to recognition. It has recently been modified by Werner and colleagues (2015) to examine the contributions of implicit and explicit processes to visuomotor adaptation. In this framework, participants are asked to either use (i.e., *inclusion* instructions; implicit + explicit adaptation are assessed) or refrain from using (i.e., *exclusion* instructions; only implicit adaptation is assessed) learned strategies when reaching in the absence of visual feedback (Werner et al., 2015; Neville & Cressman, 2018; Werner, Strüder & Donchin, 2019). The exclusion trials are similar to the post-test instructions described above, where participants are instructed to reach directly to the target. Recent work from our laboratory (Decarie, Heirani Moghaddam & Cressman, 2020), suggests that implicit adaptation is similar in magnitude regardless if participants are cued on the presence of a reaching strategy (e.g., in the exclusion trials), or merely told to aim to the target (e.g., post-test trials). Explicit adaptation is taken as the difference in performance errors between the inclusion and exclusion trials.

## Proprioception and Proprioceptive Recalibration

As indicated above, proprioceptive signals have been suggested to play a role in implicit visuomotor adaptation. First described by Sherrington (1906), proprioception is our sense of felt body position in space. It is often referred to as our ‘sixth sense’ and/or the ‘invisible sense’ because it does not have an associated sensory organ that is visibly detectable like the other five senses (i.e., sight, taste, touch, smell and audition). Proprioception functions in the absence of our direct awareness, constantly gathering information from mechanoreceptors found in muscles, tendons, and joints to help guide in the execution of accurate, smooth, and fluid movements (Roll & Vedel, 1982). Our sense of proprioception is what allows us to touch our finger to our nose with our eyes closed or reach for a glass of water without looking at it.

In the aforementioned research by Cressman and colleagues (see Cressman & Henriques, 2009, 2010; Salomonczyk et al., 2011, 2012, 2013; Mostafa et al., 2014), proprioception has been shown to be recalibrated in visuomotor adaptation studies. This recalibration was demonstrated by having participants complete a series of *proprioceptive judgments* within a hand positioning task. Specifically, the participant's unseen hand was moved to a desired location by a robotic manipulandum and participants indicated the felt position of their hand relative to a visual or proprioceptive (i.e., body midline) reference marker (i.e., participants reported if their hand was to the left or to the right of the marker; Cressman & Henriques, 2009, 2010). The hand position relative to the reference marker was then altered over trials according to participants' responses. The position at which participants reported left and right equally often was established as the location that they felt their hand was aligned with the reference marker. By having participants complete these proprioceptive judgments before and after reaching with a rotated cursor, Cressman and colleagues demonstrated that participants shifted their sense of felt hand position in the same direction as the visuomotor distortion, and that the shift was approximately one third of the size of the observed after-effects (Cressman & Henriques, 2009, 2010; Salomonczyk et al., 2011, 2012, 2013; Mostafa et al., 2014).

This phenomenon of proprioceptive recalibration has been shown to be robust, such that it arises regardless of the type of visuomotor distortion introduced (e.g., rotated cursor feedback or translated cursor feedback; Cressman & Henriques, 2009), how the visuomotor distortion is introduced (e.g., abrupt vs. gradually; Salomonczyk, Henriques & Cressman, 2012), the magnitude of the visuomotor distortion (e.g., 30° rotation vs. 70° rotation; Salomonczyk, Cressman & Henriques, 2011), which hand is trained (e.g., left or right hand; Salomonczyk, Henriques & Cressman, 2012), and age (e.g., younger or older participants; Cressman, Salomonczyk &

Henriques, 2010). Recently, Modchalingam and colleagues (2019) have shown that proprioceptive recalibration arises implicitly, as it occurs in the absence of participants' awareness of the visuomotor distortion. Moreover, it has been shown that when only the cross-sensory error signal is presented (i.e., there is no sensory prediction error; see Cressman & Henriques, 2010), the extent of proprioceptive recalibration and after-effects are similar in magnitude and significantly correlated, suggesting a critical role for the cross-sensory error signal in visuomotor adaptation.

Although proprioceptive input is important for movement execution (Harris, 1963; Roll & Vedel, 1982; Cressman & Henriques, 2009), and has been shown to play a role in visuomotor adaptation (as discussed above), research on deafferented patients (i.e., void of proprioception) has demonstrated that proprioception is not required for motor adaptation to arise. For example, Lajoie and colleagues (1992) found that a deafferented individual (G.L.) learned to quickly and accurately trace a star shape when looking in a mirror. Ingram and colleagues (2000) and Bernier and colleagues (2006) have further demonstrated preserved visuomotor adaptation following deafferentation when reaching with rotated cursor feedback in a virtual reality environment. In fact, Bernier and colleagues (2006) showed that when the visual distortion was removed, G.L. still exhibited after-effects, and hence, demonstrated implicit visuomotor adaptation.

In addition to visuomotor adaptation arising in the absence of proprioception (i.e., in deafferented individuals), Bernier and colleagues (2009) have shown that early trials during the adaptation phase with the visuomotor distortion are accompanied by initial proprioceptive suppression in healthy (Control) participants. Specifically, when participants were first learning to reach with altered visual feedback of their hand position, the magnitude of sensory evoked potentials measured using electroencephalography, and hence indicating the extent of proprioceptive processing, were reduced. In other words, when first learning to reach with the

visuomotor distortion, healthy participants acted as if they were deafferented. Over adaptation trials, participants adapted their movements and proprioceptive input was processed to a greater extent (i.e., an extent similar to what was observed in the pre-test when no visuomotor distortion was presented). This increased processing of proprioceptive input later in the adaptation phase could be related to proprioception being recalibrated as suggested by Cressman and colleagues (Cressman & Henriques, 2009, 2010; Salomonczyk et al., 2011, 2012, 2013; Mostafa et al., 2014). In support of this proposal, a review by Sarlegna & Mutha (2015) indicates that the nervous system uses all sources of sensory information available during motor adaptation, however, the contribution of information varies at different time points throughout the course of adaptation.

The question we now raise is: would an improved sense of proprioception benefit visuomotor adaption? In other words, if participants' proprioceptive sense was more accurate (i.e., enhanced proprioceptive acuity), would this lead to visuomotor adaptation arising earlier and to a greater extent. Alternatively, improved proprioceptive acuity may be of no benefit or even hinder visuomotor adaptation, as an improved proprioceptive sense may lead to difficulties in proprioceptive information being supressed or recalibrated when first learning to reach with the visuomotor distortion. Recently, researchers have investigated the effects of proprioceptive training on motor learning, including motor adaptation, to see if an improved sense of proprioception benefits performance. In the next section we discuss proprioceptive training as a potential method to help post-stroke patients reacquire proprioceptive function and lost upper-limb motor function. This is then followed by the use of proprioceptive training to help healthy individuals acquire new motor skills and adapt their movements to a velocity-dependent forcefield.

## Proprioceptive Training on Motor Learning

One of the earliest investigations into proprioceptive training was work done by Carey and colleagues (1993) in post-stroke patients. Proprioceptive deficiencies are common in individuals

who have suffered a stroke, impacting about 65% of this patient population (Feigenson et al., 1977). Over many years of study, Carey and colleagues (1993, 1995, 1996, 1997, 2000, 2002) developed a successful proprioceptive training program to help post-stroke patients improve their sense of tactile and proprioceptive discrimination in the upper-limb, producing reliable, consistent, and long-term improvements. Their training plan had patients 1) tactically explore and compare different textured surfaces, and 2) engage in passive movement training of the hand to unknown target locations and provide judgments about limb position (i.e., proprioceptive judgments). In some cases, patients received verbal and/or visual feedback about their judgments. Following proprioceptive training, Carey and colleagues (1993, 1995, 1996, 1997, 2000, 2002) showed that even patients with severe sensorimotor impairments regained proprioception to a level similar to that of their unaffected side, and in some cases, to the same level as healthy (Control) individuals. The successful use of proprioceptive training to improve post-stroke patients' tactile and proprioceptive discrimination next led the authors to ask whether enhanced proprioceptive processing leads to benefits in motor function post-stroke. Indeed, Carey and colleagues (2005, 2011) and Blennerhassett and colleagues (2006, 2007), found improvements in patients' ability to identify the tactile surface and weight of certain objects, to complete a pinch grip (even when tracking a visual object), to grasp common objects, and to perform reaching movements following proprioceptive training. However, the authors further suggested that a more tailored (i.e., patient specific) proprioceptive training plan may be required to see benefits in motor function in activities of daily living.

In a different line of inquiry, researchers have also investigated the effects of proprioceptive training on motor learning in healthy individuals. For example, Wong and colleagues (2012) tested participants' ability to learn a simple motor task (i.e., tracing a circle)

following proprioceptive training. In their study, participants were seated and attempted to trace a perfect circle using a robotic manipulandum while vision of the reaching arm was occluded. A set of baseline movements were completed, where full visual feedback of the circle and a cursor (whose motion matched the robot manipulandum) were provided on the screen. Following these baseline movements, participants began proprioceptive training. Proprioceptive training began with two visual demonstration trials. During these trials, the circle appeared on the screen and a cursor moved around the circle in the CCW direction while the participant's hand was held fixed at the starting position. Participants then completed demonstration trials and active movement trials. During the demonstration trials, the information provided during training varied across 4 groups: Group 1: the robot manipulandum passively moved participants' hand in the desired direction (CCW), Group 2: the robot manipulandum passively moved participants' hand in the opposite direction (CW), Group 3: the robot manipulandum passively moved participants' hand in the desired direction (CCW) and participants were told to actively push against the robot handle during movement, and Group 4: did not complete the passive movement trials (i.e., Control group). For Groups 1, 2 and 3, the robot motion was accompanied by participants seeing a cursor follow the same path. During the active movement trials, all groups were asked to actively move the robot manipulandum along a path that traced the desired circle in the CCW direction. Vision of the circle was not provided during these active movement trials, but vision of the cursor representing their hand position was displayed.

Altogether, proprioceptive training included 240 trials (i.e., 160 active movement trials and 80 demonstration (i.e., passive movement) trials). Trials were divided into equal blocks of 30 movements, where active movement trials and demonstration trials were presented in a 2:1 ratio. At the start of each block, two visual demonstrations (as described above) were shown to all

participants. Following proprioceptive training, all participants were asked to trace the circle as they did in the active movement trials (i.e., no circle was presented, but a cursor representing their hand motion was displayed). Participants then repeated these traces two and three days later.

Results indicated that all groups who received passive proprioceptive training (i.e., Groups 1, 2 and 3) were able to trace the circle faster and more accurately on day 1 and subsequent testing days compared to the Control group (i.e., Group 4; Wong, Kistemaker, Chin & Gribble, 2012). Interestingly, accuracy was greatest for participants who had their hand moved passively in the desired direction (i.e., Group 1) compared to participants who had their hand moved passively in the desired direction whilst being told to actively push against the robot handle (i.e., Group 3). This result is surprising because previous studies have found that proprioceptive acuity is typically better following active limb movement compared to passive limb displacement (Marteniuk, 1973; Stelmach, Kelso & McCullagh, 1976). Wong and colleagues (2012) suggested that strict passive proprioceptive training may have led to enhanced motor learning in their study because the movement being learned (i.e., tracing the circle) was externally defined (i.e., participants followed a pre-determined trajectory), therefore, the active pushing against the robot handle provided no additional benefit to learning the desired movement in their case. As expected, accuracy was greater for participants that were passively trained in the desired direction (i.e., Group 1) compared to participants that were passively trained in the opposite direction (i.e., Group 2).

Within the same study, Wong and colleagues (2012) also tested the effects of proprioceptive training on a more complex motor skill (i.e., tracing a word). Proprioceptive training was similar to that of the previous task reported, but this time only two groups were included: a passively trained group and a Control group (untrained). Passive proprioceptive training included the robot guiding the participant's hand through the word "Liz" with vision of

the cursor. Results revealed that, again, the passively trained group learned to trace the word faster and more accurately than the Control group. Taken together, the results from this study indicate that passive proprioceptive training improves motor learning for both simple and complex motor skills, and this benefit is greatest when passive training is in the desired direction.

Having established that proprioceptive training can be used to benefit motor learning of a motor skill, we next look to determine if proprioceptive training can benefit motor adaptation. Initial work by Darainy and colleagues (2013) sought to address this question in a forcefield adaptation paradigm. Participants were divided into 4 groups: Group 1: Proprioceptive training with feedback, Group 2: Proprioceptive training no feedback, Group 3: Proprioceptive training with feedback + 24 hour delay, and Group 4: Control; no proprioceptive training. All participants began by completing a set of null (i.e., no forcefield) reaches to a single target in line with their body midline (i.e., baseline reaches). Following baseline reaches, all groups completed proprioceptive training except for the Control Group (i.e., Group 4), who instead sat quietly during this time. Proprioceptive training involved 5 blocks of 100 hand positioning trials in which participants provided *proprioceptive judgments* regarding their hand position following each trial. For participants in Group 1, the robot passively moved the hand to one of ten reference locations located along a fan-shaped trajectory, distributed to the left and right of center (i.e., at 1.5°, 3°, 4°, 5° and 8° to the left and to the right of participants' body midline). Training occurred in the absence of visual feedback, such that participants did not see their hand and no reference location was displayed. On each trial, participants in Groups 1 and 3 were required to indicate if their hand was positioned to the left or to the right of their body midline. Feedback with respect to accuracy in the form of an oral response (i.e., "correct" or "incorrect") was provided by the experimenter for the last 3 blocks (i.e., 300 trials; last 60% of trials). Group 2 had their hand moved in a similar manner,

but were not asked to provide a judgment on their felt hand position and no feedback was provided. Following the proprioceptive training phase, participants again reached to the single target in another set of null (i.e., no forcefield) reaches. These reaches were then followed by a series of reaches within the velocity-dependent forcefield (150 trials when a CCW forcefield was imposed, followed by 50 trials when a CW forcefield was imposed). Group 3 completed the same training as Group 1, but they completed the second set of null reaches and forcefield reaches 24 hours after completing the proprioceptive training.

Proprioceptive training improved proprioceptive acuity for Groups 1 and 3, as their ability to correctly judge their felt limb position (as determined by their "left"/"right" responses within a block of hand positioning trials) improved across the 5 blocks of training. Furthermore, Group 1 adapted their reaches to the velocity-dependent forcefield earlier, immediately reaching with less curved trajectories when first introduced to the velocity-dependent forcefield compared to Groups 2 and 4. This improved performance suggests that proprioceptive training benefits motor adaptation (Darainy, Vahdat & Ostry, 2013). The benefits of proprioceptive training were also found to be long-lasting, as Group 3 also adapted their reaches earlier and performed less-curved reaches compared to Groups 2 and 4 when introduced to the forcefield distortion 24 hours later (Darainy, Vahdat & Ostry, 2013). Thus, the results of this study indicate that passive proprioceptive training benefits short term and long term adaptation to a velocity-dependent forcefield, but only when verbal feedback regarding position accuracy is provided during training.

A follow-up study has demonstrated similar benefits of proprioceptive training on motor adaptation, albeit when combined with observational learning. In their study, McGregor and colleagues (2018) found that if participants first completed proprioceptive training (i.e., 5 blocks of 74 hand positioning trials, with feedback provided during Blocks 2, 3 and 4) and then watched

a video of an actor adapting to a velocity-dependent forcefield, their movements were less curved when initially exposed to the forcefield compared to participants who did not complete proprioceptive training (McGregor, Cashaback & Gribble, 2018). These less-curved movements were taken as evidence that proprioceptive training benefitted motor adaptation.

## Purpose and Research Question

As outlined above, motor adaptation is typically studied in the laboratory by having participants reach (1) with a visuomotor distortion, or (2) in a velocity-dependent forcefield. It has been demonstrated that proprioceptive training can benefit motor adaptation when participants are introduced to a velocity-dependent forcefield (i.e., when a sensory prediction error signal is present; Darainy, Vahdat & Ostry, 2013; McGregor, Cashaback & Gribble, 2018). The goal of the proposed research is to determine the effects of proprioceptive training on visuomotor adaptation, a paradigm in which both a sensory prediction *and* cross-sensory error signal are experienced. Additionally, we will look to determine if visuomotor adaptation arises implicitly (i.e., unconsciously) and/or explicitly (i.e., conscious strategy engaged).

Similar to the work by Darainy and colleagues (2013) and McGregor and colleagues (2018), participants will complete proprioceptive training consisting of a hand positioning task in which their hand will be passively moved to an unknown reference location and participants will be asked to verbally indicate the position of their hand relative to their body midline. Two groups of participants will report their felt hand position on each trial, but only one group will receive feedback with respect to the accuracy of their judgments on the middle 60% of trials (i.e., Blocks 2, 3 and 4; McGregor, Cashaback & Gribble, 2018), enabling us to establish the benefit of proprioceptive training on proprioceptive acuity. A third group will also be included in the study, but this group will not participate in proprioceptive training (i.e., Control group). Following proprioceptive training, all three groups will reach with a cursor that misrepresents where their

hand is in space, such that it will be rotated 30° CW relative to hand motion. Finally, all groups will complete a series of no-cursor reaches to assess the contributions of implicit and/or explicit processes to visuomotor adaptation.

Based on previous results demonstrating that proprioceptive training benefits motor adaptation when reaching in a forcefield (Darainy, Vahdat & Ostry, 2013; McGregor, Cashaback & Gribble, 2018), we expect that proprioceptive training will benefit visuomotor adaptation. More specifically, it is hypothesized that the group that receives feedback during proprioceptive training will adapt their reaches earlier (i.e., demonstrate fewer errors when first introduced to the visuomotor distortion) compared to the other two groups. As well, it is hypothesized that these benefits will arise implicitly because adaptation to a visuomotor distortion of 30° or less has been shown to be largely unconscious in nature with minimal explicit contributions (Neville and Cressman, 2018; Modchalingam, Vachon, ‘t Hart & Henriques, 2019; Vachon et al., 2020). Alternatively, if we find that proprioceptive training does not benefit visuomotor adaptation, our results would imply that improving proprioceptive acuity does not benefit motor adaptation in a paradigm where a sensory prediction and cross-sensory error signal are experienced.

# Chapter II: Research Article

## Introduction

Proprioceptive training has been shown to benefit motor learning for both patient populations (Carey et al., 2005, 2011; Blennerhassett et al., 2006, 2007) and healthy participants (Wong, Kistemaker, Chin & Gribble, 2012; Darainy, Vahdat & Ostry, 2013; McGregor, Cashaback & Gribble, 2018). More specifically, for healthy participants, prior proprioceptive training has been shown to benefit motor adaptation when participants adapt their reaches in response to a velocity-dependent forcefield (Darainy et al., 2013; McGregor et al., 2018). Within forcefield adaptation paradigms, participants typically reach to a target in a virtual environment while experiencing a clockwise (CW) or counter-clockwise (CCW) force that pushes their hand away from the desired target position (Lackner & Dizio, 1994; Shadmehr & Mussa-Ivaldi, 1994; Mattar & Gribble, 2005). Initial errors when reaching in a velocity-dependent forcefield are common, such that reach trajectories are more curved and the hand may not land on the target as expected (Scheidt, Dingwell & Mussa-Ivaldi, 2001; Donchin, Francis & Shadmehr, 2003; Ostry et al., 2010). However, over trials, participants adapt their reaches to this new environment by pushing their hand in the opposite direction of the forcefield. In recent work, Darainy and colleagues (2013) and McGregor and colleagues (2018) have shown that this reach adaptation occurs earlier following proprioceptive training, such that participant's reaches were initially less curved when first introduced to the forcefield compared to participants that had not undergone proprioceptive training.

Darainy and colleagues' (2013) proprioceptive training included having participants judge the felt position of their unseen hand relative to their body midline within a hand positioning task. For these trials, their hand was passively moved to an unseen reference location within 8° of their body midline and participants made a judgment about whether the position of their hand was

located to the left or to the right of their body midline. One group received verbal feedback indicating if their response was correct or incorrect, whereas another group did not receive any feedback during proprioceptive training, nor did they judge their felt hand position. Proprioceptive acuity (i.e., accuracy in hand judgments) was shown to improve across proprioceptive training trials, but only for the group that provided judgments of felt hand position and received verbal feedback during training (see also McGregor, Cashaback & Gribble, 2018). This enhanced proprioceptive acuity was then shown to benefit reach adaptation to the velocity-dependent forcefield compared to the group that did not receive feedback and a Control group of participants that did not complete the proprioceptive training trials at all.

Motor adaptation to a velocity-dependent forcefield is presumed to reflect changes in reaches that arise implicitly (i.e., unconsciously) in response to a sensory prediction error signal. Specifically, participants experience a discrepancy between the predicted sensory outcome of their movement (e.g., seen position of the hand landing on the target) and the actual sensory feedback experienced (e.g., seen position of the hand heads away from the target; Tseng et al., 2007; Sarlegna & Bernier, 2010). To resolve this sensory prediction error, the internal model is updated in order to reduce future reaching errors (Wolpert, Ghahramani & Jordan, 1995; Shadmehr, Smith & Krakauer, 2010).

Having determined that proprioceptive training benefits forcefield adaptation, we asked if similar benefits arise within a visuomotor adaptation paradigm. Visuomotor adaptation is typically studied by having participants reach in virtual environments where a cursor on the screen misrepresents the location of their felt hand position in space (Ghahramani, Wolpert & Jordan, 1996; Krakauer, Ghilardi & Ghez, 1999; Krakauer, Pine, Ghilardi & Ghez, 2000; Cressman & Henriques, 2009). Similar to forcefield adaptation paradigms, visuomotor adaptation studies

introduce a sensory prediction error signal, such that the expected sensory consequences of the movement (i.e., hand/cursor landing on the target) do not match the actual sensory feedback experienced (i.e., hand/cursor does not land on the target as expected). Furthermore, unique to visuomotor adaptation paradigms, participants also experience a cross-sensory error signal when reaching due to the conflict between visual (seen cursor) and proprioceptive (felt) estimates of hand position (Cressman & Henriques, 2009; Salomonczyk, Henriques & Cressman, 2013; Maksimovic, Neville & Cressman, 2020). It has been suggested that this sensory conflict is resolved via proprioceptive recalibration, such that one shifts the felt position of their hand in the direction of the distorted visual feedback to once again form a coherent estimate of hand position (Cressman & Henriques, 2009, 2010; Salomonczyk et al., 2011, 2012, 2013; Mostafa et al., 2014).

To determine if proprioceptive training benefits visuomotor adaptation, three groups of participants were included in our study, where two of the three groups completed passive proprioceptive training prior to visuomotor adaptation as done by McGregor and colleagues 2018 (see also Darainy et al., 2013). Specifically, one group of participants received verbal feedback regarding their judgments of felt hand position after their hand was passively moved into position, and another group completed the proprioceptive judgments, but did not receive any feedback regarding their responses during training. A third group did not complete proprioceptive training and served as a Control group. Visuomotor adaptation when reaching with rotated cursor feedback (30° CW) was then assessed in all three groups. Finally, to establish if implicit processes contributed to visuomotor adaptation, we had participants complete a series of reaches to the targets in the absence of cursor (i.e., visual) feedback. During these trials, participants were instructed to refrain from using (only implicit adaptation assessed), or use (implicit + explicit adaptation assessed) any learned strategy while reaching in the absence of cursor feedback, as done

by Werner and colleagues (2015), where explicit adaptation refers to the engagement of conscious strategies.

We hypothesized that proprioceptive training would benefit visuomotor adaptation, as improving proprioceptive acuity has been shown to benefit motor adaptation to a velocity-dependent forcefield when a sensory prediction error signal is present. Thus, we expected that the group that received verbal feedback during proprioceptive training would adapt their reaches quicker when first introduced to the visuomotor distortion compared to the group that did not receive feedback during training and the Control group. Alternatively, if no benefits were found, our results would suggest that improving proprioceptive acuity does not benefit, and may even hinder visuomotor adaptation, as an improved sense of proprioception may be harder to supress or recalibrate when first learning to reach with the visuomotor distortion. We also expected motor adaptation to arise implicitly rather than explicitly, as adaptation has been shown to arise implicitly for small visuomotor distortions (i.e., cursor rotations equal to, or less than, 30°), when a small target error signal is experienced (Neville & Cressman, 2018; Modchalingam, Vachon, ‘t Hart & Henriques, 2019; Vachon et al., 2020).

## Methods

### Participants

A total of 72 participants aged 19-40 years old (M = 23 years, SD = 3.8) were recruited for this study. Initial ideal sample size was determined to be 45 participants by performing a power analysis using G*Power (Version 3.1.9.3; Faul, Erdfelder, Lang, & Buchner, 2007), with a desired power of 0.80, a probability of Type 1 error of 0.05, and an expected effect size of 0.14 with respect to the benefit of proprioceptive training (Darainy, Vahdat & Ostry, 2013; McGregor, Cashaback & Gribble, 2018). The majority of participants (n = 64) were deemed to be right-handed based on their responses on the modified version of the Edinburgh Handedness Inventory, while the

remaining 8 participants were classified as ambidextrous (M = 80.1, SD = 24.5, range = 0-100; Oldfield, 1971; see Appendix D). All participants reported having no history of neurological, motor, or sensory impairment, and had normal or corrected-to-normal vision. As well, all participants were naïve to the purpose of the study and had never participated in a visuomotor adaptation study involving reaching with distorted visual feedback in a virtual environment. Participant recruitment and data collection commenced after the Faculty of Health Sciences at the University of Ottawa approved a Safe Research plan and ethical approval was attained from the University of Ottawa's Health Sciences and Science Research Ethics Board (see Appendix A). Prior to starting the experiment, all participants provided written informed consent (see Appendix B) as well as a uOttawa Consent Information Addendum – COVID-19 Risks (see Appendix C).

## Apparatus

Testing took place in a secluded, dark room. Participants grasped the handle of the KINARM End-Point Lab (KINARM Technologies, Kingston, ON), using their right hand. As shown in Figure 1A, visual targets were projected from a downward facing monitor (LG 47LD452B-UA EzSign – 47" LCD TV; refresh rate: 60Hz, 2.6A; 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 horizontal plane as the right hand holding the robot handle. Participants were seated in a height-adjustable chair located in front of the experimental apparatus (Figure 1A). The chair was positioned so that the participant's forehead rested comfortably against the testing apparatus and they could reach to all the targets within the workspace. As well, their body midline was aligned with the starting home position and a central target position prior to beginning the experiment (Figure 1B). The position of the chair was locked in place and maintained throughout the experimental session. Participants' view of their limbs was occluded by the reflective surface and a black cloth that was draped around their neck and attached to the

apparatus. Once participants were seated comfortably, the room lights were turned off and testing began.

## Experiment Overview

### *General Overview*

Testing took place during a single session that lasted approximately 1.5 hours. Participants were randomly divided into 3 groups (n = 24/group): Proprioceptive training with feedback (PTWF), Proprioceptive training no feedback (PTNF) and Control (CTRL). Depending on group, participants completed the blocks of reaches and proprioceptive training as outlined below (also see Figure 2A&B). All instructions provided to participants during testing can be found in Appendix E.

All movements began with the hand at the home position, located approximately 20 cm in front of the participant's chest (white circle, 2 cm in diameter) and in line with their body midline (Figure 1B). All three groups first reached while seeing a cursor that was aligned with their hand (i.e., aligned reach training) to establish movement errors in a typical (i.e., baseline) visual environment (Figure 1B). All groups then completed a block of no-cursor reaches to determine how they reached to a target when no visual feedback was provided (Figure 1D). Following this, the PTWF and PTNF groups completed a series of proprioceptive training trials in which their hand was passively moved to a reference location and participants indicated if their hand was located to the left or to the right of their body midline (Figure 1E). The CTRL group did not complete proprioceptive training and instead stayed seated in the testing room for 30 minutes (i.e., time delay). Following proprioceptive training or time delay, all participants completed a second block of aligned reaches followed by a second block of no-cursor reaches. These trials were then followed by a block of reaches with a visuomotor distortion (i.e., rotated reach training; Figure

1C), followed by a third block of no-cursor reaches to assess the contributions of implicit and/or explicit processes to visuomotor adaptation.

### *Reach Training Trials*

During aligned reach training (Figure 2A & B, Box 1, 2 & 5), all three groups began by holding the robot handle at the home position. Following 500 ms, one of three targets appeared (yellow circle, 2 cm in diameter), located 15 cm away from the home position. The targets were located straight ahead of the home position (central target; 0°) and 45° to the left and right of the central target. Once a target appeared, participants were instructed to reach to it as quickly as possible with the goal of having the cursor land on the target. Real-time visual feedback of the hand position was provided via a cursor on the screen (magenta circle, 1 cm in diameter), both while the hand was held in the home position prior to the start of the reach, and throughout the duration of the movement. Once participants landed on the target (i.e., the center of the cursor and the center of the target were within 0.5 cm), the hand was held at this position for another 500 ms. The cursor and the target then disappeared, and the robot passively moved the hand back to the home position following a direct, linear path in a movement time of 1000 ms. 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. See Figure 3A for a timeline of events for aligned reach training.

Participants began by completing 9 practice aligned reach training trials (3 to each target; Figure 2A & B, Box 1). The practice trials were completed to allow participants to familiarize themselves with the reaching task and were not analyzed. Following the practice trials, participants completed 51 aligned reaches (i.e., baseline reaches; 17 to each target; Figure 2A & B, Box 2). An

additional 15 aligned reaches (5 to each target; Figure 2A & B, Box 5) were completed following proprioceptive training (PTWF and PTNF groups) or the time delay (CTRL group).

The rotated reach training trials (Figure 2A & B, Box 7) followed the same timeline of events as the aligned reach training trials explained above, in that participants were instructed to reach to the target quickly with the goal of having the cursor land on the target. However, on these trials, the cursor representing the position of the hand was rotated 30° CW relative to the participant's hand trajectory (Figure 1C). Participants were not made aware of this rotation, nor were they given instruction on how to counteract it. See Figure 3B for a timeline of events for rotated reach training trials. All 3 groups performed 99 reaches (33 to each target) with the rotated cursor following proprioceptive training or the time delay.

### *No-Cursor Reaches to Assess Implicit and Explicit Adaptation*

Two blocks of 6 no-cursor reaches (2 reaches to each target within each block) were performed 3 times: before (i.e., Time 1; Figure 2A & B, Box 3) and after (i.e., Time 2; Figure 2A & B, Box 6) proprioceptive training or time delay, and again after rotated reach training (i.e., Time 3; Figure 2A & B, Box 8). For these trials, participants reached when no visual cursor was displayed (Figure 1D). These reaches followed the same timeline of events as described above in the reach training trials (see Figure 3C). However, the end of each movement was determined online as the time at which velocity first decreased below 0.01m/s. The no-cursor reaches at Time 1 and Time 2 included two blocks of 6 *exclusion* trials, where participants were instructed to: "Reach so that your hand goes straight to the target". Following the rotated reach training trials (Time 3), participants completed 6 *exclusion* trials. These were then followed by 6 *inclusion* trials, in which participants were to: "Reach using anything you have learned during training in order to get the cursor to the target. In other words, reach so that the cursor would have gone straight to the target, as in the reaching trials you just completed when the cursor was available".

### *Proprioceptive Training*

The PTWF and PTNF groups completed proprioceptive training (Figure 2A, Box 4). This training consisted of a hand positioning task and was conducted in the absence of visual feedback (Figure 1E). Participants completed 5 blocks of 74 trials, for a total of 370 trials (as done by McGregor, Cashaback & Gribble, 2018). A 2 minute break was given at the end of each block, at which time participants remained seated at the testing apparatus with their hand hidden from view.

Proprioceptive training trials began with a participant's hand held in the home position for 500 ms. After 500 ms, the home position disappeared and the robot passively moved the hand 15 cm outward to one of ten reference locations (RL) located along a circular arc (Figure 1E). These RL were located at 1.5°, 3°, 4°, 5° and 8° to the left and to the right of center (i.e., 0°, corresponding to body midline; as used by Darainy, Vahdat & Ostry, 2013). The breakdown of trials to each RL in each block was: 10 trials to the 1.5° RL, 10 trials to the 3° RL, 7 trials to the 4° RL, 7 trials to the 5° RL and 3 trials to the 8° RL in the leftwards and rightwards direction relative to center. The RL were presented in a randomized order.

For each trial, the robot moved the participant's hand outwards with a bell-shaped velocity profile with an average speed of 15 cm/s, such that all movements took 1000 ms to complete. Once the hand reached the RL, participants were asked to verbally indicate if the position of their hand was located to the left or to the right of their body midline (i.e., the center of their body). There was no time limit to respond and their response was recorded by the experimenter. No feedback about response accuracy was provided to either group on the first and last block of proprioceptive training trials (i.e., Blocks 1 and 5). However, in the middle blocks of trials (i.e., Blocks 2, 3, and 4), feedback regarding response accuracy was provided to the PTWF group only. Specifically, they were told if their response was "correct" or "incorrect". The PTNF group did not receive feedback regarding their responses. After responses were recorded for both groups, the hand was

held at the RL for an additional 500 ms before being moved directly back to the home position in a time of 1000 ms in order to start the next trial. See Figure 3D for a timeline of events for the proprioceptive training trials.

## Data Analysis

### *Proprioceptive Training*

We first looked to establish participants' proprioceptive acuity (i.e., their ability to locate the position of their hand in space) over the course of the proprioceptive training trials by determining a participant's absolute bias (i.e., response accuracy; perceived boundary between left and right of body midline; 50$^{th}$ percentile) and uncertainty range (i.e., response consistency; interquartile range (IQR); distance between the 25$^{th}$ and 75$^{th}$ percentiles). Proprioceptive acuity was determined for each participant in the PTWF and PTNF groups for each of the five blocks of proprioceptive training trials by fitting the following binary logistic function to each participant's responses across all reference locations:

$$Y = \frac{e^{a+bX}}{1 + e^{a+bX}}$$

where 'Y' represents the probability of left responses for the different RL ('X'), 'a' represents a constant (i.e., yields Y when X is zero) and 'b' represents the slope (i.e., how quickly the probability changes with changes in RL). Absolute bias and uncertainty ranges were compared between the PTWF and PTNF groups over the 5 blocks of proprioceptive training trials using a 2 Group (PTWF and PTNF) x 5 Block (Blocks 1-5) mixed analysis of variance (ANOVA) with repeated measures (RM) on the second factor.

### *Reaching Trials*

All reaching trials (i.e., aligned reach training trials, rotated reach training trials, and no-cursor reaches) were visually inspected using custom written programs for MATLAB. The start (i.e., movement onset) and end (i.e., movement termination) points of each movement were

selected using a velocity-based criterion such that movement onset and movement termination were defined as when velocity first increased above, and decreased below, 0.01 m/s and remained above or below for 50 ms, respectively. For each trial, we determined the angular error of the hand at peak velocity (i.e., PVAE), where PVAE is equal to the angular difference between a vector from the home position to the desired target and a vector from the home position to the hand's actual position at peak velocity. Trials were removed from analysis if PVAE was greater than 50° or less than 3 standard deviations below a participants' average error on the second block of 6 no-cursor *exclusion* trials following aligned reach training (Figure 2A & B, Box 3). A total of 73 trials were removed from analysis, equal to 0.5% of all reaching trials.

### Visuomotor Adaptation: Rotated Reach Training Trials

To determine if proprioceptive training had an effect on visuomotor adaptation, we first analyzed rotated reach training trials early in adaptation (Figure 2A & B, Box 7). PVAEs were averaged across three consecutive trials for the first 15 rotated reach training trials as follows: average of trials 1-3 (Bin 1), 4-6 (Bin 2), 7-9 (Bin 3), 10-12 (Bin 4), and 13-15 (Bin 5). These values were then normalized by subtracting the average performance on the aligned reach training trials following proprioceptive training or time delay (i.e., Figure 2A & B, Box 5) using the same sequence of trials just mentioned (i.e., Bins 1-5). These normalized PVAEs were compared across groups using a 3 Group (PTWF, PTNF, CTRL) x 5 Bin (Bin 1, Bin 2, Bin 3, Bin 4, Bin 5) mixed ANOVA with RM on the second factor. The magnitude of late visuomotor adaptation observed during rotated reach training was also compared between the 3 Groups (PTWF, PTNF, CTRL), this time using a one-way ANOVA. Late adaptation was taken to be the average PVAEs over the last 15 rotated reach training trials, normalized by subtracting the average PVAEs of all 15 aligned reach training trials following proprioceptive training or time delay (i.e., Figure 2A & B, Box 5). Finally, to confirm that initial (Bin 1) and late visuomotor adaptation did not benefit from

proprioceptive training with feedback, we performed two Bayesian independent samples t-tests on average PVAE during Bin 1 and late adaptation, respectively, comparing the PTWF group and CTRL group.

### Implicit and Explicit Visuomotor Adaptation: No-Cursor Reaches

Implicit and explicit contributions to visuomotor adaptation were established using the no-cursor reach training trials. To establish implicit adaptation, we calculated the average PVAE of the 6 *exclusion* no-cursor reaches immediately after rotated reach training (i.e., Time 3; Figure 2A & B, Box 8). This value was taken to be the implicit index according to the following formula:

$$\text{Implicit index (II)} = M_{\text{PV angular error on Exclusion trials}}$$

II values were then normalized by subtracting the average PVAE on the first block of 6 *exclusion* no-cursor reaches following proprioceptive training or time delay (i.e., Time 2; Figure 2A & B, Box 6). The extent of implicit adaptation was then compared between the 3 Groups (PTWF, PTNF, CTRL) with a one-way ANOVA. To establish explicit adaptation, we calculated the average PVAE of the 6 *inclusion* no-cursor reaches after rotated reaching (i.e., Time 3; Figure 2A & B, Box 8) and subtracted the average PVAE of the 6 *exclusion* no-cursor reaches after rotated reaching (i.e., Time 3; Figure 2A & B, Box 8), according to the following formula:

$$\text{Explicit index (EI)} = M_{\text{PV angular error on Inclusion trials}} - M_{\text{PV angular error on Exclusion trials}}$$

EI values were normalized by subtracting the average PVAE of the second block of 6 *exclusion* trials following proprioceptive training or time delay (i.e., Time 2; Figure 2A&B, Box 6). The extent of explicit adaptation was then compared between the 3 Groups (PTWF, PTNF, CTRL) with a one-way ANOVA. Finally, to confirm that implicit and explicit adaptation did not benefit from proprioceptive training with feedback, we performed two Bayesian independent samples t-tests comparing the magnitude of implicit adaptation and explicit adaptation between the PTWF group and CTRL group.

The significance value for all statistical tests was set at $p < 0.05$, and Bonferonni post-hoc tests corrected for multiple comparisons were used to find the point of significant effects for all pre-planned comparisons. Where appropriate, the Greenhouse-Geisser correction was applied.

## Results

### Proprioceptive Training

As shown in Figure 4A, absolute proprioceptive biases (i.e., response accuracy) improved with proprioceptive training for the PTWF group (Block 1: M = 2.2°, SD = 2.1°; Block 5: M = 1.0°, SD = 0.9°). No such improvements were seen in the PTNF group (Block 1: M = 1.7°, SD = 1.3°; Block 5: M = 2.5°, SD = 1.6°). ANOVA revealed a significant main effect of Group ($F(1, 46) = 6.784$, $p = 0.012$, $\eta^2 = 0.129$) and a significant Group x Block interaction ($F(4, 184) = 6.249$, $p = 0.001$, $\eta^2 = 0.120$). The main effect of Block was not significant ($F(4, 184) = 0.771$, $p = 0.508$, $\eta^2 = 0.016$). Pairwise comparisons revealed that biases for the PTWF group improved with training, such that participants in this group were significantly more accurate at locating the position of their hand in space in Block 3 ($p = 0.049$), Block 4 ($p = 0.045$) and Block 5 ($p = 0.021$) of proprioceptive training compared to Block 1. Biases did not change across blocks of training for the PTNF group, such that no two blocks differed from each other (all $p > 0.57$).

In Figure 4B we display the mean uncertainty ranges (i.e., response consistency) for the PTWF and PTNF groups across proprioceptive training blocks. ANOVA revealed no significant main effects (Group: $F(1, 46) = 0.121$, $p = 0.730$, $\eta^2 = 0.003$; Block: $F(4, 184) = 2.105$, $p = 0.103$, $\eta^2 = 0.044$), and no significant Group x Block interaction ($F(4, 184) = 1.399$, $p = 0.246$, $\eta^2 = 0.030$). As seen in Figure 4B, uncertainty ranges did not significantly change across blocks of training for the PTWF group (Block 1: M = 5.2°, SD = 3.8°; Block 5: M = 4.4°, SD = 2.1°) or the PTNF group (Block 1: M = 4.6°, SD = 1.7°; Block 5: M = 3.7°, SD = 1.7°).

### Visuomotor Adaptation: Rotated Reach Training Trials

Figure 5 shows the extent of visuomotor adaptation at the start of rotated reach training (i.e., first 15 trials; average of every 3 trials (Bins 1-5)) and at the end of rotated reach training (i.e., last 15 trials) for all groups. Groups adapted their reaches as training continued across Bins ($F(4, 276) = 123.351$, $p < 0.001$, $\eta^2 = 0.641$), such that PVAE of the hand achieved in Bin 5 was significantly greater than PVAE achieved in the first 3 Bins (all $p < 0.001$). ANOVA revealed that the Groups did not significantly differ with respect to the magnitude of visuomotor adaptation early in training (Group: $F(2, 69) = 0.816$, $p = 0.446$, $\eta^2 = 0.023$; Group x Bin interaction: $F(8, 276) = 1.206$, $p = 0.299$, $\eta^2 = 0.034$). As revealed by a moderate effect (Kelter, 2020), Bayesian analysis further indicated that the PTWF group and CTRL group demonstrated similar visuomotor adaptation initially (Bin 1) when first learning to reach with a rotated cursor ($BF_{01} = 2.951$).

Late in rotated reach training, participants achieved an average PVAE of 21.9°, which did not differ between Groups ($F(2, 71) = 2.622$, $p = 0.080$, $\eta^2 = 0.066$). Although, there was a trend for the PTNF group (M = 20.9°, SD = 3.6°) to display less changes in their reaches compared to the PTWF group (M = 22.1°, SD = 2.8°) and the CTRL group (M = 22.8°, SD = 2.5°). Again, results from our Bayesian analysis supported the conclusion that the PTWF group and CTRL group demonstrated a similar magnitude of visuomotor adaptation at the end of rotated reach training ($BF_{01} = 2.340$).

### Implicit and Explicit Visuomotor Adaptation: No-Cursor Reaches

The extent of implicit and explicit adaptation following rotated reach training are shown in Figures 6A and 6B, respectively. With respect to implicit adaptation, ANOVA revealed a significant main effect of Group ($F(2, 71) = 3.149$, $p = 0.049$, $\eta^2 = 0.077$). Post hoc analysis revealed that the PTNF group (M = 9.1°, SD = 4.5°) demonstrated significantly less implicit adaptation compared to the CTRL group (M = 12.8°, SD = 4.2°) ($p = 0.048$). Implicit adaptation

for the PTWF group (M = 11.5°, SD = 6.5°) did not differ significantly from the PTNF group ($p$ = 0.319) or the CTRL group ($p$ = 1.000). As revealed by a moderate effect, Bayesian analysis suggested that the PTWF group and CTRL group demonstrated similar implicit visuomotor adaptation ($BF_{01}$ = 2.707).

With respect to explicit adaptation, ANOVA revealed no significant difference between Groups ($F(2, 71) = 0.612$, $p$ = 0.545, $\eta^2$ = 0.017), such that the PTWF group (M = 1.6°, SD = 11.4°), PTNF group (M = 2.1°, SD = 12.8°) and CTRL group (M = -1.5°, SD = 11.6°) all demonstrated minimal explicit adaptation. Finally, Bayesian analysis indicated that the PTWF group and CTRL group demonstrated similar explicit visuomotor adaptation ($BF_{01}$ = 2.487).

## Discussion

In the current experiment we tested the influence of proprioceptive training on visuomotor adaptation to establish if improving proprioceptive acuity leads to benefits in visuomotor adaptation. Two groups of participants completed proprioceptive training, where their hand was passively moved to an unseen reference location and they indicated the position of their felt hand on every trial. One group was provided with feedback regarding their response accuracy on the middle 60% of proprioceptive training trials (PTWF), while the other group did not receive any feedback during training (PTNF). A third control group (CTRL) was included in our study, but did not participate in proprioceptive training and instead sat quietly during this training time. We found that proprioceptive training with feedback lead to improved proprioceptive acuity, such that the PTWF group decreased their proprioceptive biases (i.e., improved their ability to accurately locate the position of their hand in space) over the blocks of proprioceptive training trials. That said, we found no benefit of proprioceptive training on visuomotor adaptation, either at the start or at the end of rotated reach training. Specifically, all three groups showed a similar magnitude of visuomotor adaptation across the rotated reach training trials. As well, visuomotor adaptation was

primarily driven by implicit processes for all groups, and the magnitude of implicit and explicit adaptation did not vary significantly between groups.

### Proprioceptive Training

Early proprioceptive training regimes have been successful in improving tactile sense and proprioceptive acuity of the upper limb in post-stroke individuals (Carey et al., 1993, 1995, 1996, 1997, 2000, 2002). This training has included patients identifying different tactile surfaces and providing judgments of felt limb position following passive movements to unknown locations. More recently, the benefits of proprioceptive training using a hand positioning task have been examined in healthy participants (Darainy, Vahdat & Ostry, 2013; McGregor, Cashaback & Gribble, 2018). Within the hand positioning task, participants grasp a robot handle and their hand is passively moved to an unknown reference location. Participants then judge their hand's location, and verbal feedback regarding the accuracy of their response may or may not be provided. Using this proprioceptive training regime, Darainy et al. (2013) and McGregor et al. (2018) have demonstrated that healthy individuals are able to improve their proprioceptive acuity following training when feedback is provided, such that they become more accurate at locating the position of their hand in space (Darainy, Vahdat & Ostry, 2013; McGregor, Cashaback & Gribble, 2018).

In our study, we adopted the proprioceptive training protocol used by Darainy et al. (2013) and McGregor et al. (2018). Specifically, two groups of participants had their hand passively moved to an unknown reference location within 8° of their body midline (as done by Darainy et al., 2013) and they were required to indicate if their hand was located to the left or to the right of their midline on every trial. One group (PTWF) received verbal feedback regarding response accuracy on the middle 60% of trials (as done by McGregor et al., 2018), whereas the other group (PTNF) did not receive any feedback during training. We found that proprioceptive training improved proprioceptive acuity for the group that received feedback regarding response accuracy

during training, such that the PTWF group demonstrated smaller biases by the end of the proprioceptive training blocks. Participants in our PTWF group improved their biases by 1.24° (equivalent to 0.33 cm) from the first to last block of proprioceptive training, which is similar to the 0.34 cm improvement shown by Darainy et al. (2013). In contrast, we did not see a similar improvement in response accuracy for our PTNF group. In fact, there was a trend for the PTNF group to become less accurate in their responses, such that their biases became larger by the end of proprioceptive training. Also important to note is that we did not find any significant changes when it came to response consistency (i.e., magnitude of uncertainty ranges) for either the PTWF or PTNF groups. Having established improved proprioceptive acuity in our PTWF group, we next looked to determine the influence of proprioceptive training on visuomotor adaptation.

### Proprioceptive Training and Motor Learning

We found no benefit of proprioceptive training on visuomotor adaptation in the current study. Participants in our PTWF group improved their proprioceptive acuity with training, however, this enhanced proprioceptive acuity did not lead to benefits in early or late visuomotor adaptation when compared to our PTNF group or CTRL group. In contrast, similar proprioceptive training protocols with feedback have been shown to benefit motor adaptation to a velocity-dependent forcefield. Specifically, participants adapted their reaches earlier (i.e., had less curved trajectories) when introduced to a velocity-dependent forcefield following proprioceptive training compared to participants who did not receive feedback during proprioceptive training or did not complete the proprioceptive training at all (Darainy et al., 2013; McGregor et al., 2018).

We suggest that the lack of benefits we observed in our visuomotor adaptation paradigm compared to previous forcefield adaptation paradigms may arise due to the different error signals present within the two paradigms and hence the weighting of sensory information. Reaching in a velocity-dependent forcefield generates a sensory prediction error signal, as the predicted sensory

(visual and proprioceptive) consequences of one's movement do not match the actual sensory feedback experienced during movement (Tseng et al., 2007; Sarlegna & Bernier, 2010; Shadmehr, Smith & Krakauer, 2010). In order to resolve this error signal, the internal model for reaching is updated to allow the movement to be carried out as desired, where the internal model consists of the inverse model (i.e., motor command) and the forward model (i.e., expected sensory consequences of executing the (adapted) motor command; Wolpert, Ghahramani & Jordan, 1995; Shadmehr, Smith & Krakauer, 2010).

Similar to forcefield adaptation paradigms, visuomotor adaptation paradigms also give rise to a sensory prediction error signal, as the expected (visual) position of the cursor does not match the seen position of the cursor while reaching. Visuomotor adaptation paradigms further introduce a cross-sensory error signal, due to the sensory discrepancy between one's visual estimate of hand position (i.e., seen position of the cursor) and proprioceptive estimate of hand position (i.e., felt hand position; Cressman & Henriques, 2009; Salomonczyk, Henriques & Cressman, 2013; Maksimovic, Neville & Cressman, 2020). To resolve this cross-sensory error signal, it has been shown that we recalibrate our sense of felt hand position (i.e., proprioception) in order to match the visual information provided (Cressman & Henriques, 2009, 2010; Salomonczyk et al., 2011, 2012, 2013; Mostafa et al., 2014). Specifically, one shifts their felt hand location in space so that it is more aligned with the cursor feedback provided. Cressman and Henriques (2010) have further shown that, when only the cross-sensory error signal is present (i.e., the hand is passively moved and no sensory prediction error signal is experienced), the extent of proprioceptive recalibration and visuomotor adaptation are similar in magnitude and significantly correlated. From these results, Cressman and Henriques (2010) concluded that proprioceptive recalibration contributes to visuomotor adaptation.

While proprioceptive processing has been implicated in visuomotor adaptation, our current results suggest that improving the accuracy of this sense does not benefit visuomotor adaptation in the same manner as observed for forcefield adaptation. The lack of differences in visuomotor adaptation with varying levels of proprioceptive acuity has been demonstrated by Cressman and colleagues (2010, 2021). In 2010, Cressman et al. looked to determine if healthy young and older adults demonstrated a similar magnitude of proprioceptive recalibration and resulting visuomotor adaptation, while in 2021, Cressman and colleagues compared visuomotor adaptation in individuals with Parkinson's Disease (PD) and age-matched healthy control participants. The authors hypothesized that older adults and individuals with PD would recalibrate proprioception to a greater extent than their control counterparts due to age and disease related deteriorations in proprioceptive acuity, respectively (Cressman, Salomonczyk & Henriques, 2010; Cressman et al., 2021), and hence show greater visuomotor adaptation. Contrary to their expectations, Cressman and colleagues found no differences in proprioceptive recalibration and a similar extent of visuomotor adaptation across young and older participants (2010) and patients with PD and healthy control participants (2021).

Given that proprioceptive accuracy does not impact visuomotor adaptation, one may ask how proprioception and proprioceptive recalibration are implicated in visuomotor adaptation. Early work in visuomotor adaptation has demonstrated that visuomotor adaptation can arise in the absence of proprioception (i.e., in a deafferented individual; Lajoie et al., 1992; Ingram et al., 2000; Bernier, Chua, Bard & Franks, 2006), when there is no cross-sensory error signal, and vision alone drives adaptation. Findings by Bernier and colleagues (2009) further reveal that healthy individuals suppress proprioceptive input when initially introduced to the visuomotor distortion. In their paradigm, Bernier and colleagues (2009) measured sensory evoked potentials in response to

median nerve stimulation at the wrist of the moving hand over the course of visuomotor adaptation. They found that for the first few trials, participants who demonstrated the greatest sensory suppression (i.e., had the smallest sensory evoked potentials) adapted their reaches to a greater extent, such that their movements were straighter with fewer corrections compared to participants who had larger sensory evoked potentials. As all participants gradually adapted their reaches, sensory evoked potentials increased in magnitude, indicating that proprioception was processed to a greater extent (Bernier et al., 2009). This increase in sensory processing with time may correspond to when participants recalibrated proprioception, as Zbib et al. (2016) have shown that proprioception takes time to be significantly recalibrated (~ 70 trials). Taken together, the results from the current study, combined with previous findings, suggest that the accuracy of one's proprioceptive sense does not impact visuomotor adaptation, potentially due to the flexibility in extent that proprioception is processed during initial visuomotor adaptation (i.e., visual information is weighted more initially).

In accordance with the proposal that proprioceptive acuity does not impact visuomotor adaptation, we further show no cost of proprioceptive training on visuomotor adaptation, as participants in the PTWF group performed similarly to those in the CTRL group. Interestingly, although we found no significant differences in the extent of visuomotor adaptation between groups, there was a trend for the PTNF group to show a smaller magnitude of visuomotor adaptation at the end of rotated reach training trials (20.9°) compared to the PTWF group (22.1°) and CTRL group (22.8°). Thus, it seems that continually estimating final hand position after passive movements in the absence of feedback, as experienced by the PTNF group, may reduce one's ability to adapt to a visuomotor distortion. We suspect this reduced adaptation could be due to participant fatigue, as participants provided judgments on 370 trials (i.e., for approximately 30

minutes), receiving no feedback with respect to response accuracy. Future work is required to determine the impact that (1) passively moving one's hand in directions that are not related to the upcoming goal movement, and (2) having participants provide prolonged judgments of hand position with no indication of response accuracy, have on the processes underlying visuomotor adaptation. For now, we suggest that proprioceptive training with feedback improves proprioceptive acuity, but does not influence visuomotor adaptation (i.e., neither helps, nor hinders, visuomotor adaptation).

### Mechanisms Underlying Visuomotor Adaptation

It has been suggested that motor adaptation arises implicitly (unconsciously) when adapting to both forcefield (Donchin, Francis & Shadmehr, 2003; Ostry et al., 2010) and visuomotor (Wolpert, Ghahramani & Jordan, 1995; Shadmehr, Smith & Krakauer, 2010) distortions. Particularly, when reaching with a small visuomotor distortion (less than, or equal to, 30°), it has been shown that visuomotor adaptation is primarily driven by implicit processes (Werner et al., 2015; Neville & Cressman, 2018; Modchalingam, Vachon, 't Hart & Henriques, 2019). When reaching with a small distortion, participants experience a small target error, and as a result, do not become aware that the reaching environment has changed or that they have changed their movements (i.e., participants are unable to report the presence of a visuomotor distortion, or indicate strategic changes in their reaches that they have adopted).

To determine the underlying contributions of implicit and explicit processes to visuomotor adaptation in the current paradigm, we had participants reach in the absence of cursor feedback when provided with the following instructions: (1) "Reach so that your hand goes straight to the target" and (2) "Reach using anything you have learned during training in order to get the cursor to the target". These instructions were first used in the visuomotor adaptation literature by Werner et al. (2015), and are adopted from the Process Dissociation Procedure (PDP) put forth by Jacoby

(1991). This first set of instructions, when participants are asked to reach directly to the target, is similar to typical instructions provided in after-effect trials (i.e., when the visuomotor distortion is removed and participants are once again asked to reach in a typical environment in the absence of a visuomotor distortion; Wolpert & Kawato, 1998; Baraduc & Wolpert, 2002; Cressman & Henriques, 2009; Ong & Hodges, 2010). As expected, we found that even when participants were supposed to aim directly to the target, they reached to the left of the target, demonstrating implicit adaptation of approximately 11°. Participants then continued to reach in a similar manner, even when asked to reach using any learned strategy in order to get the cursor to the target, thus demonstrating minimal explicit adaptation. In fact, explicit adaptation was only 0.7° on average across all participants.

Implicit adaptation was observed across all 3 groups of participants, but surprisingly, we found that the PTNF group displayed significantly less implicit adaptation (9.1°) compared to the CTRL group (12.8°). Implicit adaptation observed in the PTWF group (11.5°) did not differ significantly from the other two groups. This decreased implicit adaptation observed in the PTNF group could be related to the trend we saw earlier of decreased visuomotor adaptation at the end of rotated reach training for these participants (i.e., less final visuomotor adaptation led to a reduced magnitude of implicit adaptation possible).

### Summary

Proprioceptive training has been shown to improve proprioceptive acuity, and benefit motor adaptation when reaching in a velocity-dependent forcefield. Here, we asked if similar benefits are present when reaching with a visuomotor distortion. Additionally, we asked if these benefits would arise implicitly or explicitly. We found that proprioceptive training improved participant's proprioceptive acuity when feedback regarding response accuracy was provided. While proprioceptive acuity improved with proprioceptive training, this did not influence early or

late visuomotor adaptation, which was shown to arise implicitly. Thus, we conclude that improving proprioceptive acuity does not benefit, nor hinder, implicit visuomotor adaptation.

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## Figures

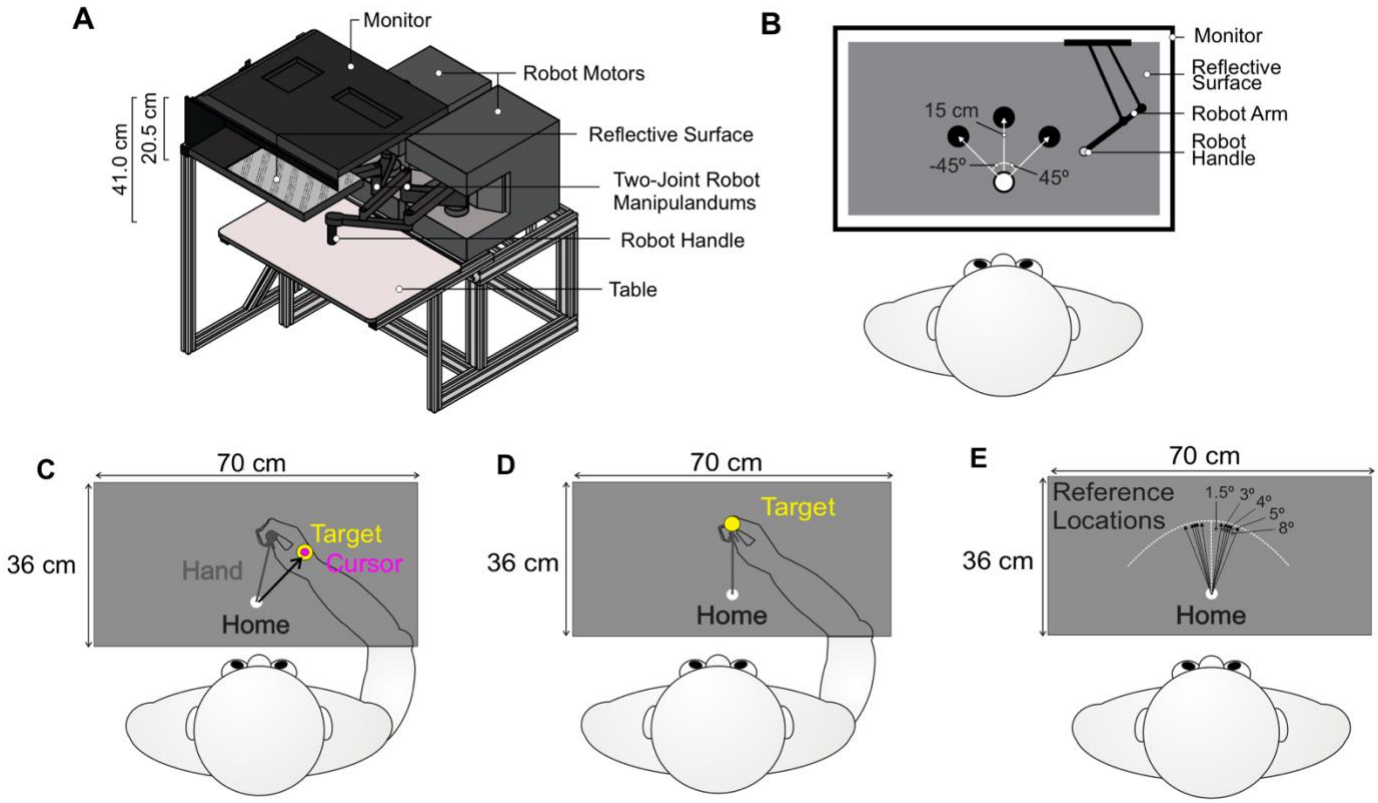



Figure 1. Experimental apparatus and types of trials

(A): Side-view of the experimental apparatus. Participants were instructed to grasp the robot handle with their right hand. (B): Top-down view of the 3 targets that participants reached to during all reaching trials. (C): Rotated Reach Training trials when the cursor was rotated 30° clockwise relative to hand motion. (D): No-Cursor Reaches, when no visual cursor was displayed. (E): The 10 reference locations used in the Proprioceptive Training trials.

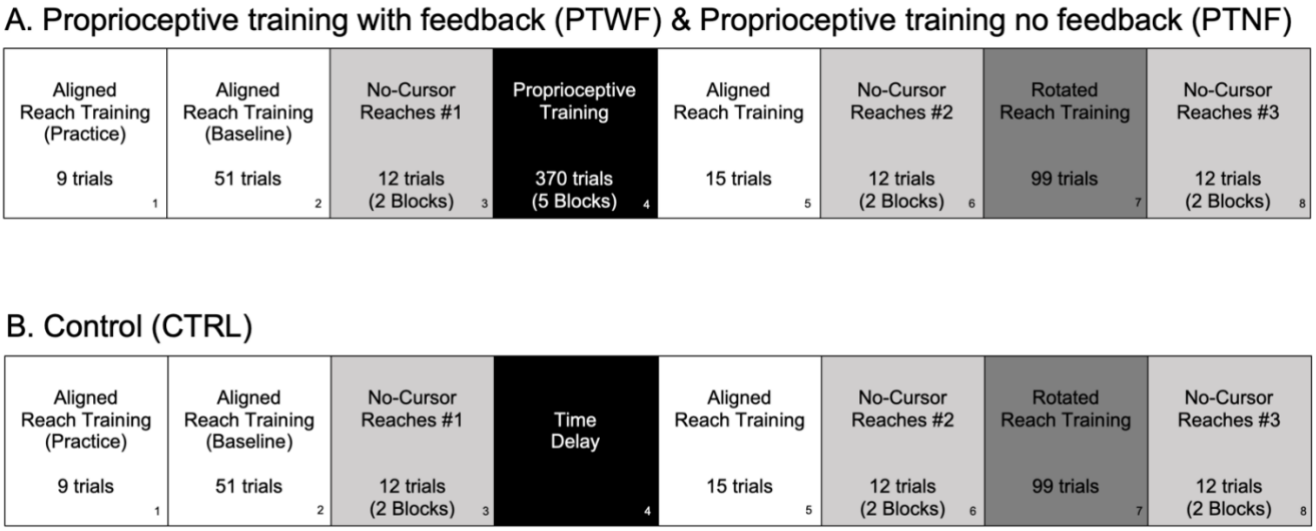
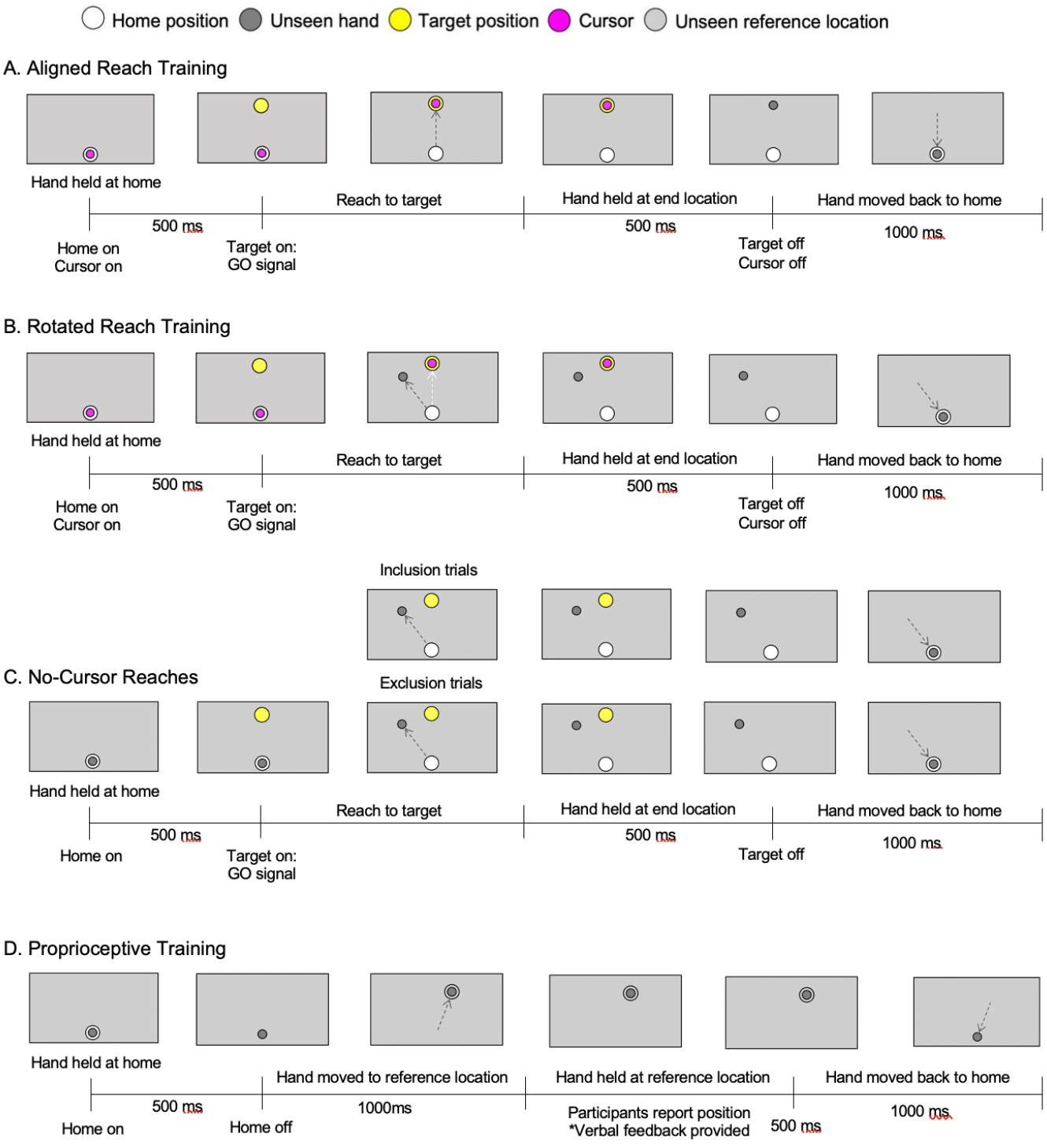



Figure 2. Breakdown of testing blocks

(A): Blocks of trials that were completed by the Proprioceptive training with feedback (PTWF) and the Proprioceptive training no feedback (PTNF) groups. (B): Blocks of trials that were completed by the Control (CTRL) group. The Proprioceptive Training consisted of 5 blocks of 74 trials with 2 minute breaks after each block. The Time Delay consisted of a 30 minute break. No-Cursor reaches #1 and #2 consisted of 2 blocks of 6 trials with *exclusion* instructions. No-Cursor reaches #3 consisted of 1 blocks of 6 trials with *exclusion* instructions, followed by 1 block of 6 trials with *inclusion* instructions.




*Feedback re response accuracy was only provided to the Proprioceptive training with feedback (PTWF) group and only during Blocks 2-4 of training.

Figure 3. Timeline of events for each trial type

(A): Aligned Reach Training trials. (B): Rotated Reach Training trials. (C): No-Cursor Reaches (i.e., exclusion and inclusion trials). (D): Proprioceptive Training trials.

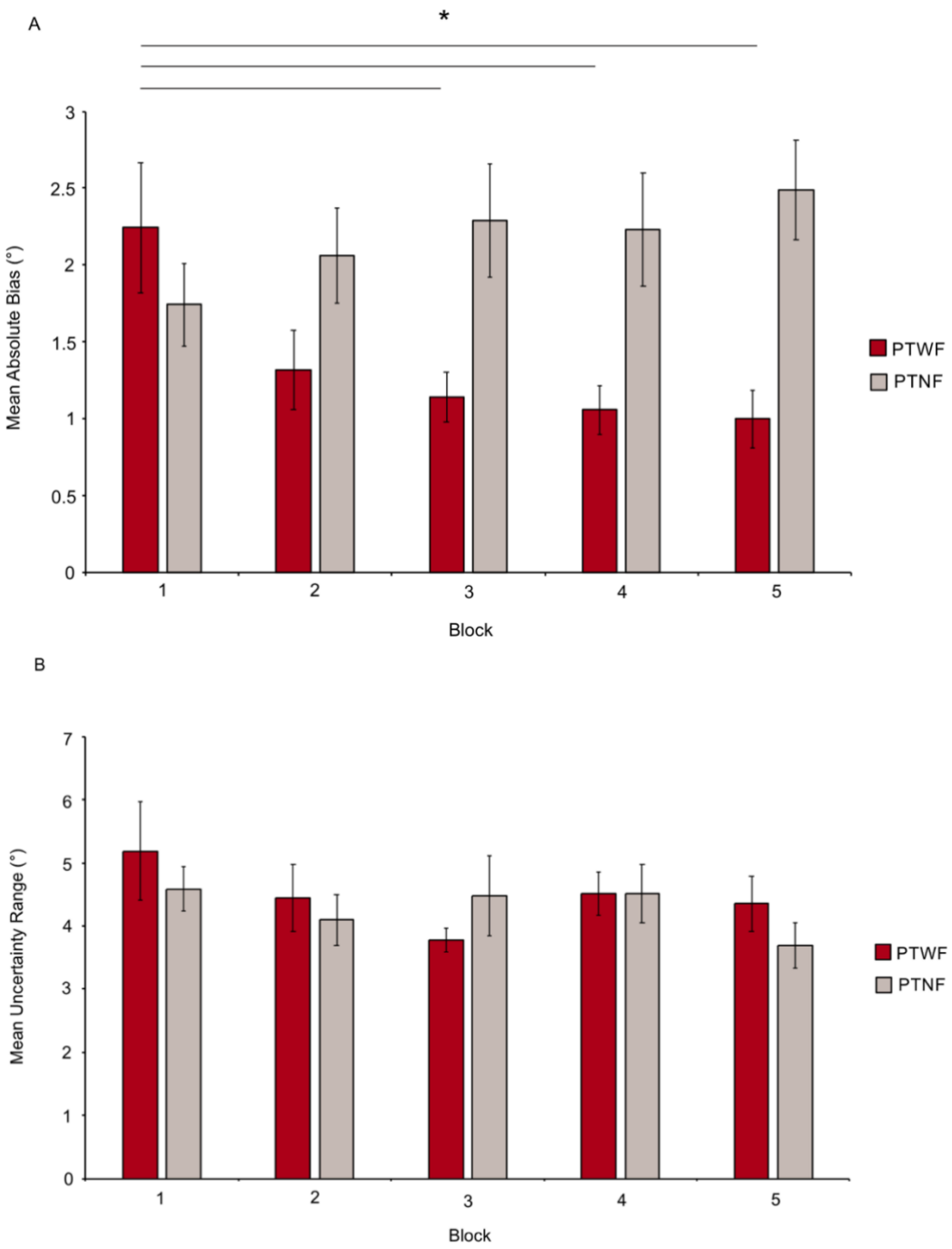



Figure 4. Proprioceptive acuity

Mean (A): absolute biases (i.e., response accuracy) and (B): uncertainty ranges (i.e., response consistency) across blocks of proprioceptive training (Blocks 1-5) for the Proprioceptive training with feedback (PTWF) group and Proprioceptive training no feedback (PTNF) group. Values closer to zero represent greater accuracy and consistency. Red and light grey bars represent proprioceptive performance for the PTWF group and the PTNF group, respectively. Error bars represent group standard error of the mean. The asterisk (*) indicates a significant difference for the PTWF group.

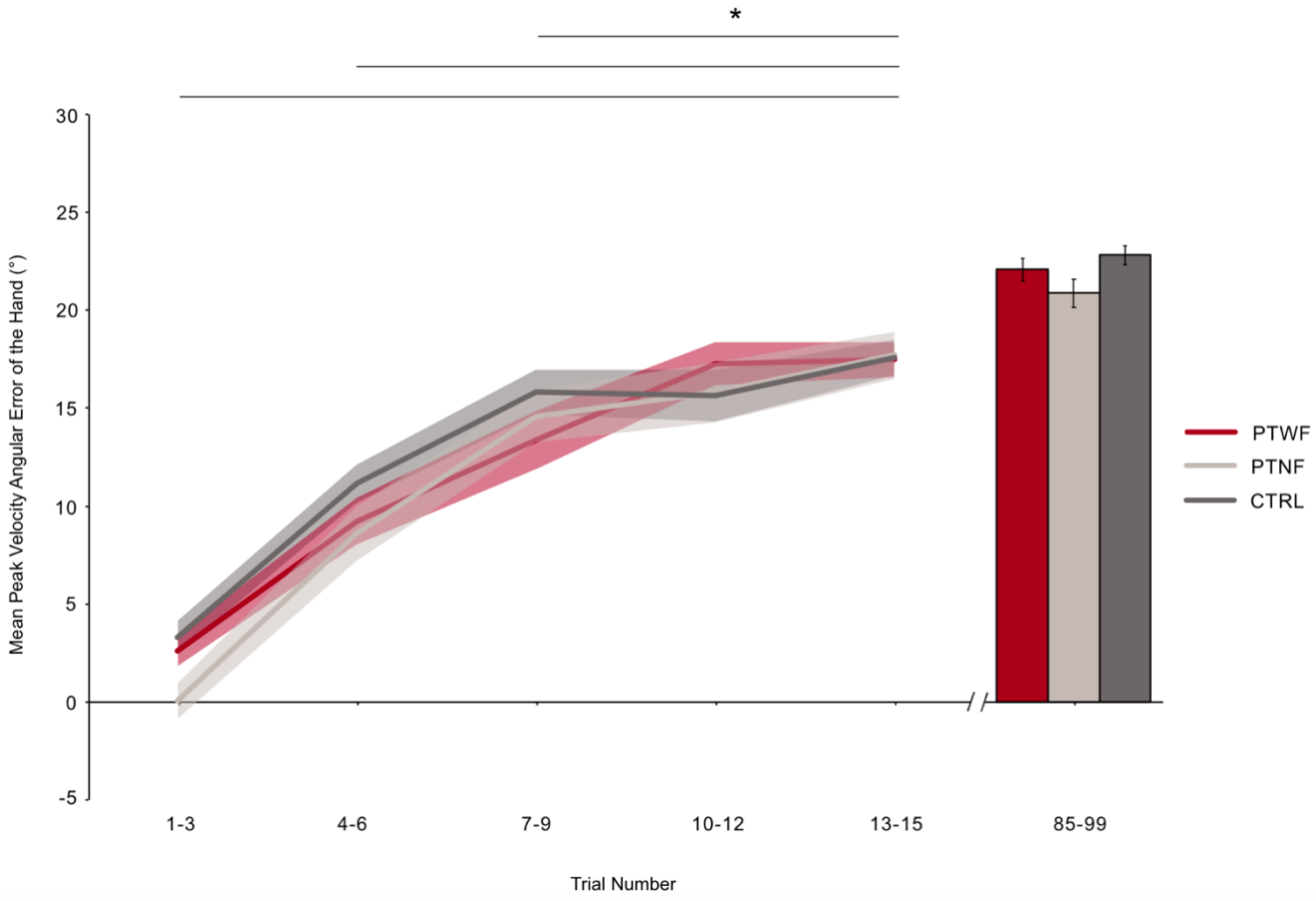



Figure 5. Visuomotor adaptation

Mean peak velocity angular error (PVAE) of the hand for all three groups of participants (Proprioceptive training with feedback (PTWF; red), Proprioceptive training no feedback (PTNF; light grey), and Control (CTRL; dark grey)) when adapting to a 30° clockwise cursor rotation. Normalized data is presented at the start of rotated reach training trials (average of three consecutive trials for trials 1-15) and at the end of rotated reaching training (average of last 15 trials). Positive values indicate reaching to the left of the target, and negative values indicate reaching to the right of the target. Shaded regions and error bars represent group standard error of the mean. The asterisk (*) indicates a significant difference for all groups.

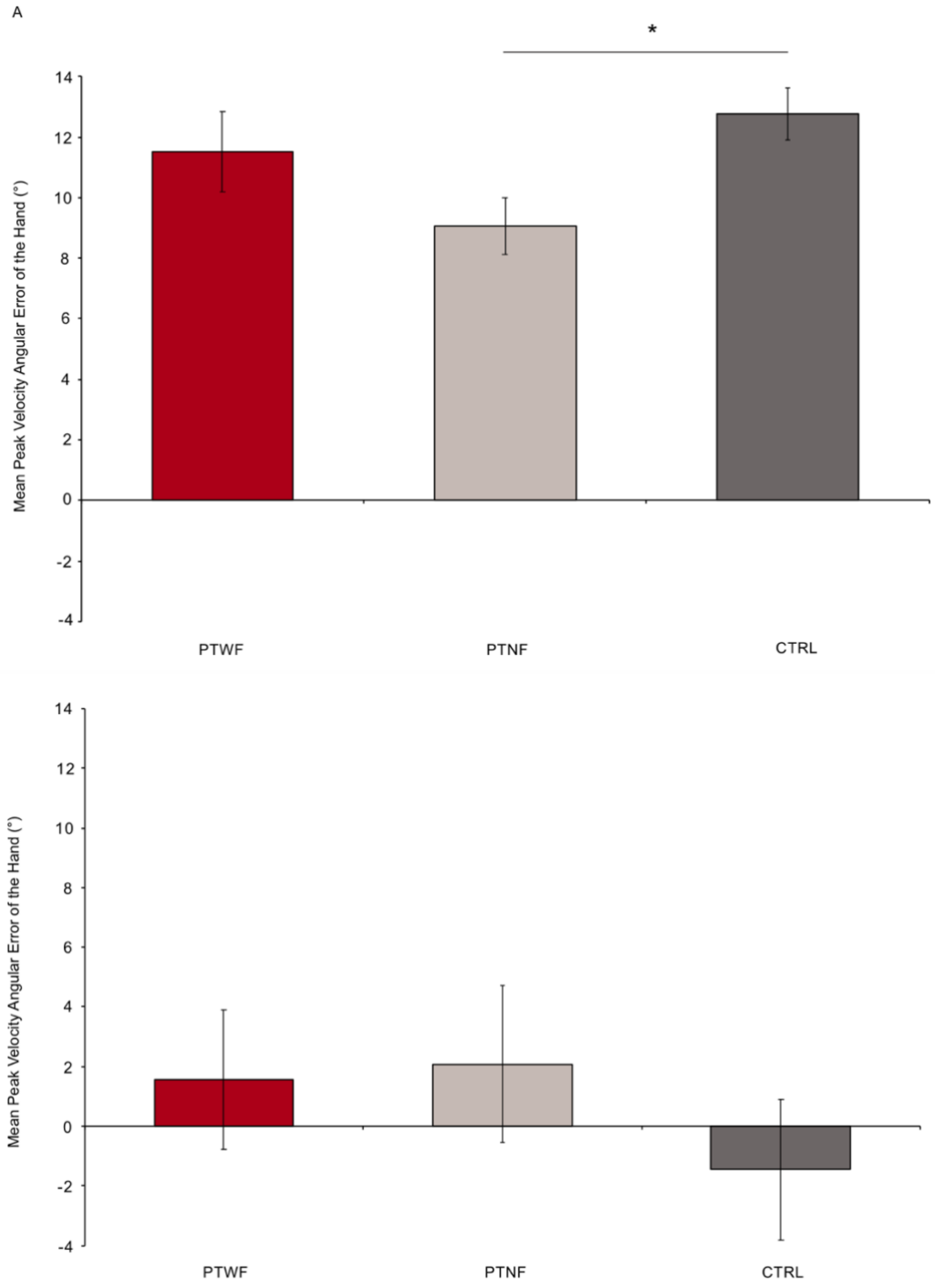



Figure 6. Implicit and explicit adaptation

Normalized mean (A): implicit adaptation and (B): explicit adaptation for all three groups of participants (Proprioceptive training with feedback (PTWF; red), Proprioceptive training no feedback (PTNF; light grey), and Control (CTRL; dark grey)), where positive values indicate reaching to the left of the target, and negative values indicate reaching to the right of the target. Error bars represent group standard error of the mean. The asterisk (*) indicates a significant difference between the PTNF group and CTRL group.

# Chapter III: General Discussion

Proprioceptive training leads to improvements in proprioceptive acuity (i.e., sense of felt hand position in space), and this improved acuity has been shown to benefit motor adaptation (Darainy, Vahdat & Ostry, 2013; McGregor, Cashaback & Gribble, 2018). Specifically, proprioceptive training has been shown to benefit reach adaptation to a forcefield distortion, when a sensory prediction error signal is present (Tseng et al., 2007; Sarlegna & Bernier, 2010; Shadmehr, Smith & Krakauer, 2010). Here, we asked if similar benefits would arise when adapting one's reaches to a visuomotor distortion, when a sensory prediction error and cross-sensory error signal are experienced. We had two groups of participants complete proprioceptive training, where their hand was moved to an unknown reference location and they had to indicate their felt hand position on every trial. One group received verbal feedback regarding accuracy during training (PTWF), and the other group did not (PTNF). A third control group (CTRL) was also included in the experiment, but did not complete proprioceptive training. All three groups then completed reaches with rotated cursor feedback, such that the cursor was rotated 30° clockwise relative to hand motion. Rotated reach training was then followed by a series of no-cursor reaches to assess the contributions of implicit (unconscious) and/or explicit (conscious strategy) processes to visuomotor adaptation.

We found improved proprioceptive acuity for our PTWF group following proprioceptive training, but not for our PTNF group. However, this improved acuity provided no additional benefit to visuomotor adaptation, as all three groups of participants adapted their reaches in a similar manner to the 30° rotated cursor. Specifically, all three groups showed a similar magnitude of reach adaptation at the start and the end of the rotated reach training trials. We also found that, on average, reach adaptation arose implicitly for all three groups, with minimal explicit contribution.

Interestingly, we did find a large amount of variability with respect to explicit adaptation within each of our three groups of participants, with explicit adaptation achieving a maximum of 30.9° (PTWF: range = -16.1° to 23.7° (M = 1.6°); PTNF: range = -14.1° to 30.9° (M = 2.1°); CTRL: range = -24.1° to 20.7° (M = -1.5°)). Implicit adaptation did not show the same variability (PTWF: range = 0.7° to 33.3° (M = 11.5°); PTNF: range = 0.7° to 18.6° (M = 9.1°); CTRL: range = 5.7° to 21.2° (M = 12.8°)). Given this variability in explicit adaptation between participants, we looked to determine if there was a difference in reach adaptation between proprioceptive training regimes when participants were categorized as having a high or low magnitude of explicit adaptation. To do so, we split each of our groups into a high and low explicit adaptation group (n = 12 per group) and compared early and late reach adaptation and implicit and explicit adaptation between PTWF, PTNF and CTRL groups (i.e., for each dependent variable two ANOVAs were completed, such that we first compared the three groups with a high magnitude of explicit adaptation and then compared the three groups with a low magnitude of explicit adaptation). The results were similar to those reported in Chapter 2, such that there were no group differences in the magnitude of reach adaptation, implicit adaptation, or explicit adaptation observed. Specifically, proprioceptive training did not influence visuomotor adaptation.

## Proprioceptive Acuity

Establishing the benefits of proprioceptive training on motor learning has been of recent interest in the literature. In an early study by Wong and colleagues (2012), a participant's hand was passively moved around a desired trajectory (i.e., circle or a word). Following proprioceptive training, participants were asked to trace the desired trajectory on their own. Wong et al. (2012) found that participants who had completed the proprioceptive training were able to trace the desired trajectory faster, and more accurately, compared to their untrained counterparts. The authors concluded that these motor learning benefits arose due to proprioceptive training.

However, it is unclear if the benefits arose due to enhanced proprioceptive acuity per se, as acuity was not assessed in their study. Instead, motor learning benefits could have arisen due to knowledge gained re muscle activation patterns required (e.g., which muscles to activate, the timing of required muscle activation, forces associated with muscle activation, etc.).

In motor adaptation paradigms, proprioceptive acuity has been assessed throughout proprioceptive training regimes, and hence benefits in motor adaptation following this training can be attributed to improved proprioceptive acuity (Darainy, Vahdat & Ostry, 2013; McGregor, Cashaback & Gribble, 2018). This proprioceptive training typically consists of a hand positioning task, where the hand is moved to an unknown reference location and participants are required to judge the position of their felt hand. Verbal feedback is provided to one group, while a second group completes the same movements, but does not receive feedback regarding their responses. Similar to our results, proprioceptive acuity has been shown to improve with training when feedback is provided (Darainy, Vahdat & Ostry, 2013; McGregor, Cashaback & Gribble, 2018). In the current study, we found improvements in proprioceptive biases of approximately 0.33 cm for our PTWF group. These improvements are consistent with previous reports (e.g., 0.34 cm as found by Darainy, Vahdat & Ostry, 2013).

At first glance, an improvement of 0.33 cm seems small. That said, proprioceptive acuity is fairly good to begin with, such that our PTWF participants demonstrated initial biases of only 2.24° (i.e., 0.59 cm). Thus, an improvement of 0.33 cm corresponds to a reduction in bias (or error) of 55.4%. We argue that this is a meaningful change, as it would mean the difference between grasping or not grasping a pen, or the handle on a cup (both approximately 0.5 cm in diameter). To ensure task success, it is crucial for this sense to be as accurate as possible.

## Observational Learning

As discussed in the introduction to the General Discussion, forcefield and visuomotor adaptation paradigms give rise to different error signals. Differences in patterns of motor adaptation between paradigms have previously been observed when looking at the impact of observation on forcefield versus visuomotor adaptation. Within a forcefield adaptation paradigm, results indicate that observational learning (i.e., watching an actor perform adaptive movements within a forcefield) benefits participants when they later have to adapt their movements to the same forcefield (Mattar & Gribble, 2005; Bernardi, Darainy, Bricolo & Ostry, 2013). More specifically, these 'observer' participants show greater learning (i.e., less error) and less variable movements compared to participants that watched an actor adapt to an incongruent forcefield, or participants who watched an actor experience randomly changing errors from trial-to-trial (i.e., the actor did not demonstrate motor adaptation; Bernardi, Darainy, Bricolo & Ostry, 2013), or control participants who did not observe an actor at all (Mattar & Gribble, 2005). Furthermore, when proprioceptive training is combined with observational learning, participants' ability to adapt to the forcefield is augmented, such that these participants had the straightest reaches (i.e., lowest error) when exposed to the forcefield compared to all other groups (McGregor, Cashaback & Gribble, 2018).

In contrast to the benefits of observation seen in forcefield adaptation paradigms, the impact of observation on visuomotor adaptation is less clear. Within a visuomotor adaptation paradigm, it has been shown that observers adapt their reaches earlier compared to participants who physically practiced reaching with the rotation (Ong & Hodges, 2010). However, these observers did not show after-effects when asked to reach to the target following rotated reach training trials, as seen in their counterparts who did not undertake observation, but instead physically adapted to the rotated cursor (Ong & Hodges, 2010; Ong, Larssen & Hodges, 2012;

Lim, Larssen & Hodges, 2014). This lack of after-effects by the observers suggests that the internal model for reaching was never updated during, or following, visuomotor adaptation observation. In a follow-up experiment, Lim and colleagues (2014) further showed that even for participants with a prior motor repertoire (i.e., having adapted to the rotated cursor previously), observation did not lead to updating of the internal model, as these participants did not display after-effects once the rotation was removed. On the other hand, the observers did indicate explicit knowledge about the rotation (Ong & Hodges, 2010; Ong, Larssen & Hodges, 2012; Lim, Larssen & Hodges, 2014; Lei, Boa & Wang 2016).

Comparing the results of the current study with forcefield adaptation literature (e.g., Darainy, Vahdat & Ostry, 2013; McGregor, Cashaback & Gribble, 2018), we once again see differences in the impact of training signals on the two paradigms. Proprioceptive training and observation benefit forcefield adaptation, but have limited impact on visuomotor adaptation, specifically implicit visuomotor adaptation. Future research is needed to explore the different impact training regimes can have on the two adaptation paradigms, and the relationship between training regime and underlying error signal(s).

## Limitations and Future Directions

In our study, we had two groups of participants complete proprioceptive training, which consisted of a hand positioning task. On each trial, a participant's hand was moved to an unknown reference location, within 8° of their body midline, and they had to indicate their felt hand position relative to their body midline. While the presentation of the 10 reference locations was randomized across trials, it is possible that the order in which these reference locations were presented, and hence participants' responses on a given trial, may have influenced their responses on the subsequent trial. For example, if the hand was led to the reference location at 8° left of the body on trial 1, and then the position at 1.5° to the left of the body on the next trial, participants may

have reported that their hand was on the right on the second trial because of the large change in hand position from one trial to the next. We attempted to minimize biases arising due to participants' responses by having a large number of hand positioning trials and by bringing the hand back to the home position to start each trial. As well, we moved the hand to the smaller reference locations on a greater number of trials compared to the larger reference locations (e.g., 40 trials for reference locations less than or equal to 3°, versus only 6 trials for reference locations equal to 8° in each block of 74 trials). Future research is needed to determine if the order of reference location presented influences responses, and hence, proprioceptive acuity established.

Also to consider with respect to proprioceptive training, is the type and timing of feedback provided. Our PTWF group received verbal feedback during training, such that they were told if their judgment was correct or incorrect on every trial. Future research could look to determine if providing more detailed feedback (e.g., response correct/incorrect and the degrees to which the hand is left or right of the body midline) would improve proprioceptive acuity. With regards to the frequency of feedback, research has shown that frequent feedback may have a "crutch-like" effect, as the learner becomes dependent on the extrinsic feedback (i.e., feedback provided) and ignores their own intrinsic feedback (i.e., proprioception), resulting in decrements in motor learning (Salmoni, Schmidt & Walter, 1984; Schmidt, Young, Swinnen & Shapiro, 1989). It has therefore been suggested that participants may achieve optimal learning if they receive summary feedback after a certain number of trials (e.g., after every 5 trials as suggested by Schmidt, Lange & Young, 1990). Additionally, self-controlled feedback (i.e., the learner decides when they receive feedback) has been shown to further benefit motor learning (Chiviacowsky & Wulf, 2002). While we found that our PTWF group did improve their proprioceptive acuity with training, perhaps providing

more detailed feedback on a varying feedback schedule or a self-controlled feedback schedule would lead to enhanced proprioceptive acuity.

Given that improved proprioceptive acuity did not benefit visuomotor adaptation in our study, one may question why improving acuity would be of importance. As mentioned previously, improved proprioceptive acuity has been shown to benefit forcefield adaptation (Darainy, Vahdat & Ostry, 2013; McGregor, Cashaback & Gribble, 2018). Thus, perhaps improving acuity would lead to greater benefits in forcefield adaptation. Furthermore, if we consider a clinical population, improving proprioceptive acuity would be of high importance for post-stroke individuals, where proprioceptive deficiencies affect nearly 65% of these patients (Feigenson et al., 1977). Carey and colleagues (1993, 1995, 1996, 1997, 2000, 2002) have shown that it is possible to improve these patients' sense of felt limb position following proprioceptive training, and perhaps using the strategies discussed above, we can further improve proprioceptive acuity, leading to benefits in motor performance.

## Conclusion

In the current study we tested if proprioceptive training benefits visuomotor adaptation, when participants experience both a sensory prediction error and cross-sensory error signal. Additionally, we examined if this visuomotor adaptation arises implicitly or explicitly. We found that proprioceptive acuity improved for our PTWF group as a result of proprioceptive training. However, this did not influence visuomotor adaptation, as all three of our groups of participants adapted similarly to the visuomotor distortion. We also found that all three groups demonstrated similar levels of implicit adaptation, with minimal contribution of explicit processes. Therefore, we conclude that proprioceptive training does not influence implicit visuomotor adaptation.

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# Appendix A

24/11/2020

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

University of Ottawa
Office of Research Ethics and Integrity

**CERTIFICAT D'APPROBATION ÉTHIQUE | CERTIFICATE OF ETHICS APPROVAL**

| | |
|---|---|
| **Numéro du dossier / Ethics File Number** | H-03-19-3433 |
| **Titre du projet / Project Title** | Explicit and Implicit Contributions to VisuoMotor Adaptation |
| **Type de projet / Project Type** | Recherche de professeur / Professor's research project |
| **Statut du projet / Project Status** | Renouvelé / Renewed |
| **Date d'approbation (jj/mm/aaaa) / Approval Date (dd/mm/yyyy)** | 25/03/2019 |
| **Date d'expiration (jj/mm/aaaa) / Expiry Date (dd/mm/yyyy)** | 24/03/2021 |

**Équipe de recherche / Research Team**

| Chercheur / Researcher | Affiliation | Role |
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**Conditions spéciales ou commentaires / Special conditions or comments**

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24/11/2020

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

University of Ottawa
Office of Research Ethics and Integrity

Le Comité d'éthique de la recherche (CÉR) de l'Université d'Ottawa, opérant conformément à l'*Énoncé de politique des Trois conseils* (2014) et toutes autres lois et tous règlements applicables, a examiné et approuvé la demande d'éthique du projet de recherche ci-nommé.

L'approbation est valide pour la durée indiquée plus haut et est sujette aux conditions énumérées dans la section intitulée "Conditions Spéciales ou Commentaires". Le formulaire « Renouvellement ou Fermeture de Projet » doit être complété quatre semaines avant la date d'échéance indiquée ci-haut afin de demander un renouvellement de cette approbation éthique ou afin de fermer le dossier.

Toutes modifications apportées au projet doivent être approuvées par le CÉR avant leur mise en place, sauf si le participant doit être retiré en raison d'un danger immédiat ou s'il s'agit d'un changement ayant trait à des éléments administratifs ou logistiques du projet. Les chercheurs doivent aviser le CÉR dans les plus brefs délais de tout changement pouvant augmenter le niveau de risque aux participants ou pouvant affecter considérablement le déroulement du projet, rapporter tout évènement imprévu ou indésirable et soumettre toute nouvelle information pouvant nuire à la conduite du projet ou à la sécurité des participants.

The University of Ottawa Research Ethics Board, which operates in accordance with the *Tri-Council Policy Statement* (2014) and other applicable laws and regulations, has examined and approved the ethics application for the above-named research project.

Ethics approval is valid for the period indicated above and is subject to the conditions listed in the section entitled "Special Conditions or Comments". The "Renewal/Project Closure" form must be completedfour weeks before the above-referenced expiry date to request a renewal of this ethics approval or closure of the file.

Any changes made to the project must be approved by the REB before being implemented, except when necessary to remove participants from immediate endangerment or when the modification(s) only pertain to administrative or logistical components of the project. Investigators must also promptly alert the REB of any changes that increase the risk to participant(s), any changes that 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 or the safety of the participant(s).

Riana MARCOTTE
Responsable d'éthique en recherche / Protocol Officer
Pour/For **Daniel LAGAREC** Président(e) du/ Chair of the **Comité d'éthique de la recherche en sciences de la santé et sciences / Health Sciences and Sciences Research Ethics Board**

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# Appendix B

Université d'Ottawa | University of Ottawa

## Explicit and Implicit Contributions in Motor Adaptation

**Supervisor:** Dr. Erin Cressman
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**Co-Investigator(s):**

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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 Montpetit Hall, Room 403B. Each participant will complete testing on 1 day, with each testing session lasting about an 1 hour. 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 403B, 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 or PhD 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 **"Explicit and Implicit Contributions in Motor Adaptation"**. I have read the information presented in the above background information and I had the opportunity to ask questions to the investigator(s). 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: _____

# Appendix C

**uOttawa Consent Information Addendum - COVID-19 Risks**

**Principal Investigator**: Amelia Decarie, School of Human Kinetics

**Study Title**: Explicit and Implicit Contributions to Visuomotor Adaptation

Please read the following statements carefully and feel free to ask questions if anything seems unclear.

We are putting in place safety precautions to reduce exposure to COVID-19, but the risk of exposure can still exist. COVID-19 can result in severe illness, medical expenses, and loss of income and in some cases, death.

If you are considered vulnerable to the effects of COVID-19 (e.g., an older adult; underlying medical conditions or a compromised immune system), please discuss your participation with the research team before consenting to participate.

**If you are feeling unwell or experiencing any potential COVID-19 symptoms leading up to the research session, please stay home and notify the research team that you cannot attend. Should you experience symptoms in days following the session, please also notify the research team.**

Potential COVID-19 symptoms include: new or worsening cough, shortness of breath or difficulty breathing, temperature equal to or over 38C (100.4F), feeling feverish, chills, fatigue or weakness, muscle or body aches, new loss of smell or taste, headache, gastrointestinal symptoms (abdominal pain, diarrhea, vomiting), or feeling very unwell.

**To reduce the possibility of COVID-19, we have implemented the following safety procedures**

☑ Regular handwashing

☑ Using hand sanitizer when handwashing is not possible

☑ Wearing of face masks/face coverings

☑ Physical distancing (as recommended by the local health authority)

☑ Limiting shared material and documents (pens, paper)

☑ Sanitizing surfaces and shared equipment

☑ Waiting 30 minutes between each session

1

☑ Collecting personal contact information for contact-tracing purposes.

Please advise a researcher if you believe a safety measure is not being taken, or that your safety is at risk.

**Considerations for the Participant:**

We ask that you:

- Wear a mask or face covering. Masks will be provided by the researcher if you do not have one. If you feel that you are unable to wear a mask, discuss your participation with the research team.
- Complete a screening assessment before each research session.
- Wash or sanitize your hands upon arrival. Hand sanitizer will be provided or a washing station will be available.
- Maintain physical distancing to the extent possible during the in-person research activities.

We ask that you follow the health-related directives above for your safety and the safety of the researchers.

**Information for Contact Tracing**

We are collecting personal contact information for contact-tracing purposes, in the event that you may have been exposed to COVID-19 at the research site.

Your name and contact information:

- Will not be stored with the research data
- Will always be securely stored
- Will only be used if requested by Public Health authorities for COVID-19 contact tracing purposes
- Will be held only for the time required by Public Health authorities

**Right to Withdraw**

You are under no obligation to participate. You can stop participating or withdraw from the study at any time by notifying the researcher using the contact information above.

Thank you for your interest and participation.

**Information for Contact Tracing (to be kept separately from research documents)**

This information:

- will not be stored with the study data;
- will always be securely stored;
- will be used only if requested by public health to provide this information for COVID-19 contact tracing purposes; and
- will be held only for the time required by public health authorities

Name (please print): _____(required)

Phone: _____(required)

Email:_____(optional)

Date: _____

# Appendix D

**Edinburgh Handedness Inventory**

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) | | |

Please stop here

# Appendix E

**Instructions for Participants**

Block 1. Aligned Reach Training (Practice)

- In this task, you will simply be reaching to a target that appears on the screen. Each trial will start with a yellow target appearing. Once it appears, reach to it quickly with the goal of having the cursor land on the target. Once you are done, hold your hand still and the robot will move your hand back to the home position (the white circle) to begin the next trial. Do you have any questions? We're going to start with 9 practice trials. Are you ready to begin?

Block 2. Aligned Reach Training (Baseline)

- Now that you have an idea of what to do, we are going to do a block of 51 trials of exact the same thing. So, a yellow target will appear and your task is to reach to it quickly with the goal of having the cursor land on the target. Once you are done, hold your hand still and the robot will move your hand back to the home position to begin the next trial. Do you have any questions? Again, there will be 51 of these trials.

Block 3. No-Cursor Reaches #1

- We are now going to change the task slightly. At this time, you are going to reach when you cannot see your hand – there will be no visual cursor on the screen. **For these trials, reach so that your hand goes straight to the target as you just did.** Once you are done, hold your hand still and the robot will guide you back to the home position to begin the next trial. Do you have any questions? We're going to do 6 trials, pause briefly, and then do 6 more.

Block 4. Proprioceptive Training (PTWF and PTNF only)

- No feedback trials (Blocks 1 & 5 for PTWF, and all 5 Blocks for PTNF)
    - OK – so we are done the first part of the experiment and now we are now going to change the task entirely. You are now going to complete a block of trials where you will **not** be reaching – the robot will do all the movement for you. For these trials, you will hold onto the handle – without pushing or pulling it. The robot will move your hand to a position within the workspace. Once the robot stops, you will have to verbally indicate if the position of your hand is located to the "left" or to the "right" of your body midline (i.e., center of your body). Once you indicate left or right, the robot will move you back to the home position to begin the next trial. Do you have any questions? We are going to begin with 3 practice trials. After that, we will complete 74 trials.
- Feedback trials (Blocks 2-4 for PTWF group only)
    - We are now going to do another block like we just did. Again, the robot will move your hand to a position within the workspace and you will have to verbally indicate if the position of your hand is located to the "left" or to the "right" of your body midline. On these trials, once you provide a response, I will tell you if your response

was "correct" or "incorrect". Again, it is very important that you do not push or pull against the robot handle during these trials. Do you have any questions? We will complete 74 trials.

Block 4. Time Delay (CTRL group only)

- We are now going to take a 30 minute break before continuing the experiment.

Block 5. Aligned Reach Training

- We are now back to our reaching trials. Like at the start of the experiment, you will see a yellow target appear. Once it appears, reach to it as quickly as possible with the goal of having the cursor land on the target. Once you are done, hold your hand still and the robot will move your hand back to the home position to begin the next trial. Do you have any questions? There will be 15 of these trials.

Block 6. No-Cursor Reaches #2

- You are now going to reach when you cannot see your hand – there will be no visual cursor on the screen. **For these trials, reach so that your hand goes straight to the target as you just did**. Once you are done, hold your hand still and the robot will guide you back to the home position to begin the next trial. Do you have any questions? We're going to do 6 of these trials, pause briefly, and then do 6 more.

Block 7. Rotated Reach Training

- **<u>This is our last block of reaching trials with the cursor</u>**. Again, you will see a yellow target appear. Once it appears, reach to it as quickly as possible with the goal of having the cursor land on the target. Once you are done, hold your hand still and the robot will move your hand back to the home position to begin the next trial. Do you have any questions? There will be 99 of these trials.

Block 8. No-Cursor Reaches #3

- Exclusion:
    - We have just a few trials left. These are the no-cursor trials. You are now going to reach when you cannot see your hand – there will be no visual cursor on the screen. **For these trials, reach so that your <u>hand</u> goes straight to the target**. Once you are done, hold your hand still and the robot will guide you back to the home position to begin the next trial. Do you have any questions? We're going to do 6 of these trials.
- Inclusion:
    - In this last set of trials, you are again going to reach when you cannot see your hand – there will be no cursor on the screen. However, the instructions for these trials are different. For these trials, I want you to use anything you have learned during training in order to get the cursor to the target. In other words, **reach so that the <u>cursor</u> would have gone straight to the target**, as in the reaching trials you just completed when the cursor was available. Once you are done, hold your hand still and the robot will guide you back to the home position to begin the next trial. Do you have any questions? We're going to do 6 of these trials.