



# Cortical preparatory activity during motor learning reflects visuomotor retention deficits after punishment feedback

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Received: 6 March 2021 / Accepted: 17 August 2021 / Published online: 28 August 2021  
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## Abstract

Previous studies have shown that reinforcement-based motor learning requires the brain to process feedback-related information after movement execution. However, whether reinforcement feedback changes how the brain processes motor preparation before movement execution is unclear. By using electroencephalography (EEG), this study investigates whether reinforcement feedback changes cortical preparatory activity to modulate motor learning and memory. Human subjects were divided in three groups [reward, punishment, control] to perform a visuomotor rotation task under different conditions that assess adaptation (learning) and retention (memory) during the task. Reinforcement feedback was provided in the form of points after each trial that signaled monetary gains (reward) or losses (punishment). EEG was utilized to evaluate the amplitude of movement readiness potentials (MRPs) at the beginning of each trial for each group during the adaptation and retention conditions of the task. The results show that punishment feedback significantly decreased MRPs amplitude during both task conditions compared to Reward and Control groups. Moreover, the punishment-related decrease in MRPs amplitude paralleled decreases in motor performance during the retention but not the adaptation condition. No changes in MRPs or motor performance were observed in the Reward group. These results support the idea that reinforcement feedback modulates motor preparation and suggest that changes in cortical preparatory activity contribute to the visuomotor retention deficits observed after punishment feedback.

**Keywords** Reinforcement feedback · Motor learning · Motor retention · Movement readiness potentials · Electroencephalography

## Introduction

Motor learning relies on the gradual reduction of movement errors either by minimizing the discrepancies between predicted and actual sensory feedback (i.e. sensory prediction errors) (Shadmehr and Krakauer 2008; Izawa and Sadtmeier

2011; Huang et al. 2011; Krakauer et al. 2019), or through maximizing reward after reinforcement feedback (i.e. reward prediction error). Previous studies have shown that reward and punishment feedback produce different effects on learning and retention of a visuomotor task (Galea et al. 2015; Song and Smiley-Oyen 2017; Huang et al. 2018; Steel et al. 2016, 2020), which suggest that the brain processing of reinforcement feedback drives motor learning (Hill et al. 2020). However, motor learning is also driven by brain mechanisms related to motor planning and movement preparation. In fact, a recent study using cortical microstimulation found a causal relationship between cortical preparatory activity and error-driven visuomotor adaptation (Vyas et al. 2020). Moreover, cortical preparatory activity seems to be critical for the development of lasting motor memories (Sheahan et al. 2016). These studies support the idea that reinforcement-based motor learning could also involve changes in cortical preparatory activity. Yet, it is currently unclear whether reinforcement feedback changes cortical preparatory activity

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Communicated by Melvyn A. Goodale.

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and whether these changes affect differently motor learning and retention.

By using electroencephalography (EEG) in humans, previous investigations have correlated cortical potentials before movement execution (i.e. cortical preparatory activity) to planning and preparation of voluntary movements. Specifically, from about 1 s to 500 ms before a voluntary movement, a gradual negative shift in electrical activity over the contralateral motor cortices to the moving limb occurs (Libet et al. 1982, 1983). This negative deflection has been termed the movement readiness potentials (MRPs) (Kirsch et al. 2010; Krigolson et al. 2012), and has been extensively examined during motor learning (Smith and Staines 2006, 2010, 2012; Jochumsen et al. 2017). MRPs have been associated with changes in the activity of the cortical motor areas such as supplementary motor areas (SMA) and primary motor cortex (M1) (Shibasaki and Hallett 2006). Critically, learning of motor skills such as the visuomotor adaptation task involves changes in the activity of M1 (Sheahan et al. 2016; Vyas et al. 2020; Kawai et al. 2015).

Changes in the amplitude of MRPs reported during motor learning (Jochumsen et al. 2017; Wright et al. 2012a, b) have been related to the outcome of motor actions during learning (i.e. action-effect contingency, reliability of action), which suggests that MRPs are sensitive to feedback (Jo et al. 2014; Pinheiro et al. 2020, Traver et al. 2021). In fact, recent studies show that the amplitude of MRPs increases with sensory feedback after voluntary movements compared to the absence of feedback (Vercillo et al. 2018; Reznik et al. 2018), which signifies the integration of sensory feedback into the motor preparatory processes that underlie self-generated actions. The changes in MRPs amplitude with sensory feedback also indicate that SMA and M1 integrate previous sensory events during motor learning (Pinheiro et al. 2020; Vercillo et al. 2018; Reznik et al. 2018). These studies, however, do not provide evidence on whether reinforcers (i.e. reward and punishment) could also modulate MRPs during motor learning. Previous work done in non-human primates demonstrate that neurons in M1 modulate their firing rates in response to reward expectation and delivery (Marsh et al. 2015; Ramkumar et al. 2016; Ramakrishnan et al. 2017) opening the possibility that MRPs (a signal derived, in part, from M1) could be modulated by motivational reinforcement.

By using EEG, in a recent study we show that punishment, but not reward, alters feedback-related cortical activity and impairs the retention of a visuomotor adaptation task (Hill et al. 2020). In our previous study, however, we did not assess whether punishment or reward changes motor preparatory activity which is also involved in visuomotor adaptation (Vyas et al. 2020; Sheahan et al. 2016). Here, we focus on whether reinforcement feedback changes motor preparatory activity. Specifically, we examine the amplitude

and latency of MRPs as an index of cortical preparatory activity during both the learning and retention phases of a visuomotor rotation task guided by reward and punishment (compared to a no feedback control). Our results show that punishment, but not reward, feedback decreases the amplitude of MRPs during both the learning and the retention phases of the task and support dissociable effects of feedback valence on cortical preparatory activity during motor learning.

## Materials and methods

### Participants

Forty-two participants (age range: 19–32, mean age  $\pm$  SD:  $21.91 \pm 2.1$  years, males; 18, females: 24) volunteered and signed an informed consent for this study. All participants were categorized as right-handed according to the Edinburgh handedness scale (Oldfield 1971). Each participant was then randomly assigned to one of three feedback groups [Reward  $n = 14$ ; Punishment  $n = 14$ ; Control  $n = 14$ ]. All procedures of this study were approved by University of Mississippi Institutional Review Board.

### Experimental procedures

Participants were seated in front of a 114.3 cm television screen at a distance of 61 cm with a Wacom tablet (sampling rate: 100 Hz) and pen, which they were instructed to hold in a similar fashion to writing. Each participant's right arm was visual occluded to limit visual feedback of the moving extremity during the task. A script was read aloud to each participant that informed them of the task procedures and goals. Participants were instructed to move quickly and accurately in straight shooting motion toward the target circle. To control for the effects of the script, participants in the Control group were given the instructions of either the Reward or Punishment groups.

The visuomotor rotation task consisted of a red starting circle and a blue target circle, displayed eight centimeters from the starting circle, that was pseudorandomly assigned to one of eight radial positions around the starting circle (target circle positions:  $0^\circ$ ,  $45^\circ$ ,  $90^\circ$ ,  $135^\circ$ ,  $180^\circ$ ,  $225^\circ$ ,  $270^\circ$ ,  $315^\circ$ ). Eight targets were used to limit the contribution of an explicit strategy to task performance (Galea et al. 2015). The participants hand was positioned over the center of the tablet, which corresponded with the starting circle position. Trials were initiated by the participant by clicking on the starting circle after which a line would follow the trajectory of the cursor. The drawn line trajectory was provided 2 cm past an invisible circle boundary that passed through the center of the target circle, after which the drawn line was

fixed and cursor movement was not available to the participant. After the presentation of the feedback, the drawn line trajectory, feedback, and target circle were cleared from the screen. A set of crosshairs, that followed the pen movement, was provided that allowed the participant to move accurately back to the starting circle at a self-selected pace.

The visuomotor rotation task consisted of 680 discrete reaching trials across five experimental conditions. Baseline and Washout feature congruent trajectories between the hand and cursor. While adaptation, no vision, and readaptation conditions featured a 30 counter-clockwise rotation of the cursor in respect to hand movement. Further descriptions of the experimental conditions are provided in Table 1. The various conditions dissect difference aspects of the motor adaptation process. Adaptation captured the overall learning of the adaptive behavior and No Vision accessed the error-less retention of previous learning by removing visual feedback of the cursor (Galea et al. 2015). Participants were instructed to “reach toward the target even without vision” during the No Vision condition, which is the same as a previous investigation that employed similar methodology to the current study (Quattrocchi et al. 2018). Reinforcement feedback was provided only during the Adaptation condition in the form of points and were displayed in accordance with the magnitude of error and their assigned group (Reward and Punishment groups). The following criteria was utilized to determine the amount of points that was awarded based on angular error:

Reward: 4 points: hit the target; 3 points: < 10° error; 2 points: < 20° error; 1 point: < 30° error; 0 points: ≥ 30° error.

Punishment: 0 points: hit the target; - 1 point: < 10° error; - 2 points: < 20° error; - 3 points: < 30° error; - 4 points: ≥ 30° error.

Null: points were replaced by two uninformative vertical lines.

All groups started with a total of zero points. Those in the Reward group earned positive points, while those in the Punishment group accrued negative points. Each point was equal to \$0.02 USD, a rule in which participants were not be made explicitly aware of. The Reward group began with \$0.00 USD and earned money based on their performance during the Adaptation condition. The Punishment group

began with \$10.00 USD and lost money during the Adaptation condition. A null feedback consisting of two vertical lines was presented for the Control group, thus no points were awarded through the task. To control for payment and time of payment, participants in the Control group were randomly selected to receive \$10.00 USD before the experiment and end the experiment with \$6.00 USD or begin with \$0.00 USD and end with \$6.00 USD.

A duration criteria of 500 ms was placed on each trial, which is similar to previous studies (Galea et al. 2015; Song and Smiley-Oyen 2017). If the trial was not completed within 500 ms, the trial was restarted with a message informing the participant to perform quicker. In order to best isolate the feedback-related neural activity from movement-related neural activity, feedback was presented 1.5 s after the end of the movement, for 1 s after each trial during Adaptation. A graphical representation of the temporal elements of the task can be found in Fig. 1.

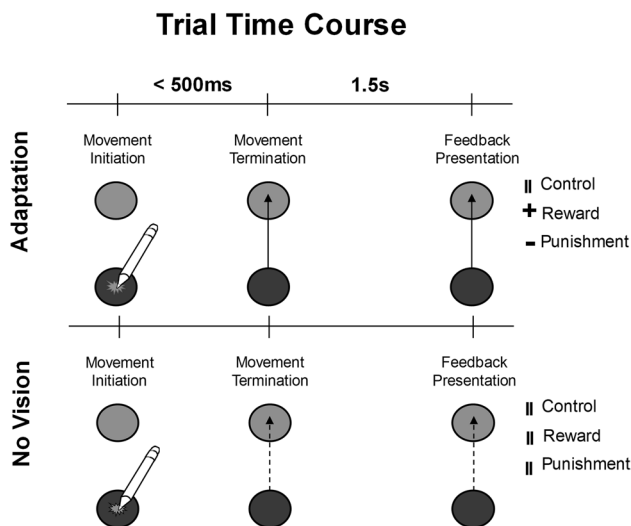
### Visuomotor rotation task analysis

Cartesian X and Y coordinates of the cursor were recorded and used to calculate our kinematic variables of interest. Movement time was defined as the time from the first movement of the cursor outside of the starting circle to the termination of the movement in the direction of the target circle. The assessment of movement time was utilized as a control parameter to ensure that all groups take similar time to move throughout the visuomotor task and that no one group benefited from a speed accuracy trade-off. Performance error was defined as the maximum angular deviation of the drawn line to the center of the target circle (Song et al. 2019). Performance errors exceeding 80° of were excluded from the analysis which is similar to previous studies (Quattrocchi et al. 2018). The Adaptation condition was divided into two learning stages: early learning was defined as the first 100 trials and Late Learning was defined as the last 100 trials. In order to best assess task retention, we compared performance error in Late Learning to No Vision. Late Learning was considered when participants had learned the task and would be the best representation of the motor skill carried over into the No Vision (retention) condition. Percent

**Table 1** Description of cursor rotation, cursor visibility, feedback type, and number trials in each task condition that was performed by the participants

Task condition	Cursor rotation	Cursor visibility	Feedback type	Number of trials
Baseline	0°	Visible	Null	80
Adaptation	30° CCW	Visible	Group assignment	200
No vision	30° CCW	Not visible	Null	200
Washout	0°	Visible	Null	100
Readaptation	30° CCW	Visible	Null	100

CCW counter-clockwise



**Fig. 1** Time course of a single trial in the Adaptation (learning) and No Vision (retention) conditions of the visuomotor task. After the trial is initiated, the participant must complete their movement in less than 500 ms (ms). Feedback (II, +, -) based on the amount of performance error is then displayed 1.5 s after the termination of the movement (see Methods for details). This time interval was set to separate movement-related neural activity from feedback-related neural activity. The solid arrow represents the visible cursor trajectory that can be viewed by the participant. The dashed arrow represents the cursor trajectory that is not visible to the participant

adaptation achieved was calculated in Early Learning, Late Learning, and No Vision conditions using the following formula from Marinelli et al. (2009):

$$100 \times \left[ 1 - \left( \frac{\text{Performance error}}{30} \right) \right]$$

A mean percent adaptation achieved was calculated in early learning, late learning, and no vision for each participant.

### EEG recording and analysis parameters

Surface EEG data was recorded with a 28 channel Quik-Cap electrode system (Victoria, Australia) and NuAmps amplifier. 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, CP3, CP4, P3, P4, T3, T4, T5, T6, TP7, TP8, O1, O2, and ground placed on the participant's right mastoid process (A2) which was used as the offline reference. A saline solution was applied with a blunt tip syringe into the individual electrodes to lower electrical signal noise. Electrical impedance for each electrode was kept below 10 k $\Omega$  throughout the data collection. All recordings were sampled at 1000 Hz, online band-pass filtered between 0.1 and 500 Hz, and notch filtered at 60 Hz.

All raw EEG data was exported and processed into Matlab, using the EEGLAB toolbox (Delorme and Makeig 2004). The raw data was down sampled from 1000 to 250 Hz, high-pass filtered at 1 Hz, and baseline corrected – 1000 ms to – 500 ms. Continuous data was segmented into time-locked data epochs. An initial visual inspection of the epochs was performed to remove trials containing artifacts. Then signal decomposition was performed using independent components analysis on each participant's data utilizing the 'runica' procedure in EEGLAB. Additional trials containing artifacts were identified using the resultant components of the signal decomposition and were removed from the analysis. Components reflecting eye blinks and electromyography activity were removed by visual inspection. Participants that retained less than 75% of original trials were excluded from the analysis.

### Movement-readiness potentials computation and analysis

Continuous EEG data were epoched into 1200 ms (– 1000 ms to + 200 ms) windows time locked to trial onset at 0 ms. Movement readiness potentials (MRPs) mean amplitude was calculated within a 50 ms window centered on the most negative peak value from – 200 to 0 ms (Krigolson et al. 2012). Peak-to-peak amplitude was calculated by subtracting the most negative peak value from – 200 to 0 ms from the positive peak during – 600 ms to – 300 ms. Similar peak to peak measurements have been utilized in other studies examining event related potentials (Palidis et al. 2019; Hill et al. 2020). Peak latency was determined by matching MRP peak to a corresponding time point in the – 200 to 0 ms time window. MRP mean amplitude, peak-to-peak amplitude, and peak latency were calculated for the FC3, FCZ, C3, and CZ electrodes and submitted separately for statistical analysis. These electrodes were chosen based on their contralateral position to the moving limb and have been previously utilized to examine MRPs in the context of motor learning (Jo et al. 2014; Jochumsen et al. 2017).

### Statistical analysis

As the primary focus of the current study was to examine the effects of reinforcement feedback on motor learning and retention, we chose to analysis the Adaptation and No Vision conditions. A 3 $\times$ 2 mixed repeated measures ANOVA was conducted to test for differences in feedback group (between-subjects factor) and task condition (within-subjects factors) on all variables of interest. Specifically, percent adaptation achieved and movement time were analyzed with a 3[Feedback Group]  $\times$  2[Learning Stage (Early Learning, Late Learning)] and 3 [Feedback Group]  $\times$  2 [Task Condition

(Late Learning, No Vision)] to test for differences in each task condition.

EEG data were analyzed with separate mixed repeated measures ANOVAs to test for differences in peak-to-peak amplitude, mean amplitude, and peak latency of MRPs for each individual electrode (FCZ, FC3, CZ, and C3). Specifically, a 3 [Feedback Group]  $\times$  2 [Learning Stage (Early Learning, Late Learning)] and a 3 [Feedback Group]  $\times$  2 [Task Condition (Adaptation, No Vision)]. All statistical analysis were conducted with SPSS<sup>®</sup> version 25 and set an a priori alpha level of 0.05.

## Results

### Movement time and percent adaptation achieved

We found that all feedback groups (Reward, Punishment and Control) displayed similar movement time during the Adaptation (Early and Late) and No Vision conditions of the visuomotor task. No significant differences were detected for movement time across conditions ( $F(1,39)=0.001$ ,  $p=0.992$ ,  $\eta^2_p=0.001$ ) and all groups demonstrated similar movement times ( $F(2,39)=0.303$ ,  $p=0.740$ ,  $\eta^2_p=0.014$ ) (Fig. 2a). This finding indicates that all participants took similar times to move throughout each task condition regardless of feedback group.

All groups demonstrated a similar increase in percent adaptation achieved in their motor performance over the course of the Adaptation condition. All groups adapted to the rotation as they progressed from Early Learning to Late Learning ( $F(2,39)=87.732$ ,  $p<0.001$ ,  $\eta^2_p=0.709$ ) (Fig. 2b). No differences were detected between groups in Early Learning and Late Learning conditions ( $F(2,39)=0.901$ ,  $p=0.415$ ,  $\eta^2_p=0.048$ ). However, when examining the percent adaptation achieved during different task conditions, the Punishment group did not maintain the same level of motor performance during No Vision (retention) ( $F(2,39)=4.24$ ,  $p=0.023$ ,  $\eta^2_p=0.191$ ) (mean difference (MD):  $-21.113\%$ ), while Reward (MD:  $2.711\%$ ) and Control (MD:  $6.296\%$ ) groups preserved their performance from Late Learning (Fig. 2c). Additionally, Punishment demonstrated a lower percent adaptation achieved during No Vision compared to Reward ( $F(2,39)=4.198$ ,  $p=0.048$ ,  $\eta^2_p=0.107$ ) and Control ( $F(2,39)=5.248$ ,  $p=0.028$ ,  $\eta^2_p=0.130$ ).

### Movement-Readiness Potentials (MRPs)

Four participants did not meet the trial inclusion criteria, leaving the sample size of 38 for MRP analysis [Reward = 13 (7 female, 6 male), Punishment = 13 (7 female, 6 male), Control = 12 (6 female, 6 male)].

## Peak-to-peak amplitude

### Task learning

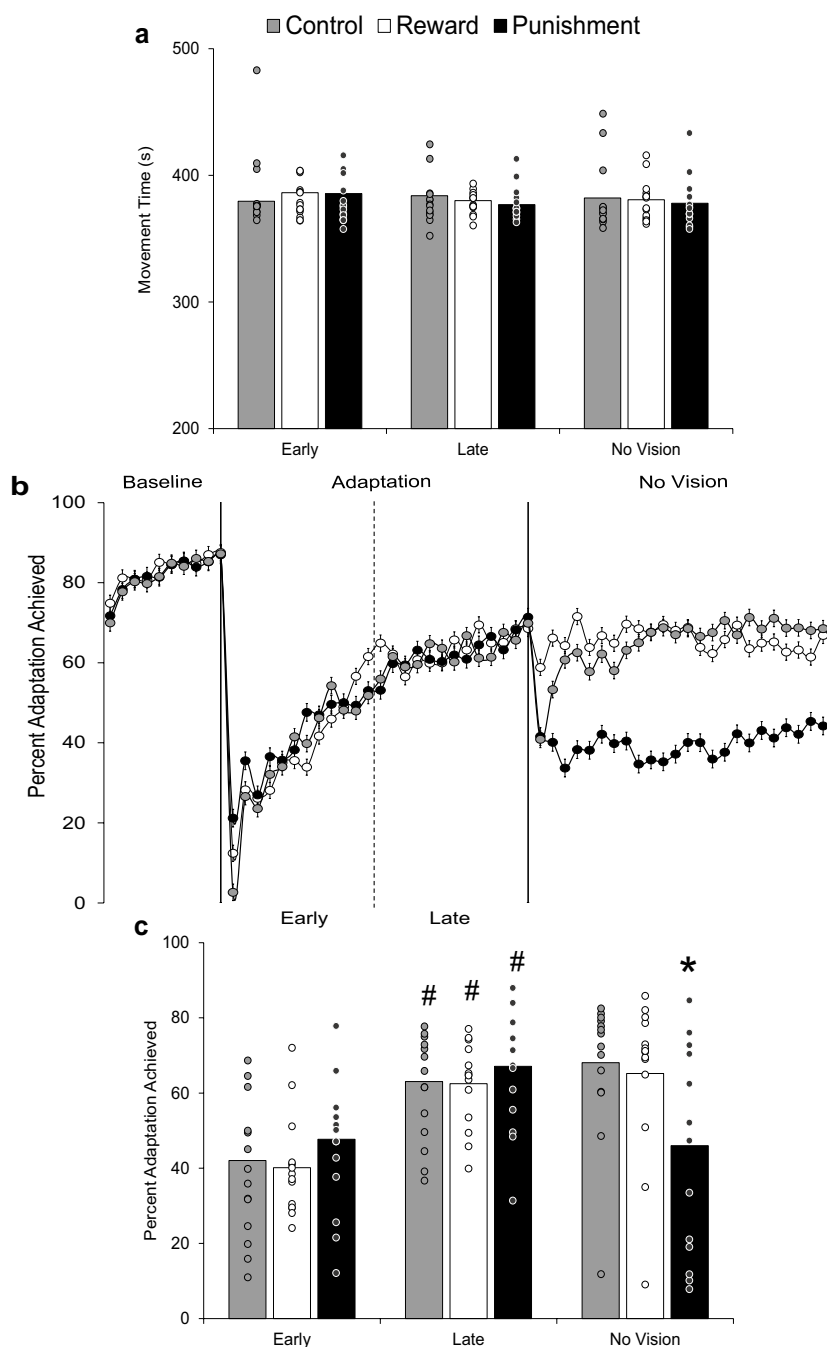
As shown in Fig. 3, we did not find any differences in the amplitude of MRPs between learning conditions, Early Learning and Late Learning, across all electrodes that were submitted for statistical analysis. We found a main effect for group (feedback valence) in each condition. In fact, midline electrodes (CZ and FCZ) demonstrated differences between groups, with Punishment displaying lower peak-to-peak amplitudes compared to the other groups. As shown in Fig. 3 the peak-to-peak amplitude of the MRP at the CZ electrode demonstrated a significant main effect for group ( $F(2,35)=4.279$ ,  $p=0.022$ ,  $\eta^2_p=0.196$ ). Reward demonstrated higher peak-to-peak amplitude compared Punishment ( $F(2,35)=11.834$ ,  $p=0.023$ ,  $\eta^2_p=0.385$ ) but not Control ( $F(2,35)=0.051$ ,  $p=0.824$ ,  $\eta^2_p=0.001$ ). Control demonstrated higher peak-to-peak amplitude compared to Punishment ( $F(2,35)=6.799$ ,  $p=0.013$ ,  $\eta^2_p=0.207$ ). A significant group difference ( $F(2,35)=4.047$ ,  $p=0.026$ ,  $\eta^2_p=0.188$ ) was found at the FCZ electrode. Reward demonstrated higher peak-to-peak amplitude compared to Punishment ( $F(2,35)=5.174$ ,  $p=0.029$ ,  $\eta^2_p=0.165$ ) but not Control ( $F(2,35)=5.174$ ,  $p=0.863$ ,  $\eta^2_p=0.005$ ). Control demonstrated higher peak-to-peak amplitude compared to Punishment ( $F(2,35)=6.780$ ,  $p=0.019$ ,  $\eta^2_p=0.206$ ).

Similar to the midline, electrodes on the lateral side (C3 and FC3) also demonstrated effects of group and not task learning phase. A significant group difference ( $F(2,35)=4.791$ ,  $p=0.014$ ,  $\eta^2_p=0.215$ ) was found at the C3 electrode. Reward demonstrated higher peak-to-peak amplitude compared to Punishment ( $F(2,35)=5.922$ ,  $p=0.02$ ,  $\eta^2_p=0.184$ ) but not Control ( $F(2,35)=0.226$ ,  $p=0.637$ ,  $\eta^2_p=0.008$ ). Control demonstrated higher peak-to-peak amplitude compared to Punishment ( $F(2,35)=6.799$ ,  $p=0.013$ ,  $\eta^2_p=0.207$ ). A significant group difference ( $F(2,35)=6.453$ ,  $p=0.004$ ,  $\eta^2_p=0.269$ ) was found at the FC3 electrode. Reward demonstrated higher peak-to-peak amplitude compared Punishment ( $F(2,35)=6.453$ ,  $p=0.001$ ,  $\eta^2_p=0.328$ ) but not Control ( $F(2,35)=2.552$ ,  $p=0.275$ ,  $\eta^2_p=0.092$ ). Control demonstrated higher peak-to-peak amplitude compared to Punishment ( $F(2,35)=2.552$ ,  $p=0.025$ ,  $\eta^2_p=0.182$ ).

### Task condition

Since no differences were found between the two learning phases of the Adaptation condition, statistical comparisons between groups were performed considering the complete Adaptation condition (Early + Late Learning). Figure 3b demonstrates the comparisons between task conditions, Adaptation (Early + Late Learning) and No Vision. Figure 4

**Fig. 2** Movement time and behavioral performance during the visuomotor task. **a** Average movement time in seconds for all groups (Control, Reward and Punishment) during Early Learning, Late Learning, and No Vision. **b** Percent adaptation achieved across epochs of eight trials in the Baseline, Adaptation, and No Vision task conditions for each of the groups. Dotted line divides Early Learning and Late Learning. Represented as mean  $\pm$  standard error. **c** Average percent adaptation achieved for all groups during Early Learning, Late Learning, and No Vision. Bars represent the mean and dots represent the individual responses. # $p < 0.05$  compared to Early Learning. \* $p < 0.05$  compared to Late Learning



showcases MRPs across select electrodes in the montage accessed in this study for the Adaptation condition as a whole. We did not find any differences between task conditions [Adaptation, No Vision] across all electrodes that were submitted for statistical analysis. However, a significant difference was noted for feedback valence, mirroring the findings of the task learning phase.

The evaluation of the midline electrodes (CZ and FCZ) revealed Punishment feedback decreased MRPs despite the task condition, compared to the other groups. A significant group difference ( $F(2,35) = 3.328$ ,  $p = 0.048$ ,

$\eta^2_p = 0.160$ ) was noted at the CZ electrode. Reward demonstrated higher peak-to-peak amplitude compared to Punishment ( $F(2,35) = 6.629$ ,  $p = 0.014$ ,  $\eta^2_p = 0.207$ ) but not Control ( $F(2,35) = 0.004$ ,  $p = 0.949$ ,  $\eta^2_p = 0.135$ ). Control demonstrated higher peak-to-peak amplitude compared to Punishment ( $F(2,35) = 4.143$ ,  $p = 0.049$ ,  $\eta^2_p = 0.138$ ). A significant group difference ( $F(2,35) = 3.594$ ,  $p = 0.038$ ,  $\eta^2_p = 0.170$ ) was noted at the FCZ electrode. Reward demonstrated higher peak-to-peak amplitude compared to Punishment ( $F(2,35) = 5.143$ ,  $p = 0.032$ ,  $\eta^2_p = 0.162$ ) but not Control ( $F(2,35) = 0.016$ ,  $p = 0.886$ ,  $\eta^2_p = 0.056$ ). Control



**Fig. 3** Movement readiness potentials (MRPs) during the visuomotor task. **a** Grand average MRP for each group (Control, Reward and Punishment) at the CZ electrode during Early Learning, Late Learning, and No Vision conditions, with zero representing movement initiation. **b** Bars represent the mean MRP amplitude for each group and dots represent the individual responses. \* $p < 0.05$  compared to Reward and Control

demonstrated higher peak-to-peak amplitude compared to Punishment ( $F(2,35) = 5.571, p = 0.024, \eta^2_p = 0.177$ ).

In the lateral side, FC3 also demonstrated a group effect for Punishment ( $F(2,35) = 3.429, p = 0.044, \eta^2_p = 0.164$ ).

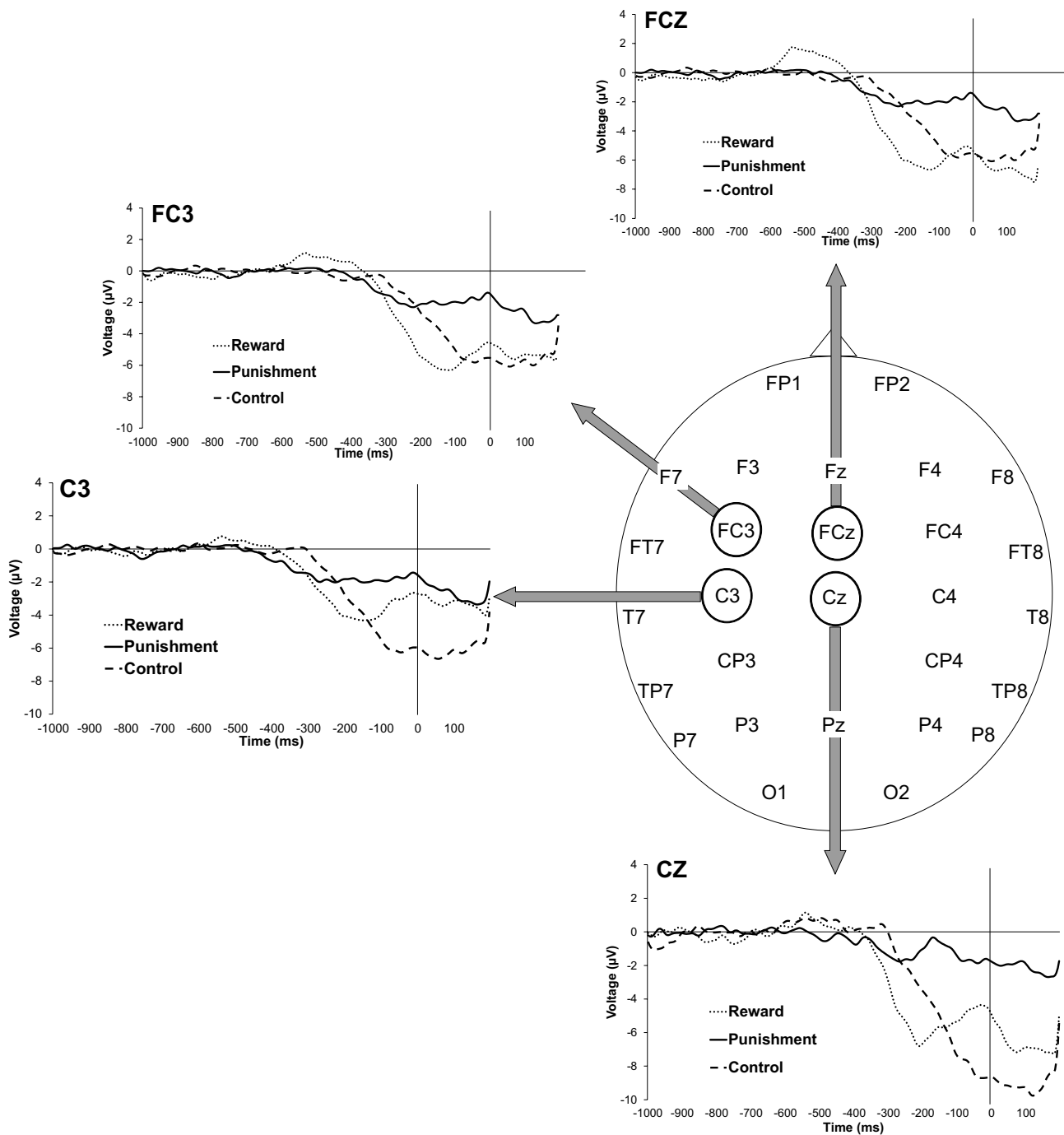
Reward demonstrated higher peak-to-peak amplitude compared to Punishment ( $F(2,35) = 6.833, p = 0.013, \eta^2_p = 0.723$ ) but not Control ( $F(2,35) = 1.312, p = 0.260, \eta^2_p = 0.031$ ). No significant differences were detected between Control and Punishment ( $F(2,35) = 2.006, p = 0.166, \eta^2_p = 0.049$ ). No significant differences were detected at the C3 electrode between groups ( $F(2,35) = 1.908, p = 0.163, \eta^2_p = 0.098$ ).

### Mean amplitude

#### Task learning

We did not find any differences in the amplitude of MRPs between learning conditions, Early Learning and Late Learning, across all electrodes that were submitted for statistical analysis. We found a main effect for group (feedback valence) in each condition. In fact, midline electrodes (CZ and FCZ) demonstrated differences between groups, with Punishment displaying lower mean amplitudes compared to the other groups. Mean amplitude of the MRP at the CZ electrode demonstrated a significant main effect for group ( $F(2,35) = 2.992, p = 0.019, \eta^2_p = 0.202$ ). Reward demonstrated a higher mean amplitude compared to Punishment ( $F(2,35) = 5.856, p = 0.042, \eta^2_p = 0.143$ ), but not Control ( $F(2,35) = 0.116, p = 0.943, \eta^2_p = 0.003$ ). Control also demonstrated a higher mean amplitude compared to Punishment ( $F(2,35) = 7.274, p = 0.032, \eta^2_p = 0.172$ ). A significant group difference ( $F(2,35) = 4.081, p = 0.016, \eta^2_p = 0.199$ ) was found at the FCZ electrode. Reward demonstrated a higher mean amplitude compared to Punishment ( $F(2,35) = 6.115, p = 0.035, \eta^2_p = 0.148$ ), but not Control ( $F(2,35) = 0.033, p = 0.982, \eta^2_p = 0.009$ ). Control also demonstrated a higher mean amplitude compared to Punishment ( $F(2,35) = 6.786, p = 0.040, \eta^2_p = 0.162$ ).

Similar to the midline, electrodes on the lateral side (C3 and FC3) also demonstrated effects of group and not task learning phase. A significant group difference ( $F(2,35) = 5.656, p = 0.007, \eta^2_p = 0.207$ ) was found at the C3 electrode. Reward demonstrated a higher mean amplitude compared to Punishment ( $F(2,35) = 7.112, p = 0.030, \eta^2_p = 0.168$ ), but not Control ( $F(2,35) = 0.229, p = 0.882, \eta^2_p = 0.006$ ). Control also demonstrated a higher mean amplitude compared to Punishment ( $F(2,35) = 9.566, p = 0.011, \eta^2_p = 0.215$ ). A significant group difference ( $F(2,35) = 6.651, p = 0.004, \eta^2_p = 0.275$ ) was found at the FC3 electrode. Reward demonstrated a higher mean amplitude compared to Punishment ( $F(2,35) = 14.371, p = 0.004, \eta^2_p = 0.291$ ), but not Control ( $F(2,35) = 0.656, p = 0.700, \eta^2_p = 0.018$ ). Control also demonstrated a higher mean amplitude compared to Punishment ( $F(2,35) = 6.843, p = 0.034, \eta^2_p = 0.164$ ).



**Fig. 4** Grand average movement readiness potential (MRP) for each group (Reward, Punishment and Control) across multiple channels during the Adaptation condition, with zero representing movement initiation

### Task condition

Since no differences were found between the two learning phases of the Adaptation condition, statistical comparisons between groups were performed considering the complete Adaptation condition (Early + Late Learning). A significant group difference was noted at the CZ

electrode ( $F(2,35) = 3.466$ ,  $p = 0.042$ ,  $\eta_p^2 = 0.165$ ). Reward demonstrated higher mean amplitude compared to Punishment ( $F(2,35) = 5.176$ ,  $p = 0.029$ ,  $\eta_p^2 = 0.114$ ) but not Control ( $F(2,35) = 0.016$ ,  $p = 0.968$ ,  $\eta_p^2 = 0.004$ ). Control demonstrated higher mean amplitude compared to Punishment ( $F(2,35) = 5.152$ ,  $p = 0.029$ ,  $\eta_p^2 = 0.128$ ). No significant differences were found for the FCZ electrode for



condition ( $F(2,35) = 1.025, p = 0.318, \eta^2_p = 0.028$ ) or group ( $F(2,35) = 2.827, p = 0.073, \eta^2_p = 0.139$ ).

In the lateral side, a significant group difference was found for the C3 electrode ( $F(2,35) = 3.843, p = 0.031, \eta^2_p = 0.180$ ). Reward demonstrated a higher mean amplitude compared to Punishment ( $F(2,35) = 5.161, p = 0.029, \eta^2_p = 0.128$ ), but not Control ( $F(2,35) = 0.073, p = 0.961, \eta^2_p = 0.002$ ). Control also demonstrated a higher mean amplitude compared to Punishment ( $F(2,35) = 6.301, p = 0.043, \eta^2_p = 0.265$ ). Similarly, a significant group difference was found for the FC3 electrode ( $F(2,35) = 4.335, p = 0.021, \eta^2_p = 0.192$ ). Reward demonstrated a higher mean amplitude compared to Punishment ( $F(2,35) = 6.115, p = 0.041, \eta^2_p = 0.148$ ) but not Control ( $F(2,35) = 0.033, p = 0.982, \eta^2_p = 0.009$ ). Control also demonstrated a higher mean amplitude compared to Punishment ( $F(2,35) = 6.786, p = 0.041, \eta^2_p = 0.162$ ).

## Peak latency

### Task learning

We did not find any differences in peak latency of MRPs between learning conditions, Early Learning and Late Learning, across all electrodes that were submitted for statistical analysis. We found a main effect for feedback valence in each condition. A significant group main effect was detected for the CZ electrode ( $F(2,35) = 6.232, p = 0.005, \eta^2_p = 0.263$ ). Control demonstrated a later peak latency compared to Reward ( $F(2,35) = 12.362, p = 0.004, \eta^2_p = 0.205$ ) but not Punishment ( $F(2,35) = 2.412, p = 0.129, \eta^2_p = 0.121$ ). No significant differences were detected between Reward and Punishment ( $F(2,35) = 4.012, p = 0.106, \eta^2_p = 0.186$ ). No significant differences for group ( $F(2,35) = 3.145, p = 0.055, \eta^2_p = 0.116$ ) or condition ( $F(2,35) = 0.041, p = 0.844, \eta^2_p = 0.002$ ) were detected for the FCZ electrode.

A significant group main effect was noted for the C3 electrode ( $F(2,35) = 3.462, p = 0.042, \eta^2_p = 0.088$ ). Control demonstrated a later peak latency compared to Reward ( $F(2,35) = 11.229, p = 0.006, \eta^2_p = 0.243$ ) and Punishment ( $F(2,35) = 8.721, p = 0.011, \eta^2_p = 0.199$ ). No significant differences were detected between Reward and Punishment ( $F(2,35) = 0.164, p = 0.687, \eta^2_p = 0.009$ ). Similar findings were noted for the FC3 electrode ( $F(2,35) = 3.462, p = 0.042, \eta^2_p = 0.165$ ). Control demonstrated a later peak latency compared to Reward ( $F(2,35) = 5.126, p = 0.032, \eta^2_p = 0.128$ ) and Punishment ( $F(2,35) = 5.396, p = 0.028, \eta^2_p = 0.236$ ). No significant differences were detected between Reward and Punishment ( $F(2,35) = 0.003, p = 0.952, \eta^2_p = 0.001$ ).

### Task condition

We found significant main effects for task conditions [Adaptation and No Vision] and groups for peak latency of MRPs.

A significant group main effect was detected for the CZ electrode ( $F(2,35) = 3.897, p = 0.031, \eta^2_p = 0.182$ ). Control demonstrated a later peak latency compared to Reward ( $F(2,35) = 7.651, p = 0.027, \eta^2_p = 0.178$ ) but not Punishment ( $F(2,35) = 1.241, p = 0.273, \eta^2_p = 0.066$ ). No significant differences were detected between Reward and Punishment ( $F(2,35) = 2.842, p = 0.202, \eta^2_p = 0.139$ ). A significant condition main effect was noted for the FCZ electrode ( $F(1,35) = 5.986, p = 0.021, \eta^2_p = 0.146$ ) with the Adaptation condition demonstrating a later peak latency compared to No Vision.

Significant group and condition main effects were found in the lateral electrodes. A significant group main effect was detected for the C3 electrode ( $F(2,35) = 4.523, p = 0.018, \eta^2_p = 0.114$ ). Control demonstrated a later peak latency compared to Reward ( $F(2,35) = 7.595, p = 0.028, \eta^2_p = 0.178$ ) and Punishment ( $F(2,35) = 6.061, p = 0.038, \eta^2_p = 0.147$ ). No significant differences were detected between Reward and Punishment ( $F(2,35) = 0.091, p = 0.765, \eta^2_p = 0.005$ ). A significant condition main effect was noted for the FC3 electrode ( $F(1,35) = 5.605, p = 0.024, \eta^2_p = 0.138$ ) with the Adaptation condition demonstrating a later peak latency compared to No Vision.

## Discussion

The purpose of this study was to determine the effects of motivational reinforcement on the neural correlates of motor preparation (i.e. MRPs) during learning and retention of a visuomotor adaptation task. We found that punishment feedback decreases motor retention and the amplitude of MRPs. Specifically, participants in the Punishment group exhibited a reduced amplitude of MRPs during both the Adaptation and No Vision conditions compared to Reward and Control groups. We also found that both reward and punishment feedback change the latency of MRPs during the visuomotor task. These results support the idea that reinforcement feedback modulates motor preparation and suggest that changes in cortical preparatory activity contribute to visuomotor retention deficits after punishment feedback.

### Cortical preparatory activity is decreased by punishment feedback

We found a decreased cortical preparatory activity in the Punishment group compared to the other two groups (i.e. Reward and Control), regardless of the task condition. In agreement with our recent study (Hill et al. 2020), we also show a decreased motor performance in the Punishment group during the No Vision condition (retention), but not the Adaptation condition, of the visuomotor task. Together these

results suggest that punishment feedback alters movement preparation in a way that is detrimental to task retention but not performance. These results further suggest that the effects of reinforcement feedback depend on valence since cortical preparatory activity and motor performance were not affected by rewards.

Recent studies postulate that changes in the amplitude of MRPs represent the outcome of movements which are implicated in the recalibration of upcoming voluntary actions (Vercillo et al. 2018; Reznik et al. 2018), and linked these changes to the modulation of the motor system by sensory parietal regions of cortex (Reznik et al. 2018; Kirsch et al. 2010). According to these studies, the depressed MRP amplitude after punishment feedback found in our study could represent a decreased sensorimotor integration into pre-movement brain processes, through sensory attenuation. More specifically, the saliency of punishment feedback could diminish attention toward the visual and proprioceptive sensory information derived from movement execution and consequently decrease MRP amplitude.

The role of punishment feedback decreasing the amplitude of MRPs and motor retention emphasizes the potential role played by the anterior cingulate cortex (ACC) and its output to motor areas (Hill et al. 2020) in motor learning. Previous work has consistently shown that punishment feedback increases the activity of the ACC (Ferdinand and Opitz 2014; Mothes et al. 2016; Monosov 2017). Furthermore, imaging studies have found functional links between the ACC and cortical motor areas (M1 and SMA) (Paus 2001; Wang et al. 2005; Nieuwenhuis et al. 2004) critically involved in both visuomotor learning and retention (Tanji and Shima 1994; Paz et al. 2005; Hadipour-Niktarash et al. 2007; Tanaka et al. 2010; Cohen et al. 2011; Dayan and Cohen 2011; Kawai et al. 2015). Therefore, it is possible that punishment feedback decreases the role of these cortical areas in motor retention, and consequently MRPs (Krigolson et al. 2012), through ACC inputs.

To impair motor retention, punishment feedback may also alter the function of the cerebellum and therefore disrupts the internal representation of the task (McNamee and Wolpert, 2019). Decrements in the MRPs have been found in clinical studies of patients with lesions in the cerebellum (Ikeda et al. 1994; Kitamura et al. 1999). Interestingly, there is a growing body of literature suggesting that the cerebellum mediates aspects of reinforcement-based motor learning. For instance, Therrien et al. (2016) found that ataxia patients were able to adapt their movement through reinforcement but learned less due to an inability to form a proper prediction of action outcome (cerebellum mediated) and reward prediction (basal ganglia mediated) contingency (Miall and Galea, 2015). Additionally, the effect for punishment feedback was not localized to a single electrode (see Fig. 4). The diminished MRP was seen in multiple electrodes throughout

the prefrontal and sensory cortices, thus it cannot be ruled out that other cortical areas contribute to motor preparation and memory deficits after punishment feedback. In fact, given the nature of the EEG technique (Kappenman and Luck 2011; Cohen 2017), identifying the cortical origin of MRPs during motor learning is challenging and would require further investigation.

Reward and null (control) feedbacks demonstrated similar MRP amplitudes throughout the visuomotor adaptation task. This finding is similar to our previous EEG study (Hill et al. 2020) and other studies (Spampinato et al. 2019) showing that the neural activity associated with the learning and retaining of a visuomotor adaptation task is not altered by the presence of reward feedback. Also, this finding aligns well with the assertion by Izawa and Shadmehr (2011) suggesting that changes of motor commands in M1, during visuomotor adaptation, are primarily derived from sensory prediction errors, and not reward prediction errors. Thusly, the lack of differences in MRP amplitude may stem from the Reward and Control groups utilizing similar brain pathways during motor preparation (Spampinato et al. 2019; Torrecillos et al. 2014).

In this study, we also found differences in peak latency between groups. Specifically, Control's peak latency occurred closer to movement onset compared to Reward and Punishment groups. This finding could be indicative of the effects of motivational factors that are presented to the groups. Control's performance is primarily being driven by sensory prediction error without influence of reinforcement, whereas the reinforcement groups (i.e., Reward and Punishment) are provided with both sensory and reward prediction errors (Izawa and Shadmehr 2011; Torrecillos et al. 2014). Consequently, the presence of both type of errors would require the brain to prepare earlier in order to maximize reward or minimize punishment during motor learning. This idea fits well with previous studies showing that the brain prepares earlier when all errors are removed from the performance space (Krigolson et al. 2012).

### **Cortical preparatory activity is not changed by task learning**

We found no differences in MRPs latency and amplitude during the Early and Late phases of the Adaptation condition, even though changes in behavior occurred. This finding could be attributed to the time course of task learning. Previous studies have noted both reductions and increases in MRP amplitude in response to task learning (Smith and Staines 2006, 2010, 2012; Wright et al. 2012a, b; Jochumsen et al. 2017). However, most of these studies designed weeks of training and feature long retention periods (Wright et al. 2012a, b; Jochumsen et al. 2017). The current study was

conducted in a single session, thus may not have allowed for adequate consolidation of the motor skill that would change MRPs. Thus, with more trials over multiple sessions, we may have seen changes in MRPs similar to those found in other studies.

## Conclusions

We found that punishment feedback not only decreases retention of a visuomotor task, but also decreases the cortical neural potentials associated with motor preparation (i.e. MRPs). These results suggest that punishment feedback alters how cortical motor areas prepare for movement limiting the ability of the brain to form a memory of the motor task and therefore impairing performance under memory-guided conditions. These results are also relevant in rehabilitation efforts, especially for those that experience neurological diseases that affect motor function, as they promote interventions that enhance sensory feedback and discourage the use of punishment feedback during task learning.

**Funding** This research was supported by the School of Applied Science at The University of Mississippi.

**Data availability** Data are available upon reasonable request.

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethics approval** All procedures of this study was approved by the University of Mississippi Institutional Review Board.

**Consent to participate** Informed consent was obtained from all individual participants included in the study.

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