

The Effect of Mental Fatigue on Explicit and Implicit Contributions to Visuomotor Adaptation

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Abstract

To date, mental fatigue has been shown to lead to a general decline in cognitive processing and motor performance. The goal of the current research was to establish the impact of mental fatigue on the contributions of explicit (i.e., conscious strategy) and implicit (unconscious) processes to visuomotor adaptation. Participants were divided into Mental Fatigue (MF) and Control groups. Mental fatigue was induced through a time load dual back task (TLDB), in which participants were required to respond as quickly and accurately as possible to letters based on recall of previously presented letters, as well as digits displayed on the screen in a choice reaction time task. The TLDB task lasted for 32 minutes, and the Control group watched a documentary for a similar length of time. Subjective feelings of mental fatigue, as indicated on a self-report scale, demonstrated that mental fatigue was significantly higher for the MF group after completion of the TLDB task. There was no similar increase in mental fatigue for the Control group. The increased mental fatigue was associated with decreased visuomotor adaptation to a 40° cursor rotation and retention of visuomotor adaptation. In particular, participants in the MF group adapted their reaches to a lesser extent early in training compared to the Control group and demonstrated less retention of visuomotor adaptation following a 20-minute rest. Furthermore, correlational analyses established that greater mental fatigue reported by participants in the MF group was associated with less explicit adaptation and greater implicit adaptation. Taken together, these results suggest that mental fatigue decreases the ability to engage in explicit processing, limiting the overall extent of visuomotor adaptation achieved.

Statement of Contributions

I hereby declare that I am the sole author of this Master of Science thesis. My contributions include: a review of literature, participant recruitment and data collection, analysis and compilation of data, statistical analysis, and the writing of this thesis. All of the aforementioned actions were performed under the guidance and mentorship of my research supervisor, Dr. Erin K. Cressman.

The original experimental design was revised in collaboration with my supervisor Dr. Cressman, taking into account the recommendations and ideas of my thesis advisory committee: Dr. Anthony Carlsen and Dr. Sarah Fraser. Dr. Cressman provided editorial feedback and is a co-author of the article presented in this thesis.

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CHAPTER 1. INTRODUCTION

We are constantly adapting our movements to meet changes in the environment.

Visuomotor adaptation is a form of motor adaptation driven by changes in the visual environment that create a discrepancy between one's seen and felt hand positions (Cressman and Henriques, 2009; Krakauer, 2006; Krakauer et al., 2019). For example, participants may be required to reach to a target when a cursor misrepresents the position of their hand in space, such that the cursor's motion on a screen is rotated clockwise relative to one's actual hand trajectory. In order to adapt their movements, participants must compensate for the visuomotor rotation by reaching in the counter clockwise direction, opposite of the imposed rotation. To date, much research has looked to establish the contributions of explicit (i.e., conscious strategy) and implicit (unconscious) processes to visuomotor adaptation (e.g., Bond and Taylor, 2015; Mazzoni and Krakauer, 2006; Neville and Cressman, 2018; Taylor et. al., 2014), with results indicating that explicit processes have a great contribution early in visuomotor adaptation, when the cursor rotation is first introduced. In contrast, implicit processes are suggested to play a more significant role in the later phases of visuomotor adaptation (Neville and Cressman, 2018; Taylor et al., 2014).

The study of visuomotor adaptation, and underlying processes, are typically examined within standardized testing environments (e.g., Cressman and Henriques, 2009; Krakauer, 2006; Krakauer et al., 2019; Severini and Zych, 2020), not reflective of, or applicable to, daily life. For example, consider that we spend much of our day under stressed or mentally fatigued conditions (as suggested by the National Sleep Foundation, 2020), when cognitive resources are limited (Sanders et al., 1997). It is possible that visuomotor adaptation and the processes underlying visuomotor adaptation may be impacted by mental fatigue. The purpose of the current research

was to determine the impact of mental fatigue on explicit and implicit contributions to visuomotor adaptation. We hypothesized that mental fatigue would impact visuomotor adaptation, in particular with respect to the engagement of explicit processes when the cursor rotation was first introduced.

In order to introduce our research question, the following review of current literature will first define motor control and visuomotor adaptation, as well as outline how visuomotor adaptation is typically examined in a laboratory setting. The literature review will then establish explicit and implicit contributions to visuomotor adaptation, as well as discuss methods for assessing their contributions. Following this, mental fatigue, including reliable measures of its incidence and how it is induced in a laboratory setting will be detailed. The potential impact of mental fatigue on motor control and visuomotor adaptation will then be discussed. Finally, the review of literature will conclude with a description of the research question and hypothesis.

CHAPTER 2. LITERATURE REVIEW

2. 1. Motor control and visuomotor adaptation

Motor control is defined as the ability to regulate mechanisms that are essential to the production of goal-directed movements (Schmidt et al., 2005). The control of goal-directed movements is constantly changing in order to meet the demands of the environment, task and individual (Kenyon and Blackinton, 2011; Shumway-Cook and Woollacott, 2007). Shumway-Cook and Woollacott (2007) discuss these changes in motor control in their Integrated Systems-Based theory, which posits that environmental attributes, as well as task attributes, define and constrain the execution of a motor task. Furthermore, they argue that individual characteristics, such as variances in action, perception, and cognition can lead to changes in task outcome (Shumway-Cook and Woollacott, 2007). This infinite combination of interacting attributes requires flexibility in motor control in order for one's movements to meet changing demands.

The study of flexibility in motor control is captured within investigations of motor adaptation. Motor adaptation is defined as the ability to adapt movements to a change in intrinsic conditions (e.g., growth and/or aging), or to extrinsic factors (e.g., our environment), and is characterized by a gradual improvement in performance in response to these altered conditions (Krakauer, 2006; Krakauer et al., 2019; Krakauer and Mazzoni, 2011; Wolpert and Flanagan, 2010). According to Krakauer and colleagues' (2019) recent definition, motor adaptation is a form of motor learning. Specifically, Krakauer et al. (2019) expand the traditional definition of motor learning (e.g., see Schmidt and Lee (2005)), so that it includes both: (1) skill acquisition, in which one acquires the ability to rapidly identify a movement goal given a particular context, correctly identify the action required to complete the movement task and execute the action with accuracy and precision, and (2) skill maintenance, which is the ability to maintain movement

performance under changing conditions. Motor adaptation falls under the umbrella of skill maintenance.

While the traditional definition of motor learning suggests a permanent change in skill level with respect to task completion, motor adaptation results in a semi-permanent change in performance arising as a result of systematic change(s) in conditions. According to Martin et. al. (1996), motor adaptation occurs when the following three criteria are met; (1) the performed movement retains its identity as a specific action (e.g. reaching), but the parameters of this action, such as force or direction, need to change, (2) adaptation occurs with repetition (i.e., practice), and the adapted behaviour appears gradually in a time span of minutes to hours, and (3) once adaptation is complete, individuals cannot perform the original movement and instead demonstrate ‘aftereffects’ as a sign that adaptation was successful. This adapted movement must then be unlearned with practice in the same manner, leading to a gradual return to the initial state, so that the original movement can once again be performed (Bastian, 2008; Martin et al., 1996).

Motor adaptation can be modelled within Wolpert and colleagues’ (1995) internal model. The internal model consists of the inverse model (i.e., motor command) and forward model (i.e., predictions of sensory feedback). Processes related to the forward model are suggested to take place in the cerebellum, where the expected sensory consequences of the movement are compared to the actual feedback received (Cullen and Brooks, 2015; Popa and Ebner, 2019; Streng et al., 2018). Any discrepancy between predicted and actual sensory feedback signals a movement error, which then leads to updating of the inverse model and forward model on subsequent movements.

Motor adaptation, in particular visuomotor adaptation, has been studied extensively in the lab (Bastian, 2008; Krakauer, 2009; Vetter et al., 1999). In a typical visuomotor adaptation paradigm, participants are introduced to a new visuomotor environment, such that visual feedback regarding their hand position is misaligned from their actual hand position (Cressman and Henriques, 2009; Krakauer, 2006; Krakauer et al., 2019; Severini and Zych, 2020). Visual feedback can be altered by having participants reach while wearing prism goggles (Redding and Wallace, 1993), or reach within a virtual reality environment, where a cursor on the screen misrepresents the position of one's hand in space (Krakauer, 2006; Krakauer et al., 2019). For example, the cursor's trajectory may be rotated 40° clockwise relative to hand motion. In this instance, the participant sees the cursor deviate 40° degrees to the right when reaching straight ahead. Participants would thus experience an error signal, such that the cursor does not move towards or land on the target as expected (Krakauer, 2009). This mismatch between expected sensory feedback and actual sensory feedback experienced creates a sensory prediction error as described above. It is this error signal that is proposed to lead to participants incrementally adjusting their reaches over trials in the absence of conscious awareness (Krakauer et al., 2000; Shadmehr et al., 2010).

Typical experiments examining visuomotor adaptation contain three testing phases (Cressman and Henriques, 2009; Krakauer et al., 2019; Mazzoni and Krakauer, 2006; Severini and Zych, 2020). In the first phase, the baseline phase, participants reach from a starting position to the target while receiving aligned cursor feedback, such that the cursor's position accurately represents their hand's position in space (Krakauer et al., 2019). These reaches establish participants' baseline level of performance. In the second phase, the adaptation phase, the visuomotor rotation is introduced. Participants initially mis-reach, such that the cursor does not

land on the target. For example, if the cursor is rotated 40° clockwise relative to hand motion, the cursor will land to the right of the target initially. However, over trials, participants adapt their reaches, such that they reach to the left of the target and the cursor once again lands on the target as desired. The final post-test phase requires participants to reach in the absence of visual feedback or when aligned cursor feedback is presented. In this last phase, the extent of visuomotor adaptation is established by comparing performance to the baseline phase. If a participant has adapted their movements, aftereffects will be present such that the participant will continue to reach to the left of the target, as if influenced by the visuomotor rotation. The presence of aftereffects is taken as evidence that the internal model has been updated and visuomotor adaptation has occurred (Bastian, 2008; Deuschl et al., 1996; Henriques and Cressman, 2012; Martin et al., 1996).

2.2. Explicit and Implicit Visuomotor Adaptation

Wolpert and colleagues (1995) suggest that the updating of the internal model arises implicitly (i.e., unconsciously). This updating of the internal model gives rise to the aftereffects observed in the post-test phase of the visuomotor adaptation paradigm, even when participants are instructed to aim to the target (Wolpert et al., 1995). Support for visuomotor adaptation arising implicitly is demonstrated by examining visuomotor adaptation in H.M., a patient diagnosed with anterograde amnesia. H.M. performed a version of a visuomotor adaptation task, in which he had to trace the shape of a star while looking at his own hand movements in a mirror (Milner, 1962). Similar to a cursor distortion introduced in a virtual reality environment, the mirror drawing task creates a discrepancy between the seen and felt locations of one's hand positions. Results indicated that while H.M. was unable to recollect having carried out the motor task in previous trials, improvements in task accuracy occurred over subsequent trials and across testing days (Milner, 1962), suggesting visuomotor adaptation did arise (Krakauer et al., 2019;

Stanley and Krakauer, 2013). Given the aforementioned evidence, it was concluded that visuomotor adaptation arises implicitly.

While traditionally visuomotor adaptation has been proposed to arise implicitly, lately there has been a focus on examining the potential contribution of explicit processes (i.e., conscious strategy) to visuomotor adaptation (see Mazzoni and Krakauer, 2006; Taylor, Krakauer and Ivry, 2014). In particular, explicit processes are proposed to be engaged when reaching with the visuomotor distortion during the adaptation phase. One of the first to suggest a contribution of explicit processes to visuomotor adaptation was Redding and Wallace (1993, 1994, 1996, 2000), who had participants reach while wearing prism goggles that laterally shifted the seen position of the target and reaching hand. Their results consistently showed a mismatch between the magnitude of aftereffects observed and the size of the visuomotor distortion introduced via the prism goggles in the adaptation phase, such that aftereffects were smaller in magnitude than the visuomotor distortion. According to Redding and Wallace (1993), if adaptation arose solely through implicit means, aftereffects would be equal in magnitude and opposite in direction to the visuomotor distortion experienced. Based on the discrepancy observed, Redding and Wallace (1993) theorized that participants compensated for the prism-induced reaching errors partially through a deliberate and explicit strategy (i.e., strategic recalibration) that could be voluntarily disengaged when the prism goggles were removed. They further suggested an implicit spatial realignment process was responsible for the aftereffects observed when the prisms were removed. According to Redding and Wallace (1993), strategic recalibration rapidly contributes to reducing initial errors through conscious changes in reaching, while spatial realignment gradually reduces reaching errors over time without conscious involvement.

Having proposed a role for explicit and implicit processes in visuomotor adaptation to a prism distortion, we next discuss the proposed contributions of explicit and implicit processes to visuomotor adaptation when a cursor distortion is introduced. In early work by Mazzoni and Krakauer (2006), they provided participants with a cognitive strategy to counteract the visuomotor rotation (i.e., participants were told to aim to a neighboring target, which would counteract the visuomotor rotation). Participants were successful in engaging in the strategy and hence negating the effects of the cursor rotation on initial trials. However, as trials progressed, participants made increasingly larger errors. Based on these results, Mazzoni and Krakauer (2006) argued that explicit processes may contribute to visuomotor adaptation initially during the adaptation phase, but that implicit processes then take over in order to resolve sensory conflicts arising from experiencing a sensory prediction error, regardless of explicit strategies being employed to mitigate task errors. In support of this proposal, recent work by Taylor et al. (2014) demonstrated that the contribution of explicit processes to visuomotor adaptation decayed over trials. In Taylor et al. (2014), the engagement of explicit processes led to large fluctuations in reaching errors in early trials as participants attempted to rapidly learn how to reach in the new visuomotor environment. In contrast, implicit adaptation increased over trials, contributing to visuomotor adaptation to a greater extent as trials progressed.

Findings by Benson, Anguera and Seidler (2011) corroborate the suggestion that explicit processes initially contribute to visuomotor adaptation. Their findings revealed that errors were greatly reduced in early adaptation trials when participants were provided with an explicit strategy to counteract the visuomotor rotation. However, participants who had been provided with an explicit strategy, demonstrated a smaller magnitude of aftereffects in the post-test phase, suggesting that engaging explicit processes during adaptation influenced the extent of implicit

adaptation achieved. In other words, increased engagement of an explicit strategy impeded the engagement of implicit processes (see also Neville and Cressman, 2018). While the engagement of explicit processes has been shown to influence implicit contributions to visuomotor adaptation, these processes have been suggested to arise independently (Bond and Taylor, 2015; Mazzoni and Krakauer, 2006; Sulzenbruck and Heuer, 2009).

Having established that explicit and implicit processes contribute to visuomotor adaptation, we next discuss methods put forth to assess their contributions. In particular, we focus on the process dissociation procedure (PDP) put forth by Jacoby in 1991. The PDP was originally introduced to dissociate the contributions of automatic processes (i.e., implicit) from intentional processes (i.e., explicit) in memory recognition tasks. Jacoby's method was then modified by Werner et al. (2015) to assess awareness of strategic changes in reaches (i.e., explicit processes), or lack thereof (i.e., implicit processes), in visuomotor adaptation. Within the PDP of Werner et al. (2015), participants are instructed to reach while (1) using what they have learned during adaptation trials (i.e., inclusion trials) and (2) refraining from using what they have learned and to perform their movements as during baseline trials (i.e., exclusion trials). Implicit adaptation is determined based on reaching errors on exclusion trials, while the difference in reaching errors between inclusion and exclusion trials establishes explicit adaptation.

Since Werner and colleagues' (2015) original work, the PDP has been used to examine explicit and implicit processes underlying visuomotor adaptation within multiple laboratories. For example, Neville and Cressman (2018) utilized the PDP to assess the contributions of explicit and implicit processes to visuomotor adaptation over time when participants adapted to different sized cursor distortions, while Modchalingham et al. (2019) assessed explicit and implicit contributions to visuomotor adaptation using the PDP in an experiment which

manipulated instructions given to participants regarding how to counteract the visuomotor rotation. In general, results show that explicit and implicit processes contribute to visuomotor adaptation, but these contributions are dependent on experimental manipulations during the adaptation phase (e.g., size of cursor distortion, instructions provided, etc.).

Recently, Heirani Moghaddam et al. (2021) assessed explicit and implicit contributions to visuomotor adaptation using the PDP over time and contrasted these results with the extent of explicit and implicit contributions as assessed by a second assessment method, the Verbal Report Framework (VRF). The Verbal Report Framework of Taylor and colleagues (2014) requires participants to reach to a target surrounded by an array of numbers. Before reaching, participants verbally declare which number they intend to reach towards in order to counteract the rotation (Taylor et al., 2014). The extent of explicit adaptation is considered to be the intended (i.e., verbally reported) reaching direction, while implicit adaptation is established to be the difference between reaching error and reported aiming direction. Results from Heirani Moghaddam et al. (2021) indicated that while the extent of explicit adaptation was similar across both methods of assessment, explicit adaptation assessed within the PDP correlated with one's reported awareness of the distortion presented, as well as reaching strategies engaged to counteract the rotation. In contrast, explicit adaptation established via the VRF did not reflect awareness of the visuomotor distortion at the end of the experiment, nor did it correlate to how participants consciously adapted their reaches (Heirani Moghaddam et al., 2021). Based on these results, we used the PDP to establish the contributions of explicit and implicit processes to visuomotor adaptation in the current experiment.

2.3. Mental fatigue

In order to examine the impact of mental fatigue on visuomotor adaptation, the concept of fatigue must first be defined. While ever present in daily life, mental fatigue is subjective, such that the perception of its onset and its effects are dependent on the individual. This individuality and subjectivity make it difficult to establish a universally accepted definition that encompasses all facets of mental fatigue (Enoka and Duchateau, 2016).

To understand mental fatigue, we first look to Chaudhuri and Behan (2000), who classified fatigue into peripheral and central components. In their classification, peripheral fatigue is attributed to strains in the mechanisms of the body, such as failure of neuromuscular transmission and metabolic disturbances, resulting in the body being unable to sustain movement (Chaudhuri and Behan, 2000). In contrast, central fatigue is represented as a failure to sustain the attention required to perform a task (Chaudhuri and Behan, 2000). Enoka and Duchateau (2016) expanded this classification and proposed their own taxonomy model for defining the broad concept of fatigue. In their model, fatigue is defined as a disabling symptom in which physical and cognitive functions are limited by interactions between performance fatigability and perceived fatigability. Performance fatigability represents the decline in an objective measure of performance over a discrete period of time, while perceived fatigability relates to changes in sensations that regulate the integrity of the performer (Enoka and Duchateau, 2016). This perceived fatigability is influenced by the maintenance of homeostasis in the body, as well as the psychological state of the individual performing the task, with contributing factors including level of arousal, mood, motivation, and performance feedback (Enoka and Duchateau, 2016). Taking these classifications into account, for the purpose of this research we define mental fatigue as “a psychobiological state caused by either prolonged and/or intense periods of demanding cognitive activity, and characterized by feelings of tiredness and lack of energy”

(Jacquet et al., 2021). This definition of mental fatigue of Jacquet et al. (2021) brings together the concepts of central fatigue as proposed by Chaudhuri and Behan (2000), and perceived fatigability as put forth by Enoka and Duchateau (2016).

According to Enoka and Duchateau (2016), fatigue, and hence mental fatigue as we have defined it, can only be measured using self-reports. Established self-reports for assessing mental fatigue include scaled questionnaires, such as the Fatigue Severity Scale (Krupp et al., 1989), the Mobility-Tiredness Scale (Fieo et al., 2013), the Modified Fatigue Impact Scale (Chwastiak et al., 2005), the Situational Fatigue Scale (Yang and Wu, 2005) and the Visual Analog Scale-Fatigue component (VAS-F) (Lee et al., 1991). These assessments vary in scope (Chaudhuri and Behan, 2004; Enoka and Duchateau, 2016; Borrigan et al., 2016). Within our research we assessed mental fatigue using 1 question from the VAS-F of Lee et al. (1991), which we refer to as the mental fatigue scale (MFS) within our experiment. Specifically, we evaluated participants' subjective experience of fatigue by asking them to indicate their feeling of mental fatigue on a visual analog scale, where the scale ranged from 0 (not at all fatigued) to 100 (extremely fatigued) (Lee et al., 1991; Figure 2.1).

Recently, Jacquet et al. (2021) looked to relate fatigue levels, measured using the same single item fatigue scale, to neural activity collected via electroencephalography (EEG). Results indicated a significant correlation between self-reported fatigue and brain activity. In particular, they found an increase in alpha power in the pre-frontal cortex during and after a mental fatiguing task, an accepted biomarker in the literature for representing a decreased level of arousal and alertness, as well as motor performance impairment (Boksem et al., 2005; Paus et al., 1997; Trejo et al., 2005; Zhao et al., 2012). These increases in alpha power correlated with participants reporting increased mental fatigue. Similarly, Cook et al. (2007) reported an

association between subjective feelings of mental fatigue as established by a single item from the VAS-F and changes in brain activity as revealed by functional magnetic resonance imaging (fMRI) following a mental fatiguing task. In particular, they saw an increase in activity in the cerebellum, as well as in the temporal, cingulate and frontal regions of the cortex, which have been shown to be important for cognitive functions (see Cabeza and Nyberg, 2000; Desmond et al., 1997; D'Esposito et al., 1995; Fletcher and Henson, 2001), in conjunction with higher self-reported mental fatigue. These studies present compelling evidence for the validity of using a single item mental fatigue scale (MFS) as a tool to establish subjective levels of mental fatigue.

Multiple theories have been put forth to explain why an individual experiences mental fatigue, including the underload theory (Manly et al., 1999), the dual regulation systems theory (Ishii et al., 2014) and the resource depletion theory (Sanders et al., 1997). According to the underload theory (Manly et al. 1999), introducing an activity that requires sustained high levels of mental processing in an environment of chronic under-stimulation will induce mental fatigue. On the other hand, the dual regulation systems theory (Ishii et al., 2014), proposes that a mental facilitation system and a mental inhibition system controlled by different areas of the central nervous system interact to raise or lower cognitive task performance. Following the onset of mentally demanding tasks, components of the mental inhibition system impair cognitive task performance over time, leading to a feeling of mental fatigue. On the other hand, the facilitation system works to improve task performance within the context of a highly demanding cognitive task but is not able to sustain this performance over a long period of time, also leading to mental fatigue. A third theory put forth to explain mental fatigue is the resource depletion theory proposed of Sanders et al. (1997). According to the resource depletion theory, attentional capacity is a limited resource that is drained progressively when engaging in a mentally

strenuous task, potentially leading to a state of mental fatigue (Sanders et al., 1997). While aspects of all three theories may be correct, recent research (e.g., Anguera et al., 2012; Jacquet et al., 2021) investigating the relationship between mental fatigue and motor control has looked to the resource depletion theory when choosing a task to induce mental fatigue. By designing a task that employs cognitive resources over a (long) period of time, mental fatigue has been shown to be reliably induced (Anguera et al., 2012; Jacquet et al., 2021).

There have been a number of experimental tasks used to induce mental fatigue (see Anguera et al., 2012; Cook et al., 2007; Jacquet et al., 2021). Typical tasks have the participant respond to a stimulus as fast as possible over a certain period of time to deplete attentional resources, or remember a sequence of numbers and letters to deplete working memory resources (Au et al., 2014). A concern when designing a task is the length of time that participants need to complete the task to experience mental fatigue. Longer duration tasks (e.g., 45-90 minutes) have the possibility of inducing both mental fatigue and boredom in participants. Thus, feelings of mental fatigue could arise due to an attentional deficit and/or lack of motivation due to boredom instead of mental strain (Chaudhuri and Behan, 2004). For example, the Stroop task, in which participants press a key on a keyboard to indicate the ink colour of a word presented on the screen, requires participants to complete over 480 trials in order for mental fatigue to be induced (Pageaux et al., 2015). This high number of trials is needed because of the low level of challenge presented in the task (Caseras et al., 2006; Magnuson et al., 2021). In order to decrease task time, more cognitively demanding tasks have been introduced to induce mental fatigue (Chaudhuri and Behan, 2004; Holtzer et al., 2010).

One example of a laboratory-based task commonly used to induce mental fatigue is the *n*-Back task (Chaudhuri and Behan, 2004; Manly et al., 1999; Jacquet et al., 2021), in which a

participant must recall if the letter being shown on the screen is the same as the one that was shown n -instances previous to the current one. This task has been shown to induce mental fatigue in only 30 minutes (Bruijell et al., 2022). A variation on the n -back task is the time load dual back task (TLDB) designed by Borrajan et al. (2016), which requires participants to recall letters and respond to interleaving integers at the same time (Figure 2.2). Using this task, Borrajan et al. (2016) reported that participants experienced mental fatigue within just 16 minutes. Furthermore, Jacquet et al. (2021) ran the TLDB task while monitoring EEG activity and determined that changes in self-reported mental fatigue and changes in alpha-waves arose within 32 minutes. In our experiment, we looked to establish mental fatigue using self reports on the single item MFS after participants completed 32 minutes of the TLDB task.

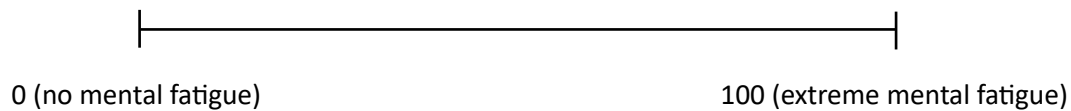


Figure 2.1. Mental Fatigue Scale: single item taken from the VAS-F

The VAS-F has been used to evaluate a participant's subjective feeling of mental fatigue (Lee et al., 1991). In this single item scale (MFS), participants are asked to indicate their feeling of mental fatigue by using a pen to mark the point on the line they feel best represents their current state of mental fatigue.

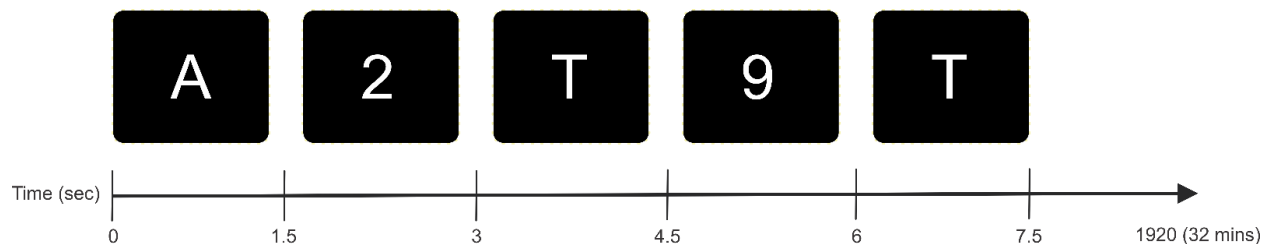


Figure 2.2. Timeline of the Time-Load Dual Back task used to induce mental fatigue.

An alternating sequence of letters and numbers, starting with letters, is shown on the screen. Participants are tasked with pressing the spacebar on a keyboard if the letter shown matches the one shown previously. In this example, the participant should press the spacebar in the 6.0 - 7.5 second interval of the sequence. Additionally, participants are tasked with pressing the number 2 if the number shown is even, and the number 3 if the number shown is odd for every number presented.

2.4. The effect of mental fatigue on visuomotor adaptation

To date, limited research has looked to establish the impact of mental fatigue on motor control. In general, mental fatigue has been shown to lead to a reduced level of alertness and impair information processing (Boksem et al., 2005, 2006; Wascher and Getzmann, 2014). Specifically, previous work from Lorist (2008) and Boksem et al. (2005) provides insight into the effect of mental fatigue on response planning within a reaction time task. Lorist (2008) determined that the influence of advance information on information processing diminished with increased mental fatigue. In other words, the ability to assimilate and process information (i.e., complete top-down processing) was reduced with increases in mental fatigue. Furthermore, Boksem et al. (2005) demonstrated that mental fatigue affects goal-directed attention, which utilizes top-down processing, while stimulus-driven attention, which utilizes bottom-up processing, remains largely untouched.

Expanding on the results of Lorist (2008) and Boksem et al. (2005), Magnuson et al. (2021) sought to quantify the impact of mental fatigue on both gross and fine motor control. Motor performance was evaluated via three tasks: a go/no-go task assessing inhibitory control, a pegboard task assessing fine motor control, and an object hit and avoid task assessing executive function and gross motor control (Magnuson et al., 2021). Results indicated that participants reported increased levels of mental fatigue after completion of the n-back task, as well as reduced motor performance on all three tasks. A mentally fatiguing task therefore impacted participants' ability to engage in gross and fine motor control functions necessary for performing reaches to a target in a task similar to the one that was carried out in our current experiment. Furthermore, within Magnuson et al.'s (2021) experiment, motor task performance continued to be impaired post completion of the mental fatigue task, such that it was not until approximately

15 to 40 minutes after completion of the mental fatigue task that performance on the motor tasks returned to baseline levels. In accordance with these findings, Jacquet et al. (2021) found the greatest performance decrements in movement time within an arm-pointing task 20 minutes after the induction of mental fatigue through a TLDB task. While it is evident that mental fatigue leads to decrements in upper limb reaching performance, it is unclear if visuomotor adaptation is also impaired.

To our knowledge, no studies have examined the impact of mental fatigue on visuomotor adaptation directly. Research has suggested that poor generalization of visuomotor adaptation may be due in part to a depletion in working memory resources imposed by an earlier adaptation task (Pine et al., 1996). Anguera et al. (2012) then went on to look at the influence of working memory resource depletion (WMRD) on visuomotor adaptation. In their research, they induced WMRD through the use of an n-back task. They found that WMRD lead to a reduction in the rate of early visuomotor adaptation, such that participants who had completed the n-back task demonstrated greater reaching errors in the early stages of visuomotor adaptation compared to control participants. While Anguera et al. (2012) focused specifically on working memory depletion as opposed to inducing mental fatigue per se, their results raise the possibility that mental fatigue may impact participants' ability to adapt to a visuomotor distortion. However, how mental fatigue impacts visuomotor adaptation with respect to the contributions of explicit and implicit processes remains to be determined.

2.5. Research question and hypothesis

While research investigating visuomotor adaptation and underlying processes has been extensive, the impact of a participant's level of mental fatigue on visuomotor adaptation has not been previously considered. In fact, investigations into the impact of mental fatigue on motor

control in general have been limited (see Anguera et al., 2012; Jacquet et al., 2021; Magnuson et al., 2021). The present research looked to determine the impact of mental fatigue on explicit and implicit contributions to visuomotor adaptation. Mental fatigue was induced in participants using a TLDB task, and confirmed through the use of our MFS. Visuomotor adaptation was then examined in a laboratory setting by having participants reach while experiencing cursor feedback that was rotated 40° CW relative to hand motion. Finally, explicit and implicit contributions to visuomotor adaptation were established via the Process Dissociation Procedure (PDP) by having participants reach while engaging in or refraining from engaging in strategic reaching.

Previous research suggests that mental fatigue leads to motor control deficits, demonstrated by longer movement times when reaching to targets following a TLDB task (Jacquet et al., 2021). Furthermore, Anguera et al. (2012) reported a lower level of visuomotor adaptation in early adaptation trials following a working memory depletion task, where early trials have been suggested to engage explicit processes (see Mazzoni and Krakauer, 2006; Taylor et al., 2014). Based on these results, we hypothesized that mental fatigue would reduce the extent of explicit adaptation observed in visuomotor adaptation, while leaving implicit adaptation largely unaffected.

CHAPTER 3. EXPERIMENT

3.1 Abstract

To date, mental fatigue has been shown to lead to a general decline in cognitive processing and motor performance. The goal of the current research was to establish the impact of mental fatigue on the contributions of explicit (i.e., conscious strategy) and implicit (unconscious) processes to visuomotor adaptation. Participants were divided into Mental Fatigue (MF) and Control groups. Mental fatigue was induced through a time load dual back task (TLDB), in which participants were required to respond as quickly and accurately as possible to letters based on recall of previously presented letters, as well as digits displayed on the screen in a choice reaction time task. The TLDB task lasted for 32 minutes, and the Control group watched a documentary for a similar length of time. Subjective feelings of mental fatigue, as indicated on a self-report scale, demonstrated that mental fatigue was significantly higher for the MF group after completion of the TLDB task. There was no similar increase in mental fatigue for the Control group. The increased mental fatigue was associated with decreased visuomotor adaptation to a 40° cursor rotation and retention of visuomotor adaptation. In particular, participants in the MF group adapted their reaches to a lesser extent early in training compared to the Control group and demonstrated less retention of visuomotor adaptation following a 20-minute rest. Furthermore, correlational analyses established that greater mental fatigue reported by participants in the MF group was associated with less explicit adaptation and greater implicit adaptation. Taken together, these results suggest that mental fatigue decreases the ability to engage in explicit processing, limiting the overall extent of visuomotor adaptation achieved.

3.1. Introduction

Mental fatigue is defined as “a psychobiological state caused by either prolonged and/or intense periods of demanding cognitive activity, and characterized by feelings of tiredness and lack of energy” (Jacquet et al., 2021). Perception of mental fatigue is subjective, varying between individuals (Enoka and Duchateau, 2016). Thus, it has been suggested that mental fatigue is best established through self-reports (Enoka and Duchateau, 2016). For example, one can track changes in participants’ mental fatigue via responses on a subjective questionnaire, such as Lee et al.’s (1991)’s Visual Analog Scale for Fatigue (VAS-F), before and after a cognitive demanding activity. Within the VAS-F, one question asks participants to specifically indicate their subjective feeling of mental fatigue on an analog scale ranging from 0 (no mental fatigue) to 100 (extreme mental fatigue), which we will refer to as the mental fatigue scale (MFS). Responses to this question have been correlated to neural biomarkers of mental fatigue (Jacquet et al., 2021, Wang et al., 2016), establishing the validity of using this single question to evaluate subjective changes in mental fatigue.

To date, research has focused on determining the influence of mental fatigue on cognitive performance, with results indicating that mental fatigue leads to a reduced level of alertness and impairs information processing (Boksem et al., 2005, 2006; Lorist et al., 2000; Norman and Shallice, 1986; Wascher and Getzmann, 2014). More recently, there has been a shift in research focus, looking to establish the influence of mental fatigue on motor control (e.g., Jacquet et al., 2021; Magnuson et al., 2021). Within these experiments, mental fatigue is typically induced through a task that requires continuous input from the participant over a period of time. For example, within the Time Load Dual Back (TLDB) task of Borrajan et al (2016), participants must press a key in response to a series of alternating letters and numbers presented on a computer monitor every 1.5 seconds. For every letter shown, the participant is to press the

spacebar on a keyboard if the letter corresponds to the previous letter presented. For every number, the participant is to complete a choice reaction time task, such that they press the “2” key on the number pad if the number is even and the “3” key if the number is odd as fast and accurately as possible. This task has been shown to induce increases in mental fatigue after completing the task for 32-minutes and responses on the single item MFS indicate that mental fatigue continues to persist even 20 minutes after task completion (Jacquet et al. 2021).

After inducing mental fatigue through the TLDB task, Jacquet et al. (2021) assessed changes in the time it took for participants to complete goal directed reaches (i.e., examined changes in movement time). Participants were required to reach as quickly and accurately as possible to targets of varying width and distance from a starting position. Results indicated a decrement in performance immediately following the TLDB task, such that movement times were longer than prior to completing the TLDB task. In addition to these findings, Magnuson et al. (2021) recently showed that mental fatigue impacts gross and fine motor control. Similar to Jacquet et al. (2021), mental fatigue was induced through the TLDB task. Motor performance was then evaluated via three tasks: a go/no-go task to assess inhibitory control, a pegboard task to assess fine motor control, and an object hit and avoid task to assess executive function and gross motor control (Magnuson et al., 2021). Participants took significantly more time to complete the pegboard task, and hit a greater number of distractor shapes on the object hit-and-avoid task compared to performance prior to mental fatigue induction. Magnuson et al. (2021) then went on to show that motor performance returned to pre-fatigue levels between 15-40 minutes following completion of the TLDB task, demonstrating a relatively quick recovery of the impact of mental fatigue on motor performance.

In the current experiment, we looked to expand this line of inquiry, focusing on establishing the influence of mental fatigue on motor learning. According to Krakauer et al. (2019), motor learning incorporates both skill acquisition and skill maintenance, where skill maintenance is the ability to maintain movement performance under changing conditions. The current research examined the impact of mental fatigue on skill maintenance, or as we refer to it, motor adaptation. Our capacity to adapt our movements to environmental changes is critical to ensure continued task success. In a laboratory setting, visuomotor adaptation can be examined by having participants reach in a novel visual environment. For example, participants reach from a home position to a target using a robot manipulandum, while the position of their hand is misrepresented on the screen by a cursor. Specifically, the cursor's trajectory can be rotated clockwise (CW) or counter clockwise (CCW) relative to a participant's actual hand motion (Cressman and Henriques, 2009; Krakauer, 2006; Krakauer et al., 2019; Severini and Zych, 2020). When first reaching with the rotated cursor feedback, participants typically experience an error, such that the cursor does not land on the target as expected. Over training trials, participants adjust their reaches to counteract the cursor rotation (Cunningham, 1989; Krakauer, 2006; Krakauer et al., 2019; Mazzoni and Krakauer, 2006; Taylor et al., 2014, Wigmore et al., 2002). Furthermore, when the cursor rotation is removed, participants display 'aftereffects', such that they continue reaching as if the cursor rotation is still present (Bastian, 2008; Deuschl et al., 1996; Henriques and Cressman, 2012; Martin et al., 1996).

The presence of aftereffects is proposed to reflect implicit (i.e., unconscious) visuomotor adaptation and arises due to participants experiencing a sensory prediction error, such that the sensory feedback arising from their movement does not reflect expected sensory feedback (Bastian, 2008; Deuschl et al., 1996; Henriques and Cressman, 2012; Martin et al., 1996;

Wolpert et al., 1995). Recent findings suggest that explicit processes (i.e., conscious strategy) may also be engaged during training trials when the cursor rotation is present (Mazzoni and Krakauer, 2006; Taylor, Krakauer and Ivry, 2014, Werner et al., 2015). Explicit processes are thought to contribute to visuomotor adaptation in the early stages of reach adaptation, with their contribution decaying over trials. In contrast, implicit processes have been shown to arise later and contribute to a greater extent as training trials progress (Mazzoni and Krakauer, 2006; Neville and Cressman, 2018; Taylor et al., 2014).

The contributions of explicit and implicit processes to visuomotor adaptation have been established through the use of the Process Dissociation Procedure (PDP; Werner et al., 2015). Within the PDP of Werner et al. (2015), participants are instructed to reach while (1) using what they learned during training trials (i.e., inclusion trials) and (2) refraining from using what they learned and to reach directly to the target (i.e., exclusion trials). Implicit adaptation is determined based on reaching errors on exclusion trials, while the difference in reaching errors between inclusion and exclusion trials is used to establish explicit adaptation.

To date, visuomotor adaptation and the processes underlying visuomotor adaptation have been studied extensively under ‘ideal’ conditions in a laboratory setting, which are not necessarily reflective of daily life. For example, previous investigations into visuomotor adaptation have not considered the potential impact of mental fatigue. According to an American survey conducted by the National Sleep Foundation in 2020, altered states of consciousness and reduced alertness permeate our day to day lives, such that on average, adults feel tired 3 days a week, with 28% of respondents stating that they felt tired 5-7 days a week (NSF, 2020).

The goal of the current experiment was to determine the impact of mental fatigue on explicit and implicit contributions to visuomotor adaptation. Two groups of participants (Mental

Fatigue (MF) and Control groups) initially reached with aligned cursor feedback. Following this, mental fatigue was induced in the MF group of participants through the TLDB task of Borrigan et al. (2016). All participants then reached with rotated cursor feedback in an adaptation phase for 45 trials, such that the cursor motion was rotated 40° CW relative to hand motion. Explicit and implicit adaptation were assessed following rotated reach training using the PDP (Modchalingham et al., 2019; Neville and Cressman, 2018; Werner et al., 2015). Participants completed the rotated reach training trials and PDP trials 3 more times to track explicit and implicit contributions to visuomotor adaptation over time, with the final block administered following a 20-minute rest in order to assess retention. Throughout the experiment, mental fatigue was assessed by having participants complete the MFS adapted from Lee and colleagues' (1991) VAS-F. Given that mental fatigue has been shown to impact reaching performance (see Jacquet et al., 2021; Magnuson et al., 2021), it was hypothesized that mental fatigue would impact visuomotor adaptation. Specifically, it was hypothesized that the MF group would take more trials to adapt their movements to the visuomotor distortion than the Control group. Furthermore, it was hypothesized that explicit contributions to visuomotor adaptation in the MF group would be affected to a larger extent than implicit contributions, such that explicit visuomotor adaptation as established via the PDP trials would be less in the MF group compared to the Control group over the course of the experiment. These results would indicate that mental fatigue impacts the conscious strategic component of visuomotor adaptation, while leaving the unconscious contribution largely unaffected.

3.2. Methods

3.2.1. Participants

40 participants (26 females) between the ages of 18-40 years (Mean age = 19.8 years, SD = 1.7 years) were recruited from the University of Ottawa and surrounding community to participate in this study. An a priori power analysis using G*Power 3.1 with the following input parameters: a power of 0.8, expected effect size of 0.89 (based on the results of Neva et al., 2019) and a Type 1 error (alpha) probability of 0.05, revealed a total sample size of 12 participants was required. However, participant number was increased to 40 in order to match previous research (see Jacquet et al., 2021). Participants were randomly assigned to one of two groups: (1) Mental Fatigue (MF, $n = 20$) or (2) Control ($n = 20$), with the same number of male and female participants in both groups (MF = 13 females; Control = 13 females).

All participants were naïve to the scope and purpose of the study and had never participated in a visuomotor adaptation experiment before. Participants were healthy, such that they reported no history of neurological disorders and/or sensorimotor dysfunction. As well, participants had normal or corrected-to-normal vision and all participants were right-handed (Edinburgh Handedness Questionnaire Mean Score = 85.5, SD = 15.0; Oldfield, 1971)

Upon arriving at the laboratory, participants confirmed they had slept for at least 7 hours the previous night, and had not consumed alcohol or engaged in strenuous physical activity the day (i.e., 24 hours) prior to the experiment. Furthermore, they indicated they had not consumed caffeine and/or nicotine in the 3 hours prior to the start of testing. In attempt to control for different levels of cognitive effort present in each participant's day, data were collected before 1 pm.

3.2.2. Experimental Overview

General Overview

The experiment was completed in a single testing session that lasted approximately two hours. In general, participants were required to complete three tasks; (1) the mental fatigue scale (MFS), (2) a Time-load Dual Back (TLDB) task or quiet rest, and (3) reaches to visual targets. See Figure 3.1 for an overview of the different tasks completed over the course of the experiment.

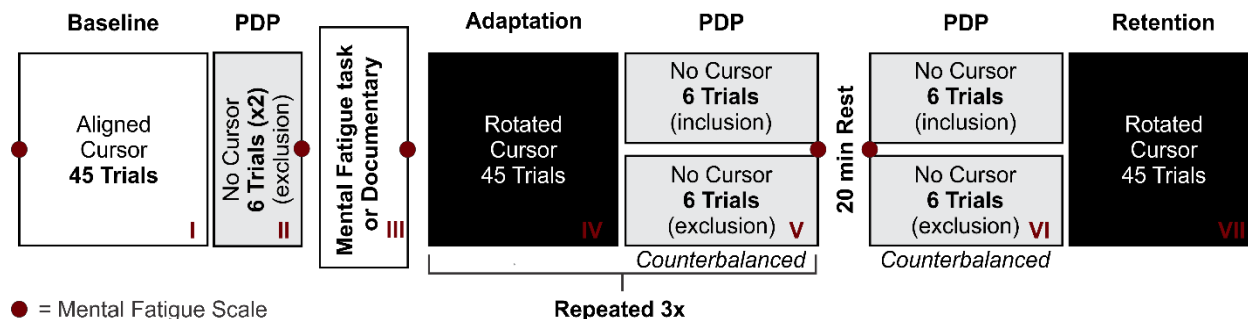


Figure 3.1. Experimental procedure. The experiment began with 45 aligned reach training trials (i.e., baseline), followed by 12 no cursor exclusion trials. This was followed by participants completing either a 32-minute fatigue protocol (MF group), or rest period (Control group). Following this, 45 rotated reach training trials were completed followed by 6 no cursor exclusion and inclusion trials. The sequence of rotated reach training trials and no cursor reaches was completed 3 times. All participants then completed a 20-minute rest period. Finally, participants completed 6 no cursor exclusion and inclusion trials followed by 45 rotated reach training trials to assess retention. The MFS was administered to participants 7 times over the course of the experiment, as indicated by placement of the red dots, to track subjective feelings of mental fatigue throughout the experiment.

All participants began the experiment by completing the MFS to establish initial levels of mental fatigue. Participants then reached in a typical environment, such that the cursor motion was aligned with their hand motion. These reaches were used to establish baseline performance. Participants then completed a block of reaches with no cursor feedback (i.e., see exclusion trials below) to determine how they reached to a target in an environment where no visual feedback was presented. Both groups then completed the MFS a second time to confirm initial levels of mental fatigue. Following this, the MF group completed the TLDB mental fatigue task, while the Control group watched a documentary for 32 minutes. Following the TLDB task or control conditions, both groups once again completed the MFS to evaluate changes in mental fatigue. Following this, the visuomotor cursor rotation was introduced. Both groups completed a block of rotated reach training trials as described below, followed by a block of no cursor reaches, which consisted of exclusion and inclusion trials. Following the no cursor reaches, participants again completed the MFS. Participants repeated the previous sequence of rotated reach training trials,

no cursor reaches and MFS assessment two more times. Following a 20-minute rest, participants then completed the MFS for a final time, followed by a final block of no cursor reaches and rotated reach training trials.

Mental Fatigue Scale (MFS)

Participants completed the MFS a total of 7 times over the course of the experiment (see Figure 3.1). Within the MFS, participants used a pen to annotate on a 10 cm line spanning from 0 to 100 their present feeling of mental fatigue, with 0 representing no mental fatigue at all and 100 representing extreme mental fatigue. After completing the MFS each time, the form was collected from the participant.

TLDB task or Rest

Participants in the MF group completed the TLDB of Borragan et al. (2016). This mental fatiguing task began with participants sitting in front of a computer screen (Dell P2210 - 22" Flat Panel Monitor; Refresh rate: 60Hz). Participants were informed of the two-component nature of the task. First, participants needed to pay attention to the white letters displayed on the black screen, which were from the following set of 8 letters: A, C, T, L, N, E, U and P. Letters were displayed in Arial font (size 16) in the middle of the screen for 1.5 seconds in duration. If the letter on the screen was the same as the previous letter shown, participants were to press the spacebar with their left index finger to indicate a match. Secondly, alternating with the letters shown on the screen, a number from a set of integers (1, 2, 3, 4, 6, 7, 8, 9) flashed on the screen for 1.5 seconds in duration. Participants were required to use their right index finger to press the number 2 on the keyboard if an even integer was displayed and the number 3 on the keyboard with their right middle finger if an odd integer was displayed. Letters and numbers alternately flashed on the screen for a total task time of 32 minutes (i.e., 1260 items were displayed) and participants were to make their responses as fast and accurately as possible. During this time, the

Control group watched a documentary for a time equal to the TLDB task duration (i.e., 32 minutes; Animal by BBC, Season 1 ep. 1: Big Cats; Netflix, Inc.).

3.2.3. Reaching task – Visuomotor Adaptation

Apparatus

Testing took place using the KINARM End-Point Lab (KINARM Technologies, Kingston, ON). As shown in Figure 3.2, visual targets were projected from a downward facing monitor (LG 47LD452B-UA EzSign – 47” LCD TV; refresh rate: 60Hz), located 20.5 cm above a reflective surface that was located 20.5 cm above the robot handle, ensuring that visual stimuli appeared to lie in the same horizontal plane as the right hand holding the robot handle. Participants seated themselves in a height and tilt adjustable chair located in front of the experimental apparatus. Participants adjusted the positioning of the chair so that their forehead rested against the testing apparatus, and they could reach comfortably to all targets presented within the workspace. Once comfortable, the position of the chair was maintained throughout all reaching trials. Participants’ view of their limbs was occluded by the reflective surface and a black cloth that was draped around their neck and attached to the apparatus. The room lights were also turned off.

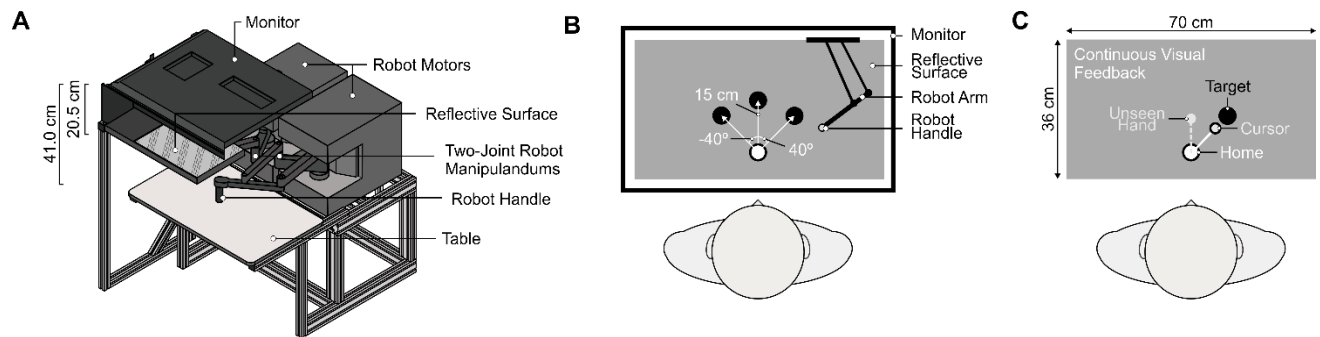


Figure 3.2. Experimental apparatus and position of the body, unseen hand, target and cursor during the reaching trials. **A.** View of the KINARM experimental apparatus. Participants grasped the robot manipulandum with their right hand. While reaching, participants did not have direct vision of their hand, but could see visual (i.e., cursor) feedback regarding the position of their hand. **B.** Aerial view of the 3 target positions participants reached to during the reaching trials. The first target was 15 centimeters in front of the home position, while the other two targets were 15 cm from the home position at 40° to the right and left of center. **C.** Example of a reach training trial in which cursor feedback was rotated 40° clockwise relative to hand motion. Participants needed to reach 40° to the left of the target to compensate for the rotated cursor feedback and have the cursor land on the target.

Reach training trials

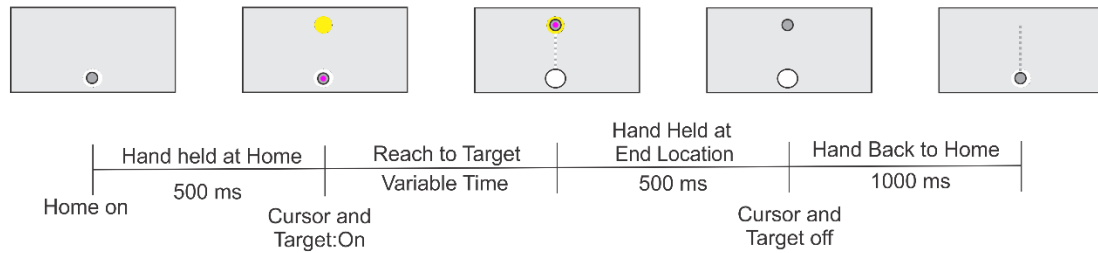
During the aligned (baseline) reach training trials, participants grasped the robot handle with their right hand. A trial began with the participant's hand held in the home position for 500 ms, where the home position (white circle, 2 cm in diameter) was located approximately 20 cm in front of their chest, in line with their body midline (Figure 3.2B). After 500 ms, one of three targets appeared (yellow circle, 2 cm in diameter) at a distance of 15 cm from the home position. The targets appeared straight ahead of the home position (central 0° target) or 40° to the left or right of center. Participants were instructed to reach to the target with the goal of having the cursor land on the target. Real-time visual feedback of the hand position was provided by the cursor on the screen (magenta circle, 1 cm in diameter) throughout the movement. Once the cursor landed on the target, (i.e., the center of the cursor and the center of the target were within 0.5 cm), the hand was held at this position for another 500 ms. The cursor and target then disappeared. Finally, the robot passively moved the hand back to the home position following a

direct, linear path in a movement time of 1000 ms. If participants attempted to move outside of the linear path, a resistance force (proportional to the depth of penetration with a stiffness of 2 N/mm and a viscous dampening of 5 N/mm) perpendicular to the grooved path was produced. The position of the KINARM robot was recorded at a sampling rate of 1000 Hz, with a spatial accuracy of 0.1 mm. Participants completed 45 aligned reach training trials at the beginning of the experiment. See Figure 3.3 for a timeline of events for aligned reach training trials.

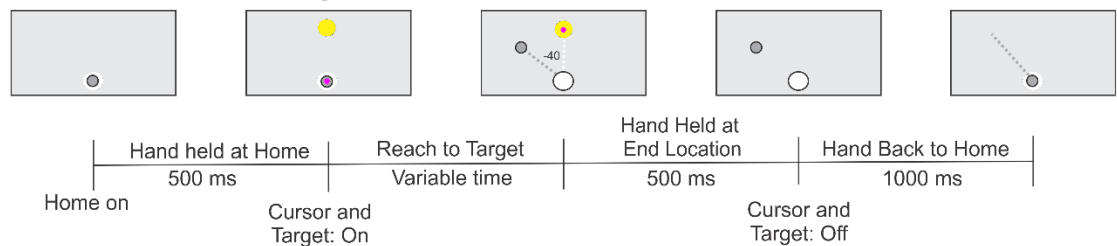
The rotated reach training trials proceeded in a similar manner. However, this time, the cursor feedback representing the position of the hand in space was rotated 40° clockwise (CW) relative to the participant's hand trajectory. Participants were not made aware of the rotation ahead of time, nor given instructions on how to counteract the visuomotor rotation, and no questions regarding the rotation were answered. As shown in Figure 3.1, participants completed 4 blocks of 45 rotated reach training trials over the course of the experiment following the induction of mental fatigue in order to determine how visuomotor adaptation changed over time in a fatigued state.

○ Home Position ● Unseen Hand Position ● Target Position ● Cursor Position

A: Aligned Cursor Reach Training Trials



B: Rotated Cursor Reach Training Trials



C: No Cursor Reach Trials

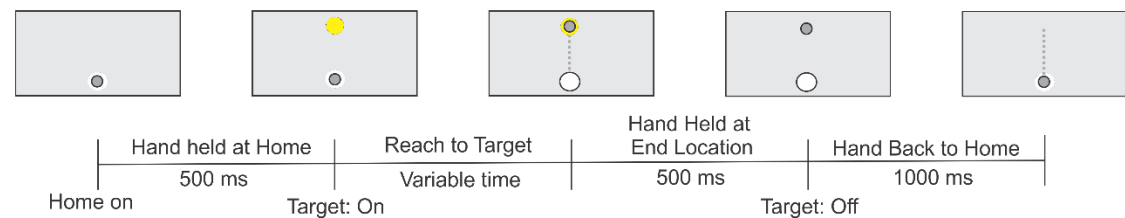


Figure 3.3. Timeline of reaching trials. **A.** Aligned reach training trials. Participants reached to a target with aligned cursor feedback. **B.** Rotated reach training trials. Participants reached to a target with rotated cursor feedback, such that the cursor's trajectory was rotated 40° clockwise relative to hand motion. **C.** No cursor reach trials. Participants reached to a target without receiving any visual feedback regarding their hand's position in space.

No cursor reaches

In these reaches, participants reached when no cursor feedback was displayed. Following aligned and rotated reach training, participants performed no cursor reaches under exclusion instructions. Specifically, they were instructed:

“You are now going to reach when you cannot see your hand, as there will be no cursor on the screen. For these trials, do not use anything you may have learned to get the cursor to the target. Instead, aim so that your hand goes straight to the target as you did during the baseline reaches.”

Participants performed 12 exclusion trials following the block of aligned reach training (4 trials to each target) and 6 exclusion trials following each block of rotated reach training (2 trials to each target).

When completing the block of no cursor reaches following rotated reach training, participants also performed 6 reaches under the inclusion instruction:

“You are now going to reach when you cannot see your hand, as there will be no cursor on the screen. For these trials, use anything you have learned during training in order to get the cursor to the target. In other words, aim so that the cursor would have gone straight to the target, as in the training trials you just completed.”

During the no cursor trials, participants reached to the target with no visual feedback and held the handle at the location they assumed to best correspond with the target. Once the velocity of their movement dropped below 0.01 m/s for more than 100 ms, the reach was considered complete.

The hand was then held at the final position for 500 ms before the robot handle brought the hand back to the home position. The order in which inclusion and exclusion trials were completed was counterbalanced across participants.

3.4. Data Analysis

3.4.1. MFS: assessment of fatigue

Responses on the MFS were determined for each participant for each of the 7 times it was completed. Responses for each participant were measured in millimeters between 0 to 100

according to the location on the continuous line at which participants indicated their level of mental fatigue, where 0 represented reporting no mental fatigue and 100 represented reports of extreme mental fatigue. A 2 Group (MF vs. Control) x 7 Time (i.e., each time the MFS was completed) mixed analysis of variance (ANOVA) with repeated measures (RM) on the last factor was conducted to establish changes in mental fatigue over the course of the experiment.

3.4.2. TLDB: induction of fatigue

Performance on the TLDB task for the MF group was evaluated by assessing response accuracy and time of responses (i.e., reaction time) relative to stimulus presentation. This analysis was performed for both types of stimuli presented (i.e., letters and digits). Accuracy was measured as the number of correct responses based on stimulus type (i.e., pressing (or not pressing) the spacebar when the current letter had appeared (or not appeared) previously; pressing the “2” (or 3) key when an even (or odd) number was shown). Reaction time for all responses was measured as the time taken to press a key after the presentation of each stimulus. Mean accuracy and reaction time for the letter and digit responses were determined for 4 time intervals (t1, t2, t3 and t4), with each time interval representing 25% of the total number of trials completed (i.e., 315 trials of the total 1260 trials), and analyzed within a 2 Stimulus Type (letters vs. digits) x 4 Time Interval (t1-4) ANOVA with RM on both factors.

3.4.3. Reaching Trials: Visuomotor adaptation

All reaching trials (i.e., aligned reach training trials, rotated reaching trials and no cursor reaches) were analyzed using custom MATLAB programs. For each trial, movement onset and termination were first determined. These events were defined as the first point in time in which resultant velocity increased above or decreased below 0.01 m/s and was maintained above or below 0.01 m/s for 100 ms, respectively. Movement time (MT), the time from movement onset to termination, was determined for each trial, as well as peak velocity angular error (PVAE),

where PVAE is the difference, in degrees, between a vector connecting the home position to the desired target and a vector connecting the home position to the position of the hand at resultant peak velocity.

PVAE was used to screen for outliers, such that trials were considered outliers if their absolute PVAE was more than 3 standard deviations above the mean PVAE of the corresponding block of trials. In total, 84 trials were initially identified as outliers. However, 32 of these trials were the first trial of a rotated reach training block, and showed similar PVAE to the aligned reach training trials, as expected. Thus, these trials were kept in the analysis, leading to the removal of 52 trials in total (or 0.46% of all trials).

Initial Adaptation: Early training

The mean PVAE of the first 15 aligned reach training trials was compared between the MF and Control groups using an independent samples t-test to check for differences between groups with respect to baseline reaching performance. We then determined the impact of mental fatigue on initial reach adaptation by comparing mean PVAE of the first 15 rotated reach training trials, across the 4 rotated training blocks, between the MF and Control groups. Specifically, the first 15 trials within each of the 4 rotated reach training blocks were first separated into 5 bins of 3 trials (i.e., trials 1-3; 4-6; 7-9; 10-12; 13-15) and the corresponding mean PVAE determined. Each bin of trials was normalized by subtracting the mean PVAE of the last 15 aligned reach training trials from the average of each bin. The normalized mean PVAE of each bin was then compared across groups in a 2 Group (MF vs. Control) x 4 Block (1st, 2nd, 3rd adaptation vs. retention block) x 5 Bin mixed ANOVA with RM on the last two factors.

Final Adaptation: Late training

The mean PVAE of the last 15 trials of aligned reach training trials were compared between the MF and Control groups using an independent samples t-test. Then, final levels of

reach adaptation were compared across groups. To do this, the mean PVAE was found for the last 15 trials of the 4 rotated training blocks. These values were again normalized relative to the average of the last 15 trials of the aligned reach training trials and compared across groups in a 2 Group (MF vs. Control) x 4 Block (1st, 2nd, 3rd adaptation vs. retention block) mixed ANOVA with RM on the last factor.

No cursor reaches

To assess the contributions of explicit and implicit adaptation to visuomotor adaptation, the no cursor trials were analyzed. The average PVAE of the no cursor reaches following the aligned cursor block were compared between the MF and Control groups in an independent samples t-test in order to ensure the two groups did not differ with respect to baseline reaching errors. The implicit index (II) was determined for each set of exclusion trials completed following rotated reach training (blocks V and VI, Figure 3.1) according to the following formula:

$$\text{Implicit index (II)} = M_{\text{PVAE Exclusion trials}}$$

The explicit index (EI) was calculated from the same blocks of trials following rotated reach training (blocks V and VI, Figure 3.1) according to the following formula:

$$\text{Explicit index (EI)} = M_{\text{PVAE Inclusion trials}} - \text{II}$$

Where M_{PVAE} is the average PVAE of the 6 exclusion or 6 inclusion trials that a participant completed. Each index was normalized by subtracting the M_{PVAE} of the corresponding exclusion trials completed following aligned reach training (block II, Figure 3.1) to establish explicit and implicit adaptation. Specifically, mean PVAE was calculated for the first and second set of 6 exclusion trials following aligned reach training. If participants completed exclusion (or

inclusion) trials immediately after rotated reach training, then the mean PVAE of the first 6 exclusion trials following aligned reach training was subtracted from the II (or EI). If participants completed the exclusion (or inclusion) trials after the inclusion (or exclusion) trials following rotated reach training, then the mean PVAE of the last 6 exclusion trials following aligned reach training was subtracted from the II (or EI). These calculations led to explicit adaptation being in the incorrect direction for 14 of the 160 values calculated (i.e., explicit adaptation was to the right of the target). These 14 values were removed from analysis and values imputed using the linear interpolation function in IBM SPSS Statistics for Windows version 28.0. Explicit and implicit adaptation were then compared between groups in a 2 Group (MF vs. Control) x 4 Block (1st, 2nd, 3rd rotation vs. retention block) mixed ANOVA with RM on the second factor.

Correlations between both explicit and implicit adaptation and changes in mental fatigue were carried out for both the MF and Control groups. A participant's explicit and implicit adaptation were defined as their average explicit and implicit adaptation across the 4 blocks of no cursor reaches following rotated reach training, while changes in mental fatigue were taken to be the difference between the mental fatigue score indicated immediately post TLDB task (MF group) or Documentary watching (Control group), and initial mental fatigue score indicated at the start of the experiment. In total, 4 correlations were performed, as explicit adaptation and implicit adaptation were correlated to changes in mental fatigue for both the MF and Control groups.

The significance value for all statistical tests was set at $p < 0.05$ and Bonferroni post-hoc tests corrected for multiple comparisons were completed for all preplanned comparisons.

3.5. Results

3.5.1. Mental Fatigue

Reports of mental fatigue over the course of the experiment are displayed in Figure 3.4A. ANOVA revealed a non-significant main effect of Group, such that both groups reported similar mean mental fatigue across the experiment (MF: $\bar{X} = 32.7$, $SE = 3.8$; Control: $\bar{X} = 26.9$, $SE = 3.8$; $F(1, 38) = 1.19$, $p = .283$). However, mental fatigue did differ across Time ($F(6, 228) = 29.47$, $p < .001$), and there was a significant Group x Time interaction ($F(6, 228) = 5.11$, $p < .001$). Post-hoc analysis revealed that initial (Time 1) mental fatigue reported was on average 18.2 ($SE = 3.3$) for the MF group and 16.5 ($SE = 4.1$) for the Control group, which did not differ from each other ($p = .747$). Mental fatigue did not differ from initial values for the Control group until the end of the second rotated training block (Time 5: $\bar{X} = 32.6$, $SE = 4.8$), at which time it increased significantly from Time 1 ($p = .006$). Mental fatigue then decreased back to initial levels following the rest period (Time 7: $\bar{X} = 26.5$, $SE = 3.9$; $p = .381$). As for the MF group, mental fatigue increased significantly immediately following the completion of the TLDB task (Time 3), such that mental fatigue was 29.5 points higher relative to initial mental fatigue reported ($p < .001$). This increase in mental fatigue was greater than that reported by the Control Group (MF group: $\bar{X} = 47.7$, $SE = 5.4$; Control group: $\bar{X} = 27.7$, $SE = 5.4$; $p = .013$). Finally, this elevated mental fatigue score was maintained until following the rest period, at which time mental fatigue did not statistically differ from initial scores reported by the MF group (Time 7: $\bar{X} = 19.0$, $SE = 3.9$; $p = 1.00$) or from the Control group at Time 7 ($p = .187$).

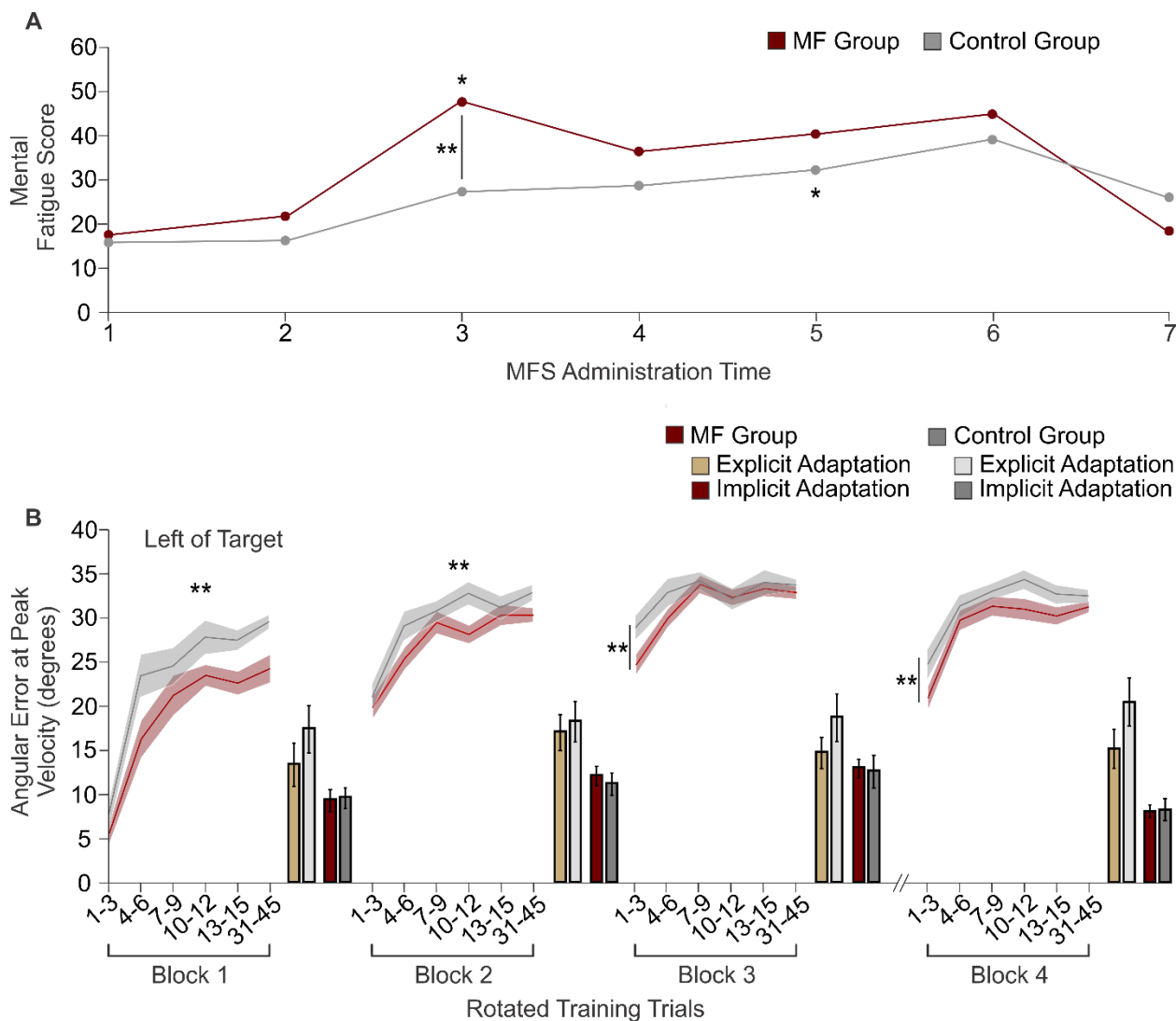


Figure 3.4. A. Mental fatigue scores for the MF group (burgundy) and Control group (grey) reported across the experiment. Asterisks (*) represent significant differences relative to baseline levels of mental fatigue ($p < .05$). **B.** Angular errors at peak velocity across blocks of rotated reach training trials. Data displayed are the average of 3 training trials early in each block (trials 1 – 15), or the last 15 training trials at the end of each block. Explicit and Implicit adaptation are presented as bars following each rotated training block. Explicit and implicit contributions for the MF group are represented by gold and garnet bars respectively, whereas for the Control group they are represented by light grey and grey bars respectively. Shaded regions and error bars represent standard errors of the mean. Double asterisks (**) represent significant differences between groups ($p < .05$).

3.5.2. Time Load Dual Back Task

Results related to the TLDB task are shown in Figure 3.5. Participants were accurate in responding to both letters and numbers across the 4 time intervals (e.g., Time Interval 1: $\bar{X}$

accuracy = 85.7%, SE = 2.2%; Time Interval 4: $\bar{X}$ accuracy = 89.9%, SE = 1.8%), surpassing the 80% benchmark that was set to indicate participant engagement in the task (Jacquet et al., 2021). ANOVA revealed a significant main effect of Time Interval with respect to percentage of correct responses ($F(3, 114) = 8.742, p < .001$), such that participants improved in accuracy from the 1st to the 2nd time interval for both stimulus types (Time Interval 1: $\bar{X}$ accuracy = 85.7%, SE = 2.2%; Time Interval 2: $\bar{X}$ accuracy = 89.3%, SE = 2.1%; $p < .001$). ANOVA did not reveal a significant main effect of Stimulus Type ($F(1, 38) = 1.395, p = .245$) or significant Stimulus Type by Time Interval interaction ($F(3, 114) = 1.465, p = .238$), indicating that participants responded with similar accuracy to letters and numbers.

As seen in Figure 3.5B, reaction time was higher overall when responding to letters compared to numbers ($F(1, 38) = 99.4, p < .001$). ANOVA also revealed a significant Stimulus Type x Time Interval interaction ($F(3, 114) = 3.99; p = .010$), with post hoc analysis indicating that reaction time for letters remained constant, showing no difference between the first and fourth time interval ($p = .964$). In contrast, reaction time for numbers decreased over the duration of the task (Time Interval 1: $\bar{X} = 0.797$ sec, SE = 0.03 sec; Time Interval 4: $\bar{X} = 0.731$ sec, SE = 0.032 sec; $p = .003$)

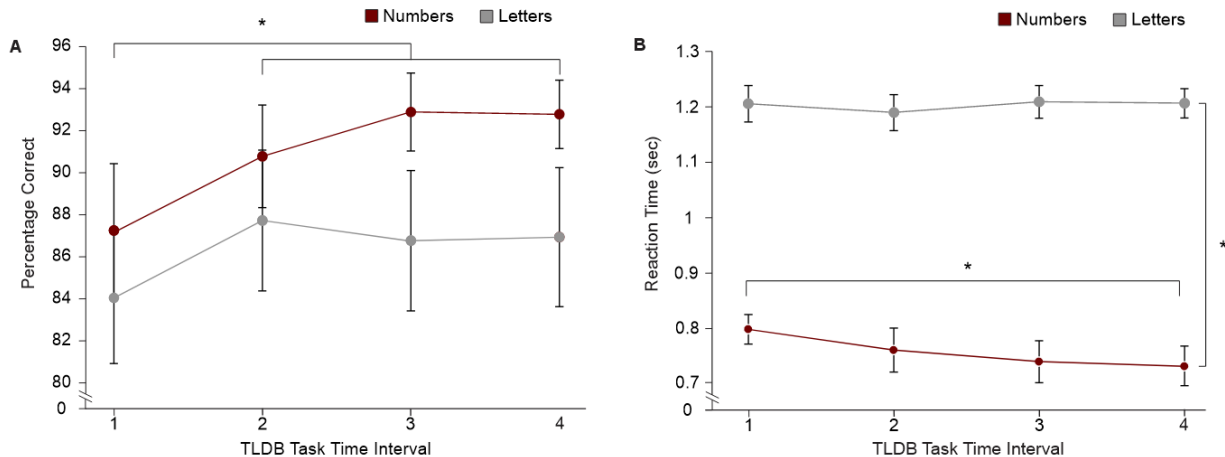


Figure 3.5. Mean performance across the 4 Time Intervals of the TLDB task for the Mental Fatigue group, separated by numbers (garnet) and letters (grey). **A.** Percentage of correct responses and **B.** Reaction time in seconds. Error bars represent standard errors of the mean. Asterisks (*) represent significant differences ($p < .05$).

3.5.3. Visuomotor Adaptation

Early visuomotor adaptation

Participants reached fairly accurately to the targets in the aligned block of trials, such that errors were minimal (MF: $\bar{X} = 2.32^\circ$, $SE = 0.35^\circ$; Control: $\bar{X} = 2.18^\circ$, $SE = 0.39^\circ$). Independent samples t-tests confirmed that initial and final reaching errors in the Aligned Reaching block did not differ between the MF and Control groups (Initial: $t(38) = 0.26$, $p = .796$; Final: $t(38) = 0.46$, $p = .647$). As can be seen in Figure 3.4, reaching direction changed with the introduction of the visuomotor distortion, such that participants began to reach to the left of the target.

Visuomotor adaptation differed between Groups during initial rotated training trials, such that ANOVA revealed a significant main effect of Group ($F(1,38) = 4.88$, $p = .033$). Overall, participants in the MF group demonstrated less initial visuomotor adaptation than participants in the Control Group across all 4 blocks of rotated training (MF: $\bar{X} = 26.94^\circ$, $SE = 0.89^\circ$; Control: $\bar{X} = 29.70^\circ$, $SE = 0.89^\circ$), indicating that mental fatigue reduced participants' ability to adapt their reaches to the visuomotor distortion. Analyses also revealed a significant main effect of Block

($F(3, 114) = 132.68, p < .001$) and Bin ($F(4, 152) = 177.29, p < .001$), as well as a significant Block by Bin interaction ($F(12, 456) = 9.03, p < .001$). Importantly, there were no significant interactions involving the factor of Group (all $p > .20$). Across both Groups, post-hoc analysis confirmed that visuomotor adaptation increased across initial Bins within each rotated training block, such that PVAE was significantly greater in Bin 2 (rotated training trials 4-6) compared to Bin 1 (rotated training trials 1-3) (all $p < .05$). PVAE plateaued by Bin 3 (e.g., rotated training trials 7-9) in each block, such that there were no further increases in PVAE (all $p > .05$). PVAE in Bin 1 also increased across the first three rotated training blocks from 19.99° in Block 1, to 28.25° in Block 2 to 30.82° in Block 3. Finally, there was no difference in PVAE between rotated training Blocks 3 and 4 across any of the Bins (all $p > .05$), suggesting that visuomotor adaptation was retained following the 20-minute rest.

Late visuomotor adaptation

ANOVA revealed a significant main effect of Group ($F(1, 38) = 6.112, p = .018$). ANOVA further revealed a significant main effect of Block ($F(3, 114) = 42.99, p < .001$) and a significant Group by Block interaction ($F(3,36) = 4.83, p = .003$). For the MF group, the level of final adaptation increased from Block 1 ($\bar{X} = 24.72^\circ, SE = 1.6^\circ$) to Block 2 ($\bar{X} = 31.36^\circ, SE = 0.85^\circ; p < .001$), and Block 2 to Block 3 ($\bar{X} = 33.16^\circ, SE = 0.78^\circ; p = .046$). Final adaptation then did not differ between Blocks 3 and 4 (Block 4: $\bar{X} = 33.57^\circ, SE = 0.69^\circ; p = 1.00$), suggesting that late adaptation peaked in Block 3 and then plateaued. For the Control group, this plateau effect was present from Block 2 onwards, such that final adaptation did not differ significantly between Blocks 2 and 3 (Block 2: $\bar{X} = 33.96^\circ, SE = 0.90^\circ$; Block 3: $\bar{X} = 34.04^\circ, SE = 0.63^\circ; p = 1.00$), and it remained at a similar level in Block 4 (Block 4: $\bar{X} = 34.79^\circ, SE = 0.74^\circ; p = 1.00$). The final level of adaptation did not differ between the MF and Control groups in Block 3 ($p = .382$) and Block 4 ($p = .215$).

The results of the adaptation trials indicate that participants in the MF group adapted their reaches to a lower extent overall in early rotated training trials compared to the Control group, and that it was only by the end of the third rotated training block, that reaching errors were similar across Groups. Thus, mental fatigue led to a decreased level of reach adaptation at the start of each rotated training block, and throughout the first two rotated training blocks.

3.5.4. No cursor reaches: Explicit and implicit visuomotor adaptation

Participants reached with no cursor feedback following aligned reach training. Again, in these trials participants reached to the target, such that across both sets of 6 trials, average mean PVAE was minimal (MF Group: $\bar{X} = 2.90^\circ$, $SE = 0.61^\circ$; Control Group: $\bar{X} = 2.81^\circ$, $SE = 0.61^\circ$; Group: $F(1,38) = .010$, $p = .922$). Furthermore, reaching errors did not differ across the two sets of 6 trials (Set 1: $\bar{X} = 2.72^\circ$, $SE = 0.52^\circ$; Set 2: $\bar{X} = 2.98^\circ$, $SE = 0.46^\circ$; $F(1,38) = .316$, $p = .577$). The subsequent no cursor trials were normalized to these baseline errors and explicit and implicit adaptation established.

Explicit adaptation

Explicit adaptation following each block of rotated training are displayed in Figure 3.4B. From this Figure, it appears that the MF group demonstrated less explicit adaptation compared to the Control group (MF: $\bar{X} = 15.14^\circ$, $SE = 2.09^\circ$; Control: $\bar{X} = 18.79^\circ$, $SE = 2.09^\circ$), however analyses indicated a non-significant main effect of Group ($F(1,38) = 1.52$, $p = .225$), and a non-significant Group by Block interaction ($F(3, 114) = 0.847$, $p = .471$). As well, the main effect of Block was not significant ($F(3, 114) = 1.39$, $p = .250$). Thus, results suggest that explicit adaptation remained relatively constant across rotated training trials and did not differ significantly with fatigue.

Implicit adaptation

Similarly, results indicated that implicit adaptation did not differ between Groups (MF: $\bar{X}$ = 10.67°, SE = 1.05°; Control: $\bar{X}$ = 10.46°, SE = 1.05°; $F(1,38) = 0.019$; $p = .890$). However, analyses did reveal a significant main effect of Block ($F(3, 114) = 13.59$, $p < .001$), but not a significant Group by Block interaction ($F(3,114) = 0.239$, $p = .869$). Post-hoc analysis revealed that implicit adaptation increased from Block 1 ($\bar{X}$ = 9.53°, SE = 0.86°) to Block 2 ($\bar{X}$ = 11.7°, SE = 0.85°; $p = .006$), where it plateaued such that implicit adaptation in Block 2 did not significantly differ from Block 3 ($\bar{X}$ = 12.85°, SE = 1.08; $p = 1.00$). Implicit adaptation then decreased after the 20-minute rest in Block 4 ($\bar{X}$ = 8.14°, SE = 0.73°), which was significantly lower than implicit adaptation in Block 3 ($p < .001$).

Taken together, these results suggest that explicit and implicit adaptation showed different trends across the experiment. Explicit adaptation remained constant for all participants across the rotated training blocks, including a 20-minute rest period. In contrast, implicit adaptation increased across the first 2 rotated training blocks and then decayed across the 20-minute reset period. Interestingly, mental fatigue did not impact the overall extent of either explicit or implicit visuomotor adaptation at a group level of analysis.

Relationship of mental fatigue to explicit and implicit adaptation

In Figure 3.6A and 3.6B, we plot individual data, such that participants' mean explicit (A) and implicit (B) adaptation are plotted relative to their changes in mental fatigue scores after the TLDB (MF group) or the documentary viewing (Control group). As shown in Figure 3.6, changes in mental fatigue for the Control group were minimal, such that scores were on average only 11.3 points greater than baseline levels. Furthermore, participant data for the Control group are clustered on the left-hand side of Figure 3.6, demonstrating a consistency in perceived changes in mental fatigue reported by participants. In contrast, there was much greater variation

in changes in mental fatigue relative to baseline levels for participants in the MF group, such that changes in mental fatigue ranged from -12 to 69. The standard deviation for changes in mental fatigue for the MF group was 22.3, compared to 14.3 for the Control group.

Correlation analyses revealed that for the MF group, changes in mental fatigue were negatively correlated with mean explicit adaptation ($r(18) = -0.491$, $p = .014$), such that explicit adaptation was less for participants who reported increased mental fatigue. Furthermore, changes in mental fatigue were found to be positively correlated with mean implicit adaptation for the MF group ($r(18) = 0.532$, $p = .008$), such that implicit adaptation was greater for participants who reported increased mental fatigue. Significant correlations were not found for the Control group with respect to explicit adaptation ($r(18) = .032$, $p = .893$) or implicit adaptation ($r(18) = .105$, $p = .657$).

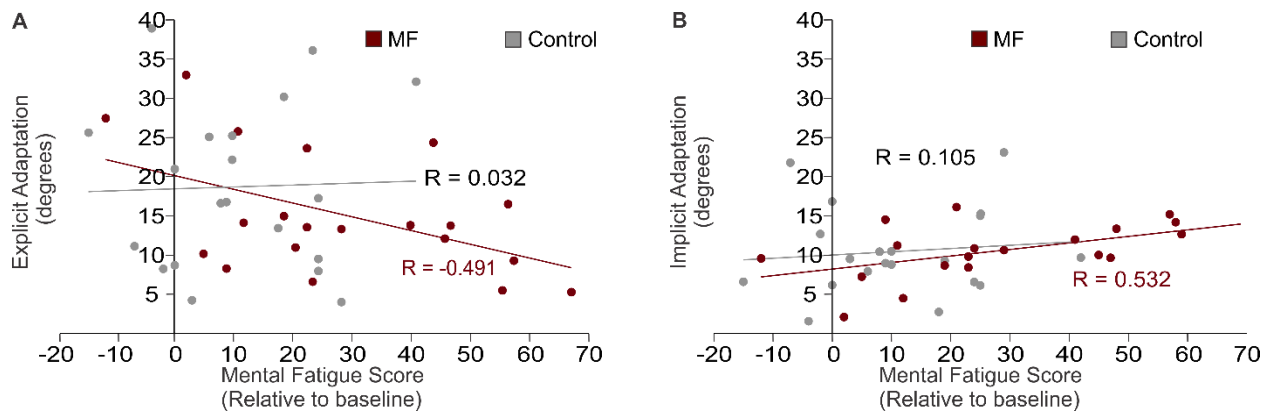


Figure 3.6. Correlations between changes in mental fatigue scores relative to baseline, following the TLDB task or documentary watching (Time 3), and **A.** mean explicit adaptation, or **B.** mean implicit adaptation. Garnet circles represent data for participants in the MF group, and grey circles represent data for participants in the Control group.

3.6. Discussion

To date, the impact of mental fatigue on motor control, specifically visuomotor adaptation, has largely been left unexplored. In the current research we looked to establish the impact of mental fatigue on explicit (conscious strategy) and implicit (unconscious) processes underlying visuomotor adaptation. Mental fatigue was induced in one group of participants (i.e., the MF group) through a time load dual back (TLDB) task, in which participants had to respond as quickly as possible to remembered letters shown on the screen, as well as respond to numbers that were presented in between the letters in a choice reaction time task for 32 minutes. Over the course of the TLDB task, participants maintained a high level of accuracy (88.7% response accuracy overall), and responses were initiated quickly. Mental fatigue increased significantly at the end of the 32 minutes for participants in the MF group. No such increase in mental fatigue was observed for the Control group, who sat and watched an animal documentary for a similar amount of time. The MF group then exhibited decreased visuomotor adaptation early in training (i.e., until the end of the third block of rotated reach training) compared to the Control group. There was no difference in the extent of explicit and implicit adaptation across groups over the

course of the experiment. However, we found significant correlations between changes in mental fatigue and the extent of both explicit and implicit adaptation for participants in the MF group. Increased mental fatigue reported following the TLDB task was negatively correlated with explicit adaptation, such that the greater the increase in mental fatigue reported by participants, the less they engaged in explicit strategies when adapting their reaches to the visuomotor distortion. In contrast, a significant positive correlation was found between increases in mental fatigue and implicit adaptation, such that the greater the increase in mental fatigue reported by participants, the more they engaged in implicit adaptation. Explicit and implicit adaptation were not significantly correlated with the minimal changes in mental fatigue reported by the Control group following watching of a documentary. Thus, results suggest that increases in mental fatigue impact visuomotor adaptation, leading to decreased explicit adaptation and increased implicit adaptation.

3.6.1. Mental Fatigue

For the purpose of this research, we adopted Jacquet et al.'s (2021) definition of mental fatigue, such that we defined mental fatigue as a psychobiological state characterized by feelings of tiredness and lack of energy that arises due to either prolonged and/or intense periods of demanding cognitive activity. We had participants complete the TLDB task of Borrigan et al. (2016), in hopes of inducing mental fatigue quickly. The TLDB task engages participants' short-term memory recall, as participants must remember letters shown on the screen for 1.5 seconds and respond if the current letter displayed corresponds to the previous one presented. While remembering letters, participants must also complete a choice reaction time task, in which they respond to even and odd numbers appearing on the screen as quickly as possible. The continuous and interchanging nature of the TLDB task requires constant attentional focus (Borrigan et al.,

2016), which is presumed to drain limited attentional resources in accordance with Sanders et al.'s (1997) resource depletion theory, quickly leading to a state of mental fatigue. The benefit of using the TLDB task is that it has reliably been shown to induce mental fatigue within a short timespan. Specifically, Borrigan et al. (2016) reported significant increases in mental fatigue following just 16 minutes of task completion, while Jacquet et al. (2021) reported increased mental fatigue in their participants and impaired motor performance after completing the TLDB task for 32 minutes.

Previous research employing the TLDB has shown changes in neural activation associated with increased mental fatigue (e.g., Jacquet et al., 2021; Wang et al., 2016). During their 32-minute TLDB task, Jacquet et al. (2021) recorded neural activity using electroencephalography (EEG). EEG results indicated an increase in alpha band oscillations within the cerebral cortex, a marker which has been accepted as reflecting decreased arousal and alertness (Boksem et al., 2005; Paus et al., 1997; Zhao et al., 2012) and thus taken as an indication of mental fatigue. These neural changes were found in parallel with increases in mental fatigue reported on a single question of Lee et al.'s (1991) Visual Analog Scale for Fatigue (VAS-F), promoting the use of the TLDB as a tool to increase mental fatigue.

Similar to Borrigan et al. (2016), as well as Jacquet et al. (2021), we saw increases in mental fatigue following the TLDB task, such that participants in our MF group indicated an increase in mental fatigue of 29.5 points following the TLDB task. This increase in mental fatigue was maintained above initial baseline levels until the end of the third block of rotated reach training trials, approximately 20 minutes post TLDB task completion. Mental fatigue was only found to decrease to initial baseline levels following an additional 20-minute rest interval, or approximately 40 minutes after completion of the TLDB task. This lasting mental fatigue

observed in our MF participants is in accordance with findings of Jacquet et al. (2021), who found that mental fatigue following their TLDB task remained elevated above baseline levels for 20 minutes.

The lingering mental fatigue we observed throughout our 20 minutes of visuomotor adaptation trials could be due to participants completing the TLDB task. Alternatively, engagement in the visuomotor adaptation trials themselves could have led to the persistence of previously induced mental fatigue or even led to the introduction of additional mental fatigue. As discussed below in Section 3.6.2., we found that participants engaged in explicit visuomotor adaptation (i.e., cognitive strategies). This explicit engagement may have led to increased levels of mental fatigue over the course of the rotated reach training blocks. In support of this proposal, we saw an increase in mental fatigue over the course of the rotated reach training blocks for the Control group, such that mental fatigue was significantly greater than initial baseline levels at the end of the third rotated reach training block, even though they did not complete the TLDB task.

The increase in mental fatigue reported by our Control group over the course of the rotated reach training trials suggests that completion of a visuomotor adaptation task itself may increase mental fatigue. Future work is required to establish the relationship between mental fatigue arising due to completing a visuomotor paradigm and the impact of this mental fatigue on visuomotor adaptation. For now, based on our current results, we are confident that mental fatigue increased in the MF group following the TLDB task.

3.6.2. Visuomotor Adaptation

Early and Late Visuomotor Adaptation

In general, visuomotor adaptation has been shown to arise quickly, with participants rapidly adapting their reaches over the course of the first few training trials and then making small adjustments as trials progress (Krakauer, 2009; Krakauer et al., 2019; Nakagawa et al., 2018). As shown in Figure 3.4, visuomotor adaptation for both our MF and Control groups followed a logarithmic learning curve, with the greatest changes in reaches occurring within the early trials of the first rotated reach training block. The patterns of visuomotor adaptation we observed are similar to Heirani Moghaddam et al. (2021), who used a similar experimental paradigm with respect to the initial number of blocks and trials completed (3 blocks of 45 rotated reach training trials). In agreement with Heirani Moghaddam et al. (2021), we observed an increase in visuomotor adaptation within each block of trials and across blocks, such that adaptation was greatest by the end of the third block of rotated reach training for both our MF and Control groups.

While visuomotor adaptation patterns were similar between our two groups, the MF group adapted their reaches to a lesser extent than the Control group over the first two rotated reach training blocks, supporting the conclusion that mental fatigue impacts visuomotor adaptation. We are aware of only one prior study (see Anguera et al., 2012) that has looked to manipulate cognitive resources prior to participants completing a visuomotor adaptation task. In Anguera and colleagues' (2012) paradigm, participants completed a task designed to deplete spatial working memory resources prior to visuomotor adaptation trials. The spatial working memory task required participants to mentally rotate shapes shown on a screen to determine if they matched previously displayed images (Anguera et al., 2012). Results indicated that

participants who performed worse on the mental rotation task also adapted their reaches to a lesser extent, leading to Anguera et al. (2012) to conclude that working memory resource depletion negatively impacts visuomotor adaptation. Their results agree with our current findings, as we show that increasing mental load prior to visuomotor adaptation impairs the extent to which participants adapt their reaches. However, our current results call into question if the findings of Anguera et al. (2012) arose due to working memory resource depletion per se or because their participants experienced mental fatigue, which Anguera et al. (2012) did not assess. In the current work, we show that the same decrements in early visuomotor adaptation found by Anguera et al. (2012) arise due to increased mental fatigue.

Retention of Visuomotor Adaptation

In addition to examining the impact of mental fatigue on visuomotor adaptation, the current research provides insight into the impact of mental fatigue during initial learning on retention of visuomotor adaptation. As shown in Figure 3.4, participants demonstrated retention of visuomotor adaptation over a 20-minute rest interval. However, early visuomotor adaptation in the retention block was less than that observed late in the third block of rotated reach training for both the MF and Control groups, suggesting some decay of visuomotor adaptation across the rest period. A similar pattern of decay in retention of visuomotor adaptation has been shown in previous work. For example, Maksimovic and Cressman (2018) found that visuomotor adaptation decayed in just 5 minutes, while Huberdeau et al. (2015) and Krakauer et al. (2005) have shown a decrease in visuomotor adaptation following a 24-hour rest period. While we found some decay of visuomotor adaptation immediately following the 20-minute rest period, participants rapidly returned to how they were reaching at the end of the third reach training block, demonstrating retention of visuomotor adaptation (Krakauer et al., 2005).

Our more critical finding with respect to the current research question is that our MF group demonstrated a lower level of visuomotor adaptation at the start of the retention block compared to the Control group. This lesser extent of visuomotor adaptation was seen even though both groups had achieved the same level of visuomotor adaptation by the end of the third rotated reach training block and mental fatigue reports had returned to baseline levels. The continued decrease in visuomotor adaptation seen in the MF group compared to the Control group suggests a persisting impact of mental fatigue on visuomotor adaptation even when participants no longer indicated increased levels of mental fatigue. As such, future research is needed to establish the duration for which mental fatigue impacts visuomotor adaptation by using more reach training trials and longer rest periods.

Interestingly, recent work by Neva et al. (2019) employing a physically fatiguing paradigm found the opposite impact of fatigue on visuomotor adaptation and retention in comparison to our current findings. In Neva et al.'s (2019) experiment, participants engaged in an acute and intense bout of cyclic exercise for 25 minutes to induce physical fatigue prior to completing a visuomotor adaptation task. Contrary to our findings following the induction of mental fatigue, Neva et al. (2019) found that fatigue arising due to physical exercise led to increased visuomotor adaptation and maintenance of visuomotor adaptation during a retention block of trials compared to control conditions. Together, our results and the findings of Neva et al. (2019) show opposite effects of mental versus physical fatigue on visuomotor adaptation, calling into question Kuppaswamy's (2021) framework of mental fatigue, which argues that changes in effort processing, be it from mental or physical efforts, are responsible for fatigue and as such the manner by which fatigue is induced should not impact performance measures. Future research is therefore needed to establish the relationship between mental and physical fatigue and

why these two types of fatigue have been shown to differentially impact visuomotor adaptation and retention (see also Zwierko and Wasik, 2019).

Explicit and Implicit Visuomotor Adaptation

In general, visuomotor adaptation to a large cursor rotation (i.e., greater than 30°) has been shown to involve both explicit and implicit processes (Bond and Taylor, 2015; Mazzoni and Krakauer, 2006; Neville and Cressman, 2018; Werner et al., 2015). These processes are proposed to be independent (Bond and Taylor, 2015; Mazzoni and Krakauer, 2006; Sulzenbruck and Heuer, 2009), with explicit processes contributing to a larger extent early in visuomotor adaptation (Taylor et al., 2014), and implicit processes increasing their contribution as visuomotor adaptation progresses (Heirani Moghaddam et al., 2021; Taylor et al., 2014). We hypothesized that mental fatigue would lead to decreased explicit adaptation given the decrease in cognitive resources available. In accordance with this observation, the MF group demonstrated less visuomotor adaptation in the early reach training trials compared to the Control group. However, no significant group differences were observed with respect to the no cursor reaches used to establish explicit and implicit visuomotor adaptation in accordance with the Process Dissociation Procedure (PDP) of Werner et al., (2015). We found explicit adaptation was 13.45° for the MF group and 17.48° for the Control group following the first block of rotated reach training trials and was maintained at a similar extent across the experiment, including in the retention block. Implicit adaptation on the other hand, increased across initial rotated reach training blocks as seen by Heirani Moghaddam et al. (2021). We then found that implicit adaptation decreased in the retention block, while explicit adaptation was maintained. Our results with respect to retention of explicit and implicit adaptation agree with Bouchard and Cressman (2021), who showed preserved explicit adaptation and limited retention of implicit adaptation following a 24-hour interval rest period. The maintenance of explicit adaptation across a rest

interval, with decaying implicit adaptation supports provides further evidence that explicit and implicit adaptation are independent processes (Bond and Taylor, 2015; Mazzoni and Krakauer, 2006; Sulzenbruck and Heuer, 2009).

While explicit adaptation did not differ significantly between groups overall, we found that mean explicit adaptation was less in the MF group compared to the Control group. Moreover, as shown in Figure 3.6, changes in mental fatigue following the TLDB task varied greatly among MF participants, with some participants reporting no change in mental fatigue, while others reported a change in mental fatigue up to 69 points. Taking individual changes in mental fatigue into account, correlational analyses revealed a significant negative correlation between changes in mental fatigue and explicit adaptation, such that a greater change in mental fatigue following the TLDB task was correlated with lower explicit adaptation in the MF group. The Control group did not demonstrate a similar significant correlation between changes in mental fatigue following watching of the documentary and explicit adaptation. Thus, it appears that increased mental fatigue prior to visuomotor adaptation impacts one's ability to engage in strategic reaching processes. The more fatigued one is, the less explicit adaptation they are capable of engaging.

Implicit adaptation was also found to be impacted by changes in mental fatigue in the MF group, but in the opposite direction. As mental fatigue increased, implicit adaptation increased in MF participants. The finding of increased implicit adaptation at the expense of explicit adaptation has been shown previously by Benson et al. (2011) and corroborated by Neville and Cressman (2018). Perhaps it is the reduction in engagement of explicit strategies that enables implicit adaptation to occur unimpeded, suggesting a compensatory mechanism that looks to preserve visuomotor adaptation. While future work is needed to firmly establish the relationship

between explicit and implicit processes, for now, we have shown that increased mental fatigue leads to a decrease in visuomotor adaptation, potentially arising due to decreased engagement of explicit adaptation.

3.7. Conclusion

Previous research has shown that visuomotor adaptation and engagement of explicit and implicit processes are influenced by the size of the visuomotor distortion introduced (Neville and Cressman, 2018; Taylor et al., 2014) and participants' awareness of the visuomotor distortion (Werner et al., 2015). Our current findings establish that mental fatigue is another factor that impacts one's ability to adapt their reaches to a visuomotor distortion. Here we show that mental fatigue reduces visuomotor adaptation and retention due to decreased engagement of explicit processes. Understanding the influence of mental fatigue on motor performance is critical, as many of us experience mental fatigue on a regular basis according to a recent survey by the National Sleep Foundation (2020). The current findings indicate that a participant's level of mental fatigue should be considered when examining visuomotor adaptation.

3.8. References

- Anguera, J. A., Bernard, J. A., Jaeggi, S. M., Buschkuhl, M., Benson, B. L., Jennett, S., Humfleet, J., Reuter-Lorenz, P. A., Jonides, J., & Seidler, R. D. (2012). The effects of working memory resource depletion and training on sensorimotor adaptation. *Behavioural Brain Research*, 228(1), 107–115. <https://doi.org/10.1016/j.bbr.2011.11.040>
- Bastian, A. J. (2008). Understanding sensorimotor adaptation and learning for rehabilitation. *Current Opinion in Neurology*, 21(6), 628–633. <https://doi.org/10.1097/WCO.0b013e328315a293>
- Benson, B. L., Anguera, J. A., & Seidler, R. D. (2011). A spatial explicit strategy reduces error but interferes with sensorimotor adaptation. *Journal of Neurophysiology*, 105(6), 2843–2851. <https://doi.org/10.1152/jn.00002.2011>
- Boksem, M. A. S., Meijman, T. F., & Lorist, M. M. (2005). Effects of mental fatigue on attention: An ERP study. *Cognitive Brain Research*, 25(1), 107–116. <https://doi.org/10.1016/j.cogbrainres.2005.04.011>
- Boksem, M. A. S., Meijman, T. F., & Lorist, M. M. (2006). Mental fatigue, motivation and action monitoring. *Biological Psychology*, 72(2), 123–132. <https://doi.org/10.1016/j.biopsycho.2005.08.007>
- Bond, K. M., & Taylor, J. A. (2015). Flexible explicit but rigid implicit learning in a visuomotor adaptation task. *Journal of Neurophysiology*, 113(10), 3836–3849. <https://doi.org/10.1152/jn.00009.2015>

Borragán, G., Slama, H., Destrebecqz, A., & Peigneux, P. (2016). Cognitive Fatigue Facilitates Procedural Sequence Learning. *Frontiers in Human Neuroscience*, 10.

<https://www.frontiersin.org/articles/10.3389/fnhum.2016.00086>

Bouchard, J.-M., & Cressman, E. K. (2021). Intermanual transfer and retention of visuomotor adaptation to a large visuomotor distortion are driven by explicit processes. *PLOS ONE*, 16(1), e0245184. <https://doi.org/10.1371/journal.pone.0245184>

Cressman, E. K., & Henriques, D. Y. P. (2009). Sensory Recalibration of Hand Position Following Visuomotor Adaptation. *Journal of Neurophysiology*, 102(6), 3505–3518. <https://doi.org/10.1152/jn.00514.2009>

Cunningham, H. A. (1989). Aiming error under transformed spatial mappings suggests a structure for visual-motor maps. *Journal of Experimental Psychology: Human Perception and Performance*, 15(3), 493–506. <https://doi.org/10.1037/0096-1523.15.3.493>

Deuschl, G., Toro, C., Zeffiro, T., Massaquoi, S., & Hallett, M. (1996). Adaptation motor learning of arm movements in patients with cerebellar disease. *Journal of Neurology, Neurosurgery & Psychiatry*, 60(5), 515–519. <https://doi.org/10.1136/jnnp.60.5.515>

Enoka, R. M., & Duchateau, J. (2016). Translating Fatigue to Human Performance. *Medicine and Science in Sports and Exercise*, 48(11), 2228–2238. <https://doi.org/10.1249/MSS.0000000000000929>

Heirani Moghaddam, S., Chua, R., & Cressman, E. K. (2021). Assessing and defining explicit processes in visuomotor adaptation. *Experimental Brain Research*, 239(7), 2025–2041. <https://doi.org/10.1007/s00221-021-06109-5>

Henriques, D. Y. P., & Cressman, E. K. (2012). Visuomotor Adaptation and Proprioceptive Recalibration. *Journal of Motor Behavior*, 44(6), 435–444.

<https://doi.org/10.1080/00222895.2012.659232>

Huberdeau, D.M., Haith, A.M., & Krakauer, J. W. (2015). Formation of a long-term memory for visuomotor adaptation following only a few trials of practice. *Journal of Neurophysiology*, 114, 969-977.

Jacquet, T., Poulin-Charronnat, B., Bard, P., & Lepers, R. (2021). Persistence of Mental Fatigue on Motor Control. *Frontiers in Psychology*, 11, 588253.

<https://doi.org/10.3389/fpsyg.2020.588253>

Juliano, J. M., Schweighofer, N., & Liew, S.-L. (2022). Increased cognitive load in immersive virtual reality during visuomotor adaptation is associated with decreased long-term retention and context transfer. *Journal of Neuroengineering and Rehabilitation*, 19(1), 1–106.

<https://doi.org/10.1186/s12984-022-01084-6>

Krakauer, J. W. (2006). Motor learning: Its relevance to stroke recovery and neurorehabilitation. *Current Opinion in Neurology*, 19(1), 84–90.

<https://doi.org/10.1097/01.wco.0000200544.29915.cc>

Krakauer, J. W. (2009). Motor learning and consolidation: The case of visuomotor rotation. *Advances in Experimental Medicine and Biology*, 629, 405–421.

https://doi.org/10.1007/978-0-387-77064-2_21

Krakauer, J. W., Ghez, C., & Ghilardi, M. F. (2005). Adaptation to Visuomotor Transformations: Consolidation, Interference, and Forgetting. *Journal of Neuroscience*, 25(2), 473–478.

<https://doi.org/10.1523/JNEUROSCI.4218-04.2005>

Krakauer, J. W., Hadjiosif, A. M., Xu, J., Wong, A. L., & Haith, A. M. (2019). Motor Learning.

In R. Terjung (Ed.), *Comprehensive Physiology* (1st ed., pp. 613–663). Wiley.

<https://doi.org/10.1002/cphy.c170043>

Kuppuswamy, A. (2022). The Neurobiology of Pathological Fatigue: New Models, New

Questions. *The Neuroscientist*, 28(3), 238–253. <https://doi.org/10.1177/1073858420985447>

Lee, K. A., Hicks, G., & Nino-Murcia, G. (1991). Validity and reliability of a scale to assess

fatigue. *Psychiatry Research*, 36(3), 291–298. [https://doi.org/10.1016/0165-1781\(91\)90027-](https://doi.org/10.1016/0165-1781(91)90027-M)

[M](https://doi.org/10.1016/0165-1781(91)90027-M)

Lorist, M. M., Klein, M., Nieuwenhuis, S., De Jong, R., Mulder, G., & Meijman, T. F. (2000).

Mental fatigue and task control: Planning and preparation. *Psychophysiology*, 37(5), 614–625.

Magnuson, J. R., Doesburg, S. M., & McNeil, C. J. (2021). Development and recovery time of mental fatigue and its impact on motor function. *Biological Psychology*, 161, 108076.

<https://doi.org/10.1016/j.biopsycho.2021.108076>

Maksimovic, S., & Cressman, E. K. (2018). Long-term retention of proprioceptive recalibration.

Neuropsychologia, 114, 65–76. <https://doi.org/10.1016/j.neuropsychologia.2018.04.009>

Martin, T. A., Keating, J. G., Goodkin, H. P., Bastian, A. J., & Thach, W. T. (1996). Throwing

while looking through prisms: II. Specificity and storage of multiple gaze—throw calibrations. *Brain*, 119(4), 1199–1211. <https://doi.org/10.1093/brain/119.4.1199>

Mazzoni, P., & Krakauer, J. W. (2006). An Implicit Plan Overrides an Explicit Strategy during

Visuomotor Adaptation. *Journal of Neuroscience*, 26(14), 3642–3645.

<https://doi.org/10.1523/JNEUROSCI.5317-05.2006>

Milner, B. (1962). Physiologie de l'Hippocampe. *Neuropsychologia*, 3(3), 273–277.

[https://doi.org/10.1016/0028-3932\(65\)90029-1](https://doi.org/10.1016/0028-3932(65)90029-1)

Modchalingam, S., Vachon, C. M., Hart, B. M. 't, & Henriques, D. Y. P. (2019). The effects of awareness of the perturbation during motor adaptation on hand localization. *PLOS ONE*, 14(8), e0220884. <https://doi.org/10.1371/journal.pone.0220884>

Nakagawa, A., Gouveia, E., & Soares, A. (2018). A Framework for Visuomotor Adaptation Studies. <https://doi.org/10.29327/cobecseb.78868>

Nakashima, A., Moriuchi, T., Matsuda, D., Nakamura, J., Fujiwara, K., Ikio, Y., Hasegawa, T., Mitunaga, W., & Higashi, T. (2022). Continuous Repetition Motor Imagery Training and Physical Practice Training Exert the Growth of Fatigue and Its Effect on Performance. *Brain Sciences*, 12(8), Article 8. <https://doi.org/10.3390/brainsci12081087>

National Sleep Foundation. (2020). *Sleep in America Poll* [Data Set].

<https://www.thensf.org/sleep-in-america-polls/>

Neva, J. L., Ma, J. A., Orsholits, D., Boisgontier, M. P., & Boyd, L. A. (2019). The effects of acute exercise on visuomotor adaptation, learning, and inter-limb transfer. *Experimental Brain Research*, 237(4), 1109–1127. <https://doi.org/10.1007/s00221-019-05491-5>

Neville, K.-M., & Cressman, E. K. (2018). The influence of awareness on explicit and implicit contributions to visuomotor adaptation over time. *Experimental Brain Research*, 236(7), 2047–2059. <https://doi.org/10.1007/s00221-018-5282-7>

Norman, D. A., & Shallice, T. (1986). Attention to Action. In R. J. Davidson, G. E. Schwartz, & D. Shapiro (Eds.), *Consciousness and Self-Regulation: Advances in Research and Theory Volume 4* (pp. 1–18). Springer US. https://doi.org/10.1007/978-1-4757-0629-1_1

Paus, T., Zatorre, R. J., Hofle, N., Caramanos, Z., Gotman, J., Petrides, M., & Evans, A. C.

(1997). Time-Related Changes in Neural Systems Underlying Attention and Arousal During the Performance of an Auditory Vigilance Task. *Journal of Cognitive Neuroscience*, 9(3), 392–408. <https://doi.org/10.1162/jocn.1997.9.3.392>

Sanders, A. F. (1997). A summary of resource theories from a behavioral perspective. *Biological Psychology*, 45(1), 5–18. [https://doi.org/10.1016/S0301-0511\(96\)05220-9](https://doi.org/10.1016/S0301-0511(96)05220-9)

Severini, G., & Zych, M. (2020). Characterization of the Adaptation to Visuomotor Rotations in the Muscle Synergies Space. *Frontiers in Bioengineering and Biotechnology*, 8, 605. <https://doi.org/10.3389/fbioe.2020.00605>

Sülzenbrück, S., & Heuer, H. (2009). Functional independence of explicit and implicit motor adjustments. *Consciousness and Cognition*, 18(1), 145–159. <https://doi.org/10.1016/j.concog.2008.12.001>

Taylor, J. A., Krakauer, J. W., & Ivry, R. B. (2014). Explicit and Implicit Contributions to Learning in a Sensorimotor Adaptation Task. *Journal of Neuroscience*, 34(8), 3023–3032. <https://doi.org/10.1523/JNEUROSCI.3619-13.2014>

Wang, C., Trongnetrpunya, A., Samuel, I. B. H., Ding, M., & Kluger, B. M. (2016). Compensatory Neural Activity in Response to Cognitive Fatigue. *Journal of Neuroscience*, 36(14), 3919–3924. <https://doi.org/10.1523/JNEUROSCI.3652-15.2016>

Wascher, E., & Getzmann, S. (2014). Rapid mental fatigue amplifies age-related attentional deficits. *Journal of Psychophysiology*, 28, 215–224. <https://doi.org/10.1027/0269-8803/a000127>

Werner, S., Aken, B. C. van, Hulst, T., Frens, M. A., Geest, J. N. van der, Strüder, H. K., &

Donchin, O. (2015). Awareness of Sensorimotor Adaptation to Visual Rotations of Different Size. *PLOS ONE*, 10(4), e0123321. <https://doi.org/10.1371/journal.pone.0123321>

Wigmore, V., Tong, C., & Flanagan, J. R. (2002). Visuomotor rotations of varying size and direction compete for a single internal model in motor working memory. *Journal of Experimental Psychology. Human Perception and Performance*, 28(2), 447–457. <https://doi.org/10.1037//0096-1523.28.2.447>

Wolpert, D. M., Ghahramani, Z., & Jordan, M. I. (1995). An internal model for sensorimotor integration. *Science (New York, N.Y.)*, 269(5232), 1880–1882. <https://doi.org/10.1126/science.7569931>

Zhao, C., Zhao, M., Liu, J., & Zheng, C. (2012). Electroencephalogram and electrocardiograph assessment of mental fatigue in a driving simulator. *Accident Analysis & Prevention*, 45, 83–90. <https://doi.org/10.1016/j.aap.2011.11.019>

Zwierko, T., and J. Wąsik. "Exercise-induced fatigue impairs visuomotor adaptability in physical education students." *Physical education of students* 23, no. 6 (2019): 327-333.

CHAPTER 4. GENERAL DISCUSSION

In this research, we examined the impact of mental fatigue on explicit and implicit contributions to visuomotor adaptation. To do so, we mentally fatigued one group of participants (MF group) and then had all participants reach with cursor feedback that was rotated 40° clockwise relative to hand motion for 3 blocks of 45 reach training trials. Explicit and implicit adaptation were assessed via no cursor reaches, in which participants were instructed to “Reach while using any strategies you have learned” (Inclusion trials) or to “Reach without using any strategies you have learned” (Exclusion trials) (PDP; Werner et al., 2015). Retention of implicit and explicit adaptation, as well as visuomotor adaptation were examined with additional no cursor reaches and a final block of 45 rotated reach training trials following a 20-minute rest period.

4.1. Explicit and implicit adaptation

Explicit adaptation is thought to arise due to neural processes occurring in the pre-frontal cortex (Anguera et al., 2010; Benson et al., 2011; Taylor and Ivry, 2014a), while implicit adaptation is mediated by activation in the cerebellum (Izawa et al., 2012; Taylor et al., 2010; Tseng et al., 2007; Tzvi et al., 2022). The pre-frontal cortex is assumed to participate in decision making and attentional focus (Arnsten, 2009). As such, it is not surprising that mental fatigue led to changes in explicit adaptation in the current study, given that participants in the MF group were given a highly demanding cognitive task that would be mediated by activation in the pre-frontal cortex (Sohn and Lee, 2007; Vassena et al., 2014). In particular, we found that increased mental fatigue led to decreased explicit adaptation.

Interestingly, we found that implicit adaptation increased with increased mental fatigue, and associated decreases in explicit adaptation. Previously, explicit and implicit adaptation have been suggested to arise independently (Bond and Taylor, 2015; Mazzoni and Krakauer, 2006;

Sulzenbruck and Heuer, 2009). Our results suggest that the interaction between explicit and implicit adaptation could be more complex, as the two processes could be interconnected. In accordance with this suggestion, previous research by Benson et al. (2011) showed that having participants engage in strategic reaching reduced the contributions of implicit processes to visuomotor adaptation. Similarly, Larssen and Hodges (2023) demonstrated that decreasing explicit adaptation through a manipulation of target veracity led to increased implicit visuomotor adaptation. Together these results suggest that explicit and implicit processes engage in a competing relationship in which the increase or decrease of explicit adaptation impedes or facilitates implicit adaptation respectively.

The potential interaction between explicit and implicit adaptation raises questions as to how the mechanisms that modulate these processes function within the brain. Recently, Jacquet et al. (2021) utilized electroencephalography (EEG) to chart brain activity during a cognitively fatiguing task, and saw increased activity in the pre-frontal cortex, the cortical area suggested to drive explicit adaptation (Anguera et al., 2010; Benson et al., 2011; Taylor and Ivry, 2014). No changes in neural activity were observed in the cerebellum, the area associated with implicit adaptation (Izawa et al., 2012; Taylor et al., 2010; Tseng et al., 2007; Tzvi et al., 2022). This then raises the question as to why we saw increased implicit visuomotor adaptation with fatigue. Within our experiment, it appears that the disruption of explicit processes through the induction of mental fatigue enabled implicit processes to contribute to a greater extent to visuomotor adaptation. Further research is needed to establish the relationship between explicit and implicit adaptation, and associated neural activity. Future studies examining visuomotor adaptation and fatigue could therefore involve monitoring neural activity (e.g., with EEG) during the cognitively fatiguing task and the visuomotor adaptation protocol. Specifically, EEG data could be collected

while participants adapt their reaches to a visuomotor rotation under normal and fatigued conditions. Emphasis should be placed on examining the areas of the brain (i.e. the pre-frontal cortex and the cerebellum) associated with explicit and implicit adaptation to determine how brain activity is modulated with fatigue during visuomotor adaptation. Results from this work would provide insight into the relationship between explicit and implicit visuomotor adaptation.

4.2. Retention of Visuomotor Adaptation

In general, the few studies that have examined the impact of mental fatigue on motor control have focussed on gross and fine motor skill performance rather than motor learning per se (e.g., Jacquet et al., 2021, Magnuson et al., 2021). Both Jacquet et al. (2021) and Magnuson et al. (2021) found decreased motor control performance following a mental fatiguing protocol for 10-17 minutes post-task (Magnuson et al., 2021) or 20 minutes post-task (Jacquet et al., 2021). These previous findings demonstrate that mental fatigue negatively impacts motor performance of previously learned skills for up to approximately 20 minutes. Our experimental results extend these findings as we investigated the ability to adapt a previously acquired skill to a novel visuomotor environment, a form of motor learning (Krakauer et al., 2019). Furthermore, we included a retention block following a 20-minute rest in our experimental design, allowing us to speak to the impact of mental fatigue on retention of a recently adapted movements.

Within our experiment, the MF group took a greater number of trials to adapt their reaches to the visuomotor distortion, such that a similar level of visuomotor adaptation to the Control group was not attained until the third block of rotated reach training. Furthermore, the MF group demonstrated less retention of visuomotor adaptation compared to the Control group, such that the level of visuomotor adaptation at the beginning of the retention block differed significantly between groups. However, the MF and Control groups demonstrated a similar

extent of visuomotor adaptation by the end of the retention block, raising questions as to how fatigue impacts retention of visuomotor adaptation. We found that visuomotor adaptation peaked by the end of the 3rd block of rotated reach training trials for the MF group, whereas it peaked earlier for the Control group (i.e., by the 2nd block of rotated reach training trials). Thus, an argument could be made that the Control group had better retention simply because they completed a greater number of reach training trials with peak visuomotor adaptation levels compared to the MF group. Future research is needed to determine the cause of the impaired retention of visuomotor adaptation observed in the MF group (i.e., mental fatigue or because of the number of reach training trials completed at peak visuomotor adaptation). Perhaps if both the MF and Control groups completed the same number of reach training trials at peak visuomotor adaptation levels before the rest period, all participants would demonstrate similar levels of retention of visuomotor adaptation.

4.3. Compensatory mechanism

We found great variability in changes in mental fatigue across participants in our MF group after they completed the TLDB task, such that mental fatigue changes ranged from -21 to 69 points on the MFS. Despite this variability in changes in perception of mental fatigue, all participants within the MF group performed well on the TLDB task. We separated our analyses of the TLDB task into quarters of time, enabling us to track response accuracy and reaction time over time. Regardless of mental fatigue, participants continued to respond accurately and quickly to the letters and numbers displayed. In fact, reaction time on the choice-reaction time component of the task (i.e., responses to the numbers displayed) decreased as the task continued, while percentage of correct responses on the working spatial memory component of the task (i.e., responses to the remembered letters) remained constant throughout the task, demonstrating

consistent participant engagement. Thus, mental fatigue did not negatively impair participants' performance on the TLDB task.

In attempt to understand why performance on the TLDB task did not deteriorate, we can look to the work of Wang et al. (2016) and their suggestion of a compensatory neural mechanisms that combats mental fatigue. Wang et al. (2016) recorded neural activity using EEG while participants completed the Stroop task (Stroop, 1935) for 160 minutes. Like the TLDB task, the Stroop task has been utilized to induce mental fatigue (Scarpina and Tagini, 2017). However, the Stroop task typically must be completed for a longer period of time compared to the TLDB task before mental fatigue is induced (Borrigan et al., 2016). During completion of the Stroop task, Wang et al. (2016) reported neural activation in the anterior frontal region of the brain that resembled an inverted U over the course of the experiment, with activation peaking 60-100 minutes into the Stroop task. This increase and subsequent decrease in neural activation corresponded with increased and decreased performance on the Stroop task respectively. In summation, Wang et al. (2016) proposed the presence of a compensatory mechanism within the anterior frontal region of the brain that enabled participants to maintain performance on the Stroop task for the first 100 minutes of task completion despite increasing mental fatigue.

In accordance with this suggestion, the maintenance of task performance we observed on the TLDB task, despite mental fatigue levels presumably rising, suggests that our participants may have engaged in a similar compensatory mechanism during completion of the TLDB task. However, visuomotor adaptation was still impacted by mental fatigue, despite performance maintenance on the TLDB task. Thus, questions remain as to why a potential compensatory mechanism identified by Wang et al. (2016) may mitigate the effects of mental fatigue on performance of the fatiguing task itself, but not ensure continued visuomotor adaptation. In order

to address this question, future research could utilize EEG to monitor neural activity during the fatiguing task and visuomotor adaptation trials to determine if similar compensatory processes are engaged as observed by Wang et al. (2016). It is possible that the compensatory mechanism identified by Wang et al. (2016) is limited in engagement to simple tasks (i.e., the Stroop task as compared to the TLDB task), and/or that visuomotor adaptation requires additional resources that cannot be effectively mitigated when mentally fatigued.

4.4. Mental Fatigue Protocols

While the TLDB task has proven useful in inducing mental fatigue, the use of different mentally fatiguing tasks within the literature leads to questions as to whether they would impact visuomotor adaptation processes in a similar manner as observed in the current experiment. Within Enoka and Duchateau's (2016) definition of mental fatigue, all fatiguing tasks are regarded as equivalent in that they induce a subjective feeling of mental fatigue. However, it remains to be determined if that is the case. In 2012, Anguera and colleagues had participants complete a task that they argued specifically targeted spatial working memory. Their results were similar to our current findings, in that after completion of a mental rotation task that engaged spatial working memory their participants demonstrated impaired early visuomotor adaptation. Anguera et al. (2012) argued that their results indicated spatial working memory was necessary for visuomotor adaptation.

However, the mental rotation task used by Anguera et al. (2012) could have induced mental fatigue, as acknowledged in their discussion. Thus, it could be asked whether the task used to induce mental fatigue (e.g., TLDB task, mental rotation task, Stroop task, etc.), could have a varying impact on visuomotor adaptation. Borrigan et al. (2016) argued that the TLDB task was efficient at inducing mental fatigue within a 16-minute time span specifically because it

engaged multiple cognitive processes (i.e., short-term memory recall and choice reaction time).

As such, it is possible that the results we obtained within our experiment are specific to the depletion of specific cognitive resources associated with short-term memory recall and/or choice reaction time rather than as a consequence of generalized mental fatigue. Future research is needed in which the impact of different mentally fatiguing tasks on visuomotor adaptation are compared in order to determine whether the nature of the mentally fatiguing task, and hence cognitive activity engaged, influences visuomotor adaptation, or if all mentally fatiguing protocols have a similar influence on visuomotor adaptation. These results would then provide insight into particular cognitive activities critical for visuomotor adaptation.

4.5. Conclusion

The purpose of this thesis was to determine the impact of mental fatigue on explicit and implicit contributions to visuomotor adaptation. We showed that mental fatigue impacts early visuomotor adaptation, such that within the first two reach training blocks of 45 trials (or 90 reach training trials in total), visuomotor adaptation was less for our MF group compared to the Control group. Furthermore, in establishing explicit and implicit visuomotor adaptation, we determined that increased mental fatigue correlated with decreased explicit and increased implicit visuomotor adaptation. Finally, we found that mental fatigue led to decreased retention of visuomotor adaptation following a 20-minute break, even though subjective feelings of mental fatigue returned to baseline levels. As such, future experiments within the field of visuomotor adaptation must take into consideration the mentally fatigued state of their participants. With further research utilizing different fatiguing protocols, in parallel with monitoring neural activity using EEG, we may be able to determine whether the nature of the fatiguing task and hence the type of cognitive resources depleted influences visuomotor adaptation, as well as map out more clearly the brain activity associated with mental fatigue and explicit versus implicit adaptation.

REFERENCES

- Anguera, J. A., Bernard, J. A., Jaeggi, S. M., Buschkuhl, M., Benson, B. L., Jennett, S., Humfleet, J., Reuter-Lorenz, P. A., Jonides, J., & Seidler, R. D. (2012). The effects of working memory resource depletion and training on sensorimotor adaptation. *Behavioural Brain Research*, 228(1), 107–115. <https://doi.org/10.1016/j.bbr.2011.11.040>
- Anguera, J. A., Reuter-Lorenz, P. A., Willingham, D. T., & Seidler, R. D. (2010). Contributions of Spatial Working Memory to Visuomotor Learning. *Journal of Cognitive Neuroscience*, 22(9), 1917–1930. <https://doi.org/10.1162/jocn.2009.21351>
- Arnsten, A. F. T. (2009). Stress signalling pathways that impair prefrontal cortex structure and function. *Nature Reviews Neuroscience*, 10(6), Article 6. <https://doi.org/10.1038/nrn2648>
- Au, J., Sheehan, E., Tsai, N., Duncan, G. J., Buschkuhl, M., & Jaeggi, S. M. (2015). Improving fluid intelligence with training on working memory: A meta-analysis. *Psychonomic Bulletin & Review*, 22(2), 366–377. <https://doi.org/10.3758/s13423-014-0699-x>
- Bastian, A. J. (2008). Understanding sensorimotor adaptation and learning for rehabilitation. *Current Opinion in Neurology*, 21(6), 628–633. <https://doi.org/10.1097/WCO.0b013e328315a293>
- Benson, B. L., Anguera, J. A., & Seidler, R. D. (2011). A spatial explicit strategy reduces error but interferes with sensorimotor adaptation. *Journal of Neurophysiology*, 105(6), 2843–2851. <https://doi.org/10.1152/jn.00002.2011>
- Bock, O. (2001). The mechanisms for human sensorimotor adaptation. *Deutsche Zeitschrift für Sportmedizin*, 52(12), 338–342. Scopus.

Bock, O., Schneider, S., & Bloomberg, J. (2001). Conditions for interference versus facilitation during sequential sensorimotor adaptation. *Experimental Brain Research*, 138(3), 359–365.

Scopus. <https://doi.org/10.1007/s002210100704>

Boksem, M. A. S., Meijman, T. F., & Lorist, M. M. (2005). Effects of mental fatigue on attention: An ERP study. *Cognitive Brain Research*, 25(1), 107–116.

<https://doi.org/10.1016/j.cogbrainres.2005.04.011>

Boksem, M. A. S., Meijman, T. F., & Lorist, M. M. (2006). Mental fatigue, motivation and action monitoring. *Biological Psychology*, 72(2), 123–132.

<https://doi.org/10.1016/j.biopsycho.2005.08.007>

Bond, K. M., & Taylor, J. A. (2015). Flexible explicit but rigid implicit learning in a visuomotor adaptation task. *Journal of Neurophysiology*, 113(10), 3836–3849.

<https://doi.org/10.1152/jn.00009.2015>

Borragán, G., Slama, H., Destrebecqz, A., & Peigneux, P. (2016). Cognitive Fatigue Facilitates Procedural Sequence Learning. *Frontiers in Human Neuroscience*, 10.

<https://www.frontiersin.org/articles/10.3389/fnhum.2016.00086>

Bruijtel, J., Vermeeren, A., Stapert, S. Z., & van Heugten, C. M. (2022). Mental effort and recovery from task-induced fatigue in people with traumatic brain injury. *Disability and Rehabilitation*, 0(0), 1–8.

<https://doi.org/10.1080/09638288.2022.2030416>

Cabeza, R., & Nyberg, L. (2000). Imaging Cognition II: An Empirical Review of 275 PET and fMRI Studies. *Journal of Cognitive Neuroscience*, 12(1), 1–47.

<https://doi.org/10.1162/08989290051137585>

Caseras, X., Mataix-Cols, D., Giampietro, V., Rimes, K. A., Brammer, M., Zelaya, F., Chalder,

T., & Godfrey, E. L. (2006). Probing the Working Memory System in Chronic Fatigue

Syndrome: A Functional Magnetic Resonance Imaging Study Using the n-Back Task.

Psychosomatic Medicine, 68(6), 947–955.

<https://doi.org/10.1097/01.psy.0000242770.50979.5f>

Chaudhuri, A., & Behan, P. O. (2000). Fatigue and basal ganglia. *Journal of the Neurological*

Sciences, 179(1), 34–42. [https://doi.org/10.1016/S0022-510X\(00\)00411-1](https://doi.org/10.1016/S0022-510X(00)00411-1)

Chaudhuri, A., & Behan, P. O. (2004). Fatigue in neurological disorders. *The Lancet*, 363(9413),

978–988. [https://doi.org/10.1016/S0140-6736\(04\)15794-2](https://doi.org/10.1016/S0140-6736(04)15794-2)

Chwastiak, L. A., Gibbons, L. E., Ehde, D. M., Sullivan, M., Bowen, J. D., Bombardier, C. H., &

Kraft, G. H. (2005). Fatigue and psychiatric illness in a large community sample of persons with multiple sclerosis. *Journal of Psychosomatic Research*, 59(5), 291–298.

<https://doi.org/10.1016/j.jpsychores.2005.06.001>

Cook, D. B., O'Connor, P. J., Lange, G., & Steffener, J. (2007). Functional neuroimaging

correlates of mental fatigue induced by cognition among chronic fatigue syndrome patients and controls. *NeuroImage*, 36(1), 108–122.

<https://doi.org/10.1016/j.neuroimage.2007.02.033>

Cressman, E. K., & Henriques, D. Y. P. (2009). Sensory Recalibration of Hand Position

Following Visuomotor Adaptation. *Journal of Neurophysiology*, 102(6), 3505–3518.

<https://doi.org/10.1152/jn.00514.2009>

- Cullen, K. E., & Brooks, J. X. (2015). Neural Correlates of Sensory Prediction Errors in Monkeys: Evidence for Internal Models of Voluntary Self-Motion in the Cerebellum. *The Cerebellum*, 14(1), 31–34. <https://doi.org/10.1007/s12311-014-0608-x>
- Desmond, J. E., Gabrieli, J. D. E., Wagner, A. D., Ginier, B. L., & Glover, G. H. (1997). Lobular Patterns of Cerebellar Activation in Verbal Working-Memory and Finger-Tapping Tasks as Revealed by Functional MRI. *Journal of Neuroscience*, 17(24), 9675–9685. <https://doi.org/10.1523/JNEUROSCI.17-24-09675.1997>
- D’Esposito, M., Detre, J. A., Alsop, D. C., Shin, R. K., Atlas, S., & Grossman, M. (1995). The neural basis of the central executive system of working memory. *Nature*, 378(6554), Article 6554. <https://doi.org/10.1038/378279a0>
- Deuschl, G., Toro, C., Zeffiro, T., Massaquoi, S., & Hallett, M. (1996). Adaptation motor learning of arm movements in patients with cerebellar disease. *Journal of Neurology, Neurosurgery & Psychiatry*, 60(5), 515–519. <https://doi.org/10.1136/jnnp.60.5.515>
- Enoka, R. M., & Duchateau, J. (2016). Translating Fatigue to Human Performance. *Medicine and Science in Sports and Exercise*, 48(11), 2228–2238. <https://doi.org/10.1249/MSS.0000000000000929>
- Fieo, R. A., Mortensen, E. L., Rantanen, T., & Avlund, K. (2013). Improving a Measure of Mobility-Related Fatigue (The Mobility-Tiredness Scale) by Establishing Item Intensity. *Journal of the American Geriatrics Society*, 61(3), 429–433. <https://doi.org/10.1111/jgs.12122>

Fletcher, P. C., & Henson, R. N. (2001). Frontal lobes and human memory: Insights from functional neuroimaging. *Brain: A Journal of Neurology*, 124(Pt 5), 849–881.

<https://doi.org/10.1093/brain/124.5.849>

Heirani Moghaddam, S., Chua, R., & Cressman, E. K. (2021). Assessing and defining explicit processes in visuomotor adaptation. *Experimental Brain Research*, 239(7), 2025–2041.

<https://doi.org/10.1007/s00221-021-06109-5>

Henriques, D. Y. P., & Cressman, E. K. (2012). Visuomotor Adaptation and Proprioceptive Recalibration. *Journal of Motor Behavior*, 44(6), 435–444.

<https://doi.org/10.1080/00222895.2012.659232>

Holtzer, R., Shuman, M., Mahoney, J. R., Lipton, R., & Verghese, J. (2010). Cognitive Fatigue Defined in the Context of Attention Networks. *Aging, Neuropsychology, and Cognition*, 18(1), 108–128. <https://doi.org/10.1080/13825585.2010.517826>

Ishii, A., Tanaka, M., & Watanabe, Y. (2014). Neural mechanisms of mental fatigue. *Reviews in the Neurosciences*, 25(4), 469–479. <https://doi.org/10.1515/revneuro-2014-0028>

Izawa, J., Criscimagna-Hemminger, S. E., & Shadmehr, R. (2012). Cerebellar Contributions to Reach Adaptation and Learning Sensory Consequences of Action. *Journal of Neuroscience*, 32(12), 4230–4239. <https://doi.org/10.1523/JNEUROSCI.6353-11.2012>

Jacoby, L. L. (1991). A process dissociation framework: Separating automatic from intentional uses of memory. *Journal of Memory and Language*, 30(5), 513–541.

[https://doi.org/10.1016/0749-596X\(91\)90025-F](https://doi.org/10.1016/0749-596X(91)90025-F)

Jacquet, T., Poulin-Charronnat, B., Bard, P., & Lepers, R. (2021). Persistence of Mental Fatigue on Motor Control. *Frontiers in Psychology, 11*, 588253.

<https://doi.org/10.3389/fpsyg.2020.588253>

Kenyon, L. K., & Blackinton, M. T. (2011). Applying Motor-Control Theory to Physical Therapy Practice: A Case Report. *Physiotherapy Canada, 63*(3), 345–354.

<https://doi.org/10.3138/ptc.2010-06>

Krakauer, J. W. (2006). Motor learning: Its relevance to stroke recovery and neurorehabilitation. *Current Opinion in Neurology, 19*(1), 84–90.

<https://doi.org/10.1097/01.wco.0000200544.29915.cc>

Krakauer, J. W., Ghez, C., & Ghilardi, M. F. (2005). Adaptation to Visuomotor Transformations: Consolidation, Interference, and Forgetting. *Journal of Neuroscience, 25*(2), 473–478.

<https://doi.org/10.1523/JNEUROSCI.4218-04.2005>

Krakauer, J. W., Hadjiosif, A. M., Xu, J., Wong, A. L., & Haith, A. M. (2019). Motor Learning. In R. Terjung (Ed.), *Comprehensive Physiology* (1st ed., pp. 613–663). Wiley.

<https://doi.org/10.1002/cphy.c170043>

Krakauer, J. W., & Mazzoni, P. (2011). Human sensorimotor learning: Adaptation, skill, and beyond. *Current Opinion in Neurobiology, 21*(4), 636–644.

<https://doi.org/10.1016/j.conb.2011.06.012>

Krakauer, J. W., Pine, Z. M., Ghilardi, M.-F., & Ghez, C. (2000). Learning of Visuomotor Transformations for Vectorial Planning of Reaching Trajectories. *Journal of Neuroscience, 20*(23), 8916–8924. <https://doi.org/10.1523/JNEUROSCI.20-23-08916.2000>

Krupp, L. B., LaRocca, N. G., Muir-Nash, J., & Steinberg, A. D. (1989). The Fatigue Severity Scale: Application to Patients With Multiple Sclerosis and Systemic Lupus Erythematosus.

Archives of Neurology, 46(10), 1121–1123.

<https://doi.org/10.1001/archneur.1989.00520460115022>

Larssen, B. C., & Hodges, N. J. (2023). Updating of Implicit Adaptation Processes through Erroneous Numeric Feedback. *Journal of Motor Behavior*, 55(5), 475–492.

<https://doi.org/10.1080/00222895.2023.2232739>

Lee, K. A., Hicks, G., & Nino-Murcia, G. (1991). Validity and reliability of a scale to assess fatigue. *Psychiatry Research*, 36(3), 291–298. [https://doi.org/10.1016/0165-1781\(91\)90027-](https://doi.org/10.1016/0165-1781(91)90027-M)

[M](https://doi.org/10.1016/0165-1781(91)90027-M)

Lorist, M. M. (2008). Impact of top-down control during mental fatigue. *Brain Research*, 1232, 113–123. <https://doi.org/10.1016/j.brainres.2008.07.053>

Lorist, M. M., Klein, M., Nieuwenhuis, S., De Jong, R., Mulder, G., & Meijman, T. F. (2000). Mental fatigue and task control: Planning and preparation. *Psychophysiology*, 37(5), 614–625.

Magnuson, J. R., Doesburg, S. M., & McNeil, C. J. (2021). Development and recovery time of mental fatigue and its impact on motor function. *Biological Psychology*, 161, 108076.

<https://doi.org/10.1016/j.biopsycho.2021.108076>

Maksimovic, S., & Cressman, E. K. (2018). Long-term retention of proprioceptive recalibration. *Neuropsychologia*, 114, 65–76. <https://doi.org/10.1016/j.neuropsychologia.2018.04.009>

- Manly, T., Robertson, I. H., Galloway, M., & Hawkins, K. (1999). The absent mind: Further investigations of sustained attention to response. *Neuropsychologia*, 37(6), 661–670.
[https://doi.org/10.1016/S0028-3932\(98\)00127-4](https://doi.org/10.1016/S0028-3932(98)00127-4)
- Martin, T. A., Keating, J. G., Goodkin, H. P., Bastian, A. J., & Thach, W. T. (1996). Throwing while looking through prisms: II. Specificity and storage of multiple gaze—throw calibrations. *Brain*, 119(4), 1199–1211. <https://doi.org/10.1093/brain/119.4.1199>
- Mazzoni, P., & Krakauer, J. W. (2006). An Implicit Plan Overrides an Explicit Strategy during Visuomotor Adaptation. *Journal of Neuroscience*, 26(14), 3642–3645.
<https://doi.org/10.1523/JNEUROSCI.5317-05.2006>
- McDougle, S. D., Bond, K. M., & Taylor, J. A. (2015). Explicit and Implicit Processes Constitute the Fast and Slow Processes of Sensorimotor Learning. *Journal of Neuroscience*, 35(26), 9568–9579. <https://doi.org/10.1523/JNEUROSCI.5061-14.2015>
- Milner, B. (1962). Physiologie de l’Hippocampe. *Neuropsychologia*, 3(3), 273–277.
[https://doi.org/10.1016/0028-3932\(65\)90029-1](https://doi.org/10.1016/0028-3932(65)90029-1)
- Modchalingam, S., Vachon, C. M., Hart, B. M., & Henriques, D. Y. P. (2019). The effects of awareness of the perturbation during motor adaptation on hand localization. *PLOS ONE*, 14(8), e0220884. <https://doi.org/10.1371/journal.pone.0220884>
- National Sleep Foundation. (2020). *Sleep in America Poll* [Data Set].
<https://www.thensf.org/sleep-in-america-polls/>

- Neva, J. L., Ma, J. A., Orsholits, D., Boisgontier, M. P., & Boyd, L. A. (2019). The effects of acute exercise on visuomotor adaptation, learning, and inter-limb transfer. *Experimental Brain Research*, 237(4), 1109–1127. <https://doi.org/10.1007/s00221-019-05491-5>
- Neville, K.-M., & Cressman, E. K. (2018). The influence of awareness on explicit and implicit contributions to visuomotor adaptation over time. *Experimental Brain Research*, 236(7), 2047–2059. <https://doi.org/10.1007/s00221-018-5282-7>
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113. [https://doi.org/10.1016/0028-3932\(71\)90067-4](https://doi.org/10.1016/0028-3932(71)90067-4)
- Pageaux, B., Marcora, S. M., Rozand, V., & Lepers, R. (2015). Mental fatigue induced by prolonged self-regulation does not exacerbate central fatigue during subsequent whole-body endurance exercise. *Frontiers in Human Neuroscience*, 9. <https://www.frontiersin.org/articles/10.3389/fnhum.2015.00067>
- Paus, T. (2001). Primate anterior cingulate cortex: Where motor control, drive and cognition interface. *Nature Reviews Neuroscience*, 2(6), Article 6. <https://doi.org/10.1038/35077500>
- Pine, Z. M., Krakauer, J. W., Gordon, J., & Ghez, C. (1996). Learning of scaling factors and reference axes for reaching movements. *Neuroreport*, 7(14), 2357–2361. <https://doi.org/10.1097/00001756-199610020-00016>
- Popa, L. S., & Ebner, T. J. (2019). Cerebellum, Predictions and Errors. *Frontiers in Cellular Neuroscience*, 12. <https://www.frontiersin.org/articles/10.3389/fncel.2018.00524>
- Redding, G. M., & Wallace, B. (1993). Adaptive Coordination and Alignment of Eye and Hand. *Journal of Motor Behavior*, 25(2), 75–88. <https://doi.org/10.1080/00222895.1993.9941642>

Redding, G. M., & Wallace, B. (1994). Effects of Movement Duration and Visual Feedback on Visual and Proprioceptive Components of Prism Adaptation. *Journal of Motor Behavior*, 26(3), 257–266. <https://doi.org/10.1080/00222895.1994.9941681>

Redding, G. M., & Wallace, B. (1996). Adaptive spatial alignment and strategic perceptual-motor control. *Journal of Experimental Psychology: Human Perception and Performance*, 22, 379–394. <https://doi.org/10.1037/0096-1523.22.2.379>

Redding, G. M., & Wallace, B. (2000). Prism Exposure Aftereffects and Direct Effects for Different Movement and Feedback Times. *Journal of Motor Behavior*, 32(1), 83–99. <https://doi.org/10.1080/00222890009601362>

Redding, G. M., & Wallace, B. (2001). Calibration and Alignment are Separable: Evidence From Prism Adaptation. *Journal of Motor Behavior*, 33(4), 401–412. <https://doi.org/10.1080/00222890109601923>

Redding, G. M., & Wallace, B. (2006). Prism adaptation and unilateral neglect: Review and analysis. *Neuropsychologia*, 44(1), 1–20. <https://doi.org/10.1016/j.neuropsychologia.2005.04.009>

Sanders, A. F. (1997). A summary of resource theories from a behavioral perspective. *Biological Psychology*, 45(1), 5–18. [https://doi.org/10.1016/S0301-0511\(96\)05220-9](https://doi.org/10.1016/S0301-0511(96)05220-9)

Scarpina, F., & Tagini, S. (2017). The Stroop Color and Word Test. *Frontiers in Psychology*, 8, 557. <https://doi.org/10.3389/fpsyg.2017.00557>

Schmidt, R. A., & Lee, T. D. (2011). *Motor control and learning: A behavioral emphasis* (5th ed). Human Kinetics.

Severini, G., & Zych, M. (2020). Characterization of the Adaptation to Visuomotor Rotations in the Muscle Synergies Space. *Frontiers in Bioengineering and Biotechnology*, 8, 605.

<https://doi.org/10.3389/fbioe.2020.00605>

Shadmehr, R., Smith, M. A., & Krakauer, J. W. (2010). Error Correction, Sensory Prediction, and Adaptation in Motor Control. *Annual Review of Neuroscience*, 33(1), 89–108.

<https://doi.org/10.1146/annurev-neuro-060909-153135>

Shumway-Cook, A., & Woollacott, M. H. (2007). *Motor Control: Translating Research Into Clinical Practice*. Lippincott Williams & Wilkins.

Sohn, J.-W., & Lee, D. (2007). Order-dependent modulation of directional signals in the supplementary and presupplementary motor areas. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 27(50), 13655–13666.

<https://doi.org/10.1523/JNEUROSCI.2982-07.2007>

Stanley, J., & Krakauer, J. (2013). Motor skill depends on knowledge of facts. *Frontiers in Human Neuroscience*, 7. <https://www.frontiersin.org/articles/10.3389/fnhum.2013.00503>

Streng, M. L., Popa, L. S., & Ebner, T. J. (2018). Modulation of sensory prediction error in Purkinje cells during visual feedback manipulations. *Nature Communications*, 9(1), Article

1. <https://doi.org/10.1038/s41467-018-03541-0>

Sülzenbrück, S., & Heuer, H. (2009). Functional independence of explicit and implicit motor adjustments. *Consciousness and Cognition*, 18(1), 145–159.

<https://doi.org/10.1016/j.concog.2008.12.001>

Taylor, J. A., & Ivry, R. B. (2014). Cerebellar and prefrontal cortex contributions to adaptation, strategies, and reinforcement learning. *Progress in Brain Research*, 210, 217–253.

<https://doi.org/10.1016/B978-0-444-63356-9.00009-1>

Taylor, J. A., Klemfuss, N. M., & Ivry, R. B. (2010). An explicit strategy prevails when the cerebellum fails to compute movement errors. *Cerebellum (London, England)*, 9(4), 580–586. <https://doi.org/10.1007/s12311-010-0201-x>

Taylor, J. A., Krakauer, J. W., & Ivry, R. B. (2014). Explicit and Implicit Contributions to Learning in a Sensorimotor Adaptation Task. *Journal of Neuroscience*, 34(8), 3023–3032. <https://doi.org/10.1523/JNEUROSCI.3619-13.2014>

Trejo, L. J., Kubitz, K., Rosipal, R., Kochavi, R. L., & Montgomery, L. D. (2015). EEG-Based Estimation and Classification of Mental Fatigue. *Psychology*, 6(5), Article 5. <https://doi.org/10.4236/psych.2015.65055>

Tseng, Y.-W., Diedrichsen, J., Krakauer, J. W., Shadmehr, R., & Bastian, A. J. (2007). Sensory prediction errors drive cerebellum-dependent adaptation of reaching. *Journal of Neurophysiology*, 98(1), 54–62. <https://doi.org/10.1152/jn.00266.2007>

Tzvi, E., Loens, S., & Donchin, O. (2022). Mini-review: The Role of the Cerebellum in Visuomotor Adaptation. *The Cerebellum*, 21(2), 306–313. <https://doi.org/10.1007/s12311-021-01281-4>

Vassena, E., Silvetti, M., Boehler, C. N., Achten, E., Fias, W., & Verguts, T. (2014). Overlapping Neural Systems Represent Cognitive Effort and Reward Anticipation. *PLoS ONE*, 9(3), e91008. <https://doi.org/10.1371/journal.pone.0091008>

- Vetter, P., Goodbody, S. J., & Wolpert, D. M. (1999). Evidence for an Eye-Centered Spherical Representation of the Visuomotor Map. *Journal of Neurophysiology*, 81(2), 935–939.
<https://doi.org/10.1152/jn.1999.81.2.935>
- Wang, C., Trongnetrpunya, A., Samuel, I. B. H., Ding, M., & Kluger, B. M. (2016). Compensatory Neural Activity in Response to Cognitive Fatigue. *Journal of Neuroscience*, 36(14), 3919–3924. <https://doi.org/10.1523/JNEUROSCI.3652-15.2016>
- Wascher, E., & Getzmann, S. (2014). Rapid mental fatigue amplifies age-related attentional deficits. *Journal of Psychophysiology*, 28, 215–224. <https://doi.org/10.1027/0269-8803/a000127>
- Werner, S., Aken, B. C. van, Hulst, T., Frens, M. A., Geest, J. N. van der, Strüder, H. K., & Donchin, O. (2015). Awareness of Sensorimotor Adaptation to Visual Rotations of Different Size. *PLOS ONE*, 10(4), e0123321. <https://doi.org/10.1371/journal.pone.0123321>
- Wolpert, D. M., & Flanagan, J. R. (2010). Motor learning. *Current Biology*, 20(11), R467–R472.
<https://doi.org/10.1016/j.cub.2010.04.035>
- Wolpert, D. M., Ghahramani, Z., & Jordan, M. I. (1995). An internal model for sensorimotor integration. *Science (New York, N.Y.)*, 269(5232), 1880–1882.
<https://doi.org/10.1126/science.7569931>
- Yang, C.-M., & Wu, C.-H. (2005). The Situational Fatigue Scale: A different approach to measuring fatigue. *Quality of Life Research*, 14(5), 1357–1362.
<https://doi.org/10.1007/s11136-004-5680-0>

Zhao, C., Zhao, M., Liu, J., & Zheng, C. (2012). Electroencephalogram and electrocardiograph assessment of mental fatigue in a driving simulator. *Accident Analysis & Prevention*, 45, 83–90. <https://doi.org/10.1016/j.aap.2011.11.019>

APPENDIX A. Participant Intake Form

Experiment Title: The effect of mental fatigue on explicit and implicit visuomotor adaptation

For Participant to Complete:

Full Name: _____ Date: _____

Date of Birth: _____ Age: _____ Sex (circle): M F
Other

Right-Handed (circle): Y N Corrected Vision (circle): Y N

7-Hour sleep (circle): Y N Caffeine Intake (circle): Y N

Alcohol intake (circle): Y N

For Experimenter to Complete:

Position Measurements:

Arm Length:

Chair Distance:

Chair Height:

Eye-Table Horizontal Distance:

Shoulder-Table Horizontal Distance:

Eye-Table Vertical Distance:

Shoulder Table Vertical Distance:

Eye-Corner Distance:

Shoulder-Corner Distance:

Testing Info

Subject Code: P

Testing Group:

Control

MF

Order of PDP instructions:

Explicit then Implicit

Implicit then Explicit

Blocks

- ☐ Baseline
- ☐ Assessment (exclusion)
- ☐ Task (Control/ MF)
- ☐ Adaptation
- ☐ Assessment
- ☐ Adaptation
- ☐ Assessment
- ☐ Adaptation
- ☐ Assessment

- ☐ Rest
- ☐ Assessment
- ☐ Retention

APPENDIX B. Edinburg Handedness Inventory

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, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9, 97-113.

APPENDIX C. Ethics Approval Letter

06/03/2023

Université d'Ottawa

Bureau d'éthique et d'intégrité de la recherche

University of Ottawa

Office of Research Ethics and Integrity

CERTIFICAT D'APPROBATION ÉTHIQUE | CERTIFICATE OF ETHICS APPROVAL

Numéro du dossier / Ethics File Number

H-03-19-3433

Titre du projet / Project Title

Explicit and Implicit Contributions
to VisuoMotor Adaptation

Type de projet / Project Type

Recherche de professeur /
Professor's research project

Statut du projet / Project Status

Renouvelé / Renewed

Date d'approbation (jj/mm/aaaa) / Approval Date (dd/mm/yyyy)

25/03/2019

Date d'expiration (jj/mm/aaaa) / Expiry Date (dd/mm/yyyy)

24/03/2023

Équipe de recherche / Research Team

Chercheur / Researcher Affiliation

Role

Erin CRESSMAN École des sciences de l'activité physique / School of
Human Kinetics

Chercheur Principal / Principal
Investigator

Sarvenaz HEIRANI École des sciences de l'activité physique / School of
MOGHADDAM Human Kinetics

Assistant de recherche / Research
Assistant

Darin WIJEYARATNAM École des sciences de l'activité physique / School of
Human Kinetics

Co-chercheur / Co-investigator

Christin SADLER École des sciences de l'activité physique / School of
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Assistant

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Student-researcher

David APREUTESEI École des sciences de l'activité physique / School of
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Conditions spéciales ou commentaires / Special conditions or comments

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Université d'Ottawa

Bureau d'éthique et d'intégrité de la recherche

University of Ottawa

Office of Research Ethics and Integrity

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

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

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

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

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

Any changes made to the project must be approved by the REB before being implemented, except when necessary to remove participants from immediate endangerment or when the modification(s) only pertain to administrative or logistical components of the project. Investigators must also promptly alert the REB of any changes that increase the risk to participant(s), any changes that considerably affect the conduct of the project, all unanticipated and harmful events that occur, and new information that may negatively affect the conduct of the project or the safety of the participant(s).

Coordonnateur / COORDINATOR

Coordonnateur de l'éthique / Ethics Coordinator

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

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