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FEEDBACK-RELATED NEURONAL PROCESSING DURING MOTOR LEARNING

By
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A thesis submitted to the faculty of The University of Mississippi in partial fulfillment of the requirements of the Sally McDonnell Barksdale Honors College.

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ABSTRACT

Feedback-Related Neuronal Processing During Motor Learning

(Under the direction of Dr. Alberto DelArco)

Motor learning has been widely examined using electroencephalography (EEG) to record event related potentials (ERP). ERPs occur in response to given stimuli and represent underlying neural processes that are either modifying or being modified by motor learning. This study seeks to examine how movement feedback changes neural activity (i.e. ERPs) in the motor cortex, and more specifically, if feedback-related neuronal activity is modified by motor learning and visual feedback. A novel visuomotor rotation task was employed in which participants adapted their movement to a 30- degree counter-clockwise rotation. Feedback was given through the presence or absence of the trajectory line of participants' movement. Surface EEG was utilized to record cortical neural activity throughout the motor task. Event related potentials were obtained at electrodes Cz and FCz. Behavioral data shows that participants successfully learned the visuomotor task over time. There was a significant difference in amplitude of ERPs between conditions where visual feedback was present and conditions where visual feedback was absent. However, the average ERPs amplitudes were not changed by learning. These results suggest that feedback-related neuronal activity contributes to processing visual sensory feedback, but not motor adaptation, during the task.

ACKNOWLEDGEMENTS

Anyone who has spent time with me over the course of the past two years has most likely experienced a reference to the ominous “thesis.” This research and everything that it embodies has easily been the most challenging academic feat of my college career, pushing me past all prior boundaries of knowledge and creativity. However, it has simultaneously been the most rewarding and fruitful academic feat of my college career.

This research endeavor was made possible and completely guided by my wonderful advisor, Dr. Alberto Del Arco, as well as Christopher Hill, an amazing PhD candidate who has been generous to allow me to research alongside him. Both of these men introduced me to the concept and process of electroencephalography analysis and expertly guided my learning and curiosity, all the while learning about it themselves. Constructing this thesis, and consequently broadening the horizons of my academic career and future professional goals, would not have been possible without them. For that, I am extremely thankful.

I would also like to acknowledge my family and friends for their consistent support and encouragement throughout the duration of this process.

This thesis project started out as an ominous, overwhelming goal, but with the aid, patience, and intelligence of these amazing influencers, it has grown into a work that I am so proud of and eager to present and share.

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LIST OF ABBREVIATIONS AND SYMBOLS

BOLD: Blood Oxygenation Level Dependent

EEG: Electroencephalography

ERP: Event Related Potential

fMRI: Functional Magnetic Resonance Imaging

FRN: Feedback-Related Negativity

M1: Primary Motor Cortex

PMc: Premotor Cortical Areas

SRTT: Simple Reaction Time Task

TMS: Transcranial Magnetic Stimulation

TTL: Transistor-Transistor Logic

ICA: Independent Components Analysis

USD: United States Dollar

(*) : Statistically Significant Results

INTRODUCTION

Motor Learning

Motor learning can be defined as underlying neural circuits becoming more efficient and faster in the transmission of task related information (Dayan et al., 2011). Manifestations of successful motor learning can be seen via increased task accuracy, faster response time, and retention of increased performance of the motor task over time (Schmidt et al., 2013). The ability to apply a new motor skill to different variations of a task, or even new environments, illustrates a high degree of successful motor learning. This specific type of motor learning is known as motor adaptation, so named because in order to translate motor skills from one context to another, one must learn to adapt movement in response to feedback (Bastian, 2008). Feedback can be given in many forms, but perhaps most often is that given in the form of error magnitude. Gradual refinement of the motor skill over the course of a learning period does not entirely change the movement or the task as a whole, but rather, allows for the modification of specific parameters such as force or direction of movement in order to improve the execution of the task. In doing so, error magnitude across the duration of the adaption period declines to resemble baseline measures. Such learned behavior can be unlearned (Bastian, 2008).

Multiple brain areas in the central nervous system contribute to the ability to learn and retain a motor skill. Most notable among these are the primary motor cortex (M1), which is primarily responsible for the acquisition of motor skill and its execution and the premotor cortical areas (PMc) (i.e. premotor cortex, supplementary motor cortex), which are primarily responsible for the preparation and coordination of movements (Kendal et.

al., 2012). Subcortical structures in the central nervous system also play a role in motor learning. The basal ganglia and the cerebellum play complimentary roles during motor learning. While the basal ganglia contributes to the planning and decision making of enacting the correct motor program to be performed (Kandel et al., 2012), the cerebellum contributes to the retention and subsequent performance of motor tasks (Galea et. al, 2012). Acting together, these cortical and subcortical areas refine and manipulate the control mechanisms of movement (Figure 1). As a result of this process throughout motor skill learning, both categories of structures can be uniquely and minutely altered for the purpose of more accurate future performance.

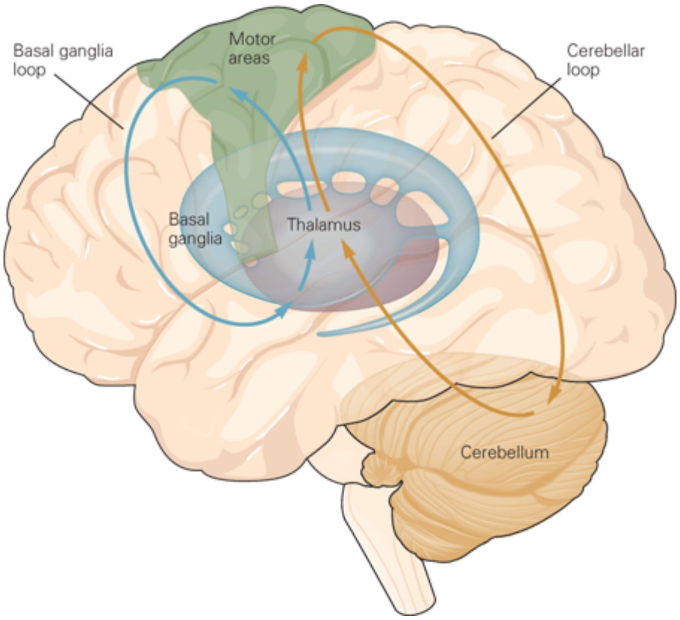


Figure 1. Cortical and subcortical brain structures involved in motor execution and learning.

Several studies have investigated the specific role of these brain areas during motor performance and learning. The primary motor cortex (M1) is involved both in the acquisition of learning a new motor skill as well as the in the progressive learning of tasks. Functional magnetic resonance imaging (fMRI) studies have reported inconclusive results regarding which of these roles is more prominent. For example, one study reported decreased blood oxygenation level dependent activity (BOLD) over the course of the skill being learned (Taubert et al., 2011), while an alternate study reported increasing BOLD levels during the course of learning the task (Mia et al., 2010). These results suggest M1 is involved in both acquisition of a motor task as well as subsequent performance of the task.

The role of M1 in learning was examined in one study by Galea et al., (2011). This study administered transcranial magnetic stimulation (TMS) to either the motor cortex or to the cerebellum as participants completed a visuomotor rotation task. The study found that when TMS was administered to M1 during the Adaptation period of the task, there was better retention of the task while the acquisition rate of the task remained the same. This suggests that the motor cortex plays a role in forming strong motor memories that are retained over time (Galea et al., 2011).

The PMc areas have been associated with the early stages of skill learning. Studies have shown that the PMc plays a role in creating links between external behavior cues and corresponding movement. For example, Steele and Penhune (2010) conducted a study that showed increases in BOLD in the PMc during learning of a finger tapping task. Furthermore, Cross, Schmitt, and Grafton (2005) illustrated that PMc activity increases when a task proves more difficult. These findings illustrate a relationship between motor preparation and decision making (Cross et al., 2005).

These cortical areas contribute to the acquisition and then continued retention and performance of motor skills. However, overarchingly, studies seem to suggest that there is decreased activity in these cortical areas once motor skills have been initially learned. This allows for the motor control system to detect new tasks and allocate cortical structure involvement appropriately, producing flexibility for other systems to take over already learned activities.

In addition to the cortical structures, subcortical structures are also vital to successful motor learning, particularly the cerebellum. As previously mentioned, Galea (2012) conducted a study during which TMS was administered to both the motor cortex and the cerebellum as participants completed a rotation visuomotor task. When TMS was administered to the cerebellum, the amount of errors decreased more quickly, but there was no effect on retention of the task. This suggests that the cerebellum plays a role in the subsequent performance and retention of a motor task (Galea et al., 2012). The basal ganglia has been shown to play a role in the consolidation of motor tasks and preparation for future premotor processes (Kandel et al., 2012).

Together, these cortical and subcortical structures play a large role in the development of motor learning while simultaneously being modified by motor learning themselves. Many techniques have been used to research these structures and their specific contributions to aspects of motor learning including fMRI, TMS, and Electroencephalography. This study utilized Electroencephalography to analyze feedback-related neuronal processing during motor learning.

1. EEG and Motor Learning

Electroencephalography (EEG) is a non-invasive technique used to examine underlying neural activity. EEG is applied by placing electrodes on the scalp in such a way that each electrode's placement corresponds with specific areas of the underlying cortex. Neurons interacting in the cortex produce an electric field that is strong enough to be detected and recorded by the electrodes. By recording these signals, EEG analysis allows for the examination of specific neural signals and the determination of their stimuli and influences in specific areas of the cortex (Cohen et al,, 2017).

One way to analyze these signals is by identifying and examining distinct time dependent signals referred to as event related potentials (ERP) (figure 2). ERPs are individual signals that appear as positive or negative deflections in voltage in response to specific environmental or motor/cognitive stimuli. Specific ERPs have been observed to change while learning a new motor skill and are associated with movement preparation, error detection, and stimuli processing:

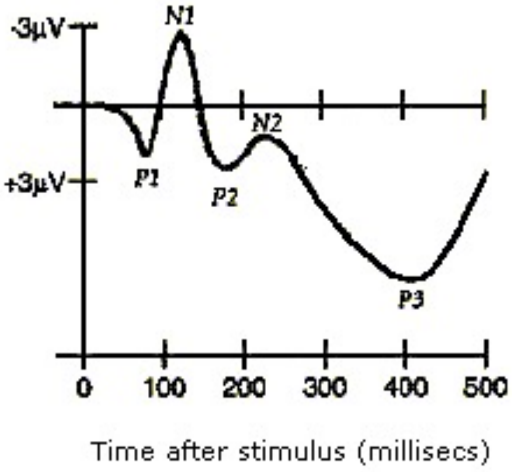


Figure 2. Depiction of components of event related potentials, post stimuli presentation. P and N refer to positive and negative deflections, respectively.

- Feedback-related negativity (FRN)

The feedback-related negativity (FRN) is a distinct fronto-central ERP elicited by an incorrect response made on a task. The FRN is typically seen as a change in voltage that occurs 200-350 milliseconds after feedback presentation. The FRN reflects activity in the anterior cingulate or supplementary motor cortical areas driven by phasic dopaminergic signaling reward processing error (Palidis et al., 2018). While the FRN is widely discussed in the current body of literature, its causes and meaning are still being examined and determined. Some studies propose that the FRN occurs in response to conflict monitoring or general prediction error (Palidis et al., 2018) while others document that relationships between the FRN and learning have been observed for tasks such as time estimation and discrete motor sequence learning (Holroyd et al., 2002). Furthermore, the FRN is elicited by multiple types of feedback. Palidis and colleagues (2018) conducted a study in which a visuomotor rotation task was implemented to assess reward and sensory error-based motor adaptation. This study found that the FRN was elicited specifically by reward feedback but not by sensory feedback. These results suggest that processes underlying the FRN may not be necessary for sensory error-based learning (Palidis et al., 2018).

Other studies demonstrated that the FRN displays different amplitudes depending on the size of the error that occurs and the experience with the new motor skill. Anguera and colleagues (2009) administered a visuomotor rotation task with a counter-clockwise rotation angle and found that during all stages of learning, FRN for large errors was significantly larger compared to small errors (Anguera et al., 2009). Furthermore, when comparing the early stages of learning with later stages, FRN for both large and small errors decreased as the participants became more accustomed to the motor task (Anguera et al., 2009). Beaulie et al., (2014) found that amplitudes of the FRN in their study depended on when in the task learning the error occurred. They administered sequential and random forms of an SRTT. Throughout the task, reaction time decreased for both sequential and random blocks. Late learning elicited higher amplitudes compared to early learning, suggesting an increased ability of the cortex to evaluate responses during online task acquisition (Beaulie et al., 2014).

- P300

The P300 is a distinct parietal ERP that represents an update to a stimulus cortical representation and the amount of attentional resources engaged in a task (Polich, 2007). The P300 is represented by a positive deflection of voltage occurring 250-500 milliseconds after a given stimulus. The three sites proposed to generate the P300 are the frontal lobe, hippocampus, and the medial temporal lobe (Polich, 2007).

The P300 ERP has been shown to decrease as a motor task is learned. MacLean and colleagues (2015) performed a prism adaption task in which participants wore distortion goggles as they reached toward a target displayed on a touchscreen. They assessed FRN and P300 ERPs. Over the course of the adaptation period, they observed a decrease in the size of the P300 ERP, suggesting that as learning occurs and participants master the motor task, an internal model is being updated, allowing for different areas of the brain to take over primary control of the continued task completion (MacLean et al., 2015).

Palidis et al., (2018) had similar findings showing a modulation in the size of P300 over the course of adaptation of a motor task. They conducted a study in which a visuomotor rotation task was implemented to assess reward and sensory error-based motor adaptation. They observed a P300 ERP in response to reach endpoint position feedback and found that the amplitude was sensitive to the magnitude of sensory error. Because learning in visuomotor rotation paradigms is thought to be driven primarily by sensory error-based learning (Izawa & Shadmehr, 2011), with both proprioceptive and visual information (Yousif et al., 2015), this suggests that the P300 observed might reflect neural activity that is related to the processing of sensory error underlying motor adaptation (Palidis et al., 2018).

Krigolson and colleagues (2015) discusses the importance of the brain's ability to process complex sensory-based visuomotor adaptations in order to realize the coordinate framework needed to execute a goal-directed movement by examining multiple studies. In one study, Krigolson and colleagues (2013) found that a visual cue notifying participants whether or not the task would be completed with or without the presence of visual feedback modulated the amplitudes of the P300 ERP. They found that memory-guided trials (those void of visual feedback) illustrated lower amplitudes in both wave forms and suggest that this potentially reflects incorrect encoding of target or movement amplitude (Krigolson et al., 2013). Similarly, Kourtis and colleagues (2011) conducted an experiment where participants completed a finger tapping task of differing difficulty levels and found modulation of the P300 ERP as a result of the presence of a visual cue that indicated the difficulty of the task prior to movement onset. These results suggest that the P300 is sensitive to visual feedback processing that drives movement planning (Kourtis et al., 2011).

In sum, it is suggested that the ability to process sensory feedback, by both constant monitoring of movement and also by following movement errors at the completion of a task, is a key skill contributing to the facilitation of motor learning (Krigolson et al., 2015). However, how the neuronal processing of sensory feedback contributes to motor learning is not fully understood. The aim of this study is to further examine feedback-related neuronal processing during motor learning by conducting EEG analysis of the discussed components during a visuomotor rotation task.

2. Specific Aims and Hypotheses

Aim 1*: To examine whether feedback-related neuronal activity is modified by motor learning.*

Previous studies have related changes in peak amplitude of feedback-related potentials to error processing by cortical areas (van der Helden et al., 2010; Beaulie et al., 2014). This study will investigate whether feedback-related neuronal activity is modified by motor learning. It is hypothesized that early learning trials will elicit greater peak amplitudes of feedback-related potentials than late learning trials, which will be associated with learning of the motor skill through practice.

Aim 2*: To examine whether feedback-related neuronal activity is modified by visual feedback.*

Kourtis and colleagues (2011) found modulations of feedback-related potentials as a result of the presence of a visual cue that indicated the difficulty of the task prior to movement onset, suggesting that these ERPs are sensitive to visual feedback processing that drives movement planning (Kourtis et al., 2011). This study will investigate whether feedback-related neuronal activity is modified by visual sensory feedback by comparing ERPs obtained during a learning period in which visual feedback was present, and then during a post-learning period in which the visual feedback was removed. It is hypothesized that the amplitude of ERPs will be lower when visual feedback is removed.

METHODS

Participants

Forty-two healthy, right handed, adult males and females aged between 18-35 with no self-reported history of musculoskeletal, orthopedic, psychiatric, and neurological abnormalities were included in the larger project as a whole. For purposes of this study, 11 of those participants were randomly selected and analyzed: six men and five women. Participants were first assessed for handedness using the Edinburgh Handedness Scale. Those scoring between 61 and 100 were considered right-handed and were included in the study (Oldfield, 1971).

Experimental Procedures

Each participant was seated in a chair and the Quik-Cap electrode system was placed on the participant's head in order to record surface electroencephalography. A saline solution was applied with a blunt tip syringe into the individual electrodes to lower the electrical signal noise (Impedance < 5kOhms). A reference electrode was placed on the right mastoid process.

The visuomotor task follows those outlined in Galea et al., (2015) and Song and Smiley-Oyen., (2017). The visuomotor rotation task consisted of several blocks of trials with congruent cursor and target movement intermixed with several blocks of trials with incongruent cursor movement. When the shift from congruent to incongruent cursor movement occurred, participants had to learn to adapt their movement in order to successfully hit the target. A Wacom tablet and pen (Saitama, Japan) was used for data collection of movement parameters such as reaction time and movement time. Participants were seated in front of an 114.3 cm television screen, at a distance of 61 cm, displaying two different circles (small red, large blue). Each trial was initiated by clicking on the small red circle in the center of the screen. Following the onset of each trial, a line followed the cursor's movement. The blue target circle was displayed eight centimeters from the starting circle in one of eight different positions given in a randomized order so that each set of eight consecutive trials included one of each of the target positions. Participants were instructed to move as quickly and accurately as possible from the starting circle to the target with the Wacom pen. A duration criterion of 400 milliseconds was placed on each trial, meaning the trial was required to be completed within 400 milliseconds. If the trial was not completed within 400 milliseconds, the trial restarted with a message informing the participant to perform quicker.

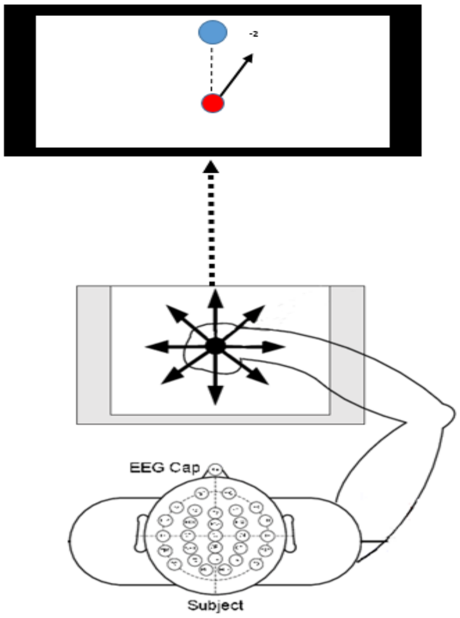


Figure 3: An illustration of the motor control task to be performed by the participants.

Participants performed a total of 680 trials. Each of these trials was completed with the participant's right hand. These 680 trials included five testing conditions: Baseline (80 trials), Adaptation (200 trials), No Vision (200 trials), Washout (100 trials), and Readaptation (100 trials). During Baseline and Washout conditions, target and cursor movement were congruent; during Adaptation, No Vision, and Readaptation conditions, target and cursor movement were incongruent, with the cursor trajectory rotated 30° counter-clockwise to the target. This manipulation of the cursor trajectory required participants to adapt their movement to hit the target successfully. During the Adaptation and Readaptation conditions, scored feedback was presented following each trial either displaying points in accordance with their assigned group or null feedback. Based on their performance, participants were either awarded or deducted points, which each corresponded to a monetary value of $0.01 USD.

However, for the purpose of this study, we will disregard the type and amount of scored feedback given and the corresponding monetary gain or loss and instead focus only on the visual feedback received via presence or absence of the cursor's trajectory line, which is given during the Adaptation condition and then removed during the No Vision condition.

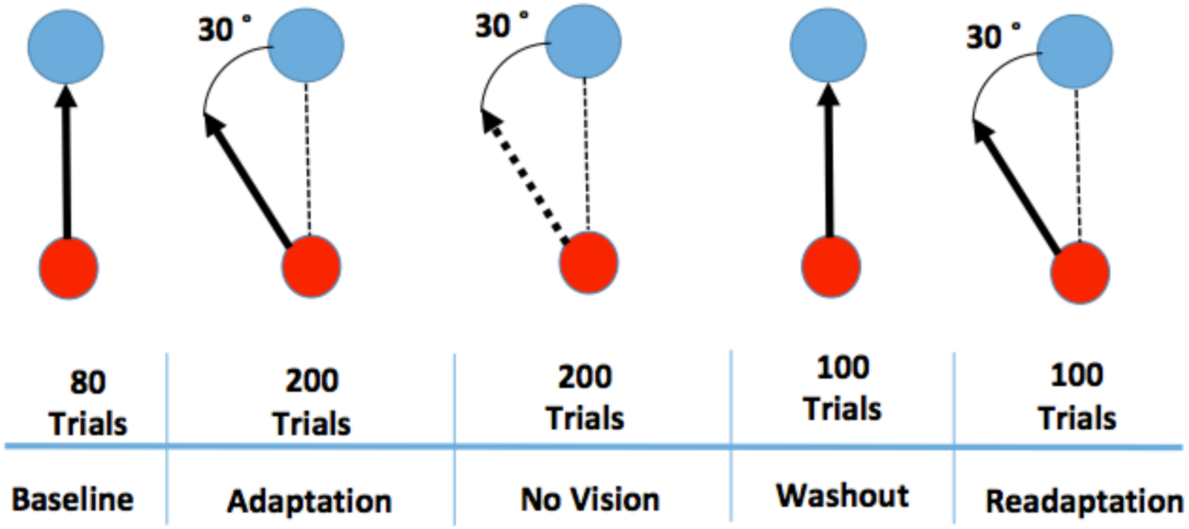


Figure 4: Illustration of the conditions of the motor task. The solid arrow represents the visible cursor trajectory that can be viewed by the participant. The dashed arrow represents cursor trajectory that is not visible to the participant. The dashed line represents the direction of the cursor moved by the participant.

Instrumentation

Surface electroencephalography (EEG) was recorded with 28 channels using Quik-Cap electrode system (Victoria, Australia). Electrodes were placed according to the 10-20 system at sites Fz, FCz, Cz, Pz, FP1, FP2, F3, F4, F7, F8, FT7, FT8, FC3, FC4, C3, C4, CP4, P3, P4, T3, T4, T5, T6, TP7, TP8, O1, O2, and ground placed on the participant's right mastoid process. All data recordings were sampled at 1000Hz, online band pass filtered between 0.1-1000Hz, and notch filtered at 60Hz. Recordings were performed at rest, with eyes open and then with eyes closed in one-minute increments before the motor learning task began. EEG data was assessed throughout each condition of the motor learning task. Motor task events of movement initiation, termination, and feedback were synchronized with the EEG recordings using a Matlab generated TTL pulse at each event onset.

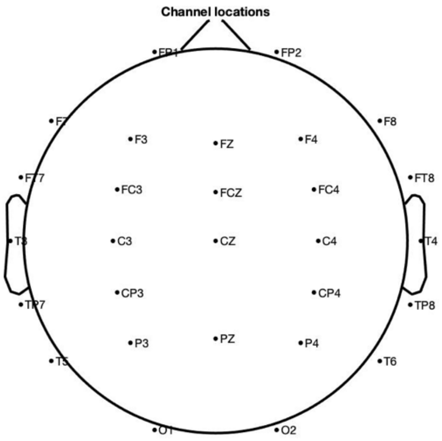


Figure 5: Scalp map showing the position of all electrodes on the Quik-Cap during EEG measurement.

Data Analysis

Motor Learning Task

Reach direction can be defined as the degree to which the participant moved the cursor to a 30° angle. Over the course of the task, the closer the participant's cursor came to the target, the better their performance, indicating successful mastering of the task. Therefore, in conditions with congruent cursor and target movement, an accurate reach direction would be 0° whereas in conditions with incongruent cursor and target movement where the target shifted to a 30° counter-clockwise rotation, an accurate reach direction would be 30°. Reaction time was considered the time between trial initiation and beginning of cursor movement. Movement time was considered the time between the beginning of the cursor's movement and the termination of the movement. Both reaction time and movement time were averaged within each condition of the behavioral task. All trials failing to be completed within the duration criteria were excluded from the analysis.

EEG

All raw EEG data was exported and processed in Matlab, using the EEGLAB toolbox (Deloreme & Makeig, 2004). Each subject's data was imported into Matlab in the form of CNT files for each condition; each participant had 5 different CNT files, which corresponded with the 5 different conditions. Before the data could be fully analyzed in Matlab, it had to be exported to Microsoft Excel in the form of text files. In Excel, the specific epochs were renamed according to which condition the data corresponded with. For example, data from the Baseline condition was manipulated so that the three events, or epochs, were named 1, 2, and 3 whereas data from the Adaptation condition was manipulated so that the same three events, or epochs, were named 4, 5, and 6, and so on.

Upon completion of this Excel work, the data was then exported as text files and imported to Matlab as "event info" per each condition. From there, the 5 data sets were appended to create one large data set consisting of all 5 conditions, with each condition possessing specifically labeled events. The data was then down sampled from 1000 Hz to 250 Hz and high pass filtered at 1 Hz. All trials that did not meet the duration criteria of 400 milliseconds were excluded from further analysis. Flat line channels VOEL, VOER, HOEL, HOER, CPz, FT9, FT10, PO1, PO2, A1, and Oz were also removed from the data. Continuous data was then segmented into epochs time-locked according to marked events. This study analyzes epoch 2, Movement Termination, which was time-locked -500 ms to + 1500 ms. In order to examine the second epoch from each condition while maintaining the knowledge of which condition each trial came from, epoch extraction also included the selection of events 2, 5, 8, 11, and 14, which were the second epochs of each condition. Epochs containing artifacts were removed using a semi-automatic algorithm for artifact rejection and visual inspection with the EEGLab Toolbox. Epochs containing artifacts flagged by the algorithm were removed after visual inspection. Independent components analysis decomposition was performed on each participant's data. Components reflecting eye blinks and electromyography activity were removed from the analysis by visual inspection. The data was then separated back into 5 smaller data sets according to condition of the task, and ERPs for each condition were obtained.

Event related potentials (ERP) were computed on an individual basis by trial averaging EEG time series epochs after artifact removal from the recordings of the frontal electrodes (FCz, F3, F4, C3, C4, Pz). This occurred for each task condition separately for each participant for two electrodes: Cz and FCz. ERPs were then summed across the eleven participants to compute a grand average ERP for each condition. Epochs used for this ERP analysis correspond to the movement termination (epoch 2). Figure 6 gives a step by step description of the data analysis.

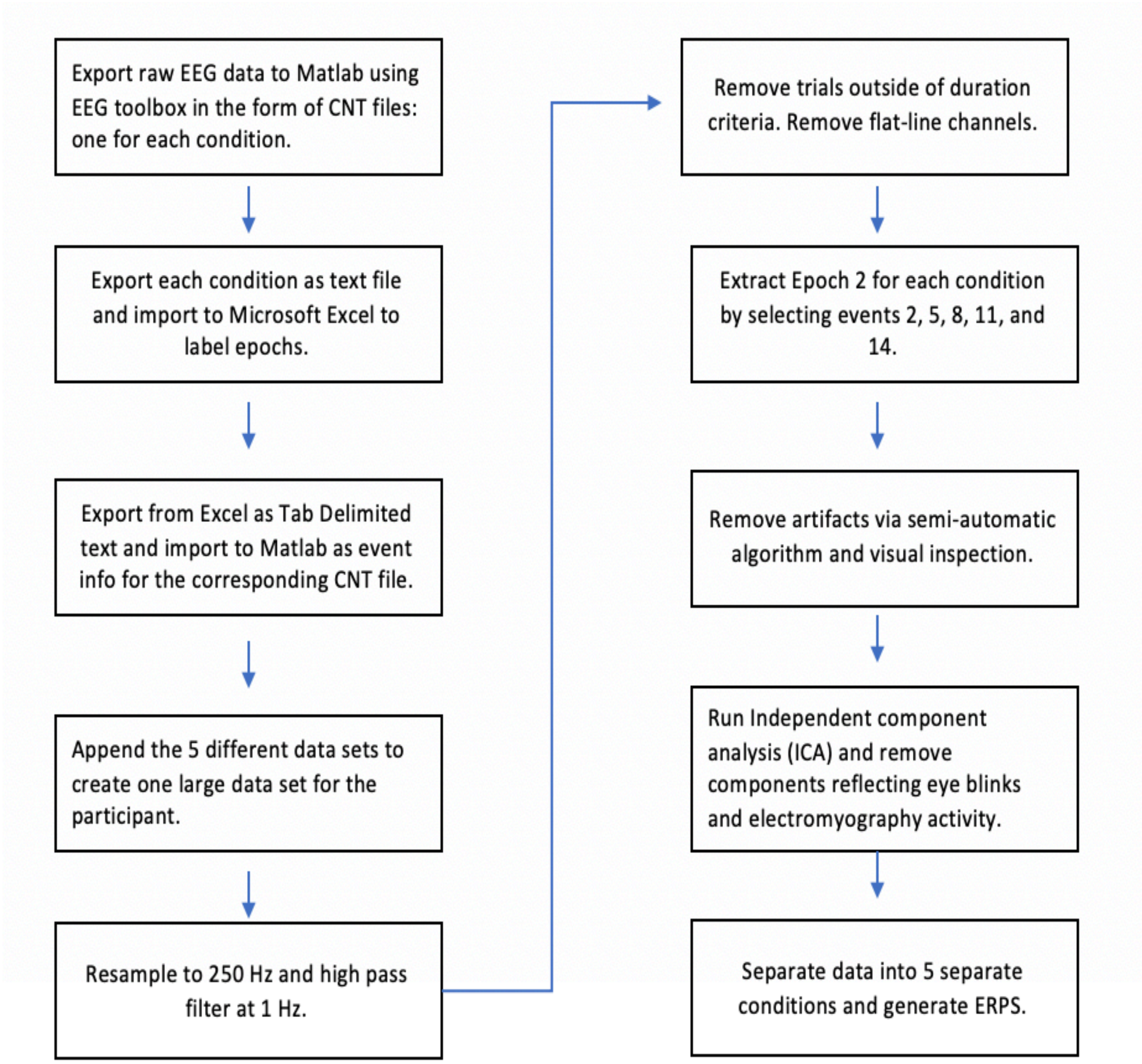


Figure 6: Flowchart representing steps of Data Analysis concerning EEG.

Early versus Late Learning

In order to examine Aim 1 regarding the ERP's amplitude over the course of the Adaptation condition, the first 60 trials and the last 60 trials of the analyzed Adaptation data sets were isolated. The first 60 trials are considered early learning while the last 60 trials are considered late learning. Data ICA and activity for these isolated data sets was then exported to Excel once more. In Excel, the average amplitudes of electrodes Cz and

FCz were determined for both the early learning data and the late learning data. Data from all 11 subjects was averaged to produce grand ERPs for early and late learning, which were then compared to each other and to behavioral data.

Statistical Analysis

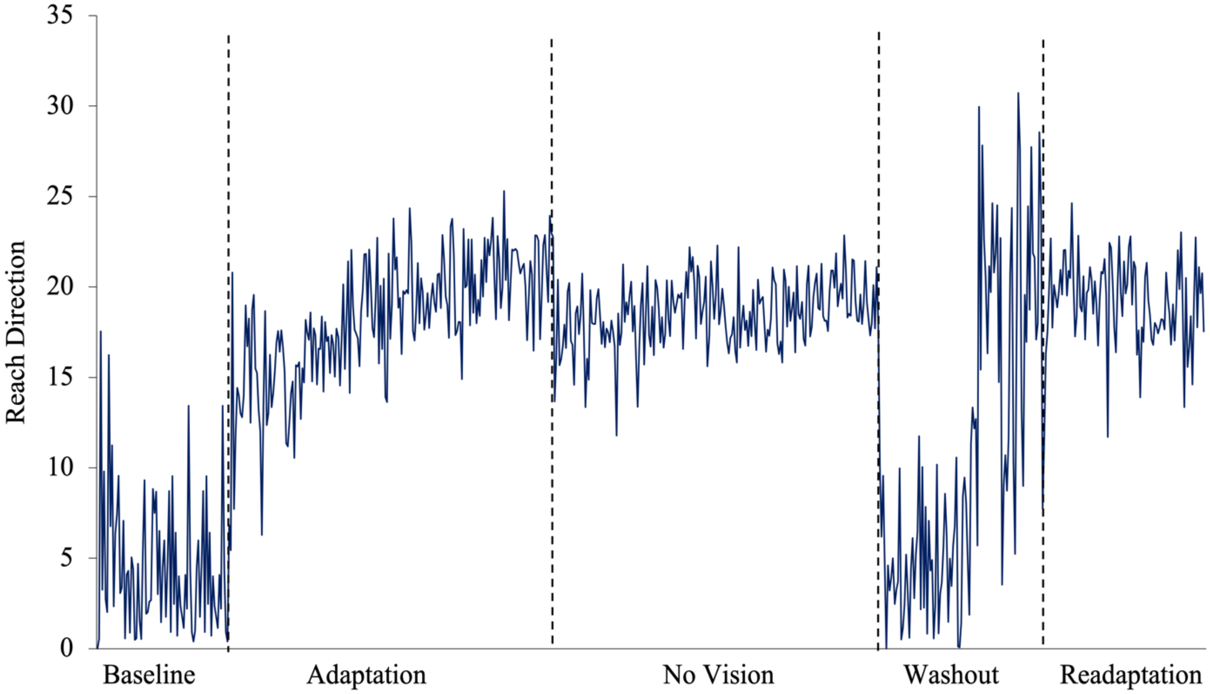
Repeated Measures ANOVAS were utilized to analyze behavior and ERPs as within subject factors across five different conditions and 680 trials. A linear regression analysis (Pearson correlation coefficient) was also conducted between the progression of trials during the Adaptation condition and the Reach Direction of each trial. All analyses were set at a priori alpha level of 0.05.

RESULTS

Behavior

Reach direction can be defined as the degree to which participants moved the cursor to the 30° counterclockwise angle. Over the course of the task, the closer the participant's cursor came to the target, the better their performance, indicating successful mastering of the task. Therefore, in conditions with congruent cursor and target movement, an accurate reach direction would be 0° whereas in conditions with incongruent cursor and target movement where the target shifted to a 30° rotation, an accurate reach direction would be 30°. As illustrated in figure 7, reach direction for Baseline and Washout conditions was relatively low, and reach direction for Adaptation, No Vision, and Readaptation was closer to 30°. These results indicate that on average, participants learned throughout the course of the task to adapt their movement in order to hit the target. No significant difference was noted between the Adaptation and No Vision conditions ($F(1,10) = 0.970$, $p= 0.348$), illustrating that participants retained the learning of the motor task (Figure 7B).

A.



B.

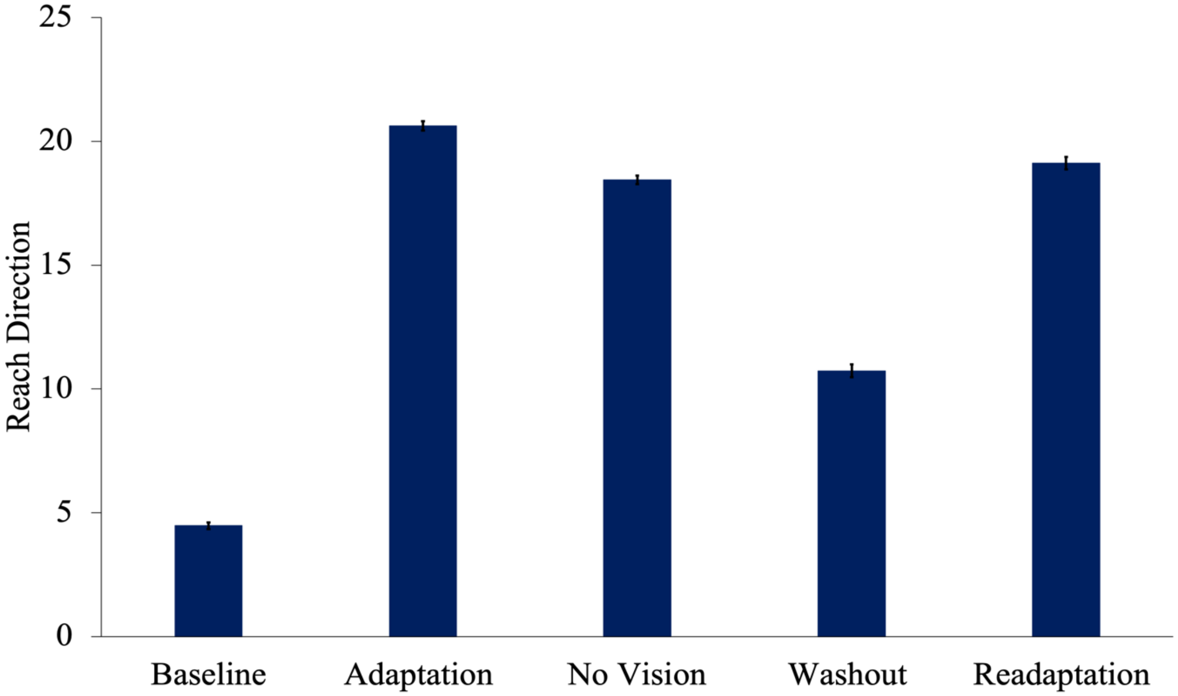


Figure 7: **A**: Illustration of average reach direction represented across blocks in the five task conditions of the motor testing. Reach direction is defined as the degree to which participants moved the cursor to a 30° counterclockwise angle. **B**: Reach direction represented across blocks in the five task conditions for motor testing. Note that the Adaptation block represents only late learning in order to prevent bias.

Throughout the five different conditions, participants adjusted their reach direction accordingly in order to hit the target at its appropriate perturbed or unperturbed angle. Figure 8 focuses specifically on the reach direction during the Adaptation (learning) condition of the task. A significant positive correlation (r=0.685, p<0.001) was noted between reach direction and trial indicating that as participants repeated the task, their performance level increased, and they learned the motor task.

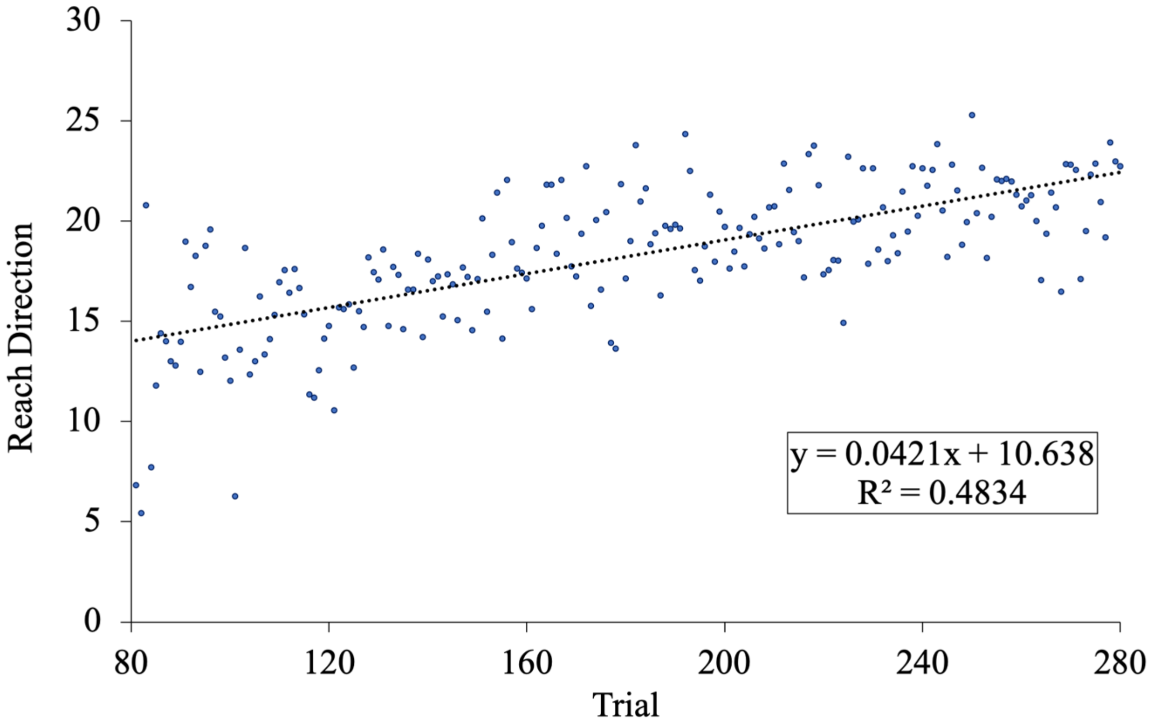


Figure 8: Illustration of the reach direction over the course of the learning (Adaptation) condition. A significant positive correlation (r=0.685, p<0.001) was noted between reach direction and trial.

In order to examine whether or not feedback-related neuronal activity is modified by motor learning, the Adaptation condition was further divided into early and late trials, with the early trials defined as the first 60 trials and the late trials defined as the last 60 trials. ERPs for two electrodes were analyzed to observe differences in the waveforms between early and late learning (Figure 9A; Figure 10A). Electrodes FCz and Cz were chosen because of their placement over the motor cortex. Average amplitudes of early and late learning were compared in two time windows, 0-200 ms and 200-500 ms. For the FCz electrode, no significant difference was noted between early and late learning in the first window ($F(1,10) = 0.003$, $p= 0.995$, $\eta p^2 < 0.01$) or in the second window ($F(1,10) = 0.882$, $p= 0.370$, $\eta p^2 = 0.081$) (Figure 9B). For the Cz electrode, no significant difference was noted between early and late learning in the first window ($F(1,10) = 0.002$, $p= 0.963$, $\eta p^2 < 0.01$) or in the second window ($F(1,10) = 0.889$, $p= 0.368$, $\eta p^2 = 0.082$) (Figure 10B).

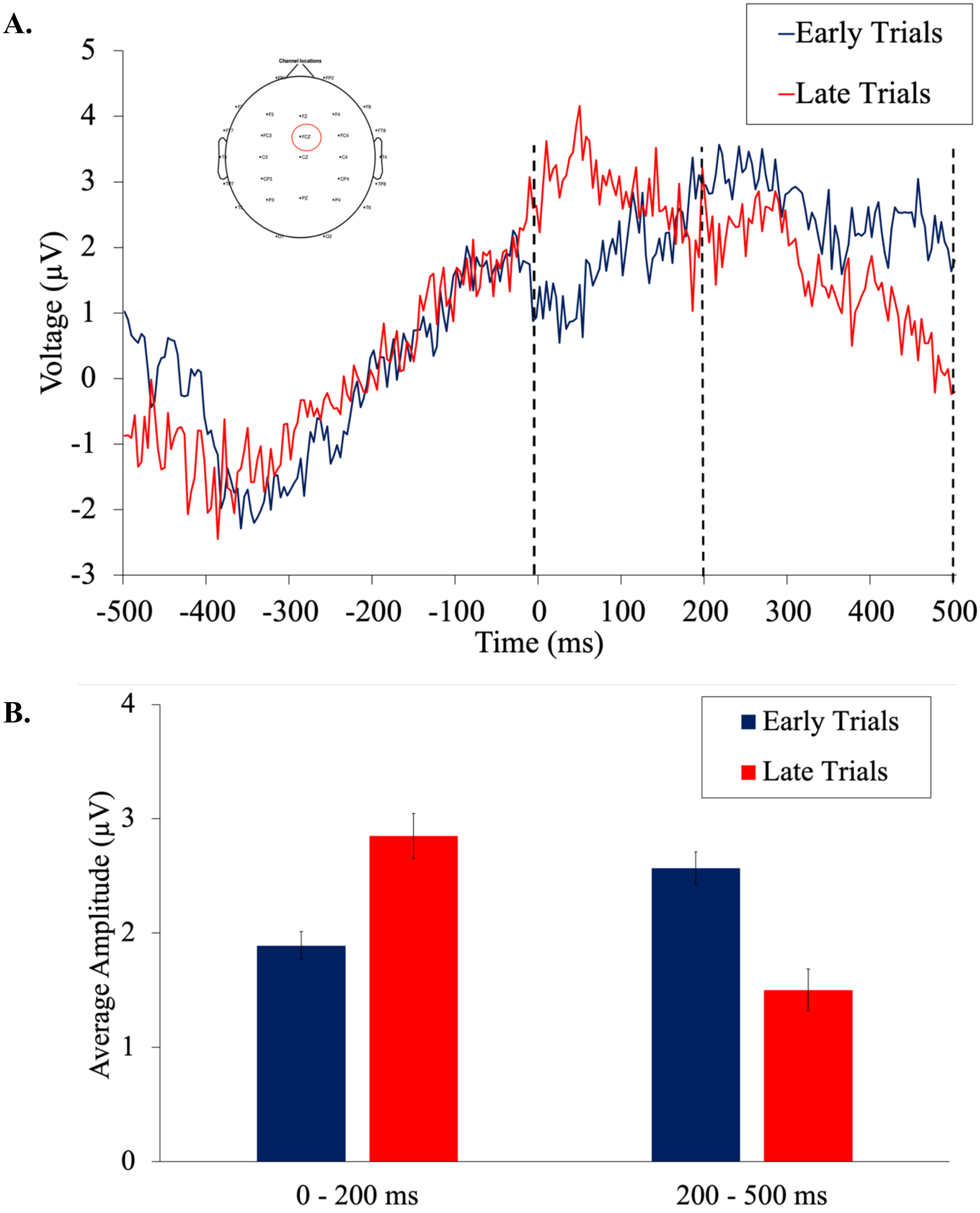


Figure 9: A: ERP of early and late trials in the FCz electrode. Early trials are defined as the first 60 trials of the Adaptation condition while late trials are defined as the last 60 trials of the Adaptation condition. **B**: Average amplitudes of early and late trials compared in two time windows. No significant difference was noted between early and late trials in either window.

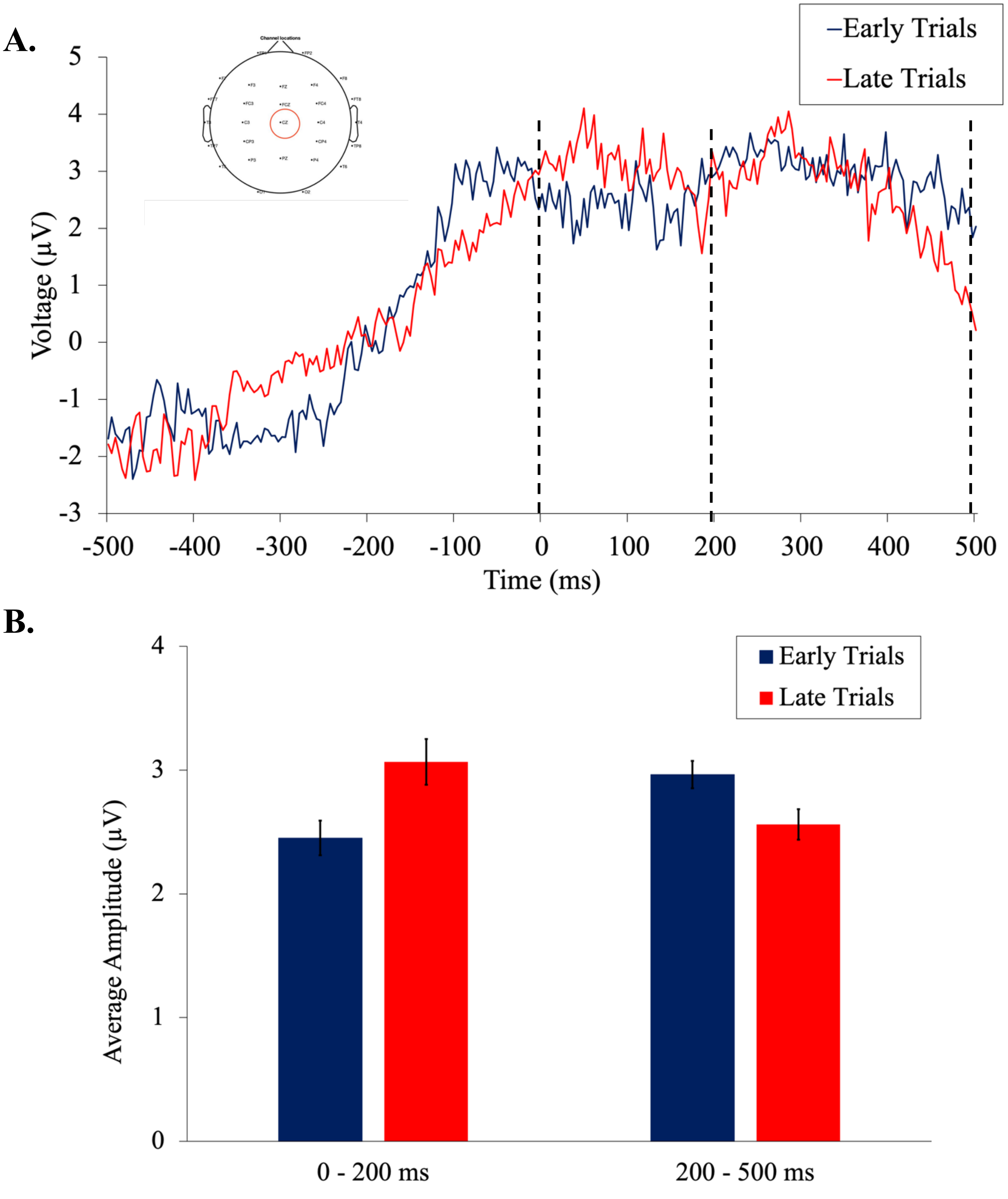


Figure 10: A: ERP of early and late trials in the Cz electrode. Early trials are defined as the first 60 trials of the Adaptation condition while late trials are defined as the last 60 trials of the Adaptation condition. **B:** Average amplitudes of early and late trials compared in two time windows. No significant difference was noted between early and late trials in either window.

In order to examine whether or not feedback related neuronal activity is modified by visual feedback, ERPs at the FCz and Cz electrodes were analyzed for the Baseline, Adaptation, and No Vision conditions of the task (Figure 11A; Figure 12A). The role of visual feedback was examined by comparing the Adaptation condition, where visual feedback in the form of the cursor's trajectory was present, to the No Vision condition, where visual feedback in the form of the cursor's trajectory was absent. The average amplitudes of the ERPs were compared in a time window of 0-500 ms (Figure 11B; Figure 12B). Data for the FCz electrode is shown in figure 11, and data for the Cz electrode is shown in figure 12.

A significant main effect for condition was noted for mean FCz amplitude ($F(2,20) = 6.021$, $p= 0.009$, $\eta p^2 = 0.376$). Baseline and Adaptation demonstrated a significantly higher mean amplitude than No Vision at $p= 0.019$ and $p= 0.029$, respectively. No significant effect was noted between Baseline and Adaptation conditions at $p=0.599$. A significant main effect for condition was noted for mean Cz amplitude ($F(2,20) =7.117$, $p=0.005$, $\eta p^2 = 0.416$). Baseline and Adaption demonstrated a significantly higher mean amplitude than No Vision at $p= 0.009$ and $p= 0.017$, respectively. No significant effect was noted between Baseline and Adaptation conditions at $p= 0.730$.

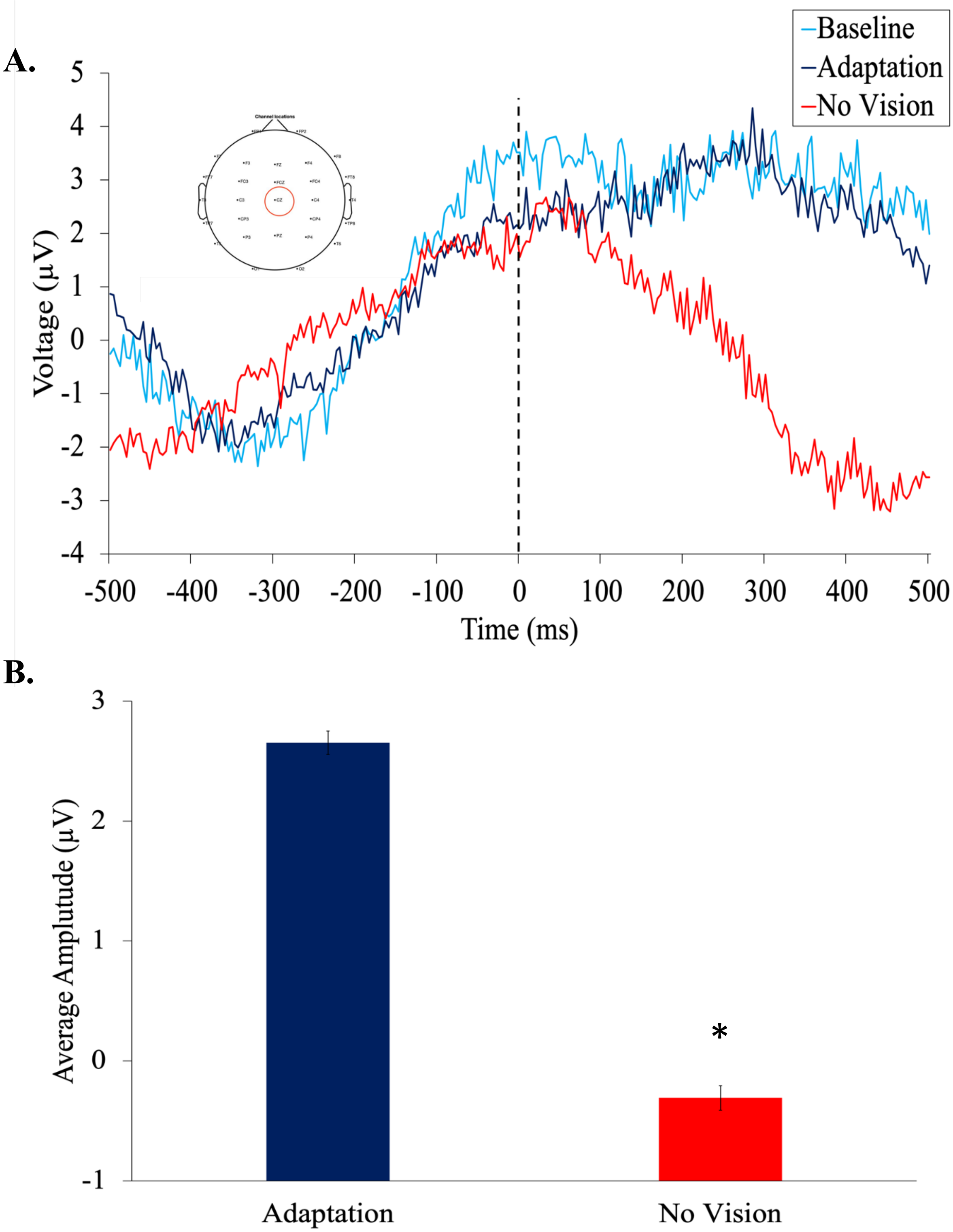


Figure 11: **A**: Grand ERP of Baseline, Adaptation, and No Vision conditions throughout duration of the task at the FCz electrode. Time zero begins the feedback time, at which time movement ceased and feedback-related processing began. Note that in the No Vision condition, visual feedback was absent. **B**: Representation of amplitudes compared between the Adaptation and No Vision conditions. Only amplitudes from the time window 0-500 ms are represented. A significant main effect for condition was noted for mean FCz amplitude between Adaptation and No Vision ($F(2,20) = 6.021$, $p = 0.029$, $\eta p^2 = 0.376$) (*).

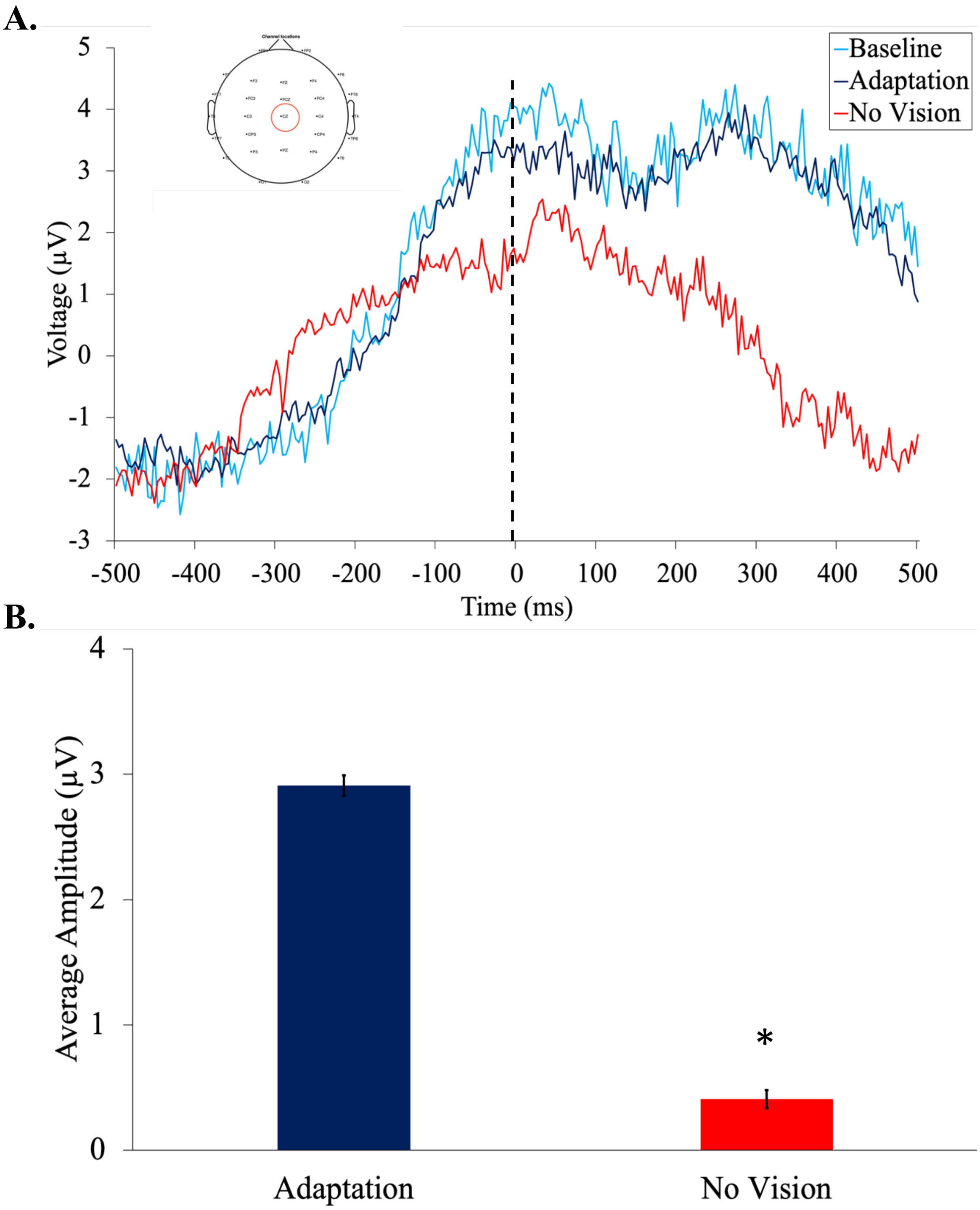


Figure 12: **A**: Grand ERP of Baseline, Adaptation, and No Vision conditions throughout duration of the task at the Cz electrode. Time zero begins the feedback time, at which time movement ceased and feedback-related processing began. Note that in the No Vision condition, visual feedback was absent. **B**: Representation of amplitudes compared between the Adaptation and No Vision conditions. Only amplitudes from the time window 0-500 ms are represented. A significant main effect for condition was noted for mean FCz amplitude between Adaptation and No Vision (F(2,20) = 6.021, p= 0.017, $\eta p^2 = 0.376$) (*).

DISCUSSION

The present study found that participants learned and retained performance in the visuomotor task, consistent with the current body of literature. Importantly, feedback-related neuronal activity was not modified by motor learning. Furthermore, it was determined that feedback-related neuronal activity was modified by the absence of visual input. These results suggest that feedback-related neuronal processing evaluated during motor performance depends, in part, on visual information, but does not contribute to motor adaptation.

Behavior

The present study found that participants learned and retained performance in the visuomotor rotation task. Consistent with the reinforcement learning theory, as the task progressed, the accuracy of participants' movement increased, signaling that they learned the task. In the Baseline and Washout conditions, during which target and cursor movement were congruent, the reach direction measured was relatively close to zero; while in the Adaptation, No Vision, and Readaptation conditions of the task, during which target and cursor movement were incongruent, reach direction was much higher. This illustrates the idea that participants learned to adapt their movement to match the perturbation during specific conditions. A significant positive correlation was noted between reach direction and trial during the learning condition (Adaptation).

No significant difference was found in the reach direction between the later stage of Adaptation condition (late learning) and the No Vision condition (retention). Taken together, these findings illustrate that participants successfully learned and retained the visuomotor rotation task.

Previous studies have investigated motor learning using a visuomotor rotation task and have found similar results. In an effort to measure the influence of positive and negative feedback on learning and retention during motor learning, Galea and colleagues (2015) implemented an identical visuomotor rotation task that required participants to adapt their movement to compensate for a 30 degree counter clockwise rotation. Participants were sorted into one of three groups: reward, punishment, or control, and during the adaptation period, they received appropriate conditional feedback based on their end-point error. While participants in all conditions successfully learned the task, as measured by end point error, they found dissociable effects for parameters of this learning. Punishment feedback caused faster learning to the fixed visuomotor rotation with no significant effect on retention while reward feedback caused greater memory retention with no significant effect on speed of acquisition of the task (Galea et al., 2015). The authors propose that the increased speed of learning observed in the punishment group is due to the enhancement of cerebellum-dependent sensory prediction error learning, potentially through increased levels of serotonin. They also propose that the increased level of retention observed in the reward group is due to the creation of a stronger memory trace for the new task in the cerebral cortex. They note that dopaminergic neurons have projections to M1, which is vital for the retention of motor adaptation and hypothesize that the enhanced retention is correlated with dopamine being transmitted to M1 during motor adaptation (Galea et al., 2015).

A larger study performed in our laboratory (Hill et al., 2019) used the same behavioral measurement tactics as Galea and colleagues (2015) as far as the visuomotor rotation task and feedback conditions. Our behavioral findings mirror Galea and colleagues (2015), thus implicating that similar changes in the cerebral cortex are taking place. However, for purposes of this analysis, the time window in which neural activity is evaluated occurs prior to the reception of conditional feedback in the form of reward or punishment. So, it is important to note that while these behavior results indicate that similar neural changes may be happening over the course of the task, the neural processing window under examination in this study seeks to examine the specific neural processing mechanisms at the end of movement and prior to the reception of reward or punishment feedback.

Palidis and colleagues (2018) conducted a study in which they implemented a visuomotor rotation task in order to examine the neural processing of sensory error-based learning compared to that of reward error-based learning. Participants alternated blocks, testing both types of learning. They moved a robotic arm to manipulate a cursor to hit a target that was viewed on a screen, while they could not view the arm itself. During the sensory error-based blocks, 50% of the trials contained perturbed movement, requiring participants to adapt their hand motion to hit the target. Feedback was given at the end of movement in the form of the final hand position. The angle of perturbation was small (.75-1.5 degrees), allowing the error and consequent reward to be held constant, and isolating sensory error-based learning. During the reward error-based blocks, participants received binary feedback indicating either a missed or hit target, but they did not receive any hand position feedback, allowing for the isolation of reward error-based learning.

Significant results were seen for both conditions, illustrating that as the task progressed, participants adapted their movement to hit the target more accurately, or more often, in response to both forms of feedback (Palidis et al., 2018).

In conclusion, the current body of literature shows consistent findings regarding motor learning in response to a visuomotor rotation task. Participants learn to adapt their movement to successfully master the task. Our results corroborate these findings.

Feedback-Related Neuronal Activity During Motor Learning

Our results indicated that feedback-related neuronal activity evaluated at the end of the movement does not change during motor learning; there was no significant difference in the average amplitudes of the early learning period, defined as the first 60 trials of the Adaptation period, and the late learning period, defined as the last 60 trials of the Adaptation period. In order to further examine this, the ERP was broken down into two time windows, and the average amplitudes were compared, yet still no significant difference in the average amplitudes was found. This suggests that the level of performance, or the degree of mastery of the task, does not affect the way feedback is processed in the cortex during motor learning.

The resulting ERPs produced during the Adaptation period show peaks in voltages following the termination of movement, beginning the window during which feedback-related processing takes place. Consistent with the current body of literature, the ERPs produced resemble a P300 ERP. Additionally, though the time window is not consistent with the typical appearance of the FRN, FRN literature is included because some researchers have found that the timing of the FRN can be considerably later when visual feedback evaluation is complex in nature (Krigolson et al., 2013). However, for both electrodes, comparing the ERPs of early trials to late trials revealed that the ERPs did not change over the course of learning.

Multiple studies have been conducted that discuss the modulation of ERPs over the course of motor learning tasks. Anguera and colleagues (2009) implemented a visuomotor rotation task as a means to examine processing during motor learning and observed an FRN. They found that the FRN amplitude was modulated by the size of errors made during the task; the bigger the error, the larger the amplitude. As participants learned the task and the size of their errors decreased, the amplitude of the FRN decreased as well (Anguera et al., 2009). Palidis and colleagues (2018) found similar results. They conducted a study that found that a P300 ERP was elicited by both reward and sensory feedback during the Adaptation period of a visuomotor rotation task. Palidis and colleagues (2018) found that during the sensory feedback condition, the amplitude of the P300 was sensitive to the magnitude of the sensory error; as participants mastered the task, the amplitude of the P300 decreased. This suggests that an internal model is being updated as the participants learn the task (Palidis et al., 2018). Van der Helden and colleagues (2010) implemented a sequence learning task in order to determine whether or not feedback would elicit an ERP that was predictive of subsequent performance of the task. They observed an FRN and found that its amplitude was predictive of future motor performance: the larger the amplitude, the more likely the performance of further trials would increase (van Der Helden et al., 2010).

In sum, while the presence of a P300 during the Adaptation portion of our task is consistent with the current body of literature, the insignificant effect of the early and late groups of trials on the amplitude of the ERP appears to be unexpected. These results could be due to the time window during which movement feedback was evaluated, or possibly the form of feedback that the participants received. It is possible that the time window that we observed is not the window that represents the greatest impact of feedback on neuronal processing of errors. Furthermore, the type of feedback given could have an effect on these results. Palidis and colleagues (2018) implemented an extremely similar visuomotor rotation task with different manipulations of way that participants received feedback and found modulations in the amplitudes of the resulting ERPs. During the first five trials of each block, participants received continuous feedback in the form of a line tracing the trajectory of their movement, as our participants did. However, following these initial trials, participants received feedback throughout their movement in the form of an arc shaped cursor that indicated their movement extent, and then upon movement termination, they received visual feedback indicating the final position of their movement (Palidis, 2018). During Adaptation, our participants received continuous feedback throughout the course of the trial but did not receive additional feedback following movement termination. Perhaps these differing forms of feedback have an effect on the presence of differential amplitude in the resulting ERP.

Our results indicate that feedback-related neuronal activity is modified by visual feedback during motor learning; there was a significant difference in the average amplitudes between the Adaptation condition and the No Vision condition in both electrodes, while the amplitudes of the Adaptation and Baseline conditions were relatively the same. This suggests that the presence of visual feedback changes the way that neuronal processing takes place over the course of motor learning.

The ERPs produced during the Adaptation and Baseline period show peaks in voltages following the termination of movement, beginning the window during which feedback-related processing takes place. The ERP produced during the No Vision condition is relatively the same shape as the Baseline and Adaptation ERPs but has significantly lower amplitude. Based on the idea that the P300 represents an internal update to cortical representation and the amount of attention allocated to a given task (Polich, 2007), and that lower amplitude corresponds with less attention allocated typically as a result of better performance (Palidis et al., 2018), combined with the idea that a decrease in amplitude of FRN indicates that the motor task is being retained (Anguera et al., 2009), the lower amplitude of the ERP during the No Vision condition suggests that the absence of visual feedback alone resulted in less attentional resources being directed to the task due to successful retention, leading to less cortical representation.

Previous studies examining the effects of visual feedback on feedback-related neuronal processing have found resulting modulation in ERPs. Krigolson and colleagues (2013) conducted an EEG study requiring participants to reach for targets that they could see or targets that they had seen but that were removed prior to the onset of movement. The trials with visible targets were deemed “visually-guided” while the trials absent of the targets were deemed “memory-guided”. Behaviorally, the memory-guided trials resulted in a small undershoot of movement. Both conditions elicited a P300 ERP. When they compared the ERPs of both conditions, they found that amplitudes of the P300 were diminished during the memory-guided trials, suggesting that the reduced amplitude induced by the presence of visual feedback reflects processes that resulted in the undershooting of movement, potentially incorrect encoding of the target (Krigolson et al., 2013).

The results of the present study are consistent with the current body of literature. Palidis et al., (2018) suggested that “surprise” results in an increased P300 amplitude. By considering surprise present in the form of visual feedback so that participants are able to gauge their success during the task, it is logical that the amplitudes during the Baseline and Adaptation conditions in the present study are significantly higher than that of the No Vision task, which does not have the element of surprise. Furthermore, the present study confirms the results of Krigolson and colleagues (2013), which found a decrease in the amplitude of memory-guided trials compared to visually-guided. By equating memory-guided trials to our No Vision condition and visually-guided trials to our Adaptation condition, we can support these results. Additionally, though it was not statistically significant, there was a marginal decrease in reach direction for the No Vision condition compared to Adaptation, which further supports the theory of Krigolson and colleagues

(2013) regarding the idea that the P300 modulation reflects processing in the undershooting movement (Krigolson et al., 2013).

In sum, the results of the present study are consistent with the current body of literature in that the visual processing of feedback during motor learning is reflected in the P300 and FRN ERPs (Krigolson et al., 2015).

Limitations

Limitations of the study were present in different forms, one being that a relatively small pool of participants was used to examine the phenomenon at hand. While the larger study had forty-two participants, only eleven were used for purposes of this analyses. Additionally, the larger study examined the effects of reward and punishment on motor learning. Because of this, feedback indicative of performance was given in the form of either reward or punishment signaling monetary gain or loss. The time window of this analyzation did not include that feedback; in fact, the present study did not wish to analyze reward-based feedback at all. However, because this study was part of a larger study that did give reward and punishment feedback, it is possible that our results are confounded by the effects of participants receiving reward or punishment feedback.

A further source of limitation could reside in the time window of the observed epoch. In this analysis, time zero was defined as the time of movement termination. However, it is possible that the movement itself is modulating the feedback activity, which could be a confounding factor.

Conclusions

The present study found that participants learned and retained performance in the visuomotor task. Feedback-related neuronal activity, evaluated at the end of movement, was not modified by learning, which suggests that this neuronal activity does not contribute to adaptation during the motor task. Lastly, feedback-related neuronal activity was modified by the absence of visual input, which suggests that this neuronal activity contributes to processing visual feedback during motor learning. More studies are needed to examine the relationship between the lack of change in feedback-related neuronal activity and motor learning as well as to elucidate when and how the neuronal processing of feedback modulates motor learning.

REFERENCES

Anguera, J. A., Seidler, R. D., & Gehring, W. J. (2009). Changes in performance monitoring during sensorimotor adaptation. *Journal of Neurophysiology*, *102*, 1868.

Bastian, A. J. (2008). Understanding sensorimotor adaptation and learning for rehabilitation. *Current Opinion in Neurology*, *21*, 628.

Beaulieu, C., Bourassa, M. È., Brisson, B., Jolicoeur, P., & De Beaumont, L. (2014). Electrophysiological correlates of motor sequence learning. *BMC Neuroscience*, *15*, 102.

Cohen, M. X. (2017). Where does EEG come from and what does it mean?. *Trends in neurosciences*, *40*, 208.

Cross, E. S., Schmitt, P. J., & Grafton, S. T. (2007). Neural substrates of contextual interference during motor learning support a model of active preparation. *Journal of Cognitive Neuroscience*, *19*, 1854.

Dayan, E., & Cohen, L. G. (2011). Neuroplasticity subserving motor skill learning. *Neuron*, *72*, 443.

Delorme, A., Makeig, S., (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *143*, 9.

Galea, J. M., Mallia, E., Rothwell, J., & Diedrichsen, J. (2015). The dissociable effects of punishment and reward on motor learning. *Nature Neuroscience*, *18*, 597.

Galea, J. M., Vazquez, A., Pasricha, N., Orban de Xivry, J. J., & Celnik, P. (2010). Dissociating the roles of the cerebellum and motor cortex during adaptive learning: the motor cortex retains what the cerebellum learns. *Cerebral cortex*, *21*, 1761.

Glazer, J. E., Kelley, N. J., Pornpattananangkul, N., Mittal, V. A., & Nusslock, R. (2018). Beyond the FRN: Broadening the time-course of EEG and ERP components implicated in reward processing. *International Journal of Psychophysiology, 132*, 184.

Hill, C., Waddell D., Del Arco, A., (2019). Reward and Punishment: The Neural Correlates of Reinforcement Feedback During Motor Learning (Dissertation in Progress).

Holroyd, C. B., & Coles, M. G. (2002). The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity. *Psychological review*, *109*, 679.

Izawa, R., & Shadmehr, R. (2011) Learning from Sensory and Reward Prediction Errors during Motor Adaptation. *PLoS Computational Biology*, *7*.

Kandel, E. R., Schwartz, J. H., Jessell, T. M. & Hudspeth, A.J. (2012). Principles of neural science (5th ed.). New York: McGraw-Hill, Health Professions Division.

Kourtis, D., Sebanz, N., & Knoblich, G. (2012). EEG correlates of Fitt's law during preparation for action, *Psychological Research, 76,* 514.

Krigolson, O. E., Hassall, C. D., & Handy, T. C. (2013). How we learn to to make decisions: rapid propagation of reinforcement learning prediction errors in humans. *Journal of Cognitive Neuroscience, 26,* 635.

Krigolson, O.E., Holroyd, C.B., Van Gyn, G., & Heath, M. (2013). Electroencephalographic correlates of target and outcome errors. *Exp Brain Res, 190*, 401.

Krigolson, O.E., Cheng, D., & Binsted, G. (2015). The Role of Visual Processing in Motor Learning and Control: Insights from Electroencephalography. *Vision Research*, *110*, 277.

Luck, S. J. (2012). Event-related potentials. *APA handbook of research methods in psychology*, *1*, 523.

MacLean, S. J., Hassall, C. D., Ishigami, Y., Krigolson, O. E., & Eskes, G. A. (2015). Using brain potentials to understand prism adaptation: the error-related negativity and the P300. *Frontiers in human neuroscience*, *9*, 335.

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

Palidis, D.J., Cashaback, J.G.A., & Gribble P.L., (2018). Neural Signatures of Reward and Sensory Prediction Error in Motor Learning. *Journal of Neurophysiology*.

Polich, J. (2007). Updating P300: an integrative theory of P3a and P3b. *Clinical neurophysiology*, *118*, 2128.

Schmidt, R., & Lee, T. (2013). Motor Learning and performance, 5E with web study guide: from principles to application. *Human Kinetics*.

Song, Y., & Smiley-Oyen, A. L. (2017). Probability differently modulating the effects of reward and punishment on visuomotor adaptation. *Experimental Brain Research*, *235*, 3605.

Steele, C. J., & Penhune, V. B. (2010). Specific increases within global decreases: a functional magnetic resonance imaging investigation of five days of motor sequence learning. *Journal of Neuroscienc*e, *30*, 8332.

Taubert, M., Lohmann, G., Margulies, D. S., Villringer, A., & Ragert, P. (2011). Long-term effects of motor training on resting-state networks and underlying brain structure. *Neuroimage*, *57*, 1492.

van der Helden, J., Boksem, M. A., & Blom, J. H. (2009). The importance of failure: feedback-related negativity predicts motor learning efficiency. *Cerebral Cortex*, *20*, 1596.

Yousif, N., Cole, J., Rothwell, J., & Diedrichsen, J. (2015). Proprioception in Motor Learning: Lessons from a Deafferented Subject. *Experimental Brain Research*, *233*, 2449.