ONLINE AND OFFLINE CONTRIBUTIONS IN ADAPTED MOVEMENTS

by

Darrin Wijeyaratnam

Supervisor: Erin K. Cressman
Committee: Romeo Chua & Anthony N. Carlsen

Thesis submitted to the University of Ottawa
in partial fulfillment of the requirements for the

MASTER OF SCIENCE

in Human Kinetics

School of Human Kinetics,
Faculty of Health Sciences
University of Ottawa

Statement of Contributors

I hereby declare that I am the sole author of this Master of Science thesis manuscript. My contributions included: a review of relevant literature, participant recruitment, data collection, analysis and compilation, statistical analysis, and the write-up of this thesis manuscript. All tasks were performed under the guidance and mentorship of my research supervisor, Dr. Erin K. Cressman.

The original conception of the experiments in this thesis was performed in collaboration with my supervisor Dr. Cressman, with recommendations from my committee: Dr. Romeo Chua (School of Kinesiology, University of British Columbia) and Anthony N. Carlsen (School of Human Kinetics, University of Ottawa). Dr. Cressman and Dr. Chua provided editorial feedback and are co-authors of the articles presented in this thesis.

Acknowledgements

My experience as Master’s student at the University of Ottawa has been exceptional. In such a short period of time, I have developed many skills all of which came through the help and support of faculty, friends and family.

I would first like to express my utmost appreciation to my supervisor, Dr. Cressman. Your mentorship and encouragement throughout the research process have really helped me be a better researcher. I recognize and appreciate all the time, feedback and finances you have invested for my success. You are truly an inspiration.

Next, I would like to extend my gratitude to my committee members. To Dr. Chua who has given me insightful feedback in the design of these experiments, as well as in the write-up of the experiments, and to Dr. Carlsen who willingly, and without hesitation, entertains my questions regarding any and all topics (research related or not).

I would like to acknowledge Jinyang Huang for his technical skills in Matlab & Simulink, as well as Mohamadou Ly and Xiaoxin Zhou. I have also had the pleasure to work alongside a number of talented researchers within Dr. Cressman’s lab, as well those under the supervision of Dr. Carlsen and Dr. Diane Ste-Marie. The discussions and laughs we have shared will not be forgotten. I would also like to thank all my friends who have really made me feel welcome in Ottawa, namely Kevin Moncion, Kaamel Haifizi, Tyler Kung, Kathryn Denize, Heather Thompson and Maji Shakih. I look forward to the future memories we will create, in spite of the many different paths we may take.

Finally, I cannot express my love and appreciation to my family who have always supported me in every and any endeavor I choose to pursue.

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Abstract

Human movements are remarkably adaptive, such that we are capable of completing movements in a novel environment with similar accuracy to those performed in a typical environment. Our ability to perform in these environments involves accurate processing of sensory feedback for online and offline control. These processes of control have been widely studied for well learned actions, but not for actions in a novel visuomotor environment. In two experiments, we examined control processes underlying reaches when participants were first introduced to a visuomotor rotation (Experiment 1) and then following visuomotor adaptation (Experiment 2). All participants completed 150 reach training trials when (1) a cursor accurately represented their hand motion (i.e., aligned cursor) and (2) a cursor was rotated 45 degrees clockwise relative to their hand motion (i.e., rotated cursor). In Experiment 1, we sought to determine if the control processes underlying movements in typical and novel visuomotor conditions were comparable. Participants (n = 16) received either continuous visual feedback or terminal visual feedback regarding movement endpoint during reach training. Analyses revealed that participants were able to demonstrate similar outcomes (i.e., movement time and endpoint errors) regardless of visual or cursor feedback, but also demonstrated more offline control (i.e., took more time planning and were less consistent in initiating their movements) when reaching with a rotated cursor compared to an aligned cursor, even at the end of training. Together, the results suggest a greater contribution of offline control processes and less effective online corrective processes when reaching in a novel environment compared to when reaching in a typical environment. In attempt to promote online corrective processes, participants (n = 16) in Experiment 2 first completed the training trials with continuous visual feedback and then completed an additional 45 reaches under (1) slow movement time (i.e., Slow MT: 800-1000 ms) and (2) fast movement time (i.e., Fast MT: 400-500ms) constraints. Results showed a shift to online control (i.e., greater endpoint accuracy) when reaching with an aligned and rotated cursor, when sufficiently more time was provided (i.e., Slow MT). Specifically, participants were able to more effectively utilize visual feedback for online control under the Slow MT constraint compared to when reaching quickly (i.e., Fast MT). Together, these experiments demonstrate a flexibility in control processes underlying reaches with rotated visual feedback of the hand. In that reaches first engage in offline control processes during adaptation to a visuomotor rotation, and then shift to online corrective processes following visuomotor adaptation.

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CHAPTER 1 INTRODUCTION

Humans are sophisticated beings that can accumulate information, produce diverse complex actions, and learn from their mistakes. With the many advancements in technology over the years, artificial systems are still unable to match the complexity in motor performance shown by a young child. We take for granted this ability to perform even the simplest of actions in continually changing environments, while also learning from incorrect actions.

The ease at which actions are adapted to meet the demands of everyday life can be attributed to our highly sophisticated central nervous system (CNS) that processes, integrates and coordinates incoming sensory and outgoing motor information, almost instantly. With respect to reaching actions, sensory information is primarily derived from vision and proprioception – which provides the sense of limb posture and orientation relative to other body segments and the environment. This sensory information is used to monitor and correct the execution of movements (i.e. online control) and to plan and adjust subsequent motor commands (i.e. offline control).

1.1 Thesis Overview

The organization of this thesis is separated into six main chapters and several appendices. Following the overview of the thesis (Chapter 1), an in-depth review of literature (Chapter 2) will primarily discuss studies that have investigated the control of movements performed in a typical environment. Specifically, the review will provide an overview of movement control models and the measures used to quantify the contributions of movement control processes (i.e., online and offline control). It will outline how visual feedback influences movement control and how these processes can be further manipulated by imposing movement constraints to promote a greater contribution of specific control processes. Altogether, the discussion of these topics (and related studies) set the stage for potential factors that may contribute to the control of movements performed in a novel visuomotor environment. In two experiments (Chapters 3 and 4), we investigated the control processes underlying movements performed in a novel visuomotor environment during adaptation (Chapter 3), and after participants had learned to perform in this novel visuomotor environment (Chapter 4). These experiments will then be discussed together (Chapter 5) in terms of participants' ability to progress through specific stages of learning, based on performance variables. Additionally, we discuss limitations of this thesis and outline potential future experiments. Finally, we conclude by stating the implications of this research and the need for future research to develop a more rigorous account of the processes underlying human motor control (Chapter 6). In view of this conclusion, we have included additional analyses in the frequency domain, that has been proposed to provide insight into movement corrections online (Appendix A).

CHAPTER 2 REVIEW OF LITERATURE

2.1 Movement Control

It is important to note that all movements discussed in this literature review will be upper limb goal-directed reaching movements primarily completed with the right (dominant) hand, typically towards a two-dimensional target. The goal-directed movements studied in our lab are usually point-to-point reaching movements in order to represent the simplest movements that closely mimic the processes required to interact with various objects in our daily environment. By reducing complex movements to these simple two-dimensional movements, we can begin to compare the kinematic measures required to plan and execute these movements when the visual reaching environment and movement constraints are manipulated (Wolpert & Kawato, 1998).

2.1.1 Models of Movement Control

In (1899a) R. S. Woodworth introduced a model describing the fundamental control of movement as consisting of two distinct phases: an initial adjustment and a current control phase. He suggested that the initial adjustment brings the limb within the vicinity of the target, while the current control phase utilizes sensory information (primarily visual in nature) gained during the movement in order to accurately achieve the target (i.e., reduce the discrepancy between limb-target positions). This model purported that more time was needed to ensure movement accuracy, as it allowed more time to correct the movement during the current control phase. More than a century later, we continue to hold on to the general notion that movements are controlled by two phases, specifically an initial adjustment phase (also referred to as impulse control) and a current control phase (also referred to as homing phase). However, in the last two decades, many experiments have led to a more sophisticated understanding of these two phases of movement (for a review, see Elliott et al., 2010, 2017; Elliott, Helsen, & Chua, 2001). Specifically, these studies, as outlined below, have identified that the impulse control phase of a goal-directed movement contains a number of interrelated and complementary limb control processes, which impact the need and type of current control.

For example, Meyer and colleagues' (1988) optimized submovement model identified a tradeoff between movement duration and spatial precision of rapid aiming movements. In line with Woodworth's phases (i.e., initial adjustment and current control), Meyer's model assumes that the phases (i.e., submovements) are optimally programmed in a way that minimizes average total movement time while maintaining a high rate of accuracy. As a result of this assumption, both phases are dependent on each other. Specifically, the time spent during the primary submovement (i.e., initial adjustment) directly impacts the number of secondary submovements (i.e., current control) when performing aiming movements. If less time is spent during the primary submovement (i.e., low movement velocity), there will then be a higher frequency of secondary submovements to accurately aim to the target. Therefore, each movement takes into account the speed at which it must be completed, while also ensuring a high percentage of target accuracy.

While this model can explain the relationship between movement time and our ability to execute accurate movements (i.e., speed-accuracy tradeoff) to targets with variable sizes and movement amplitudes, it does not explain the scaling effect of the primary submovement (i.e., initial adjustment) endpoints found in other similar studies

(Chua & Elliott, 1993; Elliott, Hansen, Mendoza, & Tremblay, 2004; Engelbrecht, Berthier, & O'Sullivan, 2003). Kinematic data from these experiments have demonstrated that the primary movement generally undershoots the target. With this in mind, the multiple-process model of limb control proposed by Elliott and colleagues (2010), builds on Woodworth (1899a) and Meyer's models by identifying two components but multiple processes that underlie most goal-directed aiming movements. Specifically, Elliott and colleagues (2010) identified a planned component (i.e., initial adjustment or impulse control), which brings the limb into the vicinity of the target, and a corrective component (i.e., homing phase or current control), which reduces any spatial discrepancy between limb and target positions late in the movement. During initial reaching attempts, participants must determine the speed at which the movement needs to be performed in order to achieve the target accurately. Similar to Meyer and colleagues, Elliott and colleagues' (2010) model builds upon the tradeoff between speed and accuracy by suggesting that over a number of trials participants adjust the central tendency of primary movement endpoints but also take into consideration the temporal and energy costs of undershooting and overshooting. Elliott and colleagues (2010) purport an additional consideration of energy expenditure as an integral factor of movement planning and execution.

Our current understanding of limb control includes the ability of making corrections in real-time as movements are being executed (commonly referred to as online control). Alternatively, the limb can also be controlled through altering the movement plan, which leads to changes in how movements are initiated (commonly referred to as offline control). In both online and offline control, the availability of sensory feedback, primarily vision, plays an important role in how the planning and execution of goal-directed movements unfold.

2.1.2 Sensory Information and Movement

Two important sources of sensory information integral for the planning and execution of a goal-directed movement are vision and proprioception. Vision is defined as the ability to see objects, as well as the surrounding environment, while proprioception is defined as the ability to sense where the body is in space (Gardner & Johnson, 2013). Together, vision and proprioception provide the ability to safely navigate ambiguous environments and to accurately complete daily activities with ease (Sober & Sabes, 2005). Moreover, studies that have manipulated the availability of visual information, clearly demonstrate that people rely on vision for information about the environment in which they are reaching and for the accurate control of their movements. Studies have manipulated vision directly, in a blocked or randomized fashion, by providing either full or no visual feedback when completing a movement (e.g., Cheng, Luis, & Tremblay, 2008; Elliott, Binsted, & Heath, 1999; Elliott, Carson, Goodman, & Chua, 1991; Khan & Franks, 2000). In general results show that in adult participants, movements are more accurate when vision is available, even when movements are performed very rapidly (e.g. within 225 ms, see Elliott et al., 2010). In no vision conditions, participants cannot use visual feedback to correct any errors, resulting in less accurate movements.

While vision may be the dominant source of sensory information for the control of movement, is it not the sole source that contributes to our perception of the surrounding environment and our movement (Sherrington, 1900). Proprioception derived from receptors within the muscle (muscle spindles embedded in the belly of the skeletal muscle), provide information related to changes in muscle length by simultaneously stretching and shortening with limb action. When a muscle spindle is stretched there is an increased rate of firing in the associated sensory neuron. Conversely, when a muscle spindle is shortened the rate of neuronal firing decreases. As such, muscle spindle activity is directly proportional with the contractile activity of the muscle and can be used to identify the location of the body in the absence of vision (Roll & Vedel, 1982).

The combination and integration of both visual and proprioceptive information provides a robust estimate of the environment and one's limb compared to when only a single source of sensory information is available (Ernst & Bülthoff, 2004). With this in mind, both sources of feedback are important for the accurate control of a goal-directed movement. In relation to Elliott and colleagues' multiple-process model (Elliott et al., 2010), sensory information related to vision and proprioception can be processed online and/or offline when controlling a goal-directed movement. For the purposes of this thesis, the primary source of sensory feedback that will be discussed is vision, which is also the sole sensory modality that will be directly manipulated.

2.1.3 Online Control

Online control refers to the ability to concurrently control and correct an ongoing movement as required. Typically, online control processes have been thought to occur near the end of the movement, after there has been sufficient time to recognize errors. Keele and Posner (1968) suggested that visual feedback could be processed and have an influence on movement within 190-260 ms. Since the 1980s, research supports the notion of early online control, such that adjustments in movements in response to visual feedback can be seen in as little as 100 ms (e.g., Carlton, 1992; Hay, Bard, Fleury, & Teasdale, 1996; Zelaznik, Hawkins, & Kisselburgh, 1983). Differences between Keele and Posner's (1968) estimate and more recent estimates can be attributed to participants' prior knowledge of the schedule of visual feedback (i.e., visual feedback provided according to a blocked or randomized schedule).

Within online control, overlapping processes such as impulse control and limb-target control are involved in order for participants to successful reach a target. Impulse control begins during the initial stages of the movement trajectory and involves a comparison of actual limb velocity and direction to an internal representation of expectations about the limb trajectory. On the other hand, limb-target control involves error-reduction based on the relative positions of the limb to the target late in the movement, which usually requires more time because it involves greater top-down control processes.

2.1.4 Offline Control

Offline control is associated with the initial planning of a movement. Studies have shown that prior information regarding the outcome of a completed movement can be used for the planning of any upcoming movements (Elliott & Allard, 1985; Elliott et al., 2004; Ghez, Gordon, & Ghilardi, 1995; Hansen, Glazebrook, Anson, Weeks, & Elliott, 2006; Zelaznik et al., 1983). Similar to online control processes, the overall goal of motor planning is to minimize error. The differentiating factor between online and offline control is with respect to the time of when sensory information is utilized to update the movement trajectory. In offline control, sensory information, obtained during the movement and/or movement termination, are evaluated, weighted and then integrated in advance of the next movement (Khan et al., 2003, 2006; Khan, Elliott, Coull, Chua, & Lyons, 2002). With every completed movement, participants become more precise at specifying the magnitude, duration and direction of the muscular forces required to accelerate and decelerate the limb (Khan, Franks, & Goodman, 1998; Krakauer, Pine, Ghilardi, & Ghez, 2000). This is evident in a study conducted by Elliott and colleagues (2004), where participants made trial-to-trial adjustments in movements such that the error on the *n*th trial was a robust predictor of error on trial *n*+1 (see also Cheng, Luis, & Tremblay, 2008). These findings support the idea that information from prior trials can be used to make direction and force-time adjustments to reduce error.

2.1.5 Feed-Forward and Feedback Models

Online control is influenced by the representation of a forthcoming action, often referred to as a forward model. Forward models are internal models, representing information about what is expected to happen in an unfolding movement (e.g., Davidson & Wolpert, 2005; Miall & Wolpert, 1996). These representations can influence online control in two ways. The first is associated with comparing the predicted limb position (i.e. efferent copy) to the desired limb position. If the actual output (efferent command) of the system differs from the desired output (efferent copy), the CNS uses this information to rapidly initiate adjustments to the movement trajectory through a feed-forward process (Elliott et al., 2010). The second method involves comparing early sensory information with an internal representation of movement direction (e.g., Hansen, Glazebrook, Anson, Weeks, & Elliott, 2006; Saunders & Knill, 2003) or velocity (e.g., Proteau & Masson, 1997). Although there may be a processing delay of sensory information, as seen in the timing of visual feedback, these sources of sensory information are typically available long before movement completion. In this latter approach of online control, participants depend on feedback to update their motor commands (inverse model) in order to achieve the target. As a result of this trial-by-trial modification of the inverse internal model, individuals begin to plan their movements differently, which is closely linked to offline control of a goal-directed movement.

In contrast to online control, offline control is influenced by feedback models that compare information about an expected movement to the actual final movement. Offline control differs from online control because real state signals driving the forward model to predict the resulting future position of the arm are not available (Passot & Arleo, 2010). Therefore, information, from the previous movement, is used to adjust a number of parameters associated with the magnitude and force of the movement but also provides a general idea of potential sensory consequences of the movement (von Holst, 1954). The main difference between the influence of forward models in both online and offline control is dependent on the timing of when sensory information is processed. In online control, sensory information is readily available concurrently throughout movement execution, whereas in the offline utilization of sensory feedback, information is processed once the movement is completed.

2.2 Kinematic Measures

The overlapping nature of online corrective processes with offline planning have made the quantification of visual feedback utilization during movement quite difficult. Over the years, researchers have identified certain variables and kinematic markers associated with the identification and quantification of online and offline control processes. In addition, novel analyses in the frequency domain have been shown to detect changes in online feedback utilization. The kinematic measures discussed in this thesis are divided into two categories: within-trial measures and between-trial measures.

2.2.1 Within-Trial Measures

Measures related to position and its derivatives have been shown to shed light onto the contributions of online and offline control processes (Elliott et al., 1991). Specifically, movement accuracy has been used to identify the contributions of online and offline processing of visual feedback (Elliott et al., 1999, 1991; Khan & Franks, 2000). Accuracy is a direct measure of an individual’s ability to complete the task, utilizing either online or offline control. Typically, we see more accurate movements possessing a larger contribution of online control due to corrections being made in real-time. In contrast, reaching accuracy can increase with offline control due to information provided from a completed movement that contributes to updating the movement plan for the following reaching movement. Several other kinematic variables such as peak velocity (PV), peak acceleration (PA), time to peak velocity (TTPV), time after peak velocity (TAPV) and jerk have also been shown to be associated with the utilization of visual feedback for limb control (Elliott et al., 2010, 2017, 2001). For example, time spent after reaching peak velocity (TAPV) during movement has been used as a marker associated with online control, such that a longer TAPV is associated with multiple corrections from processing visual feedback to achieve an accurate target position. This differs from TTPV, where longer times are associated with a larger contribution of offline control due to additional planning processes and the inability to make corrections later in the movement. Finally, jerk is the third derivative of position, which looks at the rate of change of acceleration across a movement. This means that movements with minimized jerk values are typically stereotyped, smooth movements usually not affected by the utilization of visual feedback online (i.e., controlled offline). An increase in jerk values results in less smooth movements with discontinuities which can be attributed to the utilization of visual feedback (i.e., online control) during a movement (Flash & Hogan, 1985; Richardson & Flash, 2002; Yadav & Sainburg, 2014). Together, these measures provide insight into how movements are controlled.

2.2.2 Between-Trial Measures

Both online and offline control can contribute to the decrease in trial-to-trial variability (Elliott et al., 2010; Khan et al., 2006). Trial-to-trial variability provides information regarding an individual's ability to achieve the movement demands and incorporate sensory information during or on subsequent trials. Although, this decrease is expressed through different processes. In online control, it is sufficient for an individual to make more precise corrections within each movement, which is a relatively quick process. Whereas in offline control, multiple comparisons must be made following the end of a movement to ensure that the next movement accounts for the previously made errors. As individuals become more proficient at the task, movement variability should decrease regardless of the provided sensory feedback. In a similar fashion, recent methodologies to distinguish the contributions of online and offline processing of visual feedback have analyzed between-trial variability (Khan et al., 2003, 2006, 2002; Messier & Kalaska, 1999). By looking at movement trajectories over a series of trials, different proportions of a movement can be compared to assess the influence of feedback-related processes. For example, stereotyped trajectories over a number of trials represent movements that do not utilize feedback online. Therefore, lower variability at later stages of movement proportions (i.e., 75%) is taken as evidence of increased online control processes, because a greater amount of adjustments across a trajectory (e.g. from movement start to movement end) must have been completed.

2.3 Visual Feedback

As suggested earlier, the availability of sensory feedback during and after a movement plays an important role in the contribution of online or offline control. For the purposes of this thesis, visual feedback is primarily discussed, as many consider it the dominant source for sensory information (Elliott et al., 2001; Heath, 2005; Keele & Posner, 1968; Krigolson, Cheng, & Binsted, 2015; Meyer et al., 1988; Milner & Goodale, 2008). Visual feedback can be manipulated (e.g., provided continuously versus only at movement end) in order to establish the contribution of online and offline processes to a movement.

2.3.1 Continuous Visual Feedback

In reaching tasks with continuous visual feedback, individuals are provided with concurrent view of their moving limb or a visual representation of their moving limb while executing a movement (i.e., cursor). With continuous feedback, people are able to make corrections as soon as visual errors are detected (i.e., online control), allowing for the desired target position to be achieved, provided the movement is long enough in duration (Sülzenbrück, 2012). Often studies focus on optimal performance, as determined by movement accuracy, when assessing the effects of continuous visual feedback on motor control (Eversheim & Bock, 2002; Hansen et al., 2006), but rarely mention its implications in closed-loop control systems and therefore the acquisition of novel reaching movements. Providing continuous visual feedback of a reaching movement allows subjects to adapt a closed-loop control system, which solely requires individuals to reach the target rather than learn movement mechanics. This type of non-acquisition-based reaching behaviour is evident because participants are able to perform real-time corrections and continually update their movements (Bernier, Chua, Bard, & Franks, 2006; Smeets, van den Dobbelsteen, de Grave, van Beers, & Brenner, 2006).

2.3.2 Terminal Visual Feedback

On the other hand, reaching tasks with terminal visual feedback provide individuals with information about their movement once it has been completed. This feedback can be used to plan subsequent movements, altering the movement plan in order to correct the previous movement errors. Reaching movements with terminal visual feedback differ from movements with continuous feedback because they adopt more of an open-loop control system. Movements are preprogrammed and therefore independent of any corrective processes until movement end, wherein only corrections can be made in the motor plan of the following movement. Thus, it is expected that terminal visual feedback is more effective than continuous visual feedback with regard to the acquisition of an internal model of novel reaching movements because it enables individuals to learn relationships between the input and the output processes in a novel reaching environment (Bernier, Chua, Bard, et al., 2006; Sülzenbrück & Heuer, 2011).

2.4 Movement Restrictions

Similar to manipulating visual feedback, imposing movement restrictions have also been used to assess the contributions of online and offline control processes when performing goal-directed reaching. A measure that has commonly been manipulated is movement time (MT), where MT is defined as the time required to execute the motor response; excluding reaction time (Houlihan, Campbell, & Stelmack, 1994). Researchers have put forth several models that describe the relationship between speed and accuracy when temporal constraints are imposed; the impulse variability model (Schmidt, Zelaznik, Hawkins, Frank, & Quinn Jr, 1979), later refined by Meyer and colleagues (1988) who forwarded the optimized submovement model (Meyer, Abrams, Kornblum, Wright, & Smith, 1990), which brought in aspects of the impulse variability model and the iterative correction model (Crossman & Goodeve, 1983). These models were based on the premise that movement variability in the initial impulse (i.e., muscular forces used to propel the limb toward the target) increased proportionally with the forces required to perform a particular movement type (e.g., achieve temporal constraints). In other words, experiments have shown that accuracy and precision increases as MT increases (i.e. online control), but when MT is restricted, movements become less accurate and more variable (Keele & Posner, 1968). This tradeoff between speed and accuracy has been extensively studied for well-learned movements (Khan et al., 1998; Meyer et al., 1988; Meyer, Smith, & Wright, 1982; Schmidt et al., 1979; Wright & Meyer, 1983; Zelaznik, Mone, McCabe, & Thaman, 1988). Specifically, these studies have manipulated MT directly by requiring participants to meet certain MT criterion ranging from 190-450 ms (see Beggs & Howarth, 1970; Keele & Posner, 1968). These studies provide evidence to suggest that slower MT provides individuals with sufficient time to make real-time corrections to the movement, indicative of a larger contribution of online control processes. As such, faster MT supports a greater contribution of offline control processes because additional time is not available to make movement corrections; resulting in more stereotypic movements from early in the movement compared to the end of the movement.

2.5 Novel Visuomotor Environment

An alternative strategy that researchers have used to evaluate the contributions of online and offline processes, apart from manipulating visual feedback availability and imposing movement restrictions, is to perturb an ongoing movement. This perturbation can reflect changes in a target position (Grierson & Elliott, 2008; Pisella et al., 2000), limb dynamics (Grierson, Gonzalez, & Elliott, 2009), or visual feedback related to hand position (Krakauer et al., 2000). In our research we have altered visual feedback related to hand position in order to directly compare the underlying movement control processes when reaching in novel visuomotor environments to those underlying typical environments.

Changing the requirements of the movement (i.e. motor adaptation) can be easily done using a virtual reality environment. Specifically, motor adaptation can occur in the lab by manipulating the position of the cursor representing the hand on a screen (e.g. the cursor’s motion is rotated relative to actual hand motion; Krakauer, 2009). When reaching to a target in the presence of a visual rotation, movement errors are initially large. However, over trials, participants learn to move in a direction that compensates for the rotation (Bond & Taylor, 2015; Hinder, Riek, Tresilian, de Rugy, & Carson, 2010; Hinder, Tresilian, Riek, & Carson, 2008; Krakauer et al., 2000; Maksimovic & Cressman, 2018; S. D. McDougle, Bond, & Taylor, 2015; Neville & Cressman, 2018; Shadmehr, Smith, & Krakauer, 2010; Taylor, Krakauer, & Ivry, 2014). This motor adaptation is a form of motor learning through trial-and-error processes of adjusting previously learned movements to meet the new task demands (Bastian, 2008). The brain uses these adjusted movements to calibrate and predict how the body should move, taking into account the costs associated with the task (Emken, Benitez, & Reinkensmeyer, 2007; Harris & Wolpert, 1998; Todorov, 2004).

Adaptation to a visuomotor rotation has served as an exemplary task for studying visuomotor learning (Krakauer, 2009; Pine, Krakauer, Gordon, & Ghez, 1996; Taylor et al., 2014); with the learning in such tasks attributed primarily to updating forward and inverse models (Mazzoni & Krakauer, 2006; Synofzik, Lindner, & Thier, 2008; Tseng, Diedrichsen, Krakauer, Shadmehr, & Bastian, 2007). Adaptation in this visuomotor environment is a distinct form of motor learning, as it does not require acquisition of a new pattern of muscle activation but rather an altered mapping of well-learned movements (Krakauer, 2009). For example, the requirements of moving a limb to the left in order to make a cursor on a virtual screen move upwards is indicative of acquiring a new mapping of the movement (i.e., reach left = cursor moves up) rather than learning new muscle contractions; since leftward reaching movements can be completed in daily life. With practice, one is able to quicken the speed at which they react and move within a given time window (Elliott et al., 2004).

Many people have established that a new visuomotor relationship has been learned through the use of aftereffects trials, in which participants reach in the absence of visual feedback (Krakauer et al., 2000). Changes in these trials following reaches with altered visual feedback of the hand suggest that a new representation of a reaching movement is maintained even after the distortion is removed. In addition, there is a body of literature that suggests learning can be evaluated by determining if asymptotic or saturated performance has been achieved within a given testing session when participants are continuing to reach with the distorted visual feedback (e.g., Hauptmann & Karni, 2002; Hauptmann, Reinhart, Brandt, & Karni, 2005).

Following this notion of saturation-dependent consolidation, several studies have observed a return to baseline performance when reaching to a single target with a 30° cursor rotation in as little as 20 reach training trials (e.g., Krakauer et al., 2000; Neva & Henriques, 2013; Zbib, Henriques, & Cressman, 2016) and for a 40° cursor rotation in 30 reach training trials (e.g., Yamamoto, Hoffman, & Strick, 2006). Although research supports the notion of saturation-dependent consolidation, it is unclear, from a kinematic perspective, whether movements are performed in a similar way as well learned movements (i.e. movements performed when the cursor is aligned with the hand). In addition, it has not been established if online and offline processing of visual feedback when performing movements in this novel visuomotor environment are similar to well learned reaching.

2.6 Specific Objectives

The aim of this thesis is to determine if the contributions of online and offline control processes in adapted reaching movements differ from those underlying well-learned movements. Contributions are assessed through changes in performance and kinematic variables when visual information is manipulated (i.e., continuous versus terminal visual feedback), and temporal demands imposed (i.e., reaching with goal MT; slow versus fast MT). Similarities in measures underlying reaching movements with aligned and rotated cursor feedback would suggest that movements utilize a similar form of online and offline control regardless of movement proficiency and visual feedback provided. Differences, on the other hand, would provide a novel understanding of the contributions of online and offline control to newly acquired reaching movements.

Our first objective was to establish if reaches in a novel environment (i.e., with a rotated cursor) are carried out in a similar manner as in a typical environment (i.e., with an aligned cursor). We compared traditional measures of movement control across reaching environments (i.e., typical versus novel reaching environment) when visual feedback was manipulated (continuous versus terminal visual feedback). As stated earlier, continuous feedback (CF) provides sufficient information for online control, whereas terminal feedback (TF) promotes the use of offline control. It was hypothesized that we may identify similarities in performance measures but differences in measures of movement control when reaching in a typical environment compared to reaching in a novel visuomotor environment, which may be further influenced by the availability of visual information (i.e., CF versus TF). These results would be reflective of individuals being able to complete the overall task objective of achieving the target but adopting different control processes due to participants engaging in more planning processes when reaching in this novel environment (i.e., offline control).

Our second objective was to establish whether we could promote the utilization of visual feedback for online control in newly acquired adapted movements (i.e., following visuomotor adaptation with a rotated cursor), as seen when reaching with aligned visual feedback in a typical environment. By imposing MT constraints, we could further compare the contributions of movement control processes following training, as well as determine if the relationship between speed and accuracy (i.e., speed-accuracy tradeoff), which has been extensively studied for well-learned movements, holds true for adapted movements.

Manipulations across reaching environments allowed for direct comparison of the movement control processes underlying both these movements. Focus was placed on assessing performance and kinematic measures associated with online and offline control for both well-learned reaching movements (i.e., aligned visual feedback of the hand) and adapted movements (i.e., misaligned visual feedback of the hand).

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CHAPTER 3 EXPERIMENT 1

Going offline: Differences in the contributions of movement control processes when reaching in a typical versus novel environment

Darrin O. Wijeyaratnam[1], Romeo Chua[2] and Erin K. Cressman[1]

[1]Sensorimotor Control Laboratory, School of Human Kinetics, Faculty of Health Sciences, University of Ottawa, Ottawa, ON, K1N 6N5, Canada.

[2]Perceptual-Motor Dynamics Laboratory, School of Kinesiology, Faculty of Education, University of British Columbia, Vancouver, BC, V6T 1Z1, Canada.

As of August 2018, this manuscript has yet to be submitted for publication.

3.1 Abstract

Human movements are remarkably adaptive. We are capable of completing movements in a novel visuomotor environment with similar accuracy to those performed in a typical environment. In the current study, we examined if the control processes underlying movements under typical conditions were different from those underlying novel visuomotor conditions. Sixteen participants were divided into 2 groups, one receiving continuous visual feedback during all reaches (CF), and the other receiving terminal feedback regarding movement endpoint (TF). Participants trained in a virtual environment by completing 150 reaches to 3 targets when (1) a cursor accurately represented their hand motion (i.e., typical environment) and (2) a cursor was rotated 45 degrees clockwise relative to their hand motion (i.e., novel environment). Analyses of within-trial measures across 150 reaching trials revealed that participants were able to demonstrate similar movement outcomes (i.e., movement time and angular errors) regardless of visual feedback or reaching environment by the end of reach training. Furthermore, a reduction in variability across several measures (i.e., reaction time, movement time, time after peak velocity, and jerk score) over time showed that participants improved the consistency of their movements in both reaching environments. However, participants took more time and were less consistent in the timing of initiating their movements when reaching in a novel environment compared to reaching in a typical environment, even at the end of training. As well, angular error variability at different proportions of the movement trajectory was consistently greater when reaching in a novel environment across trials and within a trial. Together, the results suggest a greater contribution of offline control processes and less effective online corrective processes when reaching in a novel environment compared to when reaching in a typical environment.

Key words: *Reaching, visuomotor adaptation, visual feedback, kinematic analysis, movement control*

3.2 Introduction

Goal-directed actions are a critical part of everyday life. Simple actions, such as reaching for a pen, become well learned over time and are eventually performed with little thought or effort. As we become proficient and well versed in our daily movements, we also gain the ability to adapt these well-learned actions to both internal and external (environmental) changes (e.g., growth, disease, changes in lighting conditions, etc.). For example, several studies have demonstrated visuomotor adaptation following the introduction of altered visual feedback via prism goggles (Clower & Boussaoud, 2000; J. C. Hay & Pick, 1966; Redding & Wallace, 2006), or within virtual reality environments in which a cursor misrepresents the position of one's hand on a screen (Hinder, Riek, Tresilian, de Rugy, & Carson, 2010; Krakauer, Ghilardi, & Ghez, 1999; Shabbott & Sainburg, 2010; Tseng, Diedrichsen, Krakauer, Shadmehr, & Bastian, 2007; Maksimovic and Cressman, 2018).

In a typical, well-experienced environment, vision and proprioception provide veridical representations of the hand's location in relation to the desired target location (Smeets et al., 2006). In general, this results in an accurate reach. When reaching in a novel environment, such as within a virtual reality environment in which the cursor's trajectory is rotated relative to the hand's trajectory, the relationship between visual and proprioceptive information and the required motor commands can be unfamiliar and unpredictable. Upon initial exposure to rotated visual feedback of the hand's trajectory, seen hand paths deviate from the planned trajectory, resulting in a visual error between the seen hand's location (i.e., cursor) and the desired target location (Shabbott & Sainburg, 2010; Tseng et al., 2007; Wolpert & Kawato, 1998). With training, movements are adapted in response to the altered visual feedback of the hand so that the cursor once again lands on the target as in the typical environment. This adaptation develops quickly, in as little as 20-30 trials, such that reaching errors in movement direction and end-point position return to similar levels as observed prior to the introduction of the rotation (i.e., baseline) (Krakauer et al., 2000; Sainburg & Wang, 2002; Yamamoto et al., 2006; Zbib et al., 2016).

Limited attention has been given to the kinematics (and hence control processes) underlying movements performed in a novel environment compared to movements completed in a typical environment. Recent work by Fernandez-Ruiz and colleagues (2011) and Simon and Bock (2016) examining visuomotor adaptation did include analyses related to performance variables, such as accuracy, response times and total movement duration, however, their primary focus was on the movement outcome. In these studies participants performed reaching movements in a novel virtual environment where a 60° counter clockwise (CCW) rotation was present (Fernandez-Ruiz, Wong, Armstrong, & Flanagan, 2011) or under 60° and 75° cursor rotations (Simon & Bock, 2016). They found that when adapting to reach in a novel environment, the rate of adaptation (i.e., reducing angular errors) depended on the number of trials performed and not on movement duration (Simon & Bock, 2016). Additionally, they observed increased response times, which the authors attributed to participants adopting a strategy (i.e., mental rotation; Fernandez-Ruiz et al., 2011). While these studies provide insight into the temporal characteristics of adapted movements, they do not speak to whether the control processes differ when reaching in a novel versus typical environment, and whether these control processes change over time.

Movements can be controlled online, using any available information to correct an ongoing movement, or they can be amended offline on a trial-by-trial basis, making use of information gathered from previous movements to optimize performance on subsequent trials. Online control processes typically occur near the end of the movement, after there has been sufficient time to recognize and correct for errors (Elliott et al., 2001; Marc Jeannerod, 1986; Meyer et al., 1988; Woodworth, 1899b). However, online adjustments can also arise early in a trajectory through the comparison of expected-to-actual sensory consequences of the movement (Desmurget & Grafton, 2000; Elliott et al., 1991; Grierson & Elliott, 2008; Scott, 2016). Offline control occurs prior to movement onset, and involves using prior information regarding the outcome of previously completed movements in the planning of an upcoming movement (Elliott & Allard, 1985; Elliott et al., 2004; Hansen et al., 2006; Khan et al., 2003, 2002; Zelaznik et al., 1983).

The goal of the current study was to determine how adapted movements are controlled relative to reaches performed in a typical environment by establishing the contributions of online and offline control processes underlying reaching movements performed in a novel visuomotor environment. Kinematic variables, previously used to characterize the contributions of online and offline control in well-learned movements (de Grosbois & Tremblay, 2016, 2017, Elliott et al., 2010, 2017, 1999, 2001, Grierson & Elliott, 2008, 2009; Khan et al., 2006), were compared between movements performed in a typical environment (i.e., aligned cursor) and movements performed in a novel visuomotor environment (i.e., rotated cursor). To promote the use of online and offline control processes across the two reaching environments, the availability of visual information was manipulated (Bernier, Chua, Franks, & Khan, 2006; Cheng et al., 2008; Gaveau, Prablanc, Laurent, Rossetti, & Priot, 2014; Heath, 2005; Khan et al., 2003, 2006; Tremblay, Hansen, Kennedy, & Cheng, 2013; Walsh, Ling, Wang, & Carnahan, 2009). Specifically, participants performed movements with either continuous visual feedback (i.e., the cursor was present throughout the duration of the movement [CF]) or terminal visual feedback (i.e., the cursor was present only once the movement was terminated [TF]). We hypothesized that training with the visuomotor rotation would quickly lead to visuomotor adaptation, perhaps through online corrective processes, such that reaching with an aligned and rotated cursor would achieve similar performance outcomes (e.g., movement time and end-point accuracy). However, we expected differences in kinematic characteristics across reaching environments. Moreover, we expected these differences to reveal a larger contribution of offline control processes when reaching with a rotated cursor compared to reaching with an aligned cursor throughout training. These results would be reflective of individuals being able to achieve the overall task objective of reaching the target but adopting different control processes depending on their experience in the reaching environment.

3.3 Method

3.3.1 Participants

Sixteen young adults (7 males, M = 23 years of age) were recruited from the University of Ottawa to participate in this experiment. Participants were naïve to the purpose of the experiment and free to withdraw at any point in the experiment without consequence. Informed consent was obtained followed by a brief handedness questionnaire (Edinburg handedness inventory, (Oldfield, 1971)). According to the handedness questionnaire, all participants were right handed, M = 80.7, range: 60-100). As well, participants had normal (n = 11) or corrected-to-normal vision (n = 5) with no self-reported history of motor, sensory of cognitive impairment. Prior to testing, participants were evenly divided into two groups (Group 1: Continuous Feedback [CF] and Group 2: Terminal Feedback [TF]). All ethical standards and safety monitoring procedures were completed in accordance with the Health Science and Science Research Ethics Board at the University of Ottawa.

3.3.2 Experimental Apparatus

Testing took place in a secluded room with a two-joint robot manipulandum (KINARM, BKIN technologies), adjacent to the experimenter's computer workstation. The KINARM set-up consisted of a downward-facing computer monitor, a reflective surface placed 20.5 cm below the computer monitor, and a robot handle placed 20.5 cm below the reflective surface that participants grasped with their right hand (see Figure 3.1A). The downward-facing computer monitor (EzSign model 47LD452B; refresh rate: 60Hz (or every 17ms); LG. Seoul, South Korea) projected visual information onto the reflective surface, which covered a workspace of 70 cm by 36 cm. Participants' movements of the robot handle were represented in the form of a cursor (i.e., magenta circle 0.5 cm in diameter) on the reflective surface. Participants were unable to see their right limb due to the reflective surface that obstructed their view and a cloth that was placed parallel to the reflective surface around their neck and shoulders.

Calibration of the KINARM was carried out prior to testing each participant according to the manufacturer's instructions. Participants were asked to sit on a standard height-adjustable office chair at a self-desired height and distance from the

KINARM, such that they were able to see and reach all of the targets comfortably. Participants grasped the vertical cylindrical handle of the KINARM with their right hand, elbow flexed at approximately 90° and the forearm in a neutral position. The position of the hand was tracked at 1000 Hz, with a spatial accuracy of 0.1 mm.

In general, participants were required to rapidly reach with the robot handle to a target (yellow circle, 1 cm in diameter) presented 15 cm away from a central home position (white circle,1 cm in diameter), located approximately 20 cm in front and aligned with each participant's midline. Participants in the CF group saw a magenta cursor that was displayed from the start of their movement up until the end of the movement (Figure 3.1C). Participants in the TF group were provided with final hand position at the end of a movement (Figure 3.1D). The end of the movement was defined online as the time when movement velocity first fell below 0.01 m/s. All participants reached to three targets (see Figure 3.1B) in both typical (aligned cursor) and novel (rotated cursor) visual training environments. Reaching targets were displayed at one of three possible locations, specifically, directly ahead of the home position (0°) and at 45° left or right of the straight ahead (Figure 3.1B). The sequence of target locations was presented randomly.

3.3.3 Procedure

Participants were required to reach in two different visual training environments: (1) reaching with aligned visual feedback of their hand, such that the cursor on the screen accurately depicted where their hand was in space (i.e., aligned cursor), and (2) reaching with distorted visual feedback of their hand such that the cursor's trajectory was rotated 45° clockwise (CW) relative to hand motion (i.e., rotated cursor). Reaching with the distortion presented participants with a novel reaching environment, which required them to adapt their reaching movements by aiming counterclockwise (i.e., left of the target) to counteract the rotation. All participants first reached with the aligned cursor (150 trials) followed by the rotated cursor (150 trials). A mandatory 5 min break separated testing times and total participation lasted approximately 1 hour.

The experiment began once the participant was seated in a comfortable position and verbally indicated they were ready to start the experiment. Each trial began with a white circle (home position) presented for 1000 ms. Participants were instructed to keep the cursor representing the hand within the home position. In the case that the cursor was outside the home position, the robot passively moved the participant’s hand into the desired home position, ensuring that the hand always started at the same position on every trial.

Participants were instructed that once a target appeared they were to reach rapidly, but comfortably, to the target and be as accurate as possible. At the end of the reach, the hand was held at the movement end location for 500 ms. During this time the target was visible and individuals in the TF feedback group were provided with terminal visual feedback regarding their final hand position in the form of the cursor. The CF group did not receive visual feedback of their hand position at this time. Following 500 ms, the robot passively moved the participant’s hand to the location of where the hand should have reached in order for the cursor to have landed on the center of the target in the absence of visual feedback. The hand was held at this location for an additional 500 ms. Finally, the robot passively moved the participant’s hand back to the home position along a linear path in a movement time of 1000 ms. The home position then became visible. The hand was held at the home position for another 1000 ms before a target appeared, signaling the start of the next trial (see Figure 3.2).

3.4 Data Analyses and Results

Data for each reaching trial were collected and analyzed using both within-trial and between-trial measures of movement control. Before analyses, the start and end of each movement was determined based on a velocity criterion (i.e., first increase in velocity greater than 0.01 m/s for 100 ms and the first decrease in velocity below 0.01 m/s, respectively). Endpoint position data were used to screen for outliers. In particular, if a participant's endpoint position in the horizontal or vertical directions was greater than 3 standard deviations above their respective mean endpoint position in the same dimension, the trial was removed from further analyses. This screening resulted in the removal of 62 trials (1.29%).

Participants' reaching data were grouped into seven bins consisting of twelve trials each: Trials 1-12, 13-24, 25-36, 37-48, 70-82, 100-112 and 130-142. A greater number of bins were defined earlier in training compared to late training, allowing us to examine early changes in reaches in detail, which were expected to happen within the first 20-30 trials (i.e., 2-3 bins; Huberdeau, Haith, & Krakauer, 2015). For the variables discussed below, data were collapsed across all targets for each subject and averaged over the 12 trials within each bin. All dependent variables were then statistically evaluated using a mixed analyses of variance (ANOVA) in SPSS (IBM, version 24). If the Mauchly's test of sphericity was significant ($p < 0.05$) then the Greenhouse-Geisser correction factor was applied and the adjusted degrees of freedom are reported. Differences with a probability of 0.05 or less were considered significant. Following a significant interaction, a simple effect analysis was conducted using the Bonferroni correction. In the case of analyses yielding significant main effects and significant interactions, only the interactions are reported and interpreted below.

3.4.1 Assessment of Performance and Adaptation

Initial analysis of the reaching trials was conducted to evaluate whether participants were able to adapt their reaches to meet the movement requirements and to observe general performance when reaching in the novel visuomotor environment. This was done by tracking changes in movement time (MT), angular errors (AE) at peak velocity (PV) and movement endpoint (EP), resultant EP error and distance in the anterior-posterior (AP) direction over time. MT was defined as the time from movement initiation until movement end. AE at PV were defined as the angular difference between a movement vector (from the home position to PV) and a reference vector (from the home position to the target location). AE EP were defined in a similar way, such that it reflected the difference between a movement vector (from the home position to movement EP) and the reference vector. Resultant EP error was defined as the absolute distance of the cursor from the target at movement end. Distance in the AP direction was defined as the cursor distance traveled in the primarily movement direction. A 2 Group (CF, TF) x 2 Reaching Environment (aligned, rotated) x 7 Time (Bins with trials: 1-12, 13-24, 25-36, 37-48, 70-82, 100-112 and 130-142) mixed analysis of variance (ANOVA) with repeated measures (RM) on the last 2 factors were used to determine if participants were able to adapt their movements in the novel environment.

Analysis of mean MT revealed a significant Reaching Environment x Time interaction (MT: $F(3.279,45.905) = 2.904$, $p = 0.041$, $\eta^2 = 0.172$), such that MT decreased over reaching trials with the rotated cursor (see Table 3.1). MTs were significantly shorter by the end of reaching (i.e., bin 7: Trials 130-142) compared to the start of reaching (i.e., bin 2: Trials 13-24, $p = 0.019$). Analysis of MT variability resulted in a three-way interaction (Group x Reaching Environment x Time: $F(6,84) = 2.652$, $p = 0.021$, $\eta^2 = 0.159$), with post hoc analysis indicating that reaching with an aligned cursor generally resulted in less variable MTs compared to reaching with a rotated cursor, across reaching trials regardless of Group. That said, participants in the CF group only demonstrated increased variability in MT when reaching with a rotated cursor compared to aligned cursor early in training (i.e., bins 1 and 2, both $p < 0.010$). In contrast, MT was more variable in the TF group when reaching with a rotated cursor compared to aligned cursor even in bin 6 ($p = 0.021$; bin 7, $p = 0.518$).

Analysis of initial reach direction errors at PV revealed similar findings. Specifically, reaching errors were greater when reaching with a rotated cursor compared to an aligned cursor early in training (Reaching Environment x Time ($F(1.969,27.563) = 4.627$, $p < 0.019$, $\eta^2 = 0.248$). By Bin 6 (Trials 100–112), reaching errors at PV were similar across reaching environments ($p > 0.216$). Errors at PV also varied between Groups ($F(1,14) = 11.662$, $p = 0.004$, $\eta^2 = 0.454$), such that participants' reaches in the TF group (M = -0.64° ± 0.45°) were initially biased more in the leftwards direction compared to reaches by the CF group (M = 1.54° ± 0.45°). Analysis of the variability of PV angular errors again revealed a significant Reaching Environment x Time interaction ($F(3.387,47.424) = 17.871$, $p < 0.001$, $\eta^2 = 0.561$), with post hoc analysis indicating that reaching with a rotated cursor was more variable than reaching with an aligned cursor across training, regardless of Group.

As shown in Figure 3.3A and B, all participants were relatively accurate when reaching with an aligned cursor over all bins of trials (mean EP angular error = -0.22° ± 0.30°). Participants then reached with greater errors, such that the cursor was right of the target, when the cursor rotation was first introduced. In accordance with these observations, an analysis of EP angular errors revealed a Reaching Environment x Time interaction ($F(1.380,19.324) = 4.421$, $p = 0.038$, $\eta^2 = 0.240$). There was no main effect of Group or interactions involving Group (all $p > 0.05$). Post hoc analysis indicated that EP angular errors were significantly greater when reaching with a rotated cursor compared to when reaching with an aligned cursor early in training across all participants. In general, participants were able to reduce their angular errors over time, such that following bin 3 (36 trials with a rotated cursor), EP angular errors did not differ significantly between reaching environments.

As seen in Figure 3.3C and D, participants in the CF group (M = 2.87° ± 0.36°) were more consistent in their EP angular errors than participants in the TF group (M = 6.14° ± 0.26°); Group ($F(1,14) = 42.190$, $p < 0.001$, $\eta^2 = 0.751$). ANOVA also revealed a significant Reaching Environment x Time interaction ($F(2.538,35.531) = 11.630$, $p < 0.001$, $\eta^2 = 0.454$), indicating that variability in EP angular error decreased over time in both reaching environments (i.e., aligned and rotated cursor). Post hoc analysis indicated that while variability in EP angular error changed over time, it was always higher when reaching with a rotated cursor compared to reaching with an aligned cursor for both groups of participants. Overall reaching with an aligned cursor did not significantly change (i.e., mean and variability) across trials for participants reaching with continuous or terminal visual feedback.

Minimal EP angular errors were also reflected in the mean resultant distance of the final cursor position from the target (M = 1.37 cm ± 0.08 cm). Main effects and interactions related to Reaching Environment and Group were observed over trials (Reaching Environment x Time: ($F(1.303,18.236) = 5.872$, $p = 0.019$, $\eta^2 = 0.296$); Group x Time: ($F(6,84) = 2.495$, $p = 0.029$, $\eta^2 = 0.151$)). Post hoc analyses indicated that endpoint distance from the target was greater when reaching with a rotated cursor (M = 1.86 cm ± 0.16 cm) compared to reaching with an aligned cursor (M = 0.9 cm ± 0.1 cm, $p < 0.003$) across all reaching trials (see Table 3.2). Additionally, post hoc analyses indicated that endpoint distance from the target was also greater in the TF group (M = 1.95 cm ± 0.01 cm) compared to the CF group (M = 0.78 cm ± 0.12 cm) across all reaching trials (see Table 3.2). An analysis of variability revealed a main effect of Group ($F(1,14) = 28.400$, $p < 0.001$, $\eta^2 = 0.670$) and an interaction between Reaching Environment and Time ($F(2.636,36.910) = 8.512$, $p < 0.001$, $\eta^2 = 0.378$). Post hoc analysis of this interaction indicated that variability when reaching with a rotated cursor decreased across reaching trials (all $p < 0.08$) but was still higher compared to reaching with an aligned cursor (all $p < 0.011$). Additionally, the TF group (M = 1.09 cm ± 0.07 cm) was more variable than the CF group (M = 0.56 cm ± 0.07 cm).

Analysis of distance in AP direction in Table 3.2. resulted in a three-way interaction between Group x Reaching Environment x Time ($F(6,84) = 1.659$, $p = 0.009$, $\eta^2 = 0.106$). Post hoc analyses indicated that participants consistently undershot when reaching with a rotated cursor (M = 13.95 cm ± 0.11 cm) and overshot when reaching with an aligned cursor (M = 17.17 cm ± 0.063 cm) regardless of Group and across all Times (all $p < 0.024$). An analysis of the variability in endpoint position in the anterior-posterior axes resulted in a main effect of Reaching Environment ($F(1,14) = 844.295$, $p < 0.001$, $\eta^2 = 0.984$), such that reaching with a rotated cursor (M = 2.12 cm ± 0.03 cm) was more variable compared to reaching with an aligned cursor (M = 6.06 cm ± 0.13 cm).

Overall, when reaching with a rotated cursor we observed decreases in the mean and variability of several performance measures (i.e., MT, PV AE, EP AE resultant EP error and distance in the AP direction) across reach training. This demonstrates participants' ability to learn the visuomotor rotation and refine their movements with continued practice. In spite of this learning, variability was always greater when reaching with a rotated cursor, indicating that movements were not as consistent across trials compared to when reaching with an aligned cursor, even at the end of reach training.

3.4.2 Assessment of Online versus Offline Control

3.4.2.1 *Movement Preparation: Offline Control*

After establishing that participants had similar levels of accuracy in PV and EP angular errors in both reaching environments, we then sought to compare movement characteristics of reaches in the two reaching environments. We used variables that have previously been used to establish online versus offline control processes in well-learned reaching environments. We first looked for evidence of offline control by examining changed in reaction time (RT), time to peak velocity (TTPV) and proportional TTPV (pTTPV). RT was defined as the time required to initiate a response from target presentation until the start of the movement and TTPV was defined as the time PV was achieved within the movement. Similarly, pTTPV was expressed as a percentage of overall MT (the time from movement initiation until movement end). Previous research has suggested that RT and TTPV provide insight into the degree of planning involved in a movement, with longer RTs and longer TTPVs indicative of a greater contribution of planning processes (i.e., offline control; Burkitt, Grierson, Straite, Elliott, & Lyons, 2013; Hansen et al., 2006; Khan et al., 2003; Elliott et al., 2001; Heath, Hodges, Chua, & Elliott, 1998; Mendoza, Elliott, Meegan, Lyons, & Welsh, 2006). A mixed 2 Group x 2 Reaching Environment x 7 Time ANOVA with RM on the last two factors, was used to determine if any of these within-trials measures differed across reaching environments over trials.

In Figure 3.4, mean and variability of RT are presented. Main effects of Reaching Environment were observed for both mean ($F(1,14) = 32.331$, $p < 0.001$, $\eta^2 = 0.698$) and RT variability ($F(1,14) = 23.174$, $p < 0.001$, $\eta^2 = 0.623$). RTs were shorter (see Figure 3.4A and B) when reaching with an aligned cursor (M = 335.6 ms ± 31.2 ms) compared to reaching with a rotated cursor (M = 496.0 ms ± 42.2 ms). This pattern was seen for both the CF and TF groups, as analysis revealed no main effect of Group or interactions with Group (all $p > 0.978$). Similarly, RT variability (see Figure 3.4C and D) was lower when reaching with an aligned cursor (M = 98.9 ms ± 13.6 ms) compared to reaching with a rotated cursor (M = 165.261 ms ± 15.364 ms). These differences in Reaching Environment continued across all trials.

Analysis of mean TTPV and pTTPV resulted in no significant main effects or interactions ($p > 0.074$; mean values can be found in Table A2 of the Appendix). On the other hand, Figure 3.5C displays variability in TTPV. TTPV was more variable in the TF group (M = 129.6 ms ± 16.9 ms) compared to the CF group (M = 68.9 ms ± 16.9 ms; $F(1,14) = 6.395$, $p = 0.024$, $\eta^2 = 0.314$) and when reaching with a rotated (M = 117.4 ms ± 14.5 ms) compared to aligned cursor (M = 81.1 ms ± 12.5 ms; $F(1,14) = 8.647$, $p = 0.011$, $\eta^2 = 0.382$).

3.4.2.2 *Movement Execution: Online Control*

To establish contributions of online control we examined the following within-trial measures: time after peak velocity (TAPV), proportional TAPV (pTAPV), and Jerk Score (JScore). TAPV was defined as the remaining time after PV until movement end and pTAPV was a proportional time, expressed as a percentage of overall MT. TAPV can be used as a preliminary indication of whether participants use visual feedback to make corrections online to reach the target (for reviews, see Elliott et al., 2010, 2017). A modified version of the Teullings et al. (1997) equation was used to calculate jerk (JScore; de Grosbois & Tremblay, 2016):

$$JScore = \sqrt{}(\frac{ssJerk}{2} x \frac{MT^5}{\left(\frac{Jerk_{Volts\ Range}}{1000}\right)^2})$$

where SS_{Jerk} represents the sum of the squared jerk across the trajectory, MT represents movement time in seconds, and $Jerk_{VoltsRange}$ represents the difference between the maximum and minimum jerks recorded from the acceleration profile across a trajectory. The final normalized JScore is a dimensionless number (Aboelnasr, Hegazy, & Altalway, 2017; Alberts, Saling, Adler, & Stelmach, 2000), which indicates the rate of change of acceleration per time across a movement. Greater JScores are reflective of many zero-line crossings in movement acceleration profiles, which is indicative of multiple online corrections (de Grosbois & Tremblay, 2016). For all within-trial measures, a mixed 2 Group x 2 Reaching Environment x 7 Time ANOVA with RM on the last two factors, was used to determine if any of these within-trials measures differed across reaching environments over trials. Finally, to gain insight into how reaching trajectories unfolded over the course of a movement, variability of angular errors (AE) was assessed at selected proportions of MT using a 2 Group x 2 Reaching Environment x 7 Time x 4 Proportion (25%, 50%, 75% and 100%) mixed ANOVA with RM on the last 3 factors. This between-trial analysis allowed us to establish early versus late modifications in trajectory and determine whether they differed depending on visual feedback and reaching environment.

As shown in Table 3.1, analysis of mean TAPV revealed a significant Reaching Environment x Time interaction ($F(2.659,37.231) = 4.093$, $p = 0.016$, $\eta^2 = 0.226$). When reaching with a rotated cursor, TAPV was significantly shorter later in reaching trials (i.e., bins 6 and 7) compared to early reaching trials (all $p < 0.013$). TAPV did not change over reaching trials when reaching with an aligned cursor. No significant differences in means were observed for pTAPV, specifically when comparing reaches with an aligned versus rotated cursor, although differences were observed between visual feedback groups (i.e., CF versus TF; see Appendix Table A3.2.). In addition, the means of several other within trial measures (i.e., TTPV, pTTPV, JScore, EP error and path length) separated by visual feedback can be found in Table A3.2. of the Appendix.

Figure 3.5 displays variability in MT, TTPV, JScore, and TAPV. Analysis of JScore variability resulted in a significant Group x Reaching Environment x Time interaction ($F(6,84) = 3.485$, $p = 0.004$, $\eta^2 = 0.199$). Post hoc analysis revealed that

JScore was more variable in the CF group, when reaching with a rotated cursor compared to reaching with an aligned cursor early in reaching trials (i.e., bin 1: Trials 1-12; bin 2: Trials 13-24, both $p < 0.012$). TAPV was also more variable in the CF group (M = 167.9 ms ± 13.6 ms) compared to the TF group (M = 120.6 ms ± 13.6 ms). This increased variability was only seen early on in training (i.e., bins 1 and 2; Group x Reaching Environment x Time: $F(6,84) = 5.339$, $p < 0.001$, $\eta^2 = 0.276$). It is important to note the three-way interactions of Group x Reaching Environment x Time seen in several of the analyses of variability outlined above, only reveal a change when reaching with a rotated cursor in the CF group. When reaching with an aligned cursor, regardless of visual feedback, variability did not change across reach training trials ($p > 0.08$).

Analysis of AE across movement proportions (i.e., 25%, 50%, 75% and 100% of the movement) resulted in a main effect of Group ($F(1,14) = 15.698$, $p = 0.001$, $\eta^2 = 0.529$), as well as a three-way interaction between Reaching Environment x Proportion x Time ($F(18,252) = 2.346$, $p = 0.002$, $\eta^2 = 0.144$). In general, variability of AE across movement proportions was greater in the TF group (M = 16.13° ± 0.80°) compared to the CF group (M = 11.64° ± 0.80°) and when reaching with a rotated cursor versus an aligned cursor. As seen in Figure 3.6, variability decreased across movement proportion when reaching with an aligned and rotated cursor (i.e., AE variability at 25% of the movement was greater than at the end of the movement (100% of the movement)) across all trials ($p < 0.006$). This same pattern was seen early in training (bin 1; Figure 3.6A and B) and late in training (bin 7; Figure 3.6C and D).

3.5 Discussion

In this study, we examined differences in movement control processes underlying reaches performed in a novel visuomotor environment compared to a typical environment. Participants reached to three targets with a cursor that was either aligned with their hand motion or was distorted 45° clockwise with respect to movement of their hand for a total of 300 trials (i.e., 150 trials in each reaching environment). Visual feedback was provided continuously until the end of the movement (i.e., continuous feedback group) or was only provided at the end of the movement (i.e., terminal feedback group) to investigate the internal control processes known to influence movement planning and execution (Abahnini, Proteau, & Temprado, 1997; Elliott et al., 2010, 2001; Hansen et al., 2006; Khan et al., 2003; Posner, Nissen, & Klein, 1976; F. R. Sarlegna & Sainburg, 2009; Tremblay et al., 2013). The objective was to compare traditional measures associated with online versus offline control across reaching environments to establish whether adapted movements (i.e., reaching in a novel environment) are carried out in a similar manner as well-learned movements (i.e., reaching in a typical environment).

3.5.1 Kinematics Underlying Visuomotor Adaptation

Traditionally, the assessment of performance measures in visuomotor adaptation paradigms has been limited to angular errors at peak velocity or movement end-point (Krakauer et al., 2000; Sainburg & Wang, 2002; Yamamoto et al., 2006; Zbib et al., 2016). As we showed here, angular errors were reduced with reach training trials to approximately baseline levels of performance (Figure 3.3). Moreover, this occurred rather quickly (e.g., following 36 trials). Recently, more attention has been given to additional kinematic variables underlying movements performed in a novel environment. For example, Simon and Bock (2016) determined the PV, curve length and MT associated with adapted movements to 60° and 75° cursor rotations. Performance on these variables were then used to split participants into two groups, differing with respect to PV, curve length or MT. They found that PV AE decreased over training regardless of PV, curve length or MT. While their results suggest that adaptive success is independent of individual differences in how movements are performed, they do not provide insight into the control processes underlying movements performed in a novel environment.

In the current study we tracked kinematic variables (including those used by Simon & Bock, 2016) over time to establish the control processes of movements performed in a novel environment. We directly compared kinematic measures underlying movements made in a novel environment to those in a typical environment. We found differences in how movements were controlled between reaching environments during training and even at the end of training, when angular errors indicated that participants had adapted their movements to the rotated cursor. Specifically, reaches in a novel environment changed over time, as shown by decreases in AE, MT and TAPV as training progressed. Decreases in the magnitude of these variables is indicative of participants having adapted to the visuomotor rotation, as participants displayed lower errors, were able to complete the movement in a shorter amount of time with practice and required less time after reaching PV. These results add support to the utilization of AE to assess adaptation, but also introduce other kinematic measures that could be employed to assess the progression and success of adaptation over time.

While AE at PV and EP when reaching in a novel environment were reduced to similar levels as in a typical environment at the end of training, other performance variables continued to differ across the reaching environments. For instance, RT and RT variability were greater in the novel environment compared to the typical environment, regardless of visual feedback even at the end of training (see Figure 3.4). Furthermore, our analysis of variability (i.e., RT variability, see Figure 3.4C and D; TTPV variability see Figure 3.5C; AE variability across a trajectory, see Figure 3.6), clearly showed that variability remained higher when reaching with a rotated cursor compared to when reaching with an aligned cursor, even at the end of reach training. These persistent differences in reaches between reaching environments suggests that movements across the two reaching environments were not performed the same way.

3.5.2 Movement Planning

Fernandez-Ruiz and colleagues (2011) have shown that reaching performance in a novel visuomotor environment differs depending on RT. In their study, they explored the relationship between RT and changes in reach errors when reaching with a cursor rotated 60° CCW relative to hand motion. Participants were asked to make continuous out and back movements, with full vision of a cursor, under constrained (RT < 350 ms) or unconstrained RT conditions. They found that RT early in learning was positively correlated with visuomotor adaptation, as assessed by both the rate and extent of decrease in reach direction errors. In other words, longer RTs (i.e., unconstrained RT) were associated with a faster rate of visuomotor adaptation as shown by a greater decrease in reach errors. They purported that participants in the unconstrained RT condition who exhibited prolonged RTs may have processed errors from the previous movements more thoroughly, prior to initiating the subsequent movement, and therefore reduced direction errors more quickly. In line with their hypothesis, the constrained RT group showed a slow error reduction rate but was less variable in direction errors compared to the unconstrained RT group. More relevant to the current study, they also found that, if provided the opportunity, average RT remained elevated even at the end of the adaptation phase (i.e., end of training in a novel environment). The authors suggested that the elevated RT that persisted until the end of training could be due to participants using a mental rotation strategy to counteract the cursor rotation.

In contrast to Fernandez-Ruiz and colleagues (2011), we did not impose RT constraints in the current study. However, we did see a rapid reduction in EP AE early in learning when RT was unconstrained, as well as RTs that remained elevated at the end of training in a novel environment compared to typical environment (see Figure 3.4). As suggested by Fernandez-Ruiz and colleagues, this increased RT may be due to participants processing errors from previous trials prior to initiating the next movement (i.e., coming up with a strategy to counteract their reaching error on the previous trial(s)). Recently, Leow and colleagues (2017) have suggested that increased preparation times (i.e., RT) in a novel environment are an indicator of some underlying strategic process being employed (i.e., explicit process; for a definition of explicit processes see Huberdeau, Krakauer, & Haith, 2015). Regardless of the strategy being employed, these findings of consistently longer RTs when reaching with a rotated cursor compared to an aligned cursor support a greater involvement of planning processes when reaching in a novel visuomotor environment compared to typical environment. Interestingly, we found that these elevated RTs at the end of training in a novel environment were present regardless of the type of visual feedback available (i.e., CF and TF). This further emphasizes the greater use of planning processes underlying these adapted movements compared to well-learned movements.

3.5.3 Models of Limb Control

The recently forwarded multiple process model of limb control explores the interplay between accuracy, training, speed, energy and strategic behaviour of movements performed in a typical environment (Elliott et al., 2017). Our current understanding of limb control includes the ability to make real-time corrections, early (i.e., impulse control) and late (i.e., limb-target control) in a trajectory, while movements are being executed (commonly referred to as online control). Alternatively, movement corrections can also be controlled through updating a movement plan, usually seen through changes in how subsequent movements are initiated (commonly referred to as offline control). In both online and offline control, the availability of sensory feedback, primarily vision, plays an important role in how the planning and execution of goal-directed movements unfold.

Overall, our findings follow the empirical evidence supporting the multiple process model. Of note, accuracy, training and strategic behaviour are the main aspects of the model that are important to the current study. Our results show that when reaching in a typical environment (i.e., aligned cursor) individuals in the CF group were more accurate overall (in terms of endpoint distance from target) compared to the TF group (see Table 3.2). This finding is expected considering individuals in the CF group can readily utilize visual information to correct an ongoing movement. Similarly, TAPV and JScores were larger in the CF vs TF group, reflecting online corrective processes being adopted early in training (i.e., within bins 1-3). Differences between groups with respect to mean performance variables and variability were reduced over reach training trials as movements were refined by updating an internal representation of the movement with repeated training (Burkitt, Grierson, Straite, Elliott, & Lyons, 2013; Elliott & Lee, 1995).

When reaching in a novel environment, several movement outcomes were consistent with the expected behaviour linked to the availability of visual feedback. For example, we found that the CF group had less variable EP AEs compared to the TF group (see Figure 3.3). Likewise, analysis of variability in other kinematic measures (i.e., TTPV, TAPV, and AE across movement proportion) indicated findings in the expected direction, such that measures were more variable in the TF group compared to the CF group, except in TAPV, where the CF group was more variable (see Table 3.2 and Figure 3.5, Figure 3.6). However, when we re-examine these variables, we see persistent differences across reaching environments with respect to performance variability (i.e., EP AE, RT, TAPV and AE across movement proportion), regardless of visual feedback availability. This suggests that the CF group also engages in more than just online error corrective processes. Specifically, the mechanisms underlying these adapted movements rely on more offline control processes (i.e., planning), even when visual feedback is available.

Measures associated with movement planning indicated distinct differences between reaching environments. In Figure 3.4, we see overall greater mean RT and associated variability when reaching with a rotated cursor compared to aligned cursor for both the CF and TF groups. Furthermore, higher AE variability was seen at various stages of movement (i.e., 25%, 50%, 75%), continuing until the end of training in both CF and TF groups (see Figure 3.6). Given these consistent differences seen between reaching environments across visual feedback groups, we suggest that when reaching in a novel environment, participants are refining their movement through offline mechanisms (i.e., planning) and may not be effective in their ability to use visual feedback even when it is continuously available. Furthermore, participants may be adopting a “play-it-safe” approach as suggested by Elliott and colleagues (2014, 2004), in that they plan their movements so that they fall short of the target (i.e., undershoot). Elliott et al. (2004) observed this behaviour when participants did not have visual feedback available during and upon completion of the movement. The fact that we see this type of behaviour when reaching in a novel environment supports the notion of ineffective use of visual information online, as well as a greater contribution of offline planning processes compared to reaching in a typical environment.

3.5.4 Mechanisms of Adaptation

While the primary focus of the current research was to determine the contributions of movement control processes underlying reaches in a novel environment, our results also speak to current models of visuomotor adaptation. In general, visuomotor adaptation has been suggested to arise due to 2 processes; (1) a fast process (i.e., strategic control; explicit process) involved in the rapid reduction of movement errors and (2) a slow process (i.e., spatial realignment; implicit process) involved in slower adjustments made as a result of incongruent sensory information between expected and actual limb positions (McDougle, Ivry, & Taylor, 2016; Redding, Rossetti, & Wallace, 2005; Redding & Wallace, 1996, 2002; Taylor & Ivry, 2011; Taylor, Krakauer, & Ivry, 2014). These processes have been studied by observing changes in angular errors at movement EP or PV in reaching trials with and without visual feedback (i.e., aftereffect trials). The results of the current study speak to an additional method to assess processes underlying visuomotor adaptation. Analyses of variability of several kinematic measures resulted in three-way interactions of Group x Reaching Environment x Time that follow the suggested trend of an initial period of fast error reduction (i.e., explicit) and then a period of slow adjustment (i.e., implicit). Our assessment of kinematic variables does not directly distinguish between the contributions of explicit processes from implicit processes. Instead, we provide evidence that preparation time may be linked to the contribution of explicit processes when reaching in a novel environment, as suggested by Leow and colleagues (2017). Our understanding of the interaction between these implicit and explicit processes remains incomplete. Our participants reduced their errors and variability with training (i.e., implicit visuomotor adaptation); however, we continued to see participants use a strategy (i.e., engage potentially explicit visuomotor adaptation processes) throughout training.

3.5.5 Newly Acquired Adapted Movements

We found a decrease in mean angular errors at movement EP and PV, so that reaching errors eventually become similar in magnitude to when reaches were completed in a typical reaching environment. This finding demonstrates participants' ability to learn in a novel environment, so that a new pattern of movement is acquired to achieve a movement outcome similar to what is seen in baseline (Batcho, Gagné, Bouyer, Roy, & Mercier, 2016; Ghilardi, Gordon, & Ghez, 1995; Kantak & Winstein, 2012; Schmidt et al., 1979). Similar outcomes in both a typical and novel environment would suggest that visuomotor adaptation in a novel environment was "complete" (Wang & Lei, 2015). While individuals achieved similar movement outcomes in our study (i.e., PV AE and EP AE), we found that performance (i.e., movement control), even at the end of training, differed with respect to several kinematic measures between reaching environments. These results indicate that visuomotor adaptation does not necessarily result in similar control mechanisms, and the discussion of visuomotor adaptation should make clear if it is with respect to adaptation of movement outcomes versus control. With respect to control, our results suggest offline control mechanisms, reflecting the engagement of an explicit strategy, had a larger contribution when reaching in a novel compared to typical environment. Our results would further suggest that this strategy continues to be engaged throughout training.

The kinematic characterization of adapted reaching in relation to well-learned movements is important for the development of rehabilitation paradigms (van der Kooij, Brenner, Van Beers, & Smeets, 2015). The goal of rehabilitation is to have an individual get back to baseline-levels of performance (i.e., movement outcomes) after they have experienced an injury. The current study sheds light on the fact that we may be able to produce similar movements outcomes with a new pattern of movement compared to a pre-injury movement, but that this does not necessarily translate to similar control. It is important to make this distinction between outcome and performance, in order to accurately assess the compensatory processes underlying similar performance outcomes post-injury. Based on our results, we suggest that when acquiring a new pattern of movement, rehabilitation paradigms need to include sufficient time for planning processes to occur.

3.6 List of Figures

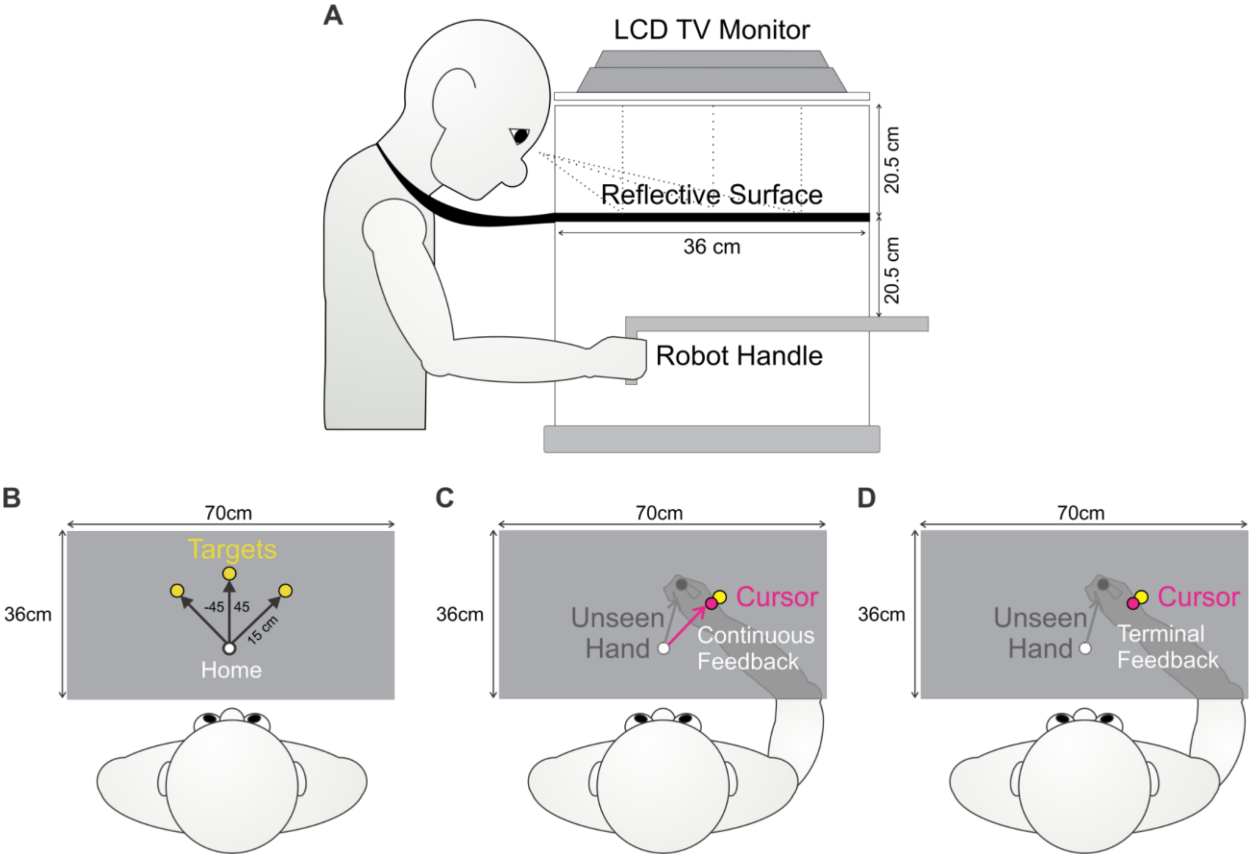


Figure 3.1. Experimental apparatus, dimensions and visuomotor training environment. **A** Side view of the experimental apparatus with a cloth that occluded vision of the limb. **B** The three target locations (yellow circles), each 15 cm away from the home position (white circle); one directly above the home position (0°) and two at 45° left and right of straight ahead. Example of on-screen feedback in the novel reaching task when provided with **C** continuous feedback (CF) and **D** terminal feedback (TF) with the cursor rotated 45° CW relative to the trajectory of the hand.

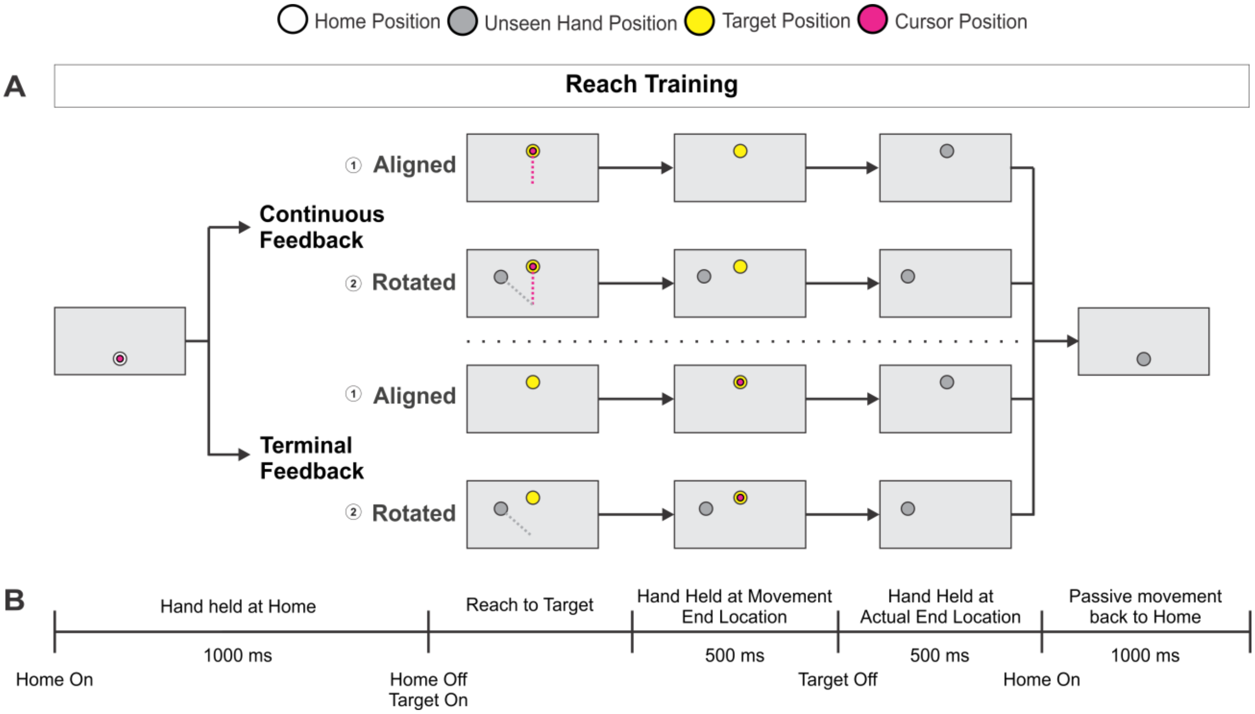


Figure 3.2. Visual events occurring within a single trial for each of the two visual feedback groups (i.e., CF and TF) and reach environments (i.e., typical and novel). **A** All reaching trials always started with a visible home position (white circle) and a visible cursor (magenta circle) held for 1000 ms at the home position until the target appeared (yellow circle), cuing participants to reach to the target. The CF group had continuous view of the cursor until the end of the movement. At movement end, the cursor was removed for the CF group. In contrast, the TF group only saw the cursor at the end of the movement. For both groups, the hand was held in the movement end position for 500 ms with view of the target. After which, the target and cursor were hidden and the unseen hand was passively moved to where the hand should have landed in order for the visual representation of the hand to be in the center of the target. The unseen hand was held at this position for 500 ms. The hand was then moved passively back to the home position in a movement time of 1000 ms. At this point, the home position and cursor were made visible once again and the hand was held for 1000 ms. **B** Timing of visual events of a single trial represented in a timeline.

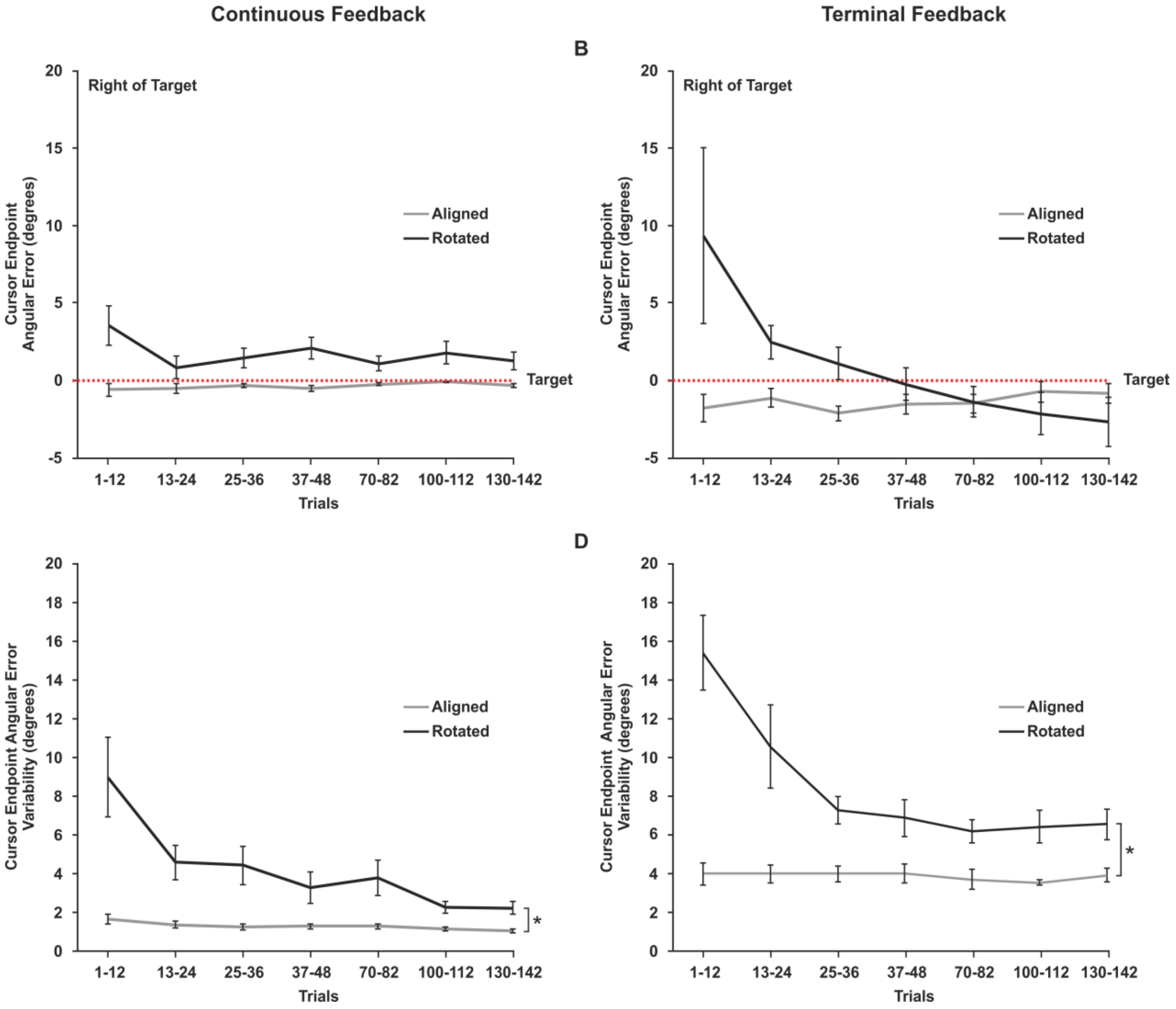


Figure 3.3. Mean and variability of cursor end-point angular errors (EP AE) measured in degrees for the continuous (CF) and terminal (TF) feedback groups over 7 bins consisting of 12 trials each. **A-B** Mean EP AE over trials in the CF and TF groups, respectively. Dotted red line represents target location. Values above the zero axis (i.e., dotted red line) represent reaches where the cursor ended up to the right of the target and values below, represent reaches where the cursor ended up to the left of the target. **C-D** Mean variability of EP AE over trials in the CF and TF groups, respectively. In **A-D** black lines represent reaches completed in a novel environment (i.e., rotated cursor) and grey lines represent reaches completed in a typical environment (i.e., aligned cursor). *Error bars* represent standard error of the mean. *Asterisks* (*) represent significant differences between reaching with an aligned versus a rotated cursor ($p < 0.05$).

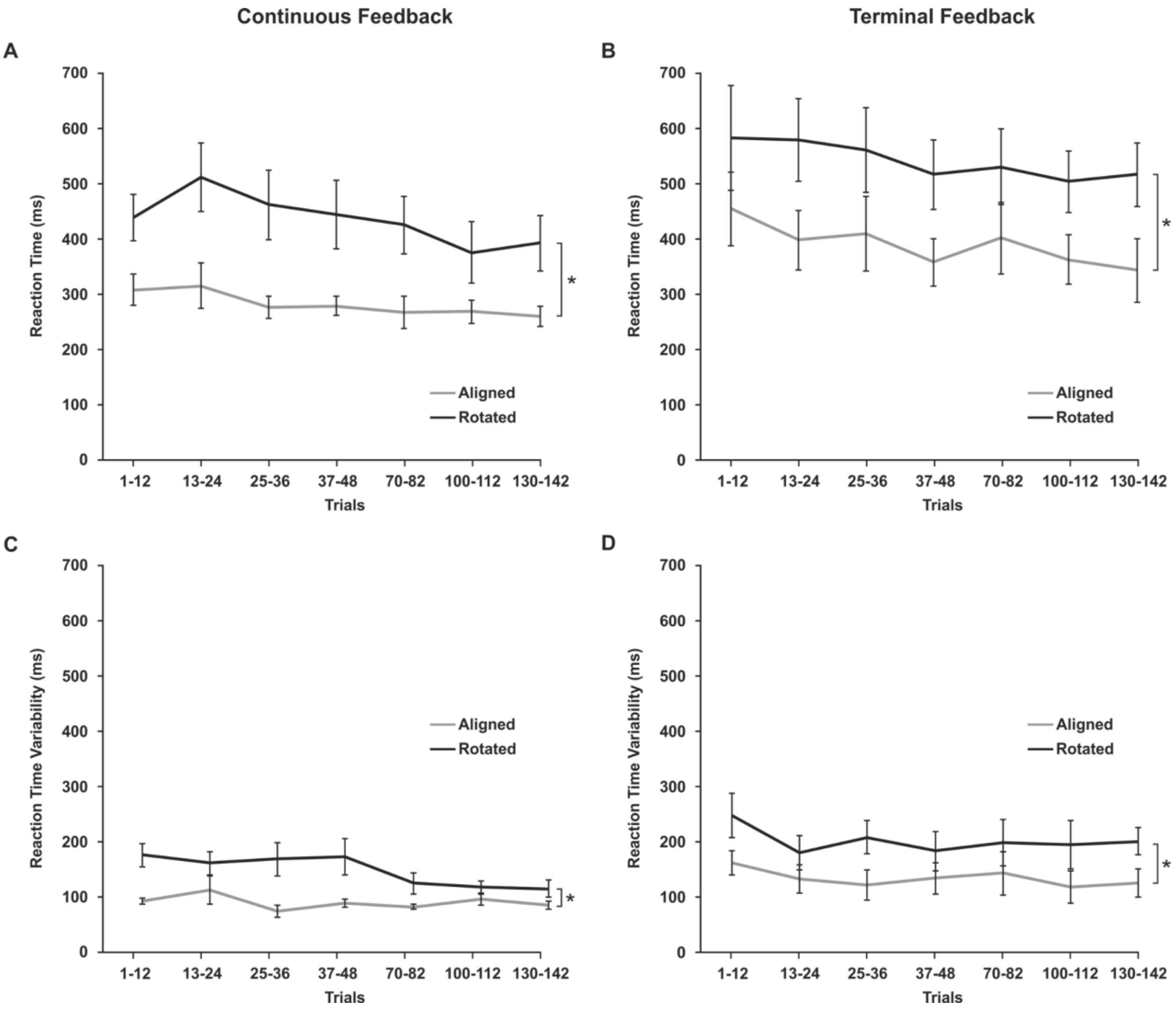


Figure 3.4. Mean RT and mean variability of reaction time (RT) measured in milliseconds for the continuous (CF) and terminal (TF) feedback groups over 7 bins consisting of 12 trials each. **A**-**B** Mean RT over trials in the CF and TF groups, respectively. **C**-**D** Mean variability of RT over trials in the CF and TF groups, respectively. In **A**-**D** Grey lines represent reaches completed in a typical environment (i.e., aligned cursor) and black lines represent reaches completed in a novel environment (i.e., rotated cursor). *Error bars* represent standard error of the mean. *Asterisks* (*) represent significant differences between reaching with an aligned versus a rotated cursor ($p < 0.05$).

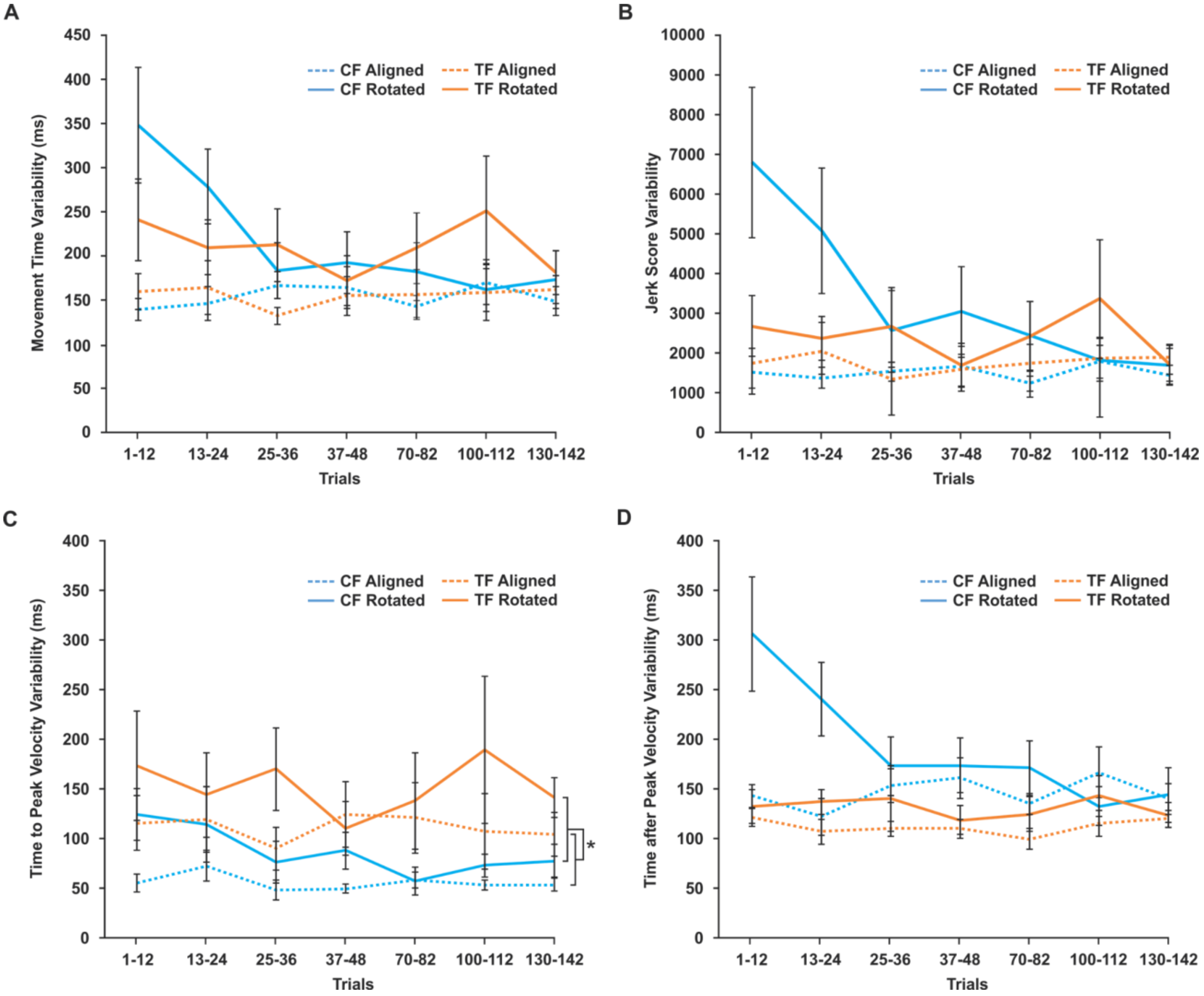


Figure 3.5. Mean variability of **A** movement time (MT), **B** jerk score (JScore), **C** time to peak velocity (TTPV) and **D** time after peak velocity (TAPV). Dotted lines represent reaching in a typical environment (i.e., aligned cursor) and solid lines represent reaching in a novel environment (i.e., rotated cursor). Blue lines represent reaches by the continuous feedback (CF) group and orange lines represent reaches by the terminal feedback (TF) group. *Error bars* represent standard error of the mean. *Asterisks* (*) represent significant differences between reaching with an aligned versus a rotated cursor ($p < 0.05$).

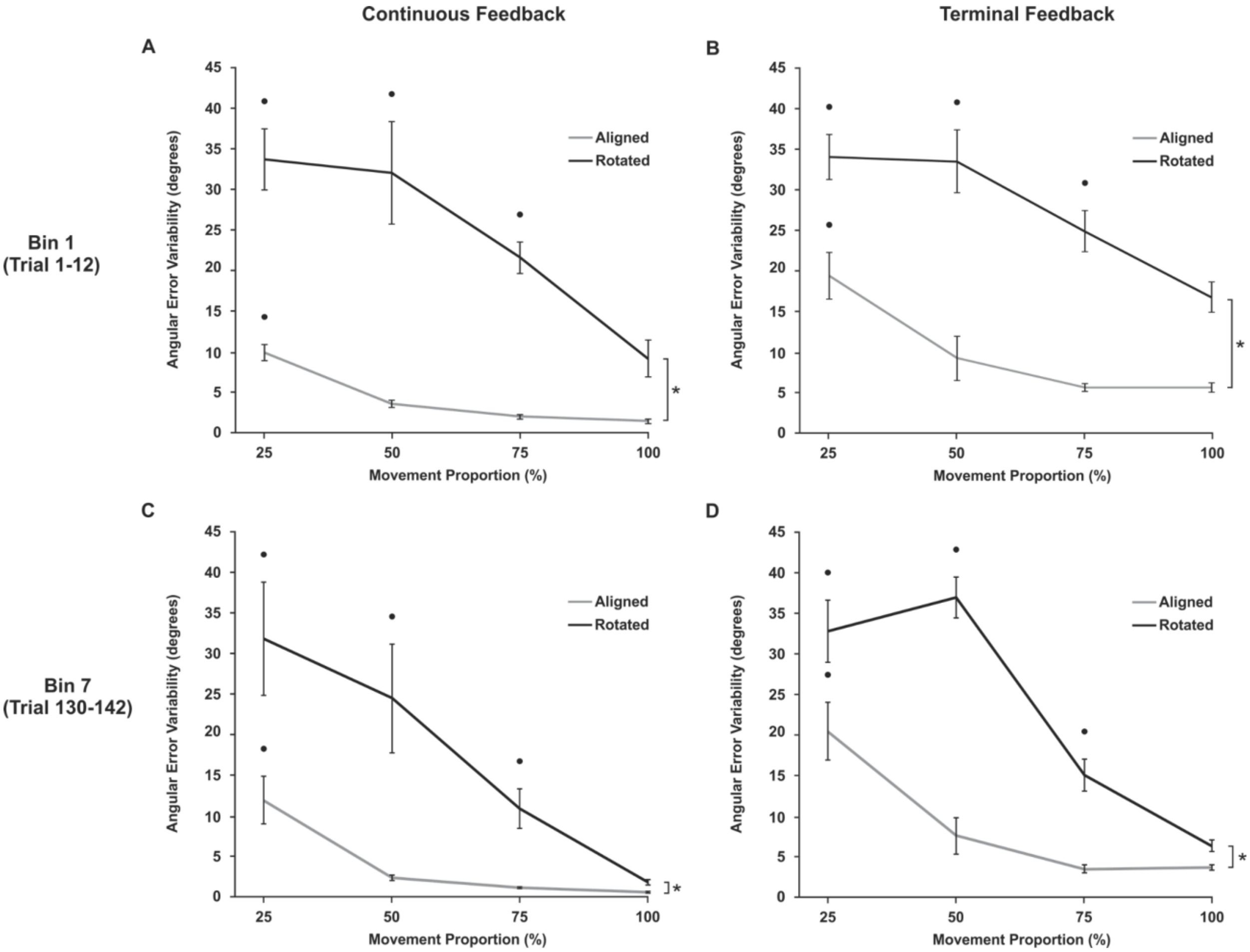


Figure 3.6. Mean variability of cursor angular error at different proportions of the movement trajectory (i.e., 25%, 50%, 75% and 100%). **A-B** Mean variability of angular error at different proportions during trials 1-12 (bin 1) in the CF and TF groups, respectively. **C-D** Mean variability of angular error at different proportion during trials 130-142 (bin 7) in the CF and TF groups, respectively. In **A-D** Grey lines represent reaches completed in a typical environment (i.e., aligned cursor) and black lines represent reaches completed in a novel environment (i.e., rotated cursor). Black dots (•) above movement proportions represent significant differences between that corresponding movement proportion compared to the end (i.e., 100% movement proportion) of the movement trajectory (p < 0.05). *Error bars* represent standard error of the mean. *Asterisks* represent differences between reaching with an aligned versus a rotated cursor ($p < 0.05$).

3.7 List of Tables

Table 3.1. Mean and standard error of the mean (in brackets) for movement time (MT) and time after peak velocity (TAPV) when reaching with an aligned and rotated cursor across all 7 bins of 12 trials.

Measure		**Trials**						
Variable	Cursor	1-12	13-24	25-36	37-48	70-82	100-112	130-142
MT (ms)	Aligned	894.4 (48.2)	844.1 (54.4)	851.2 (50.0)	882.8 (58.4)	863.1 (49.4)	891.7 (50.1)	890.1 (43.1)
	Rotated	937.8 (60.2)	922.0 (60.0)	883.9 (78.0)	873.7 (71.8)	855.2 (59.9)	828.4 (51.5)	795.7* (44.4)
TAPV (ms)	Aligned	526.0 (28.5)	473.6 (27.2)	491.3 (25.3)	508.2 (34.6)	492.4 (25.1)	522.0 (30.8)	524.1 (26.0)
	Rotated	571.4 (48.0)	558.3 (41.2)	530.2 (55.5)	522.8 (47.9)	515.5 (39.4)	473.5* (28.4)	464.5* (30.1)

Asterisks (*) represent a difference from bin 2 within the corresponding cursor type ($p < 0.05$).

Table 3.2. Mean and standard error of the mean (in brackets) for resultant endpoint (EP) error and distance in the anterior-posterior (AP) direction when reaching with an aligned and rotated cursor across all 7 bins of 12 trials.

Measure		**Trials**						
Variable	Cursor	1-12	13-24	25-36	37-48	70-82	100-112	130-142
EP Error (cm)	Aligned	1.1† (0.1)	0.9† (0.1)	0.8† (0.1)	0.8† (0.1)	0.8† (0.1)	0.8† (0.1)	0.8† (0.1)
	Rotated	3.5† (0.7)	2.0† (0.2)	1.7† (0.2)	1.5† (0.163)	1.5† (0.1)	1.4† (0.1)	1.4† (0.2)
Distance in AP direction (cm)	Aligned	16.9† (0.1)	17.1† (0.1)	17.0† (0.2)	17.4† (0.2)	17.3† (0.2)	17.2† (0.1)	17.3† (0.1)
	Rotated	13.9† (0.5)	14.5† (0.3)	14.4† (0.4)	13.6† (0.3)	14.2† (0.3)	13.5† (0.4)	13.5† (0.4)

Crosses (†) represent a difference between reaches with an aligned versus rotated cursor at the corresponding bin ($p < 0.05$).

3.8 Appendix

3.8.1 Distance Related Measures

Additional measures such as path length and horizontal displacement were used to characterize movements performed in a novel environment compared to a typically environment. Path length was defined as the length of the trajectory traversed. Horizontal displacement was defined as the greatest perpendicular distance joining the hand path to the reference vector connecting the home position to the target. A mixed 2 Group x 2 Reaching Environment x 7 Time ANOVA with RM on the last two factors was used to determine if any distance-related measures differed across reaching environments over trials.

Path lengths differed between Groups and Reaching Environments over reaching trials (Group x Time: $F(6,84) = 3.065$, $p = 0.009$, $\eta^2 = 0.180$; Reaching Environment x Time ($F(2.303,32.239) = 3.327$, $p = 0.041$, $\eta^2 = 0.192$). Post hoc analysis indicated that participants' in the TF group had shorter trajectories (M = 15.72 cm ± 0.35 cm) at the start of the reaching trials (i.e., bin 1) compared to participants in the CF group (M = 16.82 cm ± 0.35 cm; $p = 0.043$). As well, reaches with a rotated cursor were longer compared to reaches with an aligned cursor early in training, regardless of group (i.e., bins 1-3) (all $p < 0.048$). Analysis of curve length variability revealed a three-way interaction between Group x Reaching Environment x Time ($F(6,84) = 3.201$, $p = 0.007$, $\eta^2 = 0.186$). Post hoc analysis of this interaction indicated that curve length when reaching with a rotated cursor was significantly more variable than reaching with an aligned cursor in both the CF and TF groups through the majority of reaching trials. Specifically, for the CF group, participants only reached with similar curve length variability across the two Reaching Environments by bin 6 (Trials 100-112; p = 0.406). Participants in the TF group did not reach with similar curve length variability until bin 7 (Trials 130-142; *p* = 0.325).

Horizontal displacement was found to differ between Reaching Environments (*F*(1,14) = 8.269, *p* = 0.012, η^2 = 0.371), such that reaching with a rotated cursor (M = 4.50 cm ± 0.20) had a greater horizontal displacement (was more curved) compared to reaching with an aligned cursor (M = 3.98 cm ± 0.23 cm). Horizontal displacement was not affected by Group or Time (all *p* > 0.484). Similar findings were seen with respect to variability of horizontal displacement, such that reaching with a rotated cursor (M = 1.62 cm ± 0.09 cm) was more variable than reaching with an aligned cursor (M = 1.36 cm ± 0.10 cm; *F*(1,14) = 5.588, *p* = 0.033, η^2 = 0.285).

Path length findings provide kinematic support for the notion of a fast (i.e., strategic control; explicit process) and slow process (i.e., spatial realignment; implicit process) involved in visuomotor adaptation (Samuel D. McDougle et al., 2016; Redding et al., 2005; Redding & Wallace, 2002; Taylor & Ivry, 2011; Taylor et al., 2014). Here we see that following the presentation of a visual distortion, participants were able to reduce the overall distance traveled in less than 40 trials. This significant difference within 40 trials, when reaching with a rotated cursor compared to an aligned cursor (see Table A3.1), is reflective of participants developing a strategy to quickly reduce errors.

Horizontal displacement shows that reaching with a rotated cursor is consistently more curved compared to reaching with an aligned cursor throughout training (see Table A3.1) and regardless of visual feedback. This may be a result of participants engaging in planning processes early in the movement (see variability of TTPV in Figure

3.5) to correct for the altered representation of the hand’s trajectory. Furthermore, the fact that curvature is greater when reaching with a rotated cursor, regardless of available visual feedback adds to the idea of not only visually-mediated corrective processes, but also the utilization of proprioception for online control.

Although we have shown compelling evidence suggesting greater offline control processes when reaching with a rotated cursor, this does not mean that online control processes are not involved. As suggested earlier, the utilization of visual feedback online may not be effective when learning a visuomotor rotation. Perhaps, the utilization of proprioceptive feedback plays a role in the initial learning of a visuomotor rotation. With curved movements, the discrepancy between visual and proprioception is great, resulting in a faster detection and therefore corrective movement in order to achieve the target. These horizontal displacement findings are in line with our results of cursor AE at different proportions of the movement trajectory (see Figure 3.6). Specifically, participants were making corrections across movement proportions even when visual feedback was not readily available (i.e., TF group; see Figure 3.6B and D). These findings add to the idea that participants may not be solely relying on visual feedback to make corrections but are also making use of other sensory information (i.e., proprioception).

3.8.2 Visual Feedback

The means of pTTPV, TAPV and JScore for which ANOVA revealed a main effect of Group or an interaction between Group x Time are reported in Table A3.2; TAPV is also reported in Table 3.1, though ANOVA indicated it did not differ between Group. As mentioned earlier, changes in TAPV over time differed between reaches performed with an aligned versus rotated cursor (see Table 3.1). For pTTPV and JScore, ANOVA found no differences between the two Reaching Environments (all $p > 0.05$). PV was achieved on average 360.0 ms ± 21.7 ms into the movement. When TTPV was expressed as a proportion of MT (i.e., pTTPV), analysis revealed a main effect of Group ($F(1,14) = 14.547$, $p = 0.002$, $\eta^2 = 0.510$), such that participants in the TF Group spent a greater proportion of their movement achieving PV (M = 45.0% ± 1.4%) compared to participants in the CF Group (M = 37.6% ± 1.4%). Analysis of mean TAPV resulted in a significant Group x Time interaction ($F(6,84) = 2.610$, $p = 0.023$, $\eta^2 = 0.157$), with post hoc analysis indicating that individuals in the CF group spent more time during the period after PV until the end of the movement compared to individuals in the TF group at the start of reaching trials (i.e., Bin 1, Trials 1-12; $p = 0.020$). With respect to JScore, ANOVA indicated an interaction between Group x Time ($F(6,84) = 2.664$, $p = 0.020$, $\eta^2 = 0.160$). Post hoc analysis of this interaction suggested that participants in the CF group had more discontinuities (M = 5314.04 ± 751.91) compared to participants in the TF group (M = 2985.93 ± 751.91) at the start of reaching trials (Bin1, Trials 1-12: $p = 0.046$). The discontinuities in the CF group decreased over trials, such that the mean JScore later in training (Bin 7, Trials 130-142) was less than at the start of training (Bin 1, Trials 1-12; $p = 0.024$).

Together, findings related to these variables are in agreement with previous research in which visual feedback was manipulated in a typical environment (for reviews see Elliott et al., 2010, 2017, 2001). The measures that were most dependent on the influence of visual feedback were TAPV, JScore and EP error. We have shown here that following the initial presentation of a visual distortion (i.e., within 12 trials), participants perform at similar levels regardless of visual feedback. Although, EP error is not as accurate with terminal visual feedback compared to continuous visual feedback across training, as would also be expected. The fact that we have been able to reproduce similar kinematic results when reaching in a typical environment (i.e., aligned cursor) adds value for when we draw kinematic comparisons when reaching in a novel environment (i.e., rotated cursor).

Table A3.1. Mean and standard error of the mean (in brackets) for path length (PL) and horizontal displacement (HD) are presented for all 7 bins of 12 trials when reaching an aligned and rotated cursor.

Measure		**Trials**						
Variable	Cursor	1-12	13-24	25-36	37-48	70-82	100-112	130-142
PL (cm)	Aligned	15.6† (0.2)	15.6† (0.2)	15.4† (0.2)	15.5 (0.1)	15.5 (0.1)	15.5 (0.1)	15.6 (0.2)
	Rotated	17.0† (0.5)	16.2† (0.3)	16.0† (0.2)	15.9 (0.3)	15.8 (0.1)	15.7 (0.2)	15.7 (0.2)
HD (cm)♯	Aligned	1.5 (0.2)	1.3 (0.1)	1.3 (0.1)	1.5 (0.1)	1.3 (0.1)	1.4 (0.1)	1.3 (0.1)
	Rotated	2.0 (0.2)	1.6 (0.1)	1.5 (0.2)	1.5 (0.1)	1.6 (0.1)	1.6 (0.1)	1.6 (0.2)

Crosses (†) represent a difference between groups at the corresponding bin ($p < 0.05$). *Number signs* (♯) represent an overall difference between reaching environments.

Table A3.2. Mean and standard error of the mean (in brackets) for kinematic variables in both the continuous (CF) and terminal (TF) feedback groups. Time to peak velocity (TTPV), proportional time to peak velocity (pTTPV), time after peak velocity (TAPV), proportional time after peak velocity (pTAPV), jerk score (JScore), endpoint distance from target and path length are presented for all 7 bins of 12 trials.

Measure		**Trials**						
Variable	Group	1-12	13-24	25-36	37-48	70-82	100-112	130-142
Time Related Measures								
TTPV (ms)	CF	338.7 (25.2)	342.0 (32.7)	313.4 (36.1)	330.3 (38.9)	323.1 (34.3)	320.0 (40.5)	317.8 (23.9)
	TF	396.1 (25.2)	392.2 (25.2)	400.3 (36.1)	395.2 (38.9)	387.3 (35.0)	404.6 (40.5)	379.4 (23.9)
pTTPV (%)[#]	CF	35.6 (1.6)	38.3 (1.4)	36.9 (1.60)	37.6 (1.8)	37.9 (1.4)	38.5 (2.2)	38.3 (1.4)
	TF	45.9 (1.6)	45.0 (1.4)	45.3 (1.6)	45.0 (1.8)	44.2 (1.4)	44.7 (2.2)	44.4 (1.4)
TAPV (ms)	CF	638.9[†] (48.5)	566.5 (369.2)	554.7 (45.1)	565.0 (43.0)	538.2 (39.9)	519.5 (32.4)	518.5 (33.5)
	TF	458.5[†] (48.5)	465.4 (39.2)	466.7 (45.1)	465.9 (43.0)	469.6 (39.9)	475.6 (32.4)	470.1 (33.5)
pTAPV (%)	CF	64.4 (1.6)	61.7 (1.4)	63.1 (1.6)	62.4 (1.8)	62.1 (1.4)	61.5 (2.2)	61.7 (1.4)

	TF	54.1 (1.6)	55.0 (1.4)	54.7 (1.6)	55.1 (1.8)	55.8 (1.4)	55.3 (2.2)	55.6 (1.4)
JScore	CF	5314.0† (751.9)	4295.1 (905.6)	3830.4 (967.7)	4011.5 (923.8)	3329.0 (736.9)	2991.3 (667.5)	2821.8* (497.6)
	TF	2985.9† (751.9)	3125.7 (905.6)	3206.3 (967.7)	3127.3 (923.8)	3194.2 (736.9)	3506.5 (667.5)	2966.4 (497.6)
Distance Related Measures								
EP Error (cm)	CF	1.2† (0.5)	0.8† (0.153)	0.8† (0.1)	0.7† (0.2)	0.7† (0.1)	0.6† (0.1)	0.6† (0.1)
	TF	3.4† (0.5)	2.0† (0.2)	1.8† (0.1)	1.7† (0.1)	1.6† (0.1)	1.6† (0.1)	1.7† (0.1)
PL (cm)	CF	16.8† (0.4)	16.1 (0.2)	15.9 (0.2)	15.9 (0.2)	15.8 (0.1)	15.6* (0.2)	15.6 (0.2)
	TF	15.7† (0.4)	15.8 (0.2)	15.6 (0.2)	15.6 (0.2)	15.5 (0.1)	15.7 (0.2)	15.7 (0.2)

Asterisks (*) represent a difference from bin 1 within the group ($p < 0.05$). *Crosses* (†) represent a difference between groups at the corresponding bin ($p < 0.05$). *Number signs* (♯) represent an overall difference between visual feedback groups.

CHAPTER 4 EXPERIMENT 2

Shifting to online: Underlying control processes following visuomotor adaptation

Darrin O. Wijeyaratnam[1], Romeo Chua[2] and Erin K. Cressman[1]

[1]Sensorimotor Control Laboratory, School of Human Kinetics, Faculty of Health Sciences, University of Ottawa, Ottawa, ON, K1N 6N5, Canada.

[2]Perceptual-Motor Dynamics Laboratory, School of Kinesiology, Faculty of Education, University of British Columbia, Vancouver, BC, V6T 1Z1, Canada.

As of August 2018, this manuscript has yet to be submitted for publication.

4.1 Abstract

Many actions (e.g., reaching) often require striking a balance between speed and accuracy. This speed-accuracy tradeoff and resulting control processes underlying movement has been extensively studied in well-learned movements but has yet to be explored in adapted movements. In the current study, we examined how imposing temporal constraints (i.e., goal movement times [MT]) would affect the underlying control processes following visuomotor adaptation. Sixteen participants first trained to reach to 3 targets when (1) a cursor accurately represented their hand motion (i.e., aligned cursor) and (2) a cursor was rotated 45 degrees clockwise relative to their hand motion (i.e., rotated cursor) in a virtual environment. Following training, participants reached under (1) Slow MT constraints (i.e., 800-1000 ms) and under (2) Fast MT constraints (i.e., 400-500 ms) with aligned and rotated cursor feedback. Results indicated that overall accuracy was the worst and most variable when reaching with rotated cursor feedback under the Fast MT constraint. Analyses of angular errors across movement proportions, as well as resultant endpoint error further indicated that imposing temporal constraints promoted the use of different movement control processes regardless of cursor feedback. Specifically, participants were able to utilize visual feedback for online control under the Slow MT constraint, but were less effective when reaching quickly (i.e., Fast MT). These results extend our previous work in which we demonstrated that learning to reach with a rotated cursor utilizes greater offline control processes compared to reaching with an aligned cursor (see Wijeyaratnam, Chua, & Cressman, in prep). Here, once the cursor rotation is learned, results indicate a shift from predominately offline control processes to greater online control processes.

This suggests a flexibility in control once movements are learned (i.e., adapted), allowing for more effective processing of visual information online.

***Key words**: Online control, visuomotor adaptation, speed-accuracy trade-off, reaching, spatial-temporal error*

4.2 Introduction

We are capable of performing goal-directed actions across diverse environments. For example, we are able to reach to an object when vision of the object or reaching limb is manipulated (for a review, see Elliott et al., 2017). While the action may be performed to completion regardless of environment, the contributions of control processes underlying movement preparation and execution have been shown to differ when visual feedback is manipulated (Elliott et al., 2001; Ghilardi et al., 1995; Khan et al., 2002; F. R. Sarlegna & Mutha, 2015). Current models of movement control (see Elliott et al., 2010, 2017) discuss how visual feedback affects the interplay between preplanned processes (i.e., offline control) and real-time corrections made throughout the movement (i.e., online control). In general, it is widely accepted that visual feedback of an object, limb or both improves movement accuracy (Berthier, Clifton, Gullapalli, & McCall, 1996; Brenner & Smeets, 2003; Carlton, 1981; Chua & Elliott, 1993; Elliott et al., 1999; Jakobson & Goodale, 1989; Jeannerod, 1984; Newell, 1980; Pélisson, Prablanc, Goodale, & Jeannerod, 1986; Prablanc, Echallier, Jeannerod, & Komilis, 1979; Proteau, Tremblay, & Dejaeger, 1998; Sarlegna & Mutha, 2015; Tremblay et al., 2013; Woodworth, 1899a). However, in order for visual feedback to benefit performance online, the movement must be of sufficient duration (Carlton, 1981; Elliott et al., 2001; Keele & Posner, 1968; Sarlegna et al., 2003; Saunders & Knill, 2003, 2005; Zelaznik, Hawkins, & Kisselburgh, 1983).

Several studies have identified a relationship between the speed at which a movement is carried out and its resulting accuracy. Faster movements (i.e., less than 200 ms) result in greater endpoint (EP) errors compared to slower movements, in which there is sufficient time for corrective processes during the movement (Carlton, 1994; Elliott et al., 2004; Schmidt et al., 1979; Zelaznik et al., 1988). Even with sufficient time for visually-mediated online control, it is not the only factor contributing to improved EP accuracy. Participants can use visual feedback offline, by using prior information regarding the outcome of previously completed movements in the planning of an upcoming movement (Elliott & Allard, 1985; Elliott et al., 2004; Hansen et al., 2006; Khan et al., 2003, 2002; Zelaznik et al., 1983). In this respect, visual information is used as an enriched form of knowledge of results, to improve planning on subsequent trials.

Analyses of movement variability have been used to infer the contributions of online and offline control (Khan et al., 2003). When visual feedback is available for sufficient duration, spatial variability across a trajectory is typically low since modifications can be made throughout movement execution. On the other hand, when visual information is unavailable or unusable (i.e., fast movements), variability, across trials, is higher since participants may be using information gathered from the prior movement to update planning on subsequent movements (i.e., offline control). Together these results suggest that, in slow movements, participants readily use visual information for visually-mediated online control, whereas in fast movements, participants tend to use visual feedback for offline control (for a review, see Khan et al., 2006).

The findings discussed above establish the contribution of online and offline control when the MT of well learned movements was manipulated. Limited studies have looked to examine the control processes underlying newly acquired movements (e.g., following visuomotor adaptation). Visuomotor adaptation arises when reaching with altered visual feedback of the hand. For example, participants reach to a target and see a cursor on the screen with a trajectory that is rotated clockwise relative to their hand's trajectory. Having experienced a reaching error, such that the cursor does not land on the target, participants begin to adapt their movements (e.g., aim to the left of the target) (Hinder, Riek, Tresilian, de Rugy, & Carson, 2010; Krakauer, Ghilardi, & Ghez, 1999; Shabbott & Sainburg, 2010; Tseng, Diedrichsen, Krakauer, Shadmehr, & Bastian, 2007; Maksimovic and Cressman, 2018). Previous work from our lab (Wijeyaratnam et al., in prep) not only shows participants' ability to adapt their movements in response to rotated visual feedback of their hand's trajectory, but also demonstrates a difference in movement control processes when learning to reach in a novel environment compared to reaches performed in a typical environment. For instance, we observed a greater contribution of offline control processes (i.e., movement planning) when reaching in a novel environment (i.e., rotated cursor) compared to a typical environment (i.e., aligned cursor). More importantly, offline control processes persisted even after participants had adapted their reaches.

The goal of the current study was to determine whether visual feedback can be used online to correct newly learned adapted movements (i.e., following visuomotor adaptation), as seen when reaching with aligned visual feedback in a typical environment. In attempt to promote processing of visual feedback online, movement time constraints were imposed while participants reached to visual targets with aligned or rotated cursor feedback. Specifically, participants performed movements with both a slow movement time constraint (i.e., 800-1000 ms [Slow MT]) and a fast movement time constraint (i.e., 400-500 ms [Fast MT]). Kinematic markers, previously used to characterize the contributions of online and offline control in well learned movements (de Grosbois & Tremblay, 2016, 2017, Elliott et al., 2010, 2017, 1999, 2001, Grierson & Elliott, 2008, 2009; Khan et al., 2006), were compared between movements performed with the two movement time constraints when reaching with an aligned and a rotated cursor. It was hypothesized that adapted movements would continue to utilize offline control processes, regardless of movement time, but, in support of previous literature, we would see differences in control processes for well learned movements across the two MT constraints (i.e., Fast versus Slow). For example, when reaching with an aligned cursor we would expect to see differences in accuracy and variability, such that movements would be more accurate but less variable under Slow MT constraints compared to Fast MT constraints. More importantly, when reaching with a rotated cursor, we hypothesized no significant differences between the two MT constraints. These results would be reflective of individuals continuing to adopt more offline control processes when performing recently acquired movements, even when visual feedback was provided for a long duration.

4.3 Method

4.3.1 Participants

Sixteen young adults (5 females, M = 24 years of age) were recruited from the University of Ottawa community to participate in this experiment. Participants were naïve to the purpose of the experiment and free to withdraw at any point in the experiment without consequence. Participants provided informed consent and then filled out a brief handedness questionnaire (Edinburg handedness inventory, (Oldfield, 1971)). According to the handedness questionnaire, all participants were right handed, M = 79.4, range: 60-100). As well, participants had normal (n = 8) or corrected-to-normal vision (n = 8) and self-reported no history of motor, sensory of cognitive impairment. Prior to testing, participants were evenly divided into four groups that differed in the order in which they completed the different movement time constraints (Order 1: slow movement time first [Slow MT] and Order 2: fast movement time first [Fast MT]). All ethical standards and safety monitoring procedures were completed in accordance with the Health Science and Science Research Ethics Board at the University of Ottawa.

4.3.2 Experimental Apparatus

Testing took place in a secluded room with a two-joint robot manipulandum (KINARM, BKIN technologies), adjacent to the experimenter's computer workstation. The KINARM set-up consisted of a downward-facing computer monitor, a reflective surface placed 20.5 cm below the computer monitor, and a robot handle placed 20.5 cm below the reflective surface that participants grasped with their right hand (see Figure 4.1A). The downward-facing computer monitor (EzSign model 47LD452B; refresh rate: 60Hz (or every 17ms); LG. Seoul, South Korea) projected visual information onto the reflective surface, which covered a workspace of 70 cm by 36 cm. Participants' movements of the robot handle were represented in the form of a cursor (i.e., magenta circle 0.5 cm in diameter) on the reflective surface. Participants were unable to see their right limb due to the reflective surface and a cloth that was attached to the edge of the reflective surface and tied around participants' neck and shoulders.

Calibration of the KINARM was carried out prior to testing according to the manufacturer's instructions. Participants were asked to sit on a standard height-adjustable office chair at a self-desired height and distance from the KINARM, such that they were able to see and reach all of the targets comfortably. Participants grasped the vertical cylindrical handle of the KINARM with their right hand, elbow flexed at approximately 90° and the forearm in a neutral position. The position of the robot handle was recorded at a sampling rate of 1000 Hz and a spatial accuracy of 0.1 mm.

In general, participants were required to reach with the robot handle to a target (yellow circle, 1 cm in diameter) that was presented 15 cm away from a central home position (white circle,1 cm in diameter, which was located approximately 20 cm in front of, and aligned with, each participant's midline. All participants reached to three targets (see Figure 4.1B) with either aligned or rotated cursor feedback regarding their hand position. Reaching targets were displayed at one of three possible locations, specifically, directly above the home position (0°) and at 45° left or right of the 0° target (Figure 4.1B). The sequence of target locations was presented randomly. Participants were provided with continuous feedback of their hand position via the cursor, from the start of their movement up until the end of the movement, which was defined online as the time when movement velocity first fell below 0.01 m/s (Figure 4.1C).

4.3.3 Procedure

Participants were required to reach in two different cursor feedback environments: (1) reaching with aligned visual feedback of their hand, such that the cursor on the screen accurately depicted where their hand was in space (i.e., aligned cursor) and (2) reaching with altered visual representation of their hand, such that the cursor's trajectory was rotated 45° clockwise (CW) relative to hand motion (i.e., rotated cursor). When reaching with rotated cursor feedback, participants would need to aim counterclockwise (i.e., left of the target) to counteract the distortion and have the cursor land on the target. In addition to manipulating cursor feedback, participants were required to complete 45 movements in both cursor feedback environments with a slow and fast movement time (MT) goal (i.e., Slow MT or Fast MT, see Figure 4.2A). MT was defined as the time from movement initiation until movement end. For this experiment, MT between 400 ms and 500 ms was deemed fast, while MT between 800 ms and 1000 ms was considered slow. These constrained MT trials were completed following 150 reach training trials within each cursor feedback environment, as discussed below.

The experiment began once the participant was seated in a comfortable position and verbally indicated they were ready to begin. Each trial started with the presentation of a white circle (home position) for 1000 ms. Participants were instructed to keep the cursor representing their hand within the home position. In the case that the cursor was outside the home position, the robot passively moved the participant’s hand into the desired home position, ensuring that the hand started at a similar position on all trials. Figure 4.2B displays the experimental protocol undergone by an example participant. Participants first completed reach training trials with an aligned or rotated hand cursor (Time 1), followed by reaches completed according to Order 1 or Order 2 with respect to MT constraint (i.e., Slow MT or Fast MT first respectively). Following a mandatory 5-min break, participants completed all trials again, but this time with the opposite cursor feedback. For example, if participants reached with an aligned cursor in Time 1, they now reached with a rotated cursor (Time 2). When reaching with a rotated cursor, participants completed 150 rotated reach training trials followed by the same MT constraint Order that was previously performed. The order of Cursor (i.e., aligned and rotated cursor) and MT constraint (Slow and Fast) were counterbalanced across participants. Total participation time was approximately 2 hours.

Participants were instructed that once a target appeared they were to comfortably reach to the target as accurately as possible. At the end of the reach, the hand was held at their movement end location for 500 ms. At this point, visual feedback of their hand position was removed. Following 500 ms, the robot passively moved the participant’s hand to the location corresponding to where the hand should have reached to in order for the cursor to have landed on the center of the target. The hand was held at this location for an additional 500 ms. Finally, the robot passively moved the participant’s hand back to the home position along a linear path in a movement time of 1000 ms. The home position then became visible. The hand was held at the home position for another 1000 ms before a target appeared, signaling the start of the next trial (see Figure 4.3A).

In the reach training trials, participants were not provided with a MT goal. Instead they were instructed that once a target appeared they were to reach rapidly, but comfortably, to the target and be as accurate as possible. In the trials with a MT constraint additional instruction was provided. Specifically, in the Fast MT trials, participants were instructed to “reach quickly and complete the movement within 500 ms”. In the Slow MT trials, participants were instructed to “reach comfortably and complete their movement within a second”. Familiarization blocks of 21 trials were completed for each MT goal prior to experimental blocks of 45 trials, with an equal number of trials to each of the three targets within each block. The purpose of the familiarization trials was to ensure that participants understand how quickly they needed to reach to meet the goal MT criterion. All participants were able to achieve the MT criterion in at least 8 of the 10 final familiarization trials and hence continued on to complete the experimental block of trials. Trials with a MT constraint followed similar visual events as seen in reach training trails but differed with respect to feedback provided at movement completion. This difference can be seen in Figure 4.3B, during the time where the hand was held at the *actual movement end location*. Visual feedback in the form of a target colour change (red = MT constraint was not met; green = MT constraint was met) indicated participant’s ability to meet the MT criterion. Additional verbal instruction was provided by the experimenter to assist participants in achieving the MT constraint (e.g., “you need to reach a bit faster/slower”). Trials in which participants did not meet the MT constraint were discarded and repeated at the end of the block, in order to fulfill the 45 required experimental trials in a block.

4.3.4 Data Analyses

Data for each trial were collected and analyzed using both within-trial and between-trial measures of movement control. To begin, the start and end of each movement were selected based on a velocity criterion (i.e., the first increase in velocity greater than 0.01 m/s for 100 ms and the first decrease in velocity below 0.01 m/s, respectively). Endpoint position data were used to screen for outliers. In particular, if a participant’s endpoint position in the horizontal or vertical directions was greater than 3 standard deviations above their respective mean endpoint position in the same dimension, the trial was removed from further analyses. This screening resulted in the removal of 45 trials (0.6%).

For the variables discussed below, data were collapsed across all targets. All dependent variables were then statistically evaluated using a mixed analyses of variance (ANOVA) in SPSS (IBM, version 24). If the Mauchly's test of sphericity was significant ($p < 0.05$) then the Greenhouse-Geisser correction factor was applied and the adjusted degrees of freedom are reported. Differences with a probability of 0.05 were considered significant. Following a significant interaction, a simple effect analysis was conducted using Bonferroni correction. In the case of analyses yielding significant main effects and significant interactions, only the interactions are reported and interpreted below.

4.3.4.1 *Assessment of Adaptation*

Initial analysis of the reach training trials evaluated whether participants were able to adapt their reaches to meet the cursor movement requirements. Specifically, paired-samples *t*-tests were used to compare mean endpoint (EP) angular errors (AE) relative to the target, resultant EP errors and MT across the last 20 reach training trials when reaching with an aligned versus rotated cursor. Angular errors at EP were defined as the angular difference between a movement vector from the home position to movement EP and a reference vector (from the home position to the target location). Resultant EP error was defined as the absolute distance between the endpoint location of the cursor and the target.

4.3.4.2 *Within-Trial Measures*

After establishing that participants reached with similar levels of accuracy in both cursor environments, we then compared kinematic variables between reaches completed with a Fast versus Slow MT constraint. This assessment included the following within-trial measures: reaction time (RT), movement time (MT), angular errors (AE) at peak velocity (PV) and at endpoint position (EP) and resultant EP error. RT was defined as the time required to initiate a response from target presentation until the start of the movement. Angular errors at PV were defined as the difference between a movement vector (from the home position to PV) and a reference vector joining the home position to the target location. A 2 Cursor Feedback (i.e., aligned versus rotated) x 2 MT (i.e., Slow versus Fast) ANOVA with RM on both factors, was used to determine if any of these within-trial measures differed across reaching environments and MT constraints.

4.3.4.3 *Between-Trial Measures*

An analysis of variability of angular errors (AE) at selected proportions of MT was chosen to provide insight into how reaching trajectories unfolded over the course of a movement. A 2 Cursor Feedback x 2 MT x 4 Proportion (25%, 50%, 75% 100%) ANOVA with RM on the last two factors allowed us to establish early versus late modifications in trajectory and determine whether they differed depending on cursor feedback.

4.4 Results

4.4.1 Assessment of Adaptation: Reach Training Trials

EP AEs revealed that participants had a slight leftward bias (-0.3° ± 0.1°) when reaching with an aligned cursor compared to a rightward bias (-0.6° ± 0.3°) when reaching with a rotated cursor at the end of training (*t*(15) = 3.638, p = 0.002, *r* = 0.685). That said, analysis of resultant EP error of the last 20 reach training trials indicated that errors with an aligned cursor (M = 0.35 cm ± 0.02 cm) were similar to those with a rotated cursor (M = 0.55 cm ± 0.09 cm), (*t*(15) = -2.050, *p* = 0.058, *r* = 0.468). Moreover, the size of the errors indicates that participants completed reaches with both the aligned and rotated cursor such that the cursor was in contact with the target. Participants reached with an average MT of 865 ms across the last 20 reach training trials with the aligned and rotated cursor feedback. Analysis of MT of the last 20 reach training trials indicated that reaches with an aligned cursor (M = 862.3 ms ± 32.11 ms) were similar in duration to reaches with a rotated cursor (M = 870.3 ms ± 51.3 ms), (*t*(1,15) = -0.180, *p* = 0.860, *r* = 0.046).

The similarity in MT and limited EP errors across reaches with an aligned and rotated cursor suggests that participants adapted their movements. A more in-depth analysis regarding control mechanisms underlying these reach training trials, as well as reach training trials early in learning, can be found in our previous work (Wijeyaratnam et al., in prep). The results discussed below will focus on reaches in the constrained MT experimental blocks.

4.4.2 Performance Measures: MT Constraint Trials

4.4.2.1 *Within-Trials Measures: Temporal-Related Measures*

Participants were able to meet the Slow and Fast MT constraints with both an aligned (Slow MT = 892.0 ms ± 2.1 ms; Fast MT = 453.1 ms ± 1.3 ms) and rotated cursor (Slow MT = 896.7 ms ± 2.6 ms; Fast MT = 454.6 ms ± 1.2 ms). Analyses of MT revealed that MT did not differ between reaches with an aligned and rotated cursor ($F(1,15) = 3.037$, $p = 0.102$, $\eta^2 = 0.168$). Analysis of MT variability revealed a main effect of MT ($F(1,15) = 442.884$, $p < 0.001$, $\eta^2 = 0.967$), such that slow movements were more variable (M = 53.1 ms ± 1.2 ms) compared to fast movements (M = 28.0 ms ± 0.4 ms).

Figure 4.4A and B display mean RT and variability of RT, respectively. Analysis of mean RT revealed longer RTs under the Fast MT constraint (M = 437.221 ms ± 28.973 ms) compared to the Slow MT constraint (M = 334.136 ms ± 18.026 ms) ($F(1,15) = 26.292$, $p < 0.001$, $\eta^2 = 0.637$). In contrast to our previous work (Wijeyaratnam, Chua, & Cressman, in prep), we did not find a significant difference in RT when reaching with an aligned versus rotated cursor ($F(1,15) = 2.745$, $p = 0.118$, $\eta^2 = 0.155$) and no interaction between Cursor Feedback and MT ($F(1,15) = 1.396$, $p = 0.256$, $\eta^2 = 0.085$). Analysis of RT variability revealed an interaction between Cursor Feedback x MT ($F(1,15) = 5.818$, $p = 0.029$, $\eta^2 = 0.279$), with post hoc analysis indicating that fast movements had a greater variability (M = 137.3 ms ± 20.2 ms) compared to the slow movements (M = 76.6 ms ± 7.3 ms, $p = 0.020$), but only when reaching with an aligned cursor. As well, reaching with an aligned cursor under the Fast MT constraint (M = 137.3 ms ± 20.2 ms) resulted in more variable RTs compared to reaching with a rotated cursor under the Fast MT constraint (M = 103.1 ms ± 14.6 ms, $p = 0.009$). Together these results suggest that imposing MT constraints influenced the contribution of planning processes in learned movements, such that we see longer RT under the Slow MT constraint compared to under the Fast MT constraint. As well, we found lower RT variability with a rotated cursor under either temporal constraint compared to under the Fast MT constraint when reaching with an aligned cursor. The greater MT variability seen in the slow movements also lends support to the notion that participants were processing visual information online to make ongoing corrections when there was sufficient time to use visual information.

4.4.2.2 *Within-Trials Measures: Error-Related Measures*

Figure 4.5A and D display mean and variability of initial reach direction errors of the cursor at PV (i.e., PV AE), respectively. Analysis of PV AE resulted only in a main effect of Cursor Feedback ($F(1,15) = 21.465$, $p < 0.001$, $\eta^2 = 0.589$), such that reaches with an aligned cursor resulted in a leftward bias (M = -1.8° ± 0.42°) compared to a rightward bias for reaches with a rotated cursor (M = 2.3° ± 0.7°). There was no effect of MT ($F(1,15) = 0.282$, $p = 0.603$, $\eta^2 = 0.018$), as well as no interaction between Cursor Feedback x MT ($F(1,15) = 3.436$, $p = 0.084$, $\eta^2 = 0.186$). Analysis of PV AE variability again revealed a main effect of Cursor Feedback ($F(1,15) = 45.348$, $p < 0.001$, $\eta^2 = 0.751$), with greater variability in initial reach direction when reaching with a rotated cursor (M = 6.3° ± 0.4°) compared to reaching with an aligned cursor (M = 4.0° ± 0.3°).

Figure 4.5B and E display mean and variability of endpoint position (EP) angular error (AE), respectively. Analysis of EP AE revealed an interaction between Cursor Feedback x MT ($F(1,15) = 9.021$, $p = 0.009$, $\eta^2 = 0.376$). Post hoc analysis indicated a greater rightward bias when reaching with a rotated cursor compared to reaching with an aligned cursor (i.e., leftward bias) regardless of MT constraint (both $p < 0.001$). Furthermore, reaching with rotated cursor feedback under the Fast MT constraint (M = -3.2° ± 0.8°) resulted in a significantly greater rightward bias compared to reaching with rotated cursor feedback under the Slow MT constraint (M = -1.5° ± 0.3°, $p = 0.015$). No differences were found in EP AE when reaching with aligned cursor feedback between slow and fast movements (Slow MT = 0.2° ± 0.9°; Fast MT = 1.0° ± 0.4°, $p = 0.58$). Analysis of EP AE variability revealed an interaction between Cursor Feedback x MT ($F(1,15) = 14.563$, $p = 0.002$, $\eta^2 = 0.493$). Post hoc analysis revealed greater EP AE variability under the Fast MT constraint compared to under the Slow MT constraint regardless of Cursor Feedback and greater EP AE variability when reaching with rotated cursor feedback compared to aligned cursor feedback, regardless of MT constraints (all $p < 0.006$).

Figure 4.5C and F display mean and variability of resultant EP error relative to the target, respectively. Analysis revealed a significant Cursor Feedback x MT interaction ($F(1,15) = 8.722$, $p = 0.010$, $\eta^2 = 0.368$). Post hoc analysis indicated that reaching under the Fast MT constraint resulted in larger resultant EP errors than under the Slow MT constraint regardless of Cursor Feedback and larger errors when reaching with a rotated cursor compared to reaching with an aligned cursor, regardless of MT constraint (all $p < 0.005$). Analysis of resultant EP error variability revealed main effects of Cursor Feedback ($F(1,15) = 19.047$, $p = 0.001$, $\eta^2 = 0.559$) and MT ($F(1,15) = 55.141$, $p < 0.001$, $\eta^2 = 0.786$). Participants reached with greater variability when reaching with a rotated cursor (M = 0.7 cm ± 0.1 cm) compared to reaching with an aligned cursor (M = 0.5 cm ± 0.0 cm) and under the Fast MT constraint (M = 0.8 cm ± 0.1 cm) compared to the Slow MT constraint (M = 0.4 cm ± 0.0 cm).

Together, these results suggest that participants began their movements with similar initial biases (i.e., PV AE), regardless of MT constraint, and then were able to reduce these early errors, and error variability by the end of their movement (i.e., EP AE) when reaching under the Slow MT constraint. Reaching under the Slow MT constraints indicated more accurate performance with both Cursor Feedback types, suggesting that participants used the additional time available to process visual information for online control more effectively than in the Fast MT condition. Reaching under the Fast MT constraint indicated a significant decrement in performance that was greater when reaching with a rotated cursor feedback compared to aligned cursor feedback.

4.4.2.3 *Between-Trial Measures: Trajectory-Related Measure*

Variability of AE across movement proportions (i.e., 25%, 50%, 75% and 100% of the movement) resulted in a three-way interaction between Cursor Feedback x MT x Proportion ($F(1.788,26.821) = 3.685$, $p = 0.043$, $\eta^2 = 0.197$). Post hoc analysis indicated that when reaching with an aligned cursor, AE error was more variable ($p < 0.001$) at 75% and 100% of the movement under Fast MT constraints (M = 2.46° ± 0.16°; M = 2.44° ± 0.18°, respectively) compared to under Slow MT constraints (M = 1.68° ± 0.12°; M = 1.20° ± 0.12°). When reaching with a rotated cursor, the end of the movement (i.e., proportion at 100%) had a greater variability in AE under the Fast MT constraint (M = 5.16° ± 0.44°) compared to under the Slow MT constraint (M = 2.62° ± 0.41°). In general, reaching with a rotated cursor had greater variability in AE across all proportions and MT constraints (all $p < 0.012$).

4.5 Discussion

In this study, we examined differences in movement control processes when participants reached with an aligned and a rotated cursor and were required to achieve a goal MT. Slow and Fast MT constraints were imposed to investigate the internal control processes known to influence different portions of voluntary movements such as planning and online control (Abahnini et al., 1997; Elliott et al., 2010, 2001; Hansen et al., 2006; Khan et al., 2003; Posner et al., 1976; F. R. Sarlegna & Sainburg, 2009; Tremblay et al., 2013). The objective was to establish whether we could promote the utilization of visual feedback for online control in newly acquired adapted movements (i.e., following visuomotor adaptation to a rotated cursor), as seen when reaching with aligned visual feedback in a typical environment.

4.5.1 Flexible Control Processes

4.5.1.1 *Movement Planning*

In our recent work (Wijeyaratnam, Chua, & Cressman, in prep) we have suggested that participants utilize more planning processes (i.e., offline control) when reaching with altered visual feedback of the hand position compared to when performing well-learned movements. Here, using a similar analysis of mean RT and RT variability (Figure 4.4), we do not find differences between reaches performed with aligned versus rotated cursor feedback. Instead, we see similar changes in performance across MT constraints regardless of cursor feedback. Specifically, when reaching under the Slow MT constraint, RT was significantly faster than under the Fast MT constraint. This suggests that under the Slow MT constraint, participants limited planning processes and processed visual information online. In contrast, under the Fast MT constraint, participants were more inclined to processes visual feedback offline (i.e., enriched knowledge of results) through planning mechanisms in order to also meet the Fast MT demand. We observed this finding when reaching with both aligned and rotated cursor feedback, thus providing initial evidence suggesting flexible control processes following visuomotor adaptation.

The observation of online control when reaching with a rotated cursor under a Slow MT constraint in the current study compared to our previous findings can be attributed to when online and offline control was assessed. In our previous work, we evaluated the contributions of movement control process (i.e., online and offline) while participants were training (i.e., learning) in both reach environments. Here, we evaluated the contributions of movement control processes by imposing MT constraints once participants had learned the visuomotor rotation. The current results illustrate the flexibility of movement control processes once participants have adapted their movements in order to meet additional movement demands (i.e., goal MT). Furthermore, in our previous experiment, participants performed movements at their own comfort with no expectations or reference (i.e., force, speed, overall MT) for how the movement was to be executed. In contrast, the current experiment imposed an expectation (i.e., goal MT) and a reference (i.e., additional instructions to go faster or slower) in order to achieve the MT demands, in addition to performing an adapted movement (i.e., reaching with rotated cursor feedback). When specifically comparing MT performance (i.e., during reach training trials compared to under temporal constraints), we observed similar MTs regardless of whether they were self-selected (i.e., reach training trials) or when temporal constraints were imposed suggesting that participants had sufficient time to process visual feedback online, but chose not to when learning the visuomotor rotation.

4.5.1.2 *Movement Execution/Accuracy*

As suggested earlier, differences in kinematic variables across MT constraints can be used to suggest that visual feedback is being processed for online versus offline control. In Figure 4.5A and D, we see biases and variability in initial reach direction (i.e., aligned cursor: leftward bias; rotated cursor: rightward bias), which are then significantly reduced by the end of the reach, specifically under the Slow MT constraint (Figure 4.5B and E). These results suggest that, when sufficiently more time is available, participants are able to process visual feedback online in order to reduce their reaching errors. Similarly, when time is reduced (Fast MT constraint), we see greater variability in EP AE with rotated cursor feedback under the Fast MT constraint compared to reaching under the Slow MT constraint, as well as when reaching with aligned cursor feedback under the Slow and Fast MT constraints. This decrease in accuracy and precision under the Fast MT constraint when reaching with rotated cursor feedback is further emphasized by the significant increase in resultant EP error (Figure 4.5C and E). These kinematic findings suggest that participants are less effective in the processing of visual feedback online under the Fast MT constraint, especially when reaching with rotated cursor feedback.

4.5.2 Temporal-Precision Hypothesis

Similar to the current study, work by Schmidt and colleagues (1979), Meyer and colleagues (1982, 1983) and Zelaznik and colleagues (1988) also required participants to perform actions while achieving pre-specified movement times (i.e., durations that were greater than 200 ms) with continuous visual feedback. Their empirical findings led to the development of several models that describe the relationship between speed and accuracy when temporal constraints are imposed; the impulse variability model (Schmidt et al., 1979), later refined by Meyer and colleagues (1988) who forwarded the optimized submovement model (Meyer et al., 1990), which brought in aspects of the impulse variability model and the iterative correction model (Crossman & Goodeve, 1983). These models were based on the premise that movement variability in the initial impulse (i.e., muscular forces used to propel the limb toward the target) increased proportionally with the forces required to perform a particular movement type (e.g., achieve temporal constraints). In particular, Meyer and colleagues' (1982) *temporal-precision hypothesis* describes a linear-tradeoff between speed and accuracy when participants are required to produce precisely timed movements (i.e., goal MT), while a logarithmic trade-off (Fitts, 1954a) when participants are required to place emphasis on movement accuracy.

The results of the current study cannot speak to the notion of a linear versus logarithmic tradeoff, though our findings are in line with the basic principles of these models. We have shown that participants can achieve the temporal constraints (i.e., similar MTs with both cursor feedback conditions) and the increased variability in MT under the Slow MT constraint may be suggestive of participants utilizing visual feedback online compared to under the Fast MT constraint (Carlton, 1981; Elliott et al., 2010, 2017, 2001; Keele & Posner, 1968; Wallace & Newell, 1983; Zelaznik et al., 1983). Although sufficient time was available to process visual information to make corrections under both MT constraints, the speed-accuracy trade-off held true. Specifically, we saw decrements in accuracy when reaching under the Fast MT constraint regardless of cursor feedback (see Figure 4.5C and F). We show further decrements in accuracy when reaching with a rotated cursor under Fast MT constraints compared to an aligned cursor across all error-based measures. This decrease in accuracy when reaching with a rotated cursor feedback under the Fast MT constraint may arise due to attentional demands imposed by the movement.

Fernandez-Ruiz and colleagues (2011), suggest that reaching with rotated cursor feedback is attentionally demanding due to participants having to adopt a strategic process (e.g., mental rotation) to correct for the altered visual representation of one's hand motion. As well, meeting a MT constraint also requires attentional resources (Danion, Bongers, & Bootsma, 2014). Our results support the idea that temporal and spatial processes may compete for attentional resources (Carlton, 1994; Danion et al., 2014; Kahneman, 1973; Kantowitz & Knight, 1978; Newell, 1980; Zelaznik, Schmidt, & Gielen, 1986; Zelaznik, Shapiro, & McClosky, 1981) evidenced by significant differences in performance (i.e., RT, see Figure 4.4A) and kinematic measures (i.e., EP error-related, see Figure 4.5B, C, E and F). Specifically, we have shown that meeting temporal demands affected mean RTs regardless of cursor feedback (see Figure 4.4A) and a decrement in EP accuracy, as well as increased EP variability, when reaching with a rotated cursor feedback under the Fast MT constraint (see Figure 4.5C and F).

4.6 Conclusion

We have reproduced expected findings of participants adopting different control processes when temporal constraints are imposed and reaches are completed with aligned cursor feedback of the hand. We had previously characterized adapted reaches with rotated cursor feedback as adopting predominately preplanned movements (i.e., offline control; see Wijeyaratnam, Chua, & Cressman, in prep). We found that that was not the case in the current study for reaches completed after participants had adapted their movements. Reaching with rotated cursor feedback led to a speed-accuracy trade-off typically seen for reaches with aligned cursor feedback (Fitts, 1954b; Wright & Meyer, 1983; Zelaznik et al., 1988). Moreover, reaching with rotated cursor feedback under the Slow MT constraint elicited a greater contribution of visually-mediated online corrective processes compared to reaching under the Fast MT constraint; even though there was sufficient time to process visual feedback for online control in all movements

(Carlton, 1992). We suggest participants' ability to use visual feedback for online corrections in the current study when reaching with the rotated cursor can be attributed to (1) participants having learned the visuomotor rotation (i.e., similar PV and EP errors as seen in baseline) and (2) participants receiving additional cues for slow versus fast movements allowing them to effectively utilize visual feedback when sufficient time was available (i.e., Slow MT constraint).

4.7 List of Figures

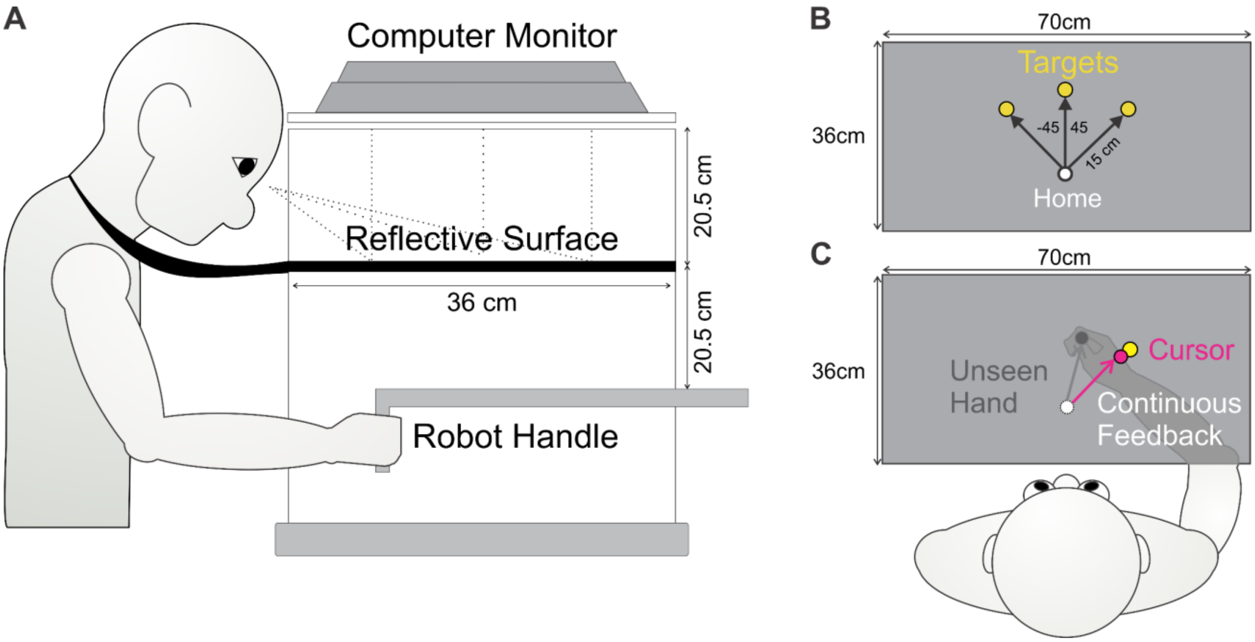


Figure 4.1. Experimental apparatus, dimensions and visuomotor reaching environment. **A** Side view of the experimental apparatus, with a cloth that occluded vision of the limb. **B** The three target locations (yellow circles), each 15 cm away from the home position (white circle); one directly above the home position (0°) and two at 45° left and right of straight ahead. **C** Example of the rotated cursor feedback. The cursor's trajectory was rotated 45° CW relative to the trajectory of the hand.

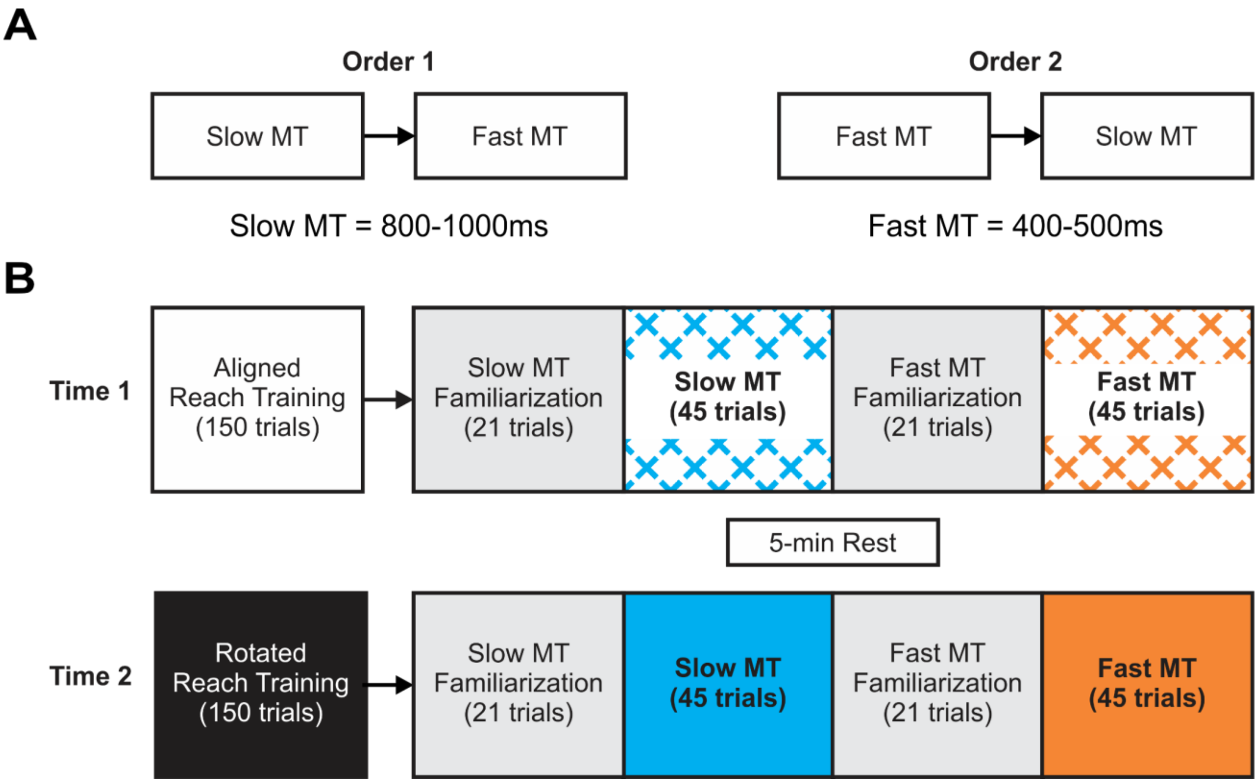


Figure 4.2. Experimental order and example protocol of reach training trials and reaches under the Slow and Fast MT constraints. **A** Participants were pseudo-randomly placed in one of two orders of MT constraints. Participants completed reaches with both MT constraints. **B** Example experimental protocol in which participants completed the MT constraint trials according to Order 1 and all trials with aligned cursor feedback first (Time 1). All participants completed both types of reach training trials (i.e., aligned and rotated) and blocks of MT constraints (i.e., Slow MT and Fast MT), with the order of cursor feedback and MT constraint counterbalanced across participants. *Patterned boxes* represent reaches with an aligned cursor and *solid boxes* represent reaches with a rotated cursor. *Blue boxes* represent reaches under the Slow MT constraint and *orange boxes* represent reaches under the Fast MT constraint.

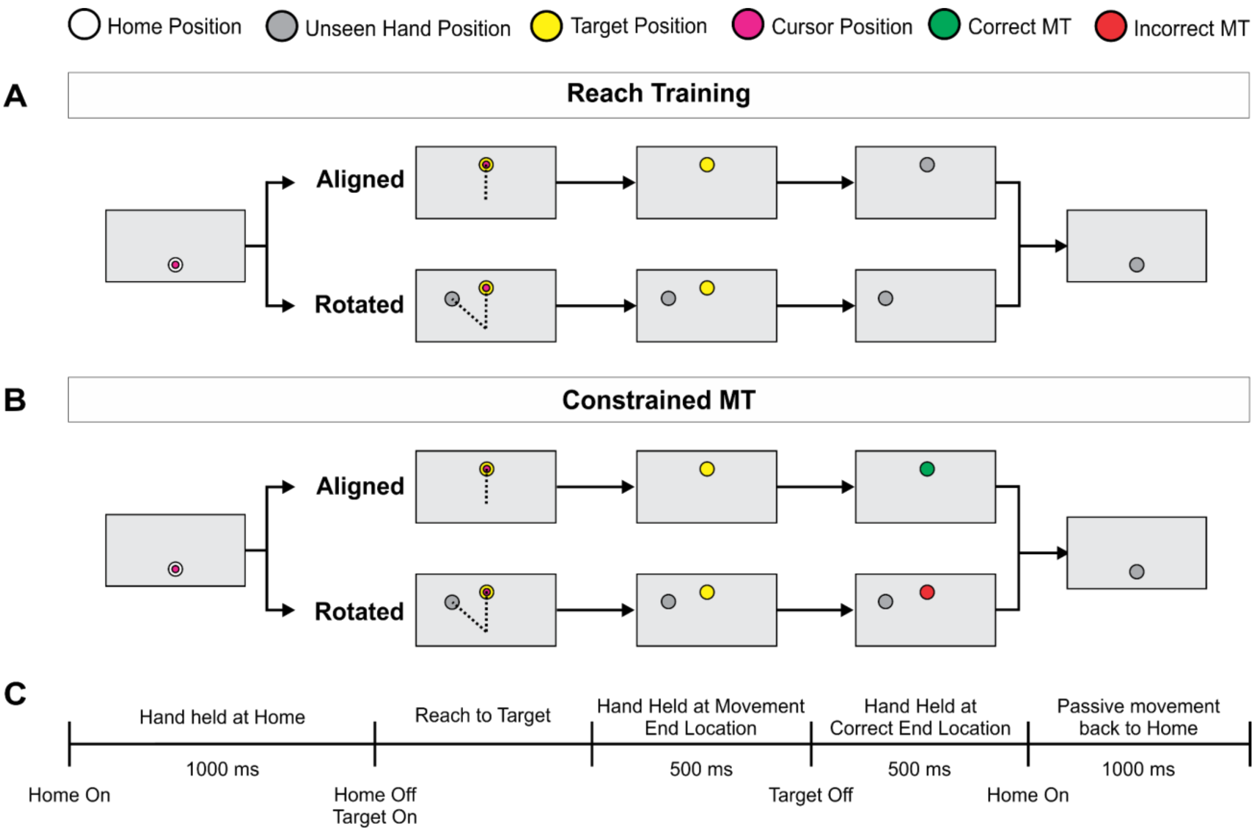


Figure 4.3. Visual events occurring within a single trial for each type of cursor feedback (i.e., aligned and rotated). **A** Reach training trials started with a visible home position (white circle) and a visible cursor (magenta circle) held for 1000 ms at the home position. The target then appeared (yellow circle), cuing participants to initiate their reach. Participants saw the cursor until the end of the movement. The unseen hand was held at their movement end position for 500 ms, while the target was still visible. The target and cursor were then hidden and the unseen hand was passively moved to where the hand should have landed in order for the visual representation of the hand to have landed on the center of the target. The unseen hand was held at this position for 500 ms. The hand was then moved back to the home position passively, with a MT of 1000 ms. At this time, the home position and cursor became visible once again, signifying the start of the next trial. **B** Constrained MT trials. Trial progression was similar to Reach Training trials except during the “Hand Held at Correct End Location” phase. At this time, participants received visual feedback regarding their ability to meet the MT constraint. Specifically, the target changed to green if the MT constraint was met and red if the MT constraint was not met. **C** Timing of events in a single trial represented in a timeline. “Reach to Target” timing varies based on individual reaches and MT constraint (i.e., Slow or Fast MT).

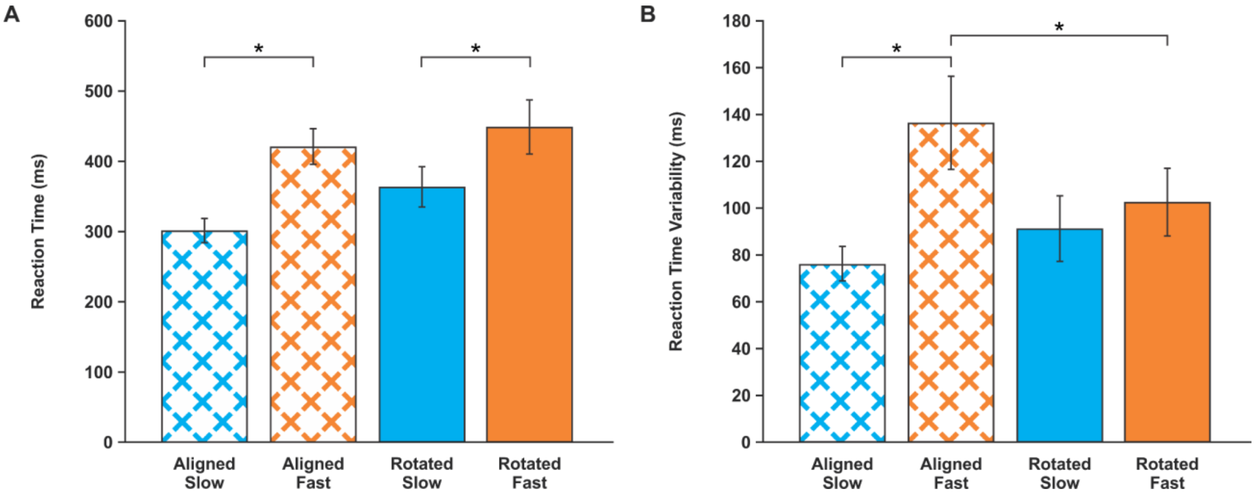


Figure 4.4. A Mean reaction time (RT) and B mean variability of RT measured in milliseconds (ms) for both types of cursor feedback (i.e., aligned and rotated). *Patterned bars* represent reaches with an aligned cursor and *solid bars* represent reaches with a rotated cursor. *Blue bars* represent reaches under the Slow MT constraint and *orange bars* represent reaches under the Fast MT constraint. *Error bars* represent standard error of the mean. *Asterisks* (*) represent significant differences between reaches with an aligned versus a rotated cursor or between the Slow versus Fast MT constraint ($p < 0.05$).

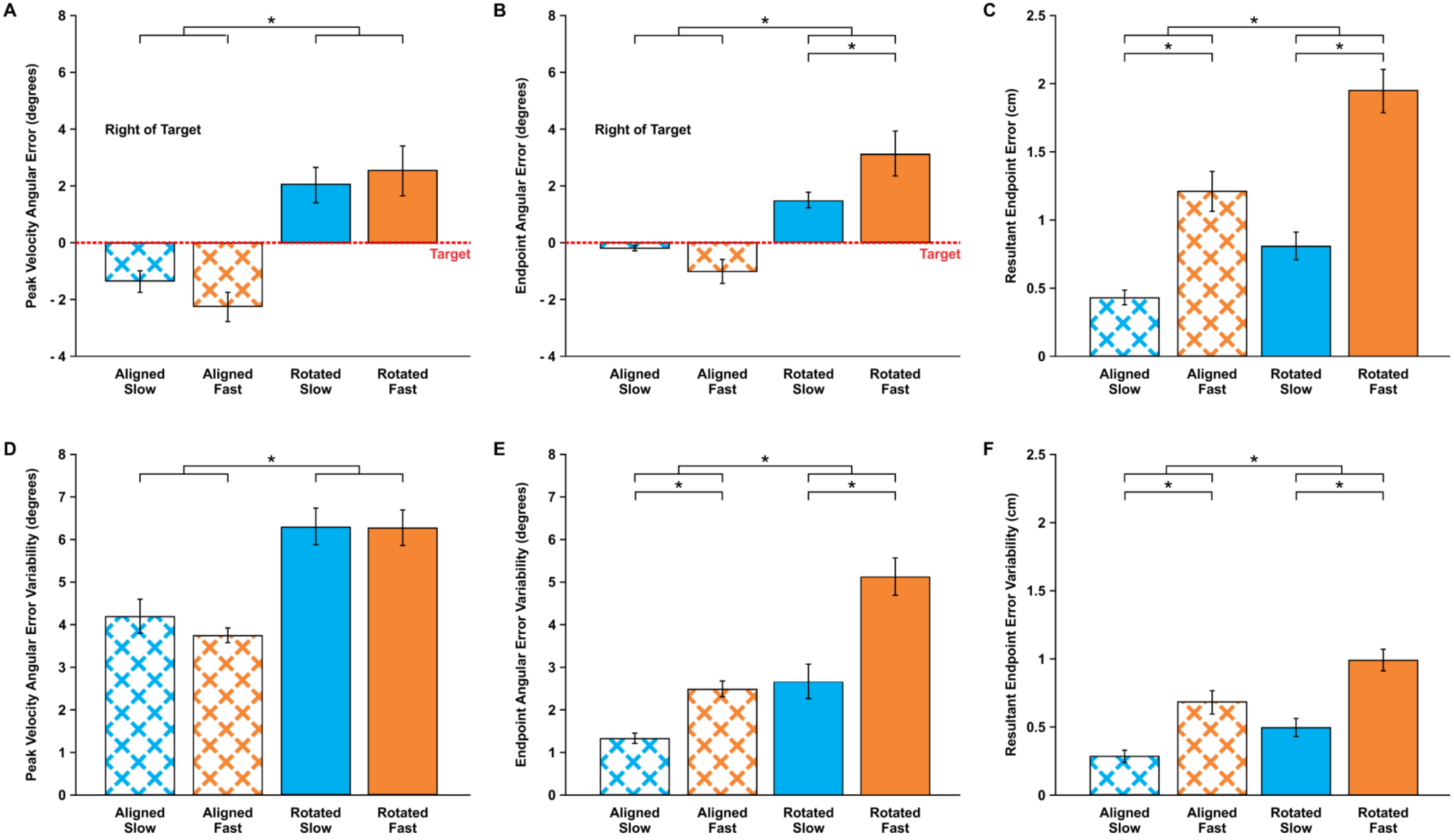


Figure 4.5. Mean and variability of error-related measures. **A** Mean and **D** variability of cursor peak velocity angular error (PV AE), measured in degrees. **B** Mean and **E** variability of cursor endpoint angular error (EP AE), measured in degrees. In **A** and **B**, *dotted red line* represents target location. Values above the zero axis (i.e., dotted red line) represent reaches that were completed to the right of the target and values below, represent reaches that were completed to the left of the target. **C** Mean and **F** variability of resultant endpoint error from the target, measured in

centimeters. *Patterned bars* represent reaches with an aligned cursor and *solid bars* represent reaches with a rotated cursor. *Blue bars* represent reaches under the Slow MT constraint and *orange bars* represent reaches under the Fast MT constraint. *Error bars* represent standard error of the mean. *Asterisks* (*) represent significant differences between reaching with an aligned versus a rotated cursor or between the Slow versus Fast MT constraint ($p < 0.05$).

4.8 Appendix

Within this appendix additional kinematic markers are provided to characterize movements performed under the Slow versus Fast temporal constraints.

4.8.1 Distance-Related Measures

Figure A4.1 display mean and variability of distance related measures. Figure A4.1A and B display mean path length and path length variability. Path length was defined as the length of the trajectory traversed. Analyses of mean path length indicated that all participants were performing movements of similar displacements (M = 15.2 cm ± 0.1 cm), regardless of Cursor Feedback ($F(1,15) = 0.341$, $p = 0.568$, $\eta^2 = 0.022$) and MT ($F(1,15) = 0.227$, $p = 0.641$, $\eta^2 = 0.015$). On the other hand, analysis of path length variability revealed a main effect of MT ($F(1,15) = 42.735$, $p < 0.001$, $\eta^2 = 0.740$), whereby reaching under the Fast MT constraint (Aligned = 0.9 cm ± 0.1 cm; Rotated = 1.0 cm ± 0.1 cm) resulted in more variable path lengths compared to reaching under the Slow MT constraint (Aligned = 0.4 cm ± 0.1 cm; Rotated = 0.6 cm ± 0.1 cm).

Horizontal displacement was defined as the greatest perpendicular distance joining the hand path to the reference vector connecting the home position to the target. Analysis of horizontal displacement resulted in a main effect of Cursor Feedback ($F(1,15) = 6.699$, $p = 0.021$, $\eta^2 = 0.309$) and MT ($F(1,15) = 51.422$, $p < 0.001$, $\eta^2 = 0.774$), such that horizontal displacement was greater when reaching with a rotated cursor compared to aligned cursor and when reaching under the Fast MT constraint (Aligned = 3.4 cm ± 0.1 cm; Rotated = 3.6 cm ± 0.1 cm) compared to under the Slow MT constraint (Aligned = 2.7 cm ± 0.1 cm; Rotated = 2.9 cm ± 0.1 cm). Analysis of horizontal displacement variability resulted in a main effect of MT ($F(1,15) = 8.732$, $p =$

0.010, $\eta^2 = 0.368$), such that reaching under the Fast MT constraint (Aligned = 0.8 cm ± 0.1 cm; 0.9 cm ± 0.1 cm) resulted in greater variability compared to reaching under the Slow MT constraint (Aligned = 0.7 cm ± 0.1 cm; 0.7 cm ± 0.1 cm).

These distance related measures speak to different control processes being adopted when temporal constraints were imposed. Overall, total path length was approximately 15 cm, which suggests that participants were able to generate the necessary forces to scale their movements to reach the target (15 cm away from the home position). A high level of path length variability was seen under the Fast MT constraint, which can be attributed to participants attempting to meet the temporal demands, through offline processes, rather than processing visual feedback online to make corrections (Newell, 1980). This idea is further supported with the low path length variability under the Slow MT constraint, where participants had sufficiently more time to utilize visual feedback online compared to under the Fast MT constraint. Important to the purpose of this study is the fact that these temporal constraints similarly affected performance regardless of whether participants were reaching with aligned or rotated cursor feedback. These findings provide evidence to support the notion of flexible movement control processes in learned adapted movements.

On the other hand, in our previous work (Wijeyaratnam, Chua, & Cressman, in prep), we have shown greater horizontal displacement when reaching with a rotated cursor compared to reaching with an aligned cursor. This kinematic characteristic still persisted when temporal constraints were imposed. However, reaches under the Fast MT constraint resulted in greater horizontal displacement compared to reaches under the Slow MT constraint when reaching with both aligned and rotated visual feedback.

Once again, these results add support to the use of visual information offline under Fast MT constraints. Although, visual feedback was continuously available, participants seem to have used this feedback to lower timing error rather than continuously change the characteristics of the ongoing movement to lower spatial error (i.e., multiple movement corrections). Essentially, for movements of short durations participants used visual feedback to control their movements primarily to meet the temporal demands first, rather than inducing online movement corrections to meet the spatial demands, which are typically found in movements of longer duration.

These distance-related measures shed light on potential control processes used to compensate for the speed-accuracy tradeoff when reaching with rotated cursor feedback. We saw the greatest horizontal displacement when reaching with rotated cursor feedback under the Fast MT constraint. Participants under the Fast MT constraint may have produced more curved movements (i.e., greater horizontal displacement) to increase their initial error in order to produce a single or limited number of corrective submovements to achieve the target (Dounskaia, Wisleder, & Johnson, 2005; Hsieh, Liu, & Newell, 2017). Specifically, larger horizontal displacement would enable participants to more easily detect the direction of the rotated cursor and once again make a single corrective movement to the target. This “strategy” further supports the idea of participants utilizing visual feedback offline to fine-tune subsequent movements, as seen with greater path length variability and horizontal displacement variability.

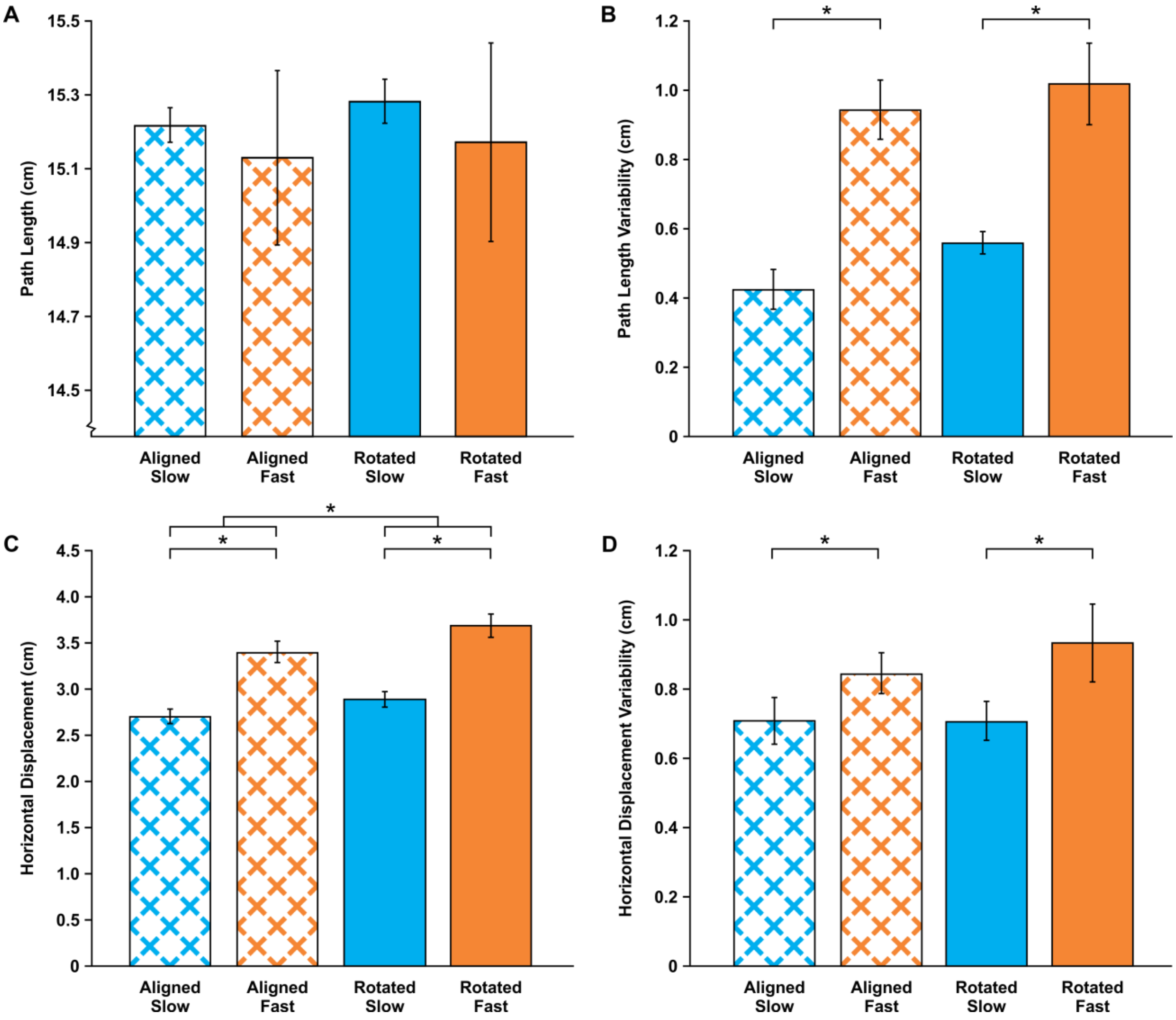


Figure A4.1. Mean and variability of distance-related measures. **A** Mean and **B** variability of path length, measured in centimeters. **C** Mean and **D** variability of horizontal displacement, measured in centimeters. *Patterned bars* represent reaches with an aligned cursor and *solid bars* represent reaches with a rotated cursor. *Blue bars* represent reaches under Slow MT constraints and *orange bars* represent reaches under Fast MT constraints. *Error bars* represent standard error of the mean. *Asterisks* (*) represent significant differences between reaching with an aligned versus a rotated cursor or between the Slow versus Fast MT constraint ($p < 0.05$).

CHAPTER 5 General Discussion

We examined the contributions of control processes underlying reaches when participants were first introduced to a visuomotor distortion (Experiment 1) and then following visuomotor adaptation (Experiment 2). In both experiments, participants completed 150 reach training trials when (1) a cursor accurately represented their hand motion (i.e., aligned cursor) and (2) a cursor was rotated 45 degrees clockwise relative to their hand motion (i.e., rotated cursor).

In Experiment 1, participants (n = 16) received either continuous visual feedback (i.e., visual feedback was provided continuously throughout the reach up until the end of the movement) or terminal visual feedback (i.e., visual feedback was only provided at the end of the movement) to investigate the contributions of movement control processes during reach training (for reviews, see Elliott et al., 2001, 2010, 2017). The objective was to compare traditional measures of movement control across reaching environments to establish whether adapted movements (i.e., reaching in a novel environment) are carried out in a similar manner as well-learned movements (i.e., reaching in a typical environment).

In Experiment 2, participants (n = 16) first completed the training trials with continuous visual feedback and then completed an additional 45 reaches under (1) slow MT (800-1000 ms) and (2) fast MT constraints (400-500 ms). The objective was to establish whether we could encourage the utilization of visual feedback for online control in learned adapted movements (i.e., following visuomotor adaptation with a rotated cursor), as seen when reaching with aligned visual feedback in a typical environment.

Together, these experiments demonstrate a flexibility in control processes underlying reaches with rotated visual feedback of the hand. We suggested that when reaching in a novel environment, participants first engage in offline control processes during learning, and then shift to online corrective processes once the visuomotor rotation is learned.

5.1 Stages of Learning

We have shown, in the two experiments described above, that (1) we utilize different control processes for adapted movement compared to well-learned movements, (2) that these control processes underlying adapted movements are flexible and (3) that we are able to strike a balance between speed and accuracy regardless of the reaching environment. The flexibility in control processes (i.e., shift from offline to online control) underlying these adapted movements, allows us to discuss potential stages of learning that participants may have engaged in during our experiments.

The traditional model of motor skill acquisition (Fitts, 1964; Fitts & Posner, 1967) has been primarily used to describe learning processes associated with acquiring a new skill (Anderson, 1982, 1995; Anson, Elliott, & Davids, 2005). In our experiments, participants were not acquiring a new skill, instead they were acquiring a new visuomotor mapping for a previously learned skill (e.g., reaching with altered visual feedback of the hand). While it is important to first make this distinction between novel skill acquisition and visuomotor adaptation, adaptation is considered to be a form of motor learning (Bastian, 2008). In particular, motor adaptation is the modification of a movement from trial-to-trial based on error feedback (Bastian, 2008). Thus, if participants continue to train under altered visual feedback, as we have done in the above experiments, they should be able to develop a new motor pattern for that movement. Given that practice is involved in both novel skill acquisition and visuomotor adaptation, participants may pass through similar stages of learning with training in both cases. Thus, we looked to determine whether our results are in line with participants transitioning through Fitts & Posner’s (1967) stages (or phases) of motor learning: the cognitive stage, associative stage and autonomous stage.

In the first stage, called the cognitive stage, movements are characterized by individuals trying to figure out *what exactly needs to be done* – what actions need to be taken in order to complete the task. Naturally, as stated in the naming of this stage, considerable cognitive activity is required in order for participants to develop an appropriate strategy (Adams, 1971). Additionally, in this stage, participants tend to pay attention to step-by-step execution of the skill (i.e., offline control), which requires considerable attentional capacity. The increased reaction time seen in our first experiment when participants were reaching with a rotated cursor suggest that they were engaging in strategic processes (e.g., mental rotation; see Fernandez-Ruiz et al., 2011) to counteract the altered visual representation of the hand. Furthermore, TTPV and AE variability across movement proportions emphasizes the notion that participants were using predominately offline control processes. Finally, our results demonstrated that when reaching in a novel environment, movements were inefficient and inconsistent throughout training.

In the second stage, called the associative stage, movements are characterized by subtle movement adjustments – how to perform the movement. Movements are considered more reliable and consistent from trial-to-trial. In addition, at least parts of the movement are controlled more automatically, and more attention can be directed to other aspects of performance. Our data reflects that participants achieved aspects of this stage, such that their movements become more consistent from trial-to-trial near the end of reach training (i.e., reduced variability in EP AE, MT, JScore, TTPV, TAPV, AE across movement proportions; see Experiment 1). Furthermore, following reach training, participants were able to achieve temporal demands with respect to MT even when reaching with rotated cursor feedback. In fact, participants were now able to utilize visual information, once they had learned this new pattern of movement (i.e., newly acquired adapted movement), to make corrections throughout the trajectory (i.e., under Slow MT constraints; see Experiment 2). This suggests that participants were devoting attentional resources to meet the MT constraints once they had learned to reach with rotated cursor feedback.

The third stage, called the autonomous stage, is typically characterized by effortless motion; movements that are not only accurate, with few or no errors, but also very consistent. Given that participants were not provided with extended practice and experience in this novel environment, we did not expect participants to achieve this stage of learning. We found that even though participants learned the visuomotor rotation and were able to attend to meeting temporal demands, AE variability across movement proportions remained elevated when reaching with rotated cursor feedback compared to when reaching with aligned cursor feedback (see Experiment 2). This adds to the idea that participants did not achieve the autonomous stage of learning, as movements were still somewhat inconsistent, even though accuracy was improved.

5.2 Limitations and Future Directions

A number of important questions/considerations arose from our experimental findings, namely the role of awareness and attention when reaching in a novel visuomotor environment. Given the objectives of the current thesis were to determine the contributions of movement control processes during and following visuomotor adaptation, we did not manipulate awareness or attention. However, we recognize the potential influences these factors may have had on the control of movements with rotated cursor feedback. Below we discuss how each factor (i.e., awareness and attention, respectively) may play a role in our results and how future studies can follow-up by directly testing their influence.

In the current experiments, we assumed that participants were aware of the visuomotor rotation and therefore, used a strategy to counteract the rotation. This assumption was based on the findings of increased reaction times paired with a rapid decrease in angular errors, resulting in a similar level of performance as seen at baseline. We did not directly assess whether participants were aware of the manipulation or the type of strategy they developed. However, several participants did verbally indicate that "*something weird*" had occurred and that they "*figured out*" how to perform under altered visual feedback of the hand. These findings support our suggestion that greater cognitive processes are involved when acquiring a new pattern of movement compared to well-learned movements; in agreement with the description of the first stage in Fitts and Posner's (1967) stages of learning. In both experiments we interpreted findings of consistently longer and more variable RT (i.e., Experiment 1), as well as stable RT variability (i.e., Experiment 2) to indicate participants engaging in strategic processes (i.e., offline control), thus suggesting that they were aware of the perturbation.

Studies have shown that awareness of a visuomotor rotation can be manipulated in which the rotation is introduced (i.e., abrupt versus gradual rotation), and the size of the rotation (i.e., ranging 15°-90°), both of which can alter the magnitude of the initial errors experienced (Bond & Taylor, 2015; Galea, Sami, Albert, & Miall, 2010; Hwang, Smith, & Shadmehr, 2006; Maksimovic & Cressman, 2018; Neville & Cressman, 2018; Redding & Wallace, 1996; Taylor et al., 2014; Werner et al., 2015; Werner, Schorn, Bock, Theysohn, & Timmann, 2014). Awareness has been associated with the involvement of strategic processes, such that participants that are aware of the cursor rotation tend to have greater involvement of strategic processes or explicit contributions, whereas participants that are unaware tend to have more implicit contributions. In general, participants are typically aware of the visuomotor rotation when it is introduced abruptly and/or is large (i.e., greater than 40°) (Neville & Cressman, 2018; Thomas & Bock, 2012; Werner et al., 2015). In contrast, participants are typically classified as being unaware of the altered representation of their hand when the cursor rotation is introduced gradually (i.e., continues to increase over a number of trials) or it is small (i.e., 30° or less).

In our experiments, we abruptly introduced a 45° visuomotor rotation. Through kinematic measures we have shown that participants can rapidly correct large initial errors (i.e., possibly through a strategy) to eventually perform with similar accuracy as seen at baseline (i.e., without a rotation). Since we did not directly assess awareness, we cannot conclusively state that these kinematic findings reflect participants becoming aware of the perturbation and using a strategy. Future studies should look to determine how performance and kinematic measures change when awareness is manipulated. For example, participants could be given a strategy in order to counteract the cursor rotation, ensuring awareness, or a small cursor rotation could be gradually introduced in attempt to have participants remain unware of that a cursor rotation. In these potential experiments, performance and kinematic measures such as RT and AE variability across a trajectory (previously used to infer offline control in newly acquired movements) may be similar regardless of cursor feedback (i.e., aligned versus rotated cursor) because participants may not need to develop a strategy if one is already provided (i.e., explicit strategy) or if one is not needed (i.e., gradual rotation). These results would suggest that participants may place more weight on online control processes compared to offline control (i.e., strategic processes; greater awareness), which may only be used to fine-tune forthcoming actions instead of engaging in strategic processes.

We found that performance (i.e., PV AE, EP AE and EP error) improved once participants learned the visuomotor rotation and were able to effectively use visual information for online control. However, we have only shown this when there was no constraint to movement planning (i.e., offline control). As a result, we cannot conclude that participants did not engage in planning (i.e., strategic processes) once they were better able to utilize visual information for online control. A potential experiment to establish if strategic processes are still engaged offline following visuomotor adaptation would be to impose RT constraints, thereby limiting planning (i.e., offline control) and encouraging the use of online control. Our results, as well as those by Fernandez-Ruiz and colleagues (2011), would suggest that imposing RT constraints would severely impact movement performance (i.e., accuracy and precision).

Finally, we suggested that when we imposed spatial and temporal demands (i.e., reaching with rotated cursor feedback under MT constraints) during reaching, these processes competed for attentional resources (see Experiment 2). This idea was primarily based on indirect measures of attention (i.e., mean RT and variability) when comparing cursor feedback (i.e., aligned versus rotated) under different MT constraints (i.e., Slow MT versus Fast MT). Posner & Boies (1971) proposed three components to attention: alertness, selectivity and processing capacity. They suggested that faster movements may be dominated by a “target selectivity”, in this case meeting a temporal constraint, whereas slower movements are not affected by this selectivity (Kahneman, 1973; Salmoni, Sullivan, & Starkes, 1976). We have shown greater RTs when reaching under the Fast MT constraint, implying greater voluntarily effort was allocated for movement planning. This was not seen when reaching under the Slow MT constraint, suggesting that planning processes were limited because participants could correct their movement throughout the trajectory. Although our indirect measures of attention are in line with studies that have specifically separated these components, we acknowledge that we cannot make definitive conclusions regarding the implications of attention when learning a visuomotor rotation or following visuomotor adaptation. Several other factors, like the instructions provided to accomplish both spatial and temporal demands of the task, can influence how participants focus their attention. Since we cannot say for sure which component of the task (i.e., spatial or temporal) participants choose to attend to first, we can only assume that the decrement in performance seen when reaching with rotated cursor feedback under the Fast MT constraint and not under the Slow MT constraint may be reflective of competing attentional processes. Future studies can look to directly measure attention, during and following visuomotor adaptation, through several techniques such as RT probes and eye tracking. This can further our understanding on whether participants choose to explore different strategies when presented with a novel reaching task and how participants may distribute their attention within a trial and across reach training.

CHAPTER 6 Conclusion

The main purpose of this thesis was to determine the contributions of movement control processes underlying movements performed in a novel environment (i.e., reaching with altered visual feedback of the hand; visuomotor rotation), during learning and following visuomotor adaptation, and whether these control processes were (kinematically) different to movements in a typical environment (i.e., well-learned movements). We have shown that participants initially engage in more offline control processes throughout training with a visuomotor rotation (i.e., during adaptation; Experiment 1), but once the new pattern of movement is acquired, they are able to better process visual feedback and therefore shift to more online corrective processes (i.e., following adaptation; Experiment 2). Together, these experiments demonstrate a flexibility in control processes at different stages of learning (i.e., cognitive and associative stages). Furthermore, our findings raise questions to be addressed in follow-up experiments, which may prove valuable in furthering our understanding of these flexible control processes and how they change over time. All-in-all, our results support models (Elliott et al., 2017) and theories of motor control (Wright & Meyer, 1983; Zelaznik et al., 1988), as well as theories of motor learning (Fitts & Posner, 1967). With continued research on the many factors (i.e., awareness, strategic processes and attentional resources) that can influence movement control processes in adapted movements, we may be able to optimize the learning and control of movement following injury through the development of effective rehabilitation paradigms.

Appendix A: Frequency Domain

Novel analyses in the frequency domain have recently been proposed by de Grosbois and Tremblay (2016, 2017, 2018) to provide an alternative assessment for detecting changes in the processing of visual feedback online. According to de Grosbois & Tremblay (2016, 2017, 2018), traditional online and offline measures (as we included in Experiments 1 and 2) are inadvertently influenced by offline control processes (i.e., trial-to-trial changes in behavior). To circumvent this problem, de Grosbois & Tremblay (2016) have suggested a method to determine the contributions of online control when visual feedback is manipulated (i.e., vision versus no-vision). In their analysis, acceleration profiles of reaching movements are first detrended by the best fitting 5th order polynomial (i.e., sine-wave shape). This is then followed by converting the residuals of the acceleration profiles to frequency representations. Finally, these frequency representations are further converted to a proportional power spectrum (pPower spectrum, % spectral power) to identify the influence of visual feedback on movement (observed as specific peaks in frequency plots). de Grosbois and Tremblay (2016) have suggested that a greater contribution of processing visual feedback for online control is associated with an increase in pPower at a particular frequency (i.e., 4-8 Hz) when compared to performance in the absence of visual feedback for online control.

We ran similar analyses on data from Experiment 1. Since the position of the robot handle was recorded at a sampling rate of 1000 Hz, we were able acquire precise estimates of iteration times (i.e.,1000 Hz/1024 samples = 0.98 Hz increments), which de Grosbois and Tremblay (2016) suggested was a limitation in their experiment (i.e., 200

Hz/128 samples = 1.56 Hz increments). pPower was first evaluated across frequencies ranging from 0.98-25.39 Hz on the average of the last 80 reaches, during reach training, performed to all targets under both reaching environments (see Figure A1A). A 2 Group (CF, TF) x 2 Reaching Environment (aligned, rotated) x 26 Frequency (0.98, 1.95, 2.93, 3.91, 4.88, 5.86, 6.84, 7.81, 8.79, 9.77, 10.74, 11.72, 12.70, 13.67, 14.65, 15.63, 16.60, 17.58, 18.55, 19.53, 20.51, 21.48, 22.46, 23.44, 24.41, 25.39) mixed ANOVA with RM on the last 2 factors was used to determine if observable peaks were influenced by visual feedback and reaching environment.

Additionally, analyses were conducted on peak pPower and associated frequencies averaged across trials for each participant. This analysis was further separated by two specific frequency ranges based upon the suggested frequencies being associated with the use of visual feedback for online control. The first range (0.98 to 10.74 Hz) was determined based on the hypothesized influence of visual feedback at 10 Hz (i.e. 100 ms per cycle, Carlton, 1981; Saunders & Knill, 2003), whereas the second range (11.72 – 25.39 Hz) was determined based on modifications in trajectories suggested to arise due to non-visual (e.g., proprioceptive) mechanisms (de Grosbois & Tremblay, 2016, 2017, 2018). Mean peak pPower and associated frequencies were compared in 2 Group x 2 Reaching Environment ANOVAs with RM on the last factor to evaluate the influence of visual feedback and reaching environment.

Figure A1A displays mean pPower across frequencies for the last 80 reaches, averaged across all participants and targets for each group and cursor feedback condition (i.e., aligned and rotated cursor feedback). It was expected that each frequency would be significantly different from each other, therefore we have omitted discussion of any main effects of frequency. Analysis of pPower resulted in no main effects of Group ($F(1,14) = 1.302$, $p = 0.273$, $\eta^2 = 0.085$) and Reaching Environment ($F(1,14) = 0.165$, $p = 0.691$, $\eta^2 = 0.012$), as well as no interactions (Group x Reaching Environment: $F(1,14) = 1.266$, $p = 0.279$, $\eta^2 = 0.083$); Group x Frequency: $F(24,336) = 0.873$, $p = 0.640$, $\eta^2 = 0.059$; Reaching Environment x Frequency: $F(3.546, 49.648) = 0.622$, $p = 0.630$, $\eta^2 = 0.043$; Group x Reaching Environment x Frequency: $F(24,336) = 0.461$, $p = 0.742$, $\eta^2 = 0.032$).

Further analysis was conducted on average peak pPower and the associated frequencies for both sets of frequency ranges (i.e., 0.98 to 10.74 Hz, see Figure A1B and C; 11.72 – 25.39 Hz, see Figure A1D and E). Analysis of peak pPower for the first frequency range resulted in no main effects (Reaching Environment: $F(1,14) = 0.710$, $p = 0.414$, $\eta^2 = 0.048$; Group: $F(1,14) = 0.202$, $p = 0.660$, $\eta^2 = 0.014$) or interaction of Group x Reaching Environment ($F(1,14) = 0.022$, $p = 0.885$, $\eta^2 = 0.002$). Analysis of the associated frequency of peak pPower also resulted in no main effects (Reaching Environment: $F(1,14) = 0.604$, $p = 0.450$, $\eta^2 = 0.041$; Group: $F(1,14) = 0.806$, $p = 0.384$, $\eta^2 = 0.054$) or interaction of Group x Reaching Environment ($F(1,14) = 0.519$, $p = 0.483$, $\eta^2 = 0.036$). Analysis of peak pPower for the second frequency range also resulted in no main effects (Reaching Environment: $F(1,14) = 1.301$, $p = 0.273$, $\eta^2 = 0.085$; Group: $F(1,14) = 0.009$, $p = 0.927$, $\eta^2 = 0.001$) or interaction of Group x Reaching Environment ($F(1,14) = 0.043$, $p = 0.840$, $\eta^2 = 0.003$). Analysis of the frequency associated with peak pPower also resulted in no main effects (Reaching Environment: $F(1,14) = 0.292$, $p = 0.598$, $\eta^2 = 0.020$; Group: $F(1,14) = 0.169$, $p = 0.687$, $\eta^2 = 0.012$) or interaction of Group x Reaching Environment ($F(1,14) = 2.248$, $p = 0.156$, $\eta^2 = 0.138$).

The design of de Grosbois and Tremblay's experiments are much different from those described in this thesis. They required participants to reach in the horizontal direction (always rightward) to targets that were 10 and 30 cm away under various conditions of visual feedback (i.e., full vision, no-vision, memory-guided no-vision and terminal feedback). In attempt to match their analysis, we isolated reaches that were performed primarily in a single direction (i.e., anterior-posterior direction). In other words, we compared reaches when participants' actual hand was moving straight-ahead (i.e., to the 0° target) in both reaching environments (see Figure A2). Analysis revealed no main effect of Group ($F(1,14) = 0.417$, $p = 0.529$, $\eta^2 = 0.029$), but we did see an interaction between Reaching Environment x Frequency ($F(24,336) = 2.085$, $p = 0.002$, $\eta^2 = 0.130$). Post hoc analysis revealed higher pPower at 5.86 Hz when reaching with a rotated cursor (M = 11.93% ± 1.39%) compared to reaching with an aligned cursor (M = 9.32% ± 1.36%, $p = 0.039$). Additionally, reaching with an aligned cursor resulted in greater pPower specifically at 11.72 Hz and between 13.67-25.39 Hz compared to reaching with a rotated cursor (all $p < 0.035$, see Figure A2A).

Analysis of peak pPower for the first frequency range resulted in only a main effect of Reaching Environment ($F(1,14) = 7.115$, $p = 0.018$, $\eta^2 = 0.337$), such that reaching with a rotated cursor (M = 36.79% ± 1.41%) resulted in higher pPower compared to reaching with an aligned cursor (M = 31.25% ± 1.76%). Analysis of the frequencies associated with peak pPower also resulted in a main effect of Reaching Environment ($F(1,14) = 11.072$, $p = 0.005$, $\eta^2 = 0.442$), such that peak pPower was achieved at a higher frequency when reaching with an aligned cursor (M = 5.14 Hz ± 0.53 Hz) compared to when reaching with a rotated cursor (M = 3.45 Hz ± 0.26 Hz).

Analysis of peak pPower for the second frequency range also resulted in no main effects (Reaching Environment: $F(1,14) = 0.244$, $p = 0.629$, $\eta^2 = 0.017$; Group: $F(1,14) = 0.593$, $p = 0.454$, $\eta^2 = 0.041$) or interaction of Group x Reaching Environment ($F(1,14) = 1.932$, $p = 0.186$, $\eta^2 = 0.121$). Analysis of the frequencies associated with peak pPower also resulted in no main effects (Reaching Environment: $F(1,14) = 1.064$, $p = 0.320$, $\eta^2 = 0.071$; Group: $F(1,14) = 0.639$, $p = 0.437$, $\eta^2 = 0.044$) or interaction of Group x Reaching Environment ($F(1,14) = 3.081$, $p = 0.101$, $\eta^2 = 0.180$).

We additionally investigated the implications of the frequency analysis when visual feedback of the hand was similar. This analysis differed from the analysis conducted in the AP direction, such that we now compared reaches when visual representations of the hand (i.e., cursor) instead of actual hand position were similar. Thus, we compared reaches to the 0° target when participants reached with aligned visual feedback to reaches to the -45° target when participants reached with rotated cursor feedback (see Figure A3A). Analysis revealed no main effects (Group: $F(1,14) = 0.001$, $p = 0.982$, $\eta^2 = 0.000$; Reaching Environment: $F(1,14) = 1.255$, $p = 0.281$, $\eta^2 = 0.082$) but we did observe an interaction between Reaching Environment x Frequency ($F(24,336) = 2.186$, $p = 0.001$, $\eta^2 = 0.135$), such that peak pPower was significantly higher when reaching with an aligned cursor at 8.79 Hz, 9.77 Hz and 23.44 Hz compared to reaching with a rotated cursor (all $p < 0.49$).

Analysis of peak pPower for the first frequency range resulted in no main effects (Reaching Environment: $F(1,14) = 3.214$, $p = 0.095$, $\eta^2 = 0.187$; Group: $F(1,14) = 0.322$, $p = 0.580$, $\eta^2 = 0.022$) or interaction of Group x Reaching Environment ($F(1,14) = 0.033$, $p = 0.859$, $\eta^2 = 0.002$). Analysis of the frequencies associated with peak pPower resulted in only a main effect of Reaching Environment ($F(1,14) = 5.343$, $p = 0.037$, $\eta^2 = 0.276$) such that peaks achieved when reaching with an aligned cursor (M = 6.36 Hz ± 0.23 Hz) were achieved at a higher frequency compared to when reaching with a rotated cursor (M = 5.72 Hz ± 0.17 Hz). Analysis of peak pPower for the second frequency range also resulted in no main effects (Reaching Environment: $F(1,14) = 1.748$, $p = 0.207$, $\eta^2 = 0.111$; Group: $F(1,14) = 0.003$, $p = 0.956$, $\eta^2 = 0.000$) or interaction of Group x Reaching Environment ($F(1,14) = 0.001$, $p = 0.977$, $\eta^2 = 0.000$). Analysis of the frequencies associated with peak pPower also resulted in no main effects (Cursor: $F(1,14) = 0.219$, $p = 0.647$, $\eta^2 = 0.015$; Group: $F(1,14) = 0.401$, $p = 0.531$, $\eta^2 = 0.028$) or interaction of Group x Reaching Environment ($F(1,14) = 0.212$, $p = 0.653$, $\eta^2 = 0.015$).

de Grosbois and Tremblay have identified two peaks in the spectra, one at a relatively low frequency, denoted as the alpha peak and the other at a higher frequency, denoted as the beta peak. Upon visual inspection of our pPower curves, we observed alpha peak frequencies at 3.91 Hz (see Figure A1), 4.88 Hz (see Figure A2) and 5.86 Hz (see Figure A3), which are earlier than those observed at the critical frequency of 6.25 Hz (adjusted from 4.68 Hz, see de Grosbois & Tremblay, 2016), 6.70 Hz (de Grosbois & Tremblay, 2017) and 7.7 Hz (de Grosbois & Tremblay, 2018). The observed pPower magnitudes obtained at each specific frequency interval, averaged over participants, is not representative of the actual peak pPower for each participant. Therefore, we conducted additional analyses on peak pPower and its associated frequencies, which resulted in peak pPower being observed in the range of 5-8 Hz. This frequency range is more in line with previously estimated processing times for visual information (Saunders & Knill, 2003, 2005; Zelaznik et al., 1983). On the other hand, we did not observe a secondary pPower peak at relatively higher frequencies (i.e., beta peak), but an analysis of local peaks at associated frequencies ranged from 15-18 Hz (see Figure A1D; Figure A2D; Figure A3D), similar to those in de Grosbois and Tremblay's (2016, 2017) experiments.

We were able to produce similar results of de Grosbois and Tremblay (2016, 2017) in terms of the general shape of the pPower spectra, peak pPower and associated frequencies. That said, there remain many questions regarding the interpretation and hence implications of analyses completed in the frequency domain. In particular, can alpha peaks be used as an indicator for visually-mediated changes in online control? We had participants reach with continuous or terminal visual feedback. Thus, we would expect (and saw in the other variables we reported (Experiment 1) a greater contribution of online control when reaches were completed with continuous visual feedback compared to terminal visual feedback, in particular when reaching with an aligned cursor. We did not find a difference between our continuous versus terminal visual feedback groups in the frequency domain. In fact, peak pPower and associated frequencies were similar under both visual feedback conditions, which limit our ability to confidently say that an alpha peak at a particular frequency is indicative of online control. These same trends were observed when reaches were performed in a novel environment (i.e., rotated cursor feedback). Moreover, analyses and results outlined in Experiment 1 would suggest that participants elected to use predominately offline control processes (i.e., preplanning) when reaching with a rotated cursor. Therefore, in our results, the observed significant differences between cursor feedback (i.e., greater peak magnitudes when reaching with a rotated cursor), cannot be attributed to any specific mechanism of control since peaks were similar between groups (i.e., continuous feedback and terminal feedback).

Our results raise questions regarding the generalizability of this frequency analysis to targets at diagonal locations (i.e., 45° Targets), and, as consequence, the scaling (i.e., magnitudes) of the peaks across frequencies in the primary direction versus resultant direction. In Figure A1A and Figure A3A (reaches in the resultant direction) display more changes in peaks from frequency-to-frequency compared to Figure A2A (reaches in the AP direction). This finding may suggest that this analysis may be more sensitive to reaches performed primarily in a single direction (e.g., 1-dimensional horizontal movement), compared to reaches performed in 2 dimensions). This raises the question of whether specific conditions need to be met in order for analysis in the frequency domain to reveal distinct differences in the processing of visual feedback for online control. Altogether, before we can make definitive conclusions regarding the utility and implications of analyses in the frequency domain, we must first address the questions and limitations raised from our work, as well as those of de Grosbois and Tremblay (2016, 2017, 2018).

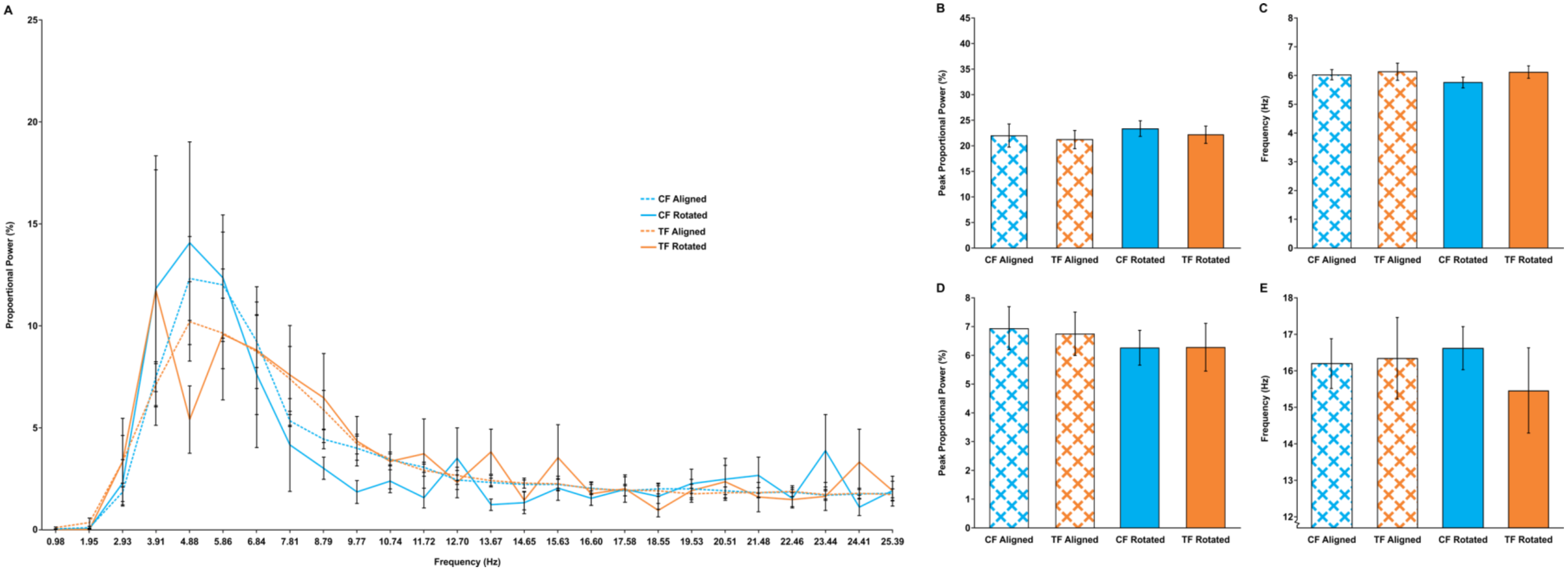


Figure A1. Resultant peak proportional power and frequency. **A** Resultant proportional power (pPower) across frequency bands (i.e., 0.98-25.39 Hz) averaged across the last 80 reach training trials, collapsed across targets. **B** Max proportional peak power and **C** associated frequency within 0-10 Hz for each Group (i.e., CF and TF) and Cursor Feedback condition (i.e., aligned and rotated). **D** Max proportional peak power and E associated frequencies within 11-25 Hz for each Group and Visual Feedback condition.

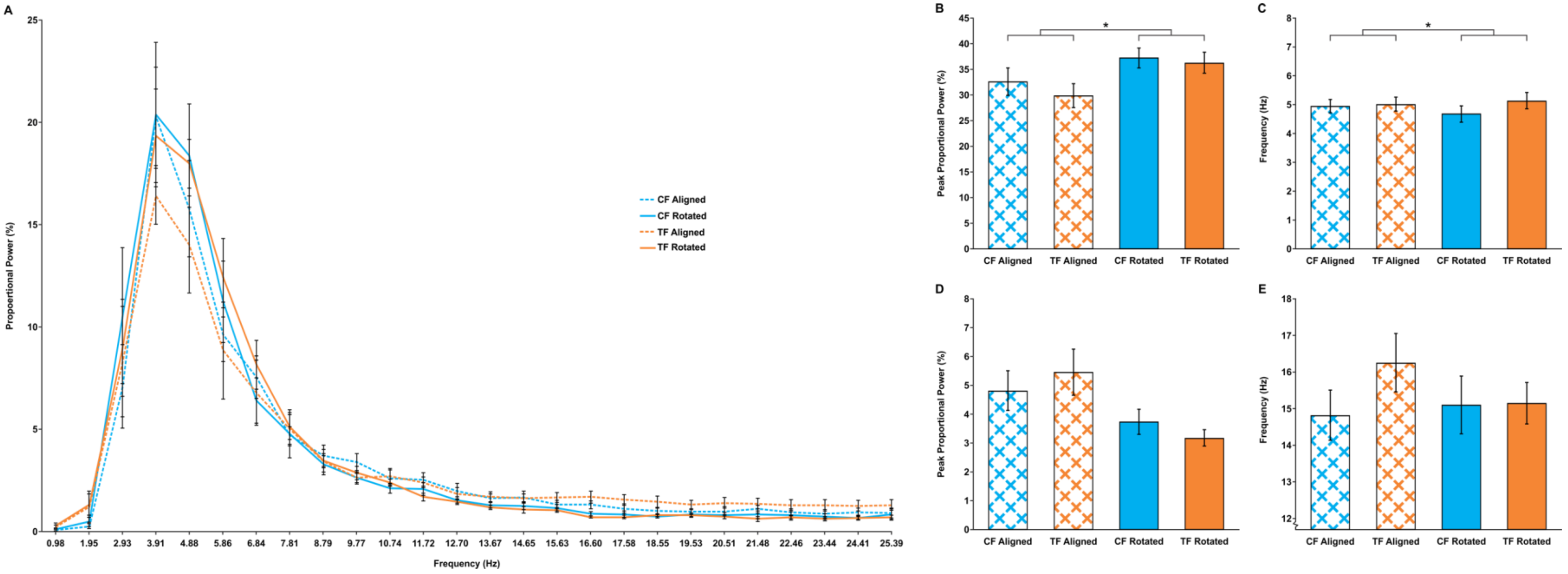


Figure A2. Anterior-Posterior peak proportional power and frequency. **A** Anterior-Posterior proportional power (pPower) across frequency bands (i.e., 0.98-25.39 Hz) averaged across reach training trials when reaching to the 0° target (i.e., 15 cm straight ahead). **B** Max proportional peak power and **C** associated frequency within 0-10 Hz for each Group (i.e., CF and TF) and Cursor Feedback condition (i.e., aligned and rotated). **D** Max proportional peak power and **E** associated frequencies within 11-25 Hz for each Group and Visual Feedback condition.

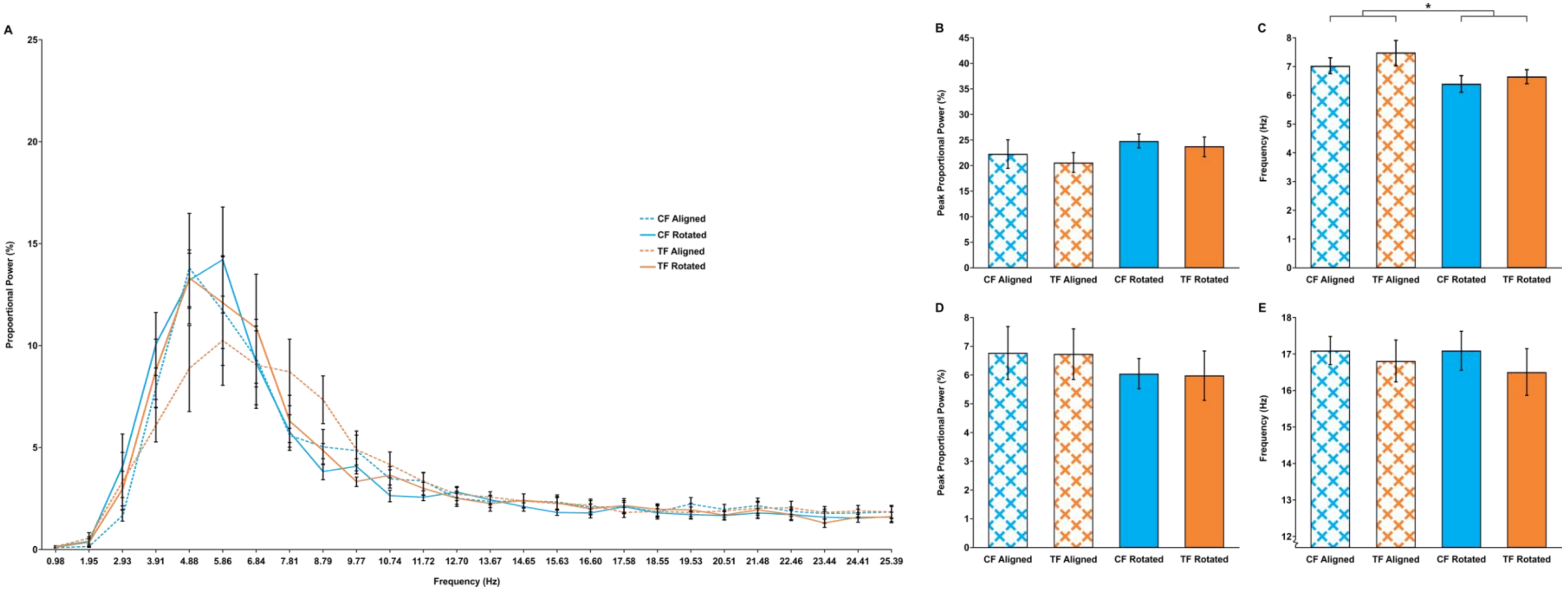
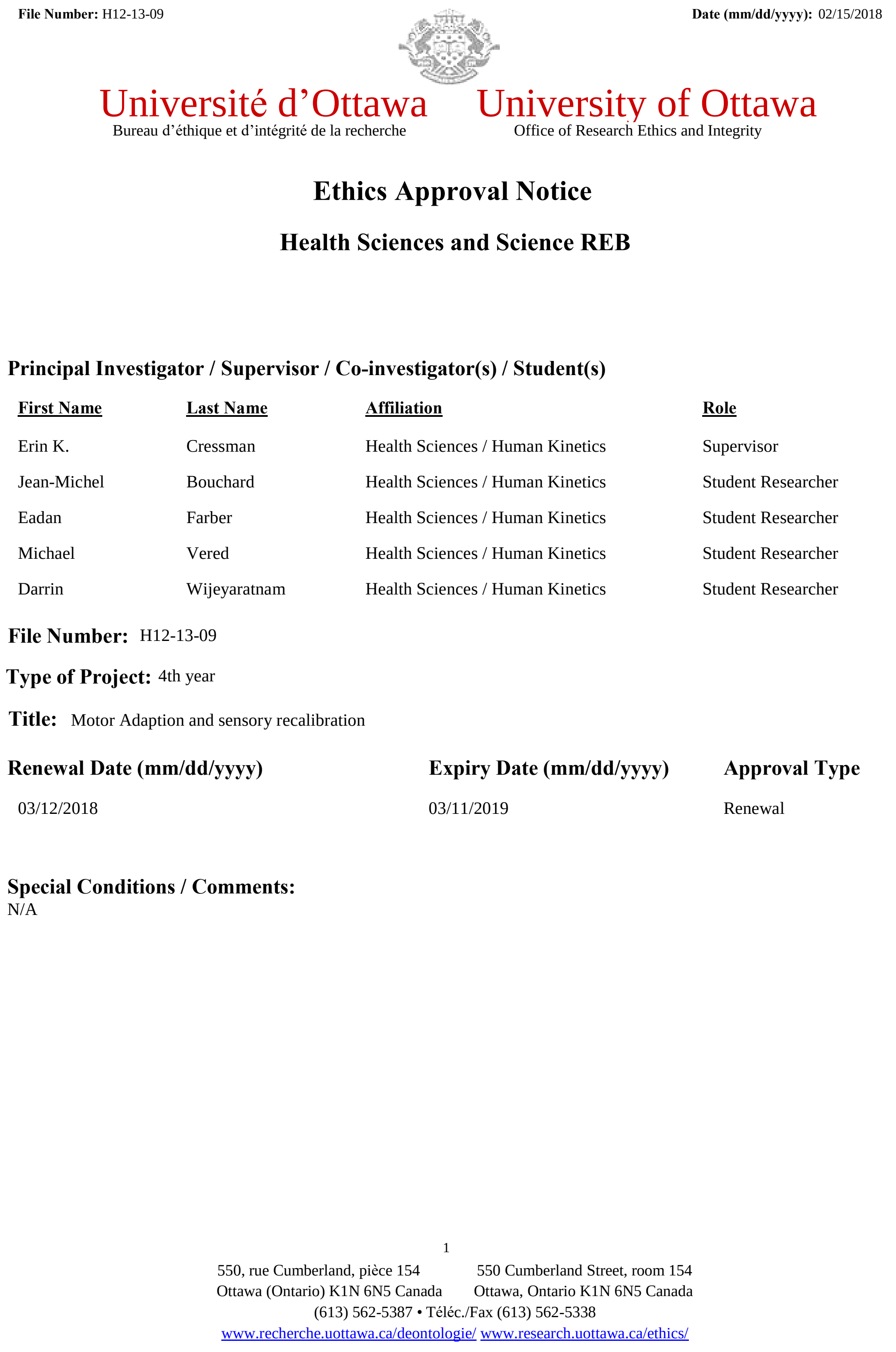


Figure A3. Resultant peak proportional power and frequency with cursor feedback going straight ahead. **A** Resultant proportional power (pPower) across frequency bands (i.e., 0.98-25.39 Hz) averaged across reach training trials when reaching to the 0° target (i.e., 15 cm straight ahead). **B** Max proportional peak power and **C** associated frequency within 0-10 Hz for each Group (i.e., CF and TF) and Cursor Feedback condition (i.e., aligned and rotated). **D** Max proportional peak power and **E** associated frequencies within 11-25 Hz for each Group and Visual Feedback condition.

Appendix B: Ethics Approval Notice



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

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

Ethics Approval Notice

Health Sciences and Science REB

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

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

File Number: H12-13-09

Type of Project: 4th year

Title: Motor Adaption and sensory recalibration

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

Special Conditions / Comments:
N/A

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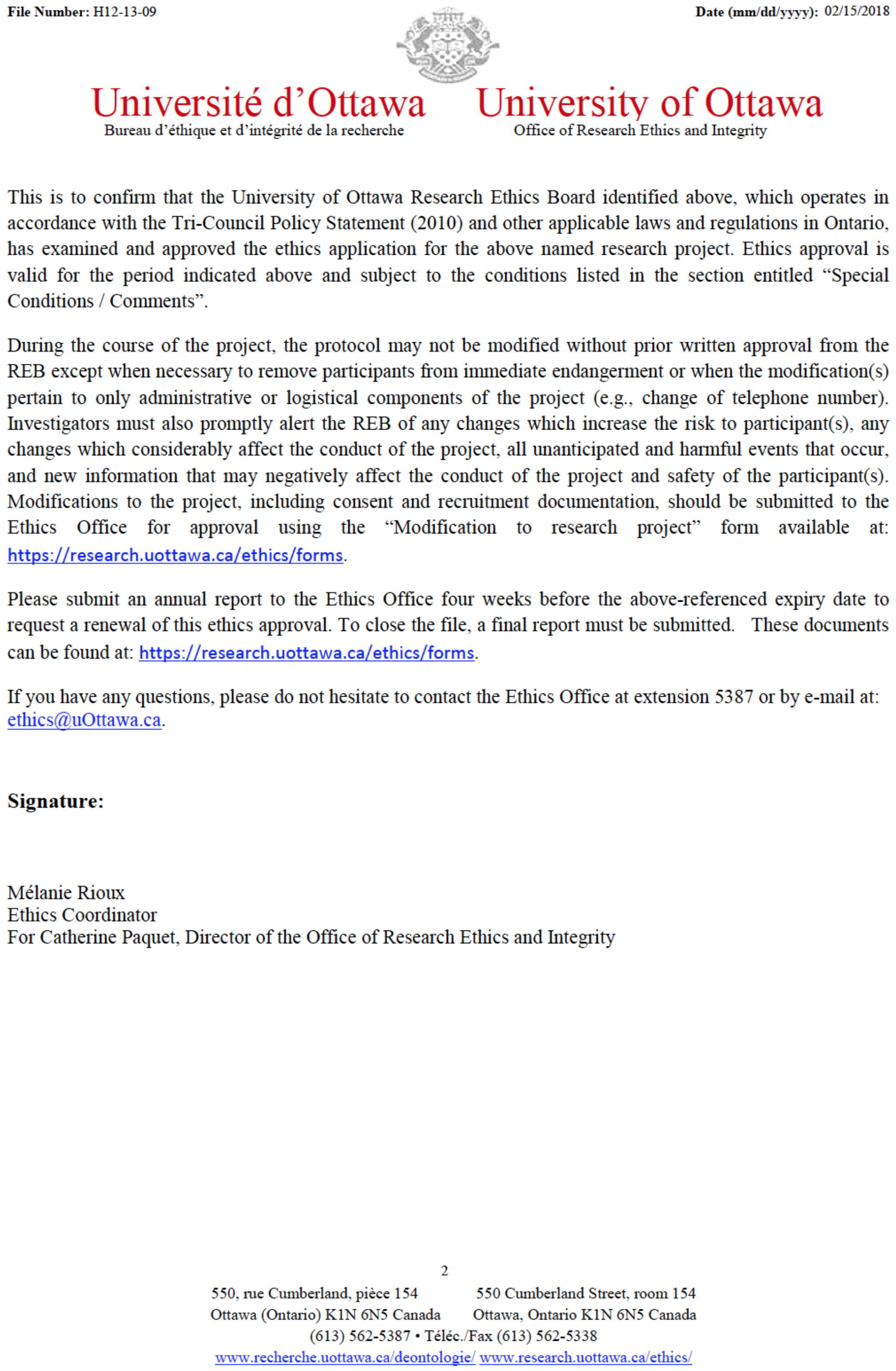
550, rue Cumberland, pièce 154 550 Cumberland Street, room 154
Ottawa (Ontario) K1N 6N5 Canada Ottawa, Ontario K1N 6N5 Canada
(613) 562-5387 • Téléc./Fax (613) 562-5338
www.recherche.uottawa.ca/deontologie/ www.research.uottawa.ca/ethics/



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

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

University of Ottawa
Office of Research Ethics and Integrity

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

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

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

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

Signature:

Mélanie Rioux
Ethics Coordinator
For Catherine Paquet, Director of the Office of Research Ethics and Integrity

Appendix C: Edinburg Handedness Inventory

Name: ______________________________ Date: ___________

Please **indicate with a number (1 or 2)** 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 the number 2.
>
> Where there is a general preference that you are more likely to use the one hand over the other, put the number 1.
>
> If you are indifferent, put a 1 in each column (1 **|** 1)

Task/Object	Left Hand	Right Hand
1. Writing		
2. Drawing		
3. Throwing		
4. Scissors		
5. Toothbrush		
6. Knife		
7. Spoon		
8. Broom (upper hand)		
9. Striking a Match (match)		
10. Opening a box (lid)		
Total Checks:	LH =	RH =

Modified from Oldfield (1971).

Participants will not see the below section.

Handedness will be determined using the following equation(s):

Cumulative Total:	CT = LH + RH =
Difference:	D = RH – LH =
Result:	R = (D/CT) x 100 =

Interpretation:
(Left Handed: $R < -40$)
(Ambidextrous: $-40 \leq R \leq +40$)
(Right Handed: $R > +40$)

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