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# 2           **Distinct Neural Signatures of Outcome Monitoring** 3           **following Selection and Execution Errors**

4

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36 **Abstract**

37 Losing a point in tennis could result from poor shot selection or faulty stroke execution. To explore  
38 how the brain responds to these different types of errors, we examined feedback-locked EEG  
39 activity while participants completed a modified version of a standard three-armed bandit  
40 probabilistic reward task. Our task framed unrewarded outcomes as either the result of errors of  
41 selection or errors of execution. We examined whether amplitude of a medial frontal negativity (the  
42 Feedback-Related Negativity; FRN) was sensitive to the different forms of error attribution.  
43 Consistent with previous reports, selection errors elicited a large FRN relative to rewards and  
44 amplitude of this signal correlated behavioral adjustment following these errors. A different pattern  
45 was observed in response to execution errors. These outcomes produced a larger FRN, a  
46 frontocentral attenuation in activity preceding this component, and a subsequent enhanced error  
47 positivity in parietal sites. Notably, the only correlations with behavioral adjustment were with the  
48 early frontocentral attenuation and amplitude of the parietal signal; FRN differences between  
49 execution errors and rewarded trials did not correlate with subsequent changes in behavior. Our  
50 findings highlight distinct neural correlates of selection and execution error processing, providing  
51 insight into how the brain responds to the different classes of error that determine future action.

52

53 **Key words:** Credit Assignment, Medial Frontal Negativity, Feedback-Related Negativity, Prediction  
54 Error, Reinforcement Learning

## 55 Introduction

56 When an action fails to produce the desired goal, there is a “credit assignment” problem to resolve:  
57 Did the lack of reward occur because the wrong course of action was selected, or was it because  
58 the selected action was poorly executed? Consider a tennis player who, mid-game, must  
59 determine whether losing the last point was the result of selecting the wrong action or executing  
60 the action poorly. The player might have attempted a lob rather than the required passing shot, an  
61 error in action selection. Alternatively, a lob might have been appropriate but hit with insufficient  
62 force, an error in motor execution.

63 Reinforcement learning presents a framework for understanding adaptive behavior through  
64 trial and error interactions with the environment. According to numerous models (e.g. temporal  
65 difference learning; Sutton & Barto, 1998), the discrepancy between expected and actual  
66 outcomes, the reward prediction error, provides a learning signal that allows an agent to refine its  
67 predictions and update its action selection policy. But what happens when a negative prediction  
68 error could arise from either poor action selection or poor response execution?

69 To address this question, McDougle et al. (2016) used a “bandit” task in which participants  
70 chose between two stimuli to maximize reward. In one condition, choices were made using a  
71 standard button-press method, a situation in which the negative prediction errors on unrewarded  
72 trials were attributed to poor action selection (given the negligible demands on motor execution). In  
73 a second condition, choices were made by reaching to the desired bandit. Here, unrewarded trials  
74 were attributed to movement execution errors. In the latter condition, participants strongly  
75 discounted the negative prediction errors on unrewarded trials relative to the former condition. The  
76 authors hypothesized that errors credited to the motor execution system block value updating in  
77 the action selection system. Consistent with this hypothesis, McDougle et al. (2019) reported that  
78 reward prediction error coding in the human striatum was attenuated following execution errors,  
79 relative to selection errors. Differences between responses to selection and execution errors have  
80 been attributed to a greater sense of “agency” in the latter, with participants’ choice biases  
81 indicating a belief that they can reduce execution errors by making more accurate movements  
82 (Parvin et al., 2018).

83 A window into the processes that underlie outcome monitoring is offered through the  
84 discovery of the Feedback-Related Negativity (FRN), a negative deflection in the EEG first  
85 identified following the presentation of feedback indicating incorrect responses (Miltner et al.,  
86 1997). Following its identification, the component quickly became the subject of intense  
87 investigation as a marker signaling gains and losses (Gehring & Willoughby, 2002) and outcomes  
88 that are worse than expected (Holroyd et al., 2006). The most prominent explanation of its  
89 significance, the “reinforcement learning theory of the error-related negativity” (RL-ERN; Holroyd &  
90 Coles, 2002) holds that the component (and its response-locked variant, the Error-Related  
91 Negativity, the ERN) indexes the activity of signals from the midbrain dopamine that are conveyed  
92 to the anterior cingulate cortex for adaptive modification of behaviour (Holroyd & Coles, 2002;

93 Holroyd & Umemoto, 2016). Recent developments reveal that much of the variation in this  
94 component is driven by a positive going component (a Reward Positivity; RewP) responding to  
95 outcomes that are better than expected (Foti et al., 2011; Holroyd et al., 2008; Proudfit, 2015).  
96 Irrespective of whether this signal is framed as a feedback negativity or reward positivity (here, we  
97 refer to this component as the FRN- the most widely label), there is a consensus, as indicated by a  
98 meta-analysis of 55 datasets (Sambrook & Goslin, 2015), that it is sensitive to reward prediction  
99 error.

100 The FRN's sensitivity to errors of action is more contentious. A series of experiments  
101 (Krigolson et al., 2008; Krigolson & Holroyd, 2006, 2007a) contrasting high level (goal-attainment)  
102 errors, variously operationalized as a failure to reach a target (Krigolson et al., 2008; Krigolson &  
103 Holroyd, 2007a), avoid a collision (Krigolson & Holroyd, 2006, 2007b), and the erroneous selection  
104 of the wrong hand or force (de Bruijn et al., 2003) with low-level errors (i.e. mismatch between  
105 actual and intended motor command), concluded that the latter do not elicit a FRN. Instead,  
106 reflecting a hierarchical error processing system (Krigolson & Holroyd, 2006), these motor errors  
107 are proposed to be mediated within posterior parietal cortex (Desmurget et al., 1999, 2001;  
108 Diedrichsen, 2005). Further elaborations indicated that the FRN may only be generated for action  
109 errors that cannot be corrected (Krigolson et al., 2008; Krigolson & Holroyd, 2007a), indicating a  
110 binary high level coding of outcomes in the FRN (i.e. signaling whether the goal was achieved or  
111 not). In line with this, a recent experiment isolating reward-based and sensory error-based motor  
112 adaptation reported a FRN in response to binary reward feedback, but not sensory error feedback-  
113 which instead generated a P300 (Palidis et al., 2019). Previous work on the P300's sensitivity to  
114 "low level" motor execution errors led to the proposal that this later parietally distributed component  
115 might reflect the revision of an internal forward model in posterior parietal cortex (Krigolson &  
116 Holroyd, 2007a).

117 A contrasting set of results suggest that the FRN (and its response-locked variant, the  
118 ERN) may in fact be sensitive to motor errors and reflect more than binary coding of outcomes,  
119 with evidence showing that it scales with the magnitude of error during sensorimotor adaptation  
120 (Anguera et al., 2009) and correlates with the size of hand-path deviations following externally  
121 perturbation to target reaches (Torrecillos et al., 2014). These findings are more in line with a  
122 growing body of work suggesting that the FRN indexes a general salience prediction error (Oliveira  
123 et al., 2007; Torrecillos et al., 2014). A computational model attempting to unify a broad range of  
124 findings on medial prefrontal cortex function (Alexander & Brown, 2011) proposes that this region  
125 is responsible for tracking discrepancies between expectations and outcomes, which are reflected  
126 in the FRN. Viewed in this way, the processing of execution and selection error may share a  
127 common neural network that signals a mismatch between the outcome and expectations in the  
128 service of behavioural adaptation (Cavanagh et al., 2012; Torrecillos et al., 2014).

129 To test whether outcome errors of action and selection can be dissociated in the medial  
130 frontal cortex, we recorded feedback-locked ERPs while participants engaged in a modified bandit

131 task where choices were selected via rapid arm movements. Unrewarded trials were either framed  
132 as errors in choosing the wrong bandit (a selection error) or the result of an inaccurate movement  
133 (an execution error). Following a large body of evidence reporting that the FRN is sensitive to RPE  
134 (Sambrook & Goslin, 2015), we expected that unrewarded outcomes attributed to selection error  
135 would elicit an FRN response. If this medial frontal monitoring system also tracks general action-  
136 outcome discrepancies, then we should expect a deflection following errors of action execution too.  
137 However, should the recently proposed movement-dependent account of RL hold, the FRN  
138 response should be attenuated when errors can be ascribed to the motor system. We would  
139 expect P300 amplitude, a putative index of internal forward model revision (Krigolson & Holroyd,  
140 2007a), to be largest for execution errors.

141 In addition to these predictions, we also examined the relationship between the FRN and  
142 behavioral modification. Specifically, we predicted that participants who exhibited a larger change  
143 in the FRN would be more likely to switch between the different options. Notably, we expected this  
144 brain-behavior relationship would hold for selection errors, but not for execution errors. Reasoning  
145 that action errors may instead be encoding information about the size of the execution error, with  
146 this feedback used to correct discrepancies between the planned and actual outcome, we explored  
147 the possibility that these signals may be correlated with the magnitude of error and subsequent  
148 change in motor response.

## 149 Materials and Methods

### 150 Participants

151 Using an effect size estimate derived from our previous work on the FRN ( $\eta^2p = .167$ ; Mushtaq et  
152 al., 2016), with a desired statistical power of 0.8 and alpha criterion set at 0.05, we set a minimum  
153 sample size of 28 participants. In total we tested thirty-two right-handed participants (EHI > 40;  
154 Oldfield, 1971). Two participants were excluded due to excessive EEG artifacts, and a technical  
155 error during data collection rendered one participant's dataset unusable. All analyses were  
156 performed on the resulting sample of 29 participants (19 females, 10 males,  $\mu$  age = 26.75 years,  
157  $\pm 9.51$  years).

158 Participants were told they would be remunerated based on their performance. However,  
159 due to the pseudo-veridical nature of outcomes (see Procedure), all received a fixed payment of  
160 £10.00. Participants signed an informed consent document, were fully debriefed, and the  
161 experiment was approved by the Ethics Committee in the School of Psychology at the University of  
162 Leeds, United Kingdom.

## 163 Design and Procedure

164 We employed a novel three-armed bandit task (**Figure 1**) where the absence of reward on a given  
165 trial could be the product of a poorly executed action or an error in action selection (McDougle et  
166 al., 2019). Following EEG set-up, the participant was seated in a chair approximately 50 cm away  
167 from a 24" ASUS monitor (53.2 X 30 cm [2560 x 1600 pixels], 100 Hz refresh rate). The participant  
168 was instructed to make a choice by making a reaching movement, sliding their right arm across a  
169 graphics tablet (49.3 X 32.7 cm, Intuos 4XL; Wacom, Vancouver, WA) while holding a digitizing  
170 pen encased inside a customized air hockey paddle. The tablet was placed below the monitor on  
171 the table and between an opaque platform that occluded the hand.

172 The experimental session comprised 400 trials, with opportunity for self-paced breaks. To  
173 initiate each trial, the participant made a reaching movement, sliding their right arm to position a  
174 white cursor (diameter of 0.5 cm) inside the home position, indicated by a solid white circle at the  
175 center of the screen. After maintaining this position for 400 ms, the start circle turned green and  
176 three bandits appeared on the screen (positioned at a radial distance 8 cm from the center at 90°,  
177 210° and 330° degrees relative to the origin). The bandits were colored light blue, dark blue, or  
178 purple and the color-position mappings were maintained for the entire experiment (randomized  
179 across participants).

180 Following the appearance of the 3 bandits, participants had 2 seconds to initiate a reaching  
181 movement. If the reaction time (RT) was greater than 2 s, the trial was aborted and the message  
182 "Too Slow" appeared. After movement onset, participants had 1 s (Movement Time; MT) to  
183 complete a rapid straight-line "shooting" movement through one of the bandits. Upon movement  
184 initiation, the cursor indicating hand position disappeared and did not reappear until feedback  
185 presentation. If the movement was not completed within the required 1 s window, the trial was  
186 terminated and the error message "Too Slow" was displayed. If the movement was completed  
187 within the 1 s window, there were three possible outcomes: If the movement was accurate (hand  
188 passed through the bandit) the cursor was displayed within the spatial extent of the bandit. On  
189 these trials, there were two possible outcomes: (1) The bandit could turn green, indicating that a  
190 reward would be earned for the trial (reward outcome), or (2) the bandit would turn red, indicating  
191 that, while the movement was accurate, no reward would be given on that trial (selection error). If  
192 the movement missed the bandit, a cursor would appear indicating the position when the hand was  
193 at the radial distance of the bandits, and thus indicate if the execution error was clockwise or  
194 counterclockwise relative to the target. The bandit would turn yellow, further signaling an execution  
195 error. Participants were informed of the three possible outcomes prior to the start of the experiment  
196 and presented with demonstrations of the three outcomes.

197 Following McDougle et al. (McDougle et al., 2019), each bandit had its own fixed  
198 probabilities for the three trial outcomes. All bandits had a 40% reward outcome, and thus, the  
199 expected value for the three bandits were identical. However, the frequency of selection error and



200 execution error trials varied. For one bandit, 50% of the trials resulted in execution errors and 10%  
201 resulted in selection errors. We refer to this as the “High Execution/Low Selection Error” bandit. A  
202 second bandit resulted in execution errors on 10% of trials and 50% resulted in selection errors (a  
203 “Low Execution/High Selection Error” bandit). A third, “Neutral” bandit produced an equal number  
204 (30%) of execution and selection errors.

205 To achieve these probabilities, outcomes were surreptitiously perturbed so that they aligned  
206 with predetermined feedback (a randomized sequence for each run) for the selected bandit. On  
207 trials in which the actual movement produced the desired outcome in terms of hitting or missing the  
208 bandit, the cursor was shown at its veridical position. However, if the participant’s movement  
209 missed the bandit, but the trial outcome was set as either a reward or selection error (i.e.,  
210 outcomes requiring successful motor execution), the feedback showed the cursor landing inside  
211 the bandit, albeit near the side consistent with the actual hand position. Conversely, where a trial  
212 was set to be an execution error, but the stylus successfully intersected the bandit, the cursor was  
213 shifted just outside the bandit, with the side again consistent with the actual hand position (e.g., if  
214 the hit was slightly clockwise to the center of the bandit, the cursor appeared outside the spatial  
215 boundary of the bandit on the clockwise side). On trials in which feedback needed to be perturbed  
216 (i.e., deliver a false hit or false miss) to control the frequency of outcomes, the cursor position was  
217 shifted by randomly sampling from a normal distribution ( $\pm 6.24^\circ$ , equivalent to .5 cm with an 8 cm  
218 reach) until a new cursor position was chosen that landed inside the bandit (for false hits) or  
219 outside the bandit (false misses).

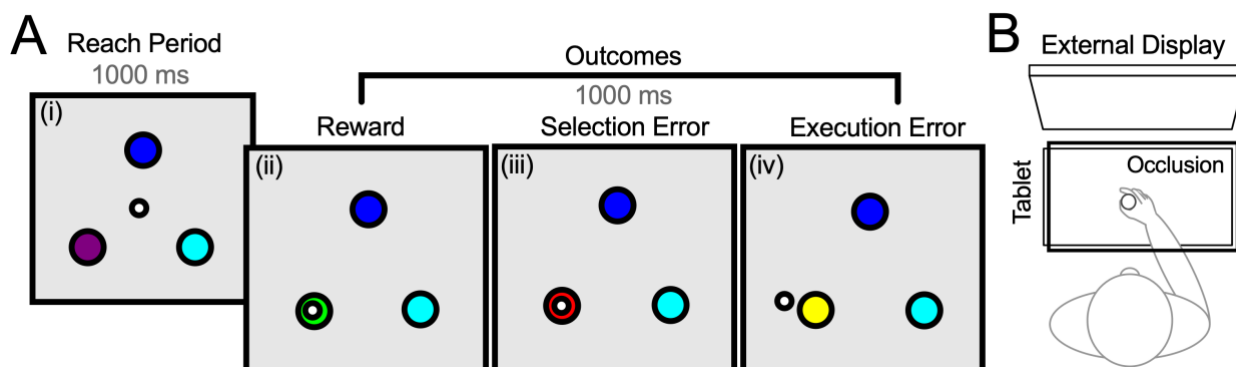
220 We included three further constraints to minimize the likelihood that participants would  
221 recognize that the outcomes were not always directly reflective of their movements: (i) No online  
222 movement feedback was available; (ii) end-point feedback was presented 1 s after the stylus had  
223 passed the bandit location (this also helped reduce the impact of motor artefacts contaminating the  
224 ERP); and (iii) if the actual reaching angle was greater than  $10^\circ$  from the closest bandit on any trial  
225 (irrespective of the set outcome), no outcome was shown, the experiment software instructed  
226 participants to “Please Reach Closer to the Bandit.” Trials in which the movement was not  
227 completed within 1 s of the onset of the bandits or in which the reach angle was greater than  $10^\circ$   
228 from the closest bandit were repeated, ensuring a full data set of 400 trials for each participant.

229 To increase motivation, participants were told that at the end of the experiment the software  
230 would randomly select five trials, and based on the outcomes from these trials, a cash bonus  
231 between £1-5 would be provided. As such, the goal was to accumulate as many reward trials as  
232 possible. In actuality, all participants received a fixed payment of £10 for taking part in the  
233 experiment.

234 Finally, given that it is possible that the execution error feedback could be interpreted in  
235 different ways (for example, participants may have assumed these errors were the result of faulty  
236 technical equipment), participants were invited to complete a brief optional post-experiment survey  
237 where they were asked to rate their agreement with the statement “I felt that that the miss (yellow)

238 outcomes were the result of poor arm reaches" on a 7-point Likert scale, where a score of 7  
239 indicated strongly agree and 1 indicated strongly disagree. From 21 respondents, a mean score of  
240 5.57 (SD = 1.6), which was statistically significantly different to the mid-point (neither agree nor  
241 disagree) on the scale ( $t(20) = 4.41, p < .001$ ), indicated general agreement with the intended  
242 experimental manipulation.

243 The experimental task was programmed using the Psychophysics Toolbox (Brainard, 1997;  
244 Kleiner et al., 2007) and lasted approximately 35 minutes, with an additional 25-30 minutes of  
245 technical set up for EEG data acquisition.



246  
247 **Figure 1- Experimental Task:** (A) Participants moved a stylus on a tablet to make rapid shooting  
248 movements (i) through one of 3 bandits (large circles) at 90°, 210° and 330° degrees relative to the  
249 home position (small circle). Following a 1000 ms delay (not pictured), pseudo-veridical feedback (white  
250 cursor) was provided indicating if the outcome was a reward (ii), a selection error (iii) or an execution  
251 error (iv). (B) The hand was occluded throughout, and stimuli were presented on a monitor positioned in  
252 front of the participants at approximately eye level.

253

## 254 Electrophysiological Data Recording and Preprocessing

255 EEG data were recorded continuously from 64 scalp locations at a sampling rate of 1024 Hz using  
256 a BioSemi Active-Two amplifier (BioSemi, Amsterdam). Four electrooculograms (EOG) – above  
257 and below the left eye, and at the outer canthi of each eye – were recorded to monitor eye  
258 movements. Two additional electrodes were placed on the left and right mastoids. The CMS and  
259 DRL active electrodes placed close to the Cz electrode of the international 10-20 system served as  
260 reference and ground electrodes, respectively. EEG pre-processing was performed using the  
261 EEGLAB (Delorme & Makeig, 2004) and Fieldtrip (Oostenveld et al., 2011) toolboxes, combined  
262 with in-house procedures running using Matlab (The MathWorks, Inc., Natick, Massachusetts).

263 All data were first re-referenced offline to the average of all channels, and downsampled  
264 from 1024 Hz to 256 Hz. The continuous time series data were filtered using a high-pass filter with  
265 a cut-off at 0.1 Hz (Kaiser windowed-sinc FIR filter, beta = 5.653, transition bandwidth = .2 Hz,  
266 order = 4638) and a low-pass filter with a cut-off at 30 Hz (Kaiser windowed-sinc FIR, beta = 5.653,  
267 transition bandwidth = 10 Hz, order = 126). A second filtering of the data was performed for  
268 subsequent independent component analysis using a high-pass filter cut-off at 1 Hz (Kaiser  
269 windowed-sinc FIR filter, beta = 5.653, transition bandwidth = 2 Hz, order = 4666). ICA typically  
270 attains better decompositions on data with a 1 Hz high-pass filter (Winkler et al., 2015). The data

271 were segmented into epochs beginning 1s before and lasting 1s after the onset of feedback.

272 Infomax ICA, as implemented in the EEGLAB toolbox, was run on the 1 Hz high-pass-filter  
273 epoched data, and the resulting component weights were copied to the .1 Hz high-pass-filter  
274 epoched data. All subsequent steps were conducted on the .1 Hz high-pass-filtered data.  
275 Potentially artefactual components were selected automatically using SASICA (Chaumon et al.,  
276 2015), based on low autocorrelation, high channel specificity, and high correlation with the vertical  
277 and horizontal eye channels. The selections were visually inspected for verification purposes and  
278 adjusted when necessary. After removal of artefactual components, the Fully Automated Statistical  
279 Thresholding for EEG Artefact Rejection plugin for EEGLAB (Nolan et al., 2010) was used for  
280 general artefact rejection and interpolation of globally and locally artefact contaminated channels,  
281 supplemented by visual inspection for further periods of non-standard data, such as voltage jumps,  
282 blinks, and muscle noise.

283 Following artifact-removal, 93.5% of total trials were available for analysis. There was no  
284 difference in the percentage of trials removed across conditions ( $F(2, 56) = 2.09, p = .133$ ).  
285 However, as a product of the experimental design, there was a difference in the total number of  
286 trials between the conditions ( $F(2, 56) = 85.2, p < .001$ ), with more reward trials ( $\mu = 150, \pm 9$ )  
287 available for analysis relative to execution error ( $\mu = 114, \pm 12; t(28) = 12.21, p < .001$ ) and  
288 selection error trials ( $\mu = 110, \pm 11; t(28) = 13.89, p < .001$ ). There was no difference in trial counts  
289 for the two types of errors ( $t(28) = .82, p = .693$ ). To increase the reliability of our conclusions by  
290 addressing potential problems of distribution abnormalities and outliers, averaged waveforms were  
291 constructed for each individual by taking the bootstrapped ( $n = 100,000$ ) means from the EEG time  
292 series epochs. The waveforms were baseline corrected using a 200 ms time window pre-feedback  
293 onset.

294

### 295 **ERP Quantification**

296 Given that we had specific hypotheses, we focused our analysis on two locations. First, meta-  
297 analyses (Sambrook & Goslin, 2015; Walsh & Anderson, 2012) have shown the feedback-locked  
298 FRN effect to be maximal over the frontocentral region of the scalp. As such, we averaged activity  
299 across three frontocentral electrodes FC1, FCz, and FC2. Second, given that the P300  
300 (specifically, the P3b sub-component) is commonly present in feedback-locked ERPs and typically  
301 maximal over parietal electrodes (Polich, 2007), we averaged over electrodes P1, Pz, and P2.  
302 Averaging across electrodes improves the signal-to-noise ratio of the ERP measures (Oken &  
303 Chiappa, 1986).

304 To test whether our results might be biased by the specific configurations of electrodes  
305 included in the averaged cluster and use of bootstrapped waveforms, we calculated the similarity  
306 between four different approaches to calculating the ERPs: (i) grand averaged activity from the raw  
307 waveforms in the clustered electrodes, (ii) grand averaged activity from the bootstrapped  
308 waveforms in the clustered electrodes, (iii) grand averaged activity from raw waveforms from a

309 single electrode (FCz for frontocentral analysis and Pz for parietal); and (iv) grand averaged  
310 activity from bootstrapped means extracted from a single electrode. An intraclass correlation  
311 coefficient indicated a high level of agreement between all four approaches (Frontocentral ICC =  
312 .995, 95% CI 0.989- 0.997; Parietal ICC: = .996, 95% CI 0.994- 0.997). Clustered bootstrapped  
313 averaged ERP waveforms are reported here.

314 With growing evidence that most of the variation in the FRN is driven by a reward positivity,  
315 we decided to make use of difference waveforms for our analysis to detect differences irrespective  
316 of whether they were driven by positive or negative deflections in the ERP (Krigolson, 2018). A  
317 difference waveform procedure has the added benefit of more easily isolating the FRN from  
318 components that precede (P2) and follow (a large P3 component comprising a frontal P3a and  
319 parietal P3b), eliminating activity in common between two conditions (Kappenman & Luck, 2017).  
320 The majority of research on the FRN has typically computed “reward prediction error” (RPE)  
321 difference waveforms, derived by subtracting error/loss trials from reward trials (Sambrook &  
322 Goslin, 2015). Here, we created a “Selection Error” difference waveform by subtracting the  
323 average activity associated with Selection Error trials from the average activity related to all  
324 Reward trials, and an “Execution Error” difference waveform by subtracting the average activity  
325 associated with Execution Error trials from the average activity associated with Reward trials.  
326 Finally, we directly contrasted Execution and Selection Error ERPs by subtracting the Execution  
327 Error waveform from the Selection Error waveform to create an “Error Sensitivity” difference  
328 waveform. For statistical analysis, the parent waveform outcome trials were subjected to a one-  
329 way ANOVA and where main effects emerged, one-sample t tests were conducted to identify  
330 where these difference waveforms were significantly different to zero.

331 To reduce the number of false positives (Luck & Gaspelin, 2017), the ERP data were  
332 downsampled to 250 Hz and only activity between 150 and 500 ms (spanning the P2, FRN and P3  
333 ERPs) was analysed. For each analysis, p values were corrected by applying a false discovery  
334 rate (FDR) control algorithm (Benjamini & Hochberg, 1995; Lage-Castellanos et al., 2010). The  
335 Benjamin-Hochberg correction approach was adopted as previous studies have shown it to reliably  
336 control the FDR when data are correlated, even when the number of comparisons are relatively  
337 small (Hemmelmann et al., 2005). This method is also ideally suited for the exploration of focally  
338 distributed effects (Groppe et al., 2011).

339 To aid the interpretation of the difference waveforms, we first visualised the grand averaged  
340 ERPs related to each outcome. For every statistically significant contrast, we present the mean  
341 amplitude from the cluster for each parent waveform. Differences between relevant conditions at  
342 each electrode site are also visualized through topographical maps to support interpretation of  
343 underlying components: Predicated on previous research (Walsh & Anderson, 2012), we  
344 anticipated that the FRN should show a frontocentral topography and, following an early  
345 frontocentral peak, there would be a subsequent posterior maximum corresponding to the P3b  
346 sub-component of the P300 (Holroyd & Krigolson, 2007).

## 347 Brain-Behavior Relationships

348 A key question in this study is whether electrophysiological signatures of different types of  
349 outcomes correlate with the participants' choice behavior (see San Martín, 2012 for a review).  
350 Based on a reinforcement learning account of the FRN (Holroyd and Coles, 2002), we would  
351 expect the amplitude of the FRN to scale with the degree of behavioral adjustment: large  
352 differences in the FRN should be more likely to lead to changes in choice behavior compared to  
353 small differences in the FRN. Here we can ask this question with respect to both selection and  
354 execution errors.

355 To examine brain-behavior correlations, we calculated a behavioral adjustment score, or  
356 "Switch Bias" rate, for each participant (operationalized as the ratio of the percentage of trials that  
357 the participant switched following an error to the percentage of switching following a reward). This  
358 served as an intuitive index of how much participants favored one outcome over another. Mean  
359 amplitudes from the statistically significant clusters of EEG activity were then correlated with these  
360 behavioral adjustment scores.

361 Rather than signaling a need to switch from one target to another, feedback from Execution  
362 Errors might be more readily used to modify a motor plan for future action. To quantify the  
363 magnitude of cursor error, we calculated the angular deviation of the cursor relative to the center of  
364 the selected target. Hand error was calculated as the position of the hand relative to the center of  
365 the selected target and was different to cursor error only on trials with perturbed outcomes. The  
366 degree of motor correction was examined on a subset of data where participants selected the  
367 same target on consecutive trials and quantified as the degree of angular change in hand position  
368 relative to cursor position on the previous outcome. Mean cursor error and motor correction scores  
369 were correlated with mean amplitudes from the previously identified statistically significant clusters  
370 of EEG activity.

371

## 372 Statistical Analysis

373 For reporting purposes, time points are rounded to the nearest millisecond, amplitude (in  
374 microvolts;  $\mu\text{V}$ ) to two decimal places and p values to three decimal places. The range for the  
375 scalp maps was time-interval specific and determined by the 1st and 99th percentile values across  
376 all electrodes. Spearman's rho ( $r_s$ ) was used to examine correlations between amplitude and  
377 behavior. For correlations between behavior and neural activity, peak and mean amplitudes were  
378 extracted. Both are reported and the strongest correlations are visualized. Where appropriate,  
379 pairs of correlations were directly compared with Hittner, May, and Silver's (2003) modification of  
380 Dunn and Clark's (1969) approach, using a back-transformed average Fisher's Z procedure as  
381 implemented in the R package Cocor v. 1.1-3 (Diedenhofen & Musch, 2015). The statistical  
382 significance threshold was set at  $p < .05$ . Generalized eta squared ( $\eta_G^2$ ) is used as a measure of  
383 effect size for repeated measures ANOVAs. This measure was selected over eta squared and  
384 partial eta squared because it provides comparability across between- and within-subjects designs  
385 (Bakeman, 2005; Olejnik & Algina, 2003); we considered  $\eta_G^2 = 0.02$  to be small,  $\eta_G^2 = 0.13$  medium  
386 and  $\eta_G^2 = 0.26$  to be a large effect size. All statistical analyses were performed using R (R Core  
387 Team, 2015).

## 388 Results

### 389 Behavioral Responses

390 A one-way ANOVA revealed a significant difference in bandit preference ( $F [2, 56] = 8.27, p < .001,$   
391  $\eta^2_g = .23$ ), with participants exhibiting bias towards the High Execution/Low Selection Error bandit.  
392 Overall, this bandit was chosen on average on 39% (SE = 2%) of the trials, which was significantly  
393 greater than the Low Execution/High Selection error bandit ( $M = 29\%; SE = 1\%; t(28) = 4.03, p =$   
394  $.001$ ) and Neutral bandit ( $M = 32\%; SE = 2\%; t(28) = 2.58, p = .046$ ), with no difference for the  
395 latter two ( $t(28) = 1.07, p = .877$ ). Consistent with previous work, when expected value is equal, the  
396 data show that participants prefer choices in which unrewarded trials are attributed to errors in  
397 movement execution rather than errors in action selection (Parvin et al., 2018; Green et al., 2010;  
398 Wu et al., 2009).

399 We then examined the effect of the different outcomes on the subsequent choice, asking  
400 how they influenced switching behavior (**Figure 2A**). Participants exhibited high switching rates  
401 overall (54%), but the rate differed according to outcome type ( $F [2, 56] = 10.23, p < .001, \eta^2_g =$   
402  $.11$ ). Switching was highest following selection errors ( $M = 66\%; SE = 5\%$ ) and markedly lower  
403 following execution errors ( $M = 42\%, SE = 5\%; t(28) = 5.22, p < .001$ ). This difference is consistent  
404 with the hypothesis that motor errors attenuate value updating, perhaps because participants  
405 believe they have more control to correct for execution errors (Parvin et al., 2018).

406 Interestingly, switch rates following rewarded trials fell between the other two outcome  
407 types ( $M = 55\%, SE = 6\%$ ). There was no difference between switch rates following reward relative  
408 to selection errors ( $t(28) = 1.85, p = .227$ ) or execution errors, although the latter approached  
409 significance ( $t(28) = 2.46, p = .062$ , following Bonferroni correction). The fact that many participants  
410 (18 of 29) were so prone to switching after a rewarded outcome and even more so (numerically)  
411 than after an execution error was unexpected. The high switching rates would suggest a bias  
412 towards exploratory behavior in this task- which might have been promoted by the relatively low  
413 rewards and/or the highly probabilistic nature of the outcomes (Cohen et al., 2007; Daw et al.,  
414 2006). Notably, there were very large individual differences in the treatment of the outcomes:  
415 Switch rates ranged from 3% to 98% following rewards, 7%-99% following selection errors and  
416 4%-81% following execution errors.

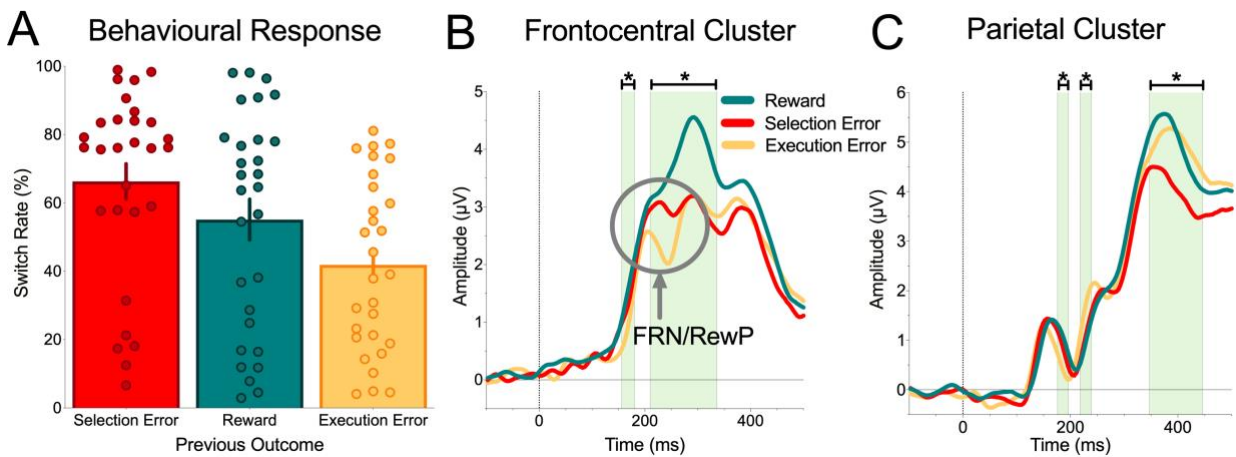
417

### 418 ERP Responses

419 Our primary aim was to examine whether selection and execution errors could be reliably  
420 distinguished in outcome-locked ERPs. To start, we ran an exploratory 3 (Bandit Type: High  
421 Execution/Low Selection Error vs. Low Execution/High Selection Error vs. Neutral) X 3 (Outcome:  
422 Reward vs. Selection Error vs. Execution Error) ANOVA at each time point for the frontocentral and  
423 parietal clusters. The main effect of Bandit Type was not significant ( $p's \geq .702$ ) and there was no  
424 Bandit Type X Outcome interaction ( $p's \geq .671$ ). Thus, we collapsed across the three bandits in

425 our primary analyses of the three outcomes, allowing us to avoid increasing the family-wise error  
426 rate.

427 The grand averaged ERPs related to each outcome are shown in **Figure 2B and 2C**. F  
428 tests revealed two significant clusters in the frontocentral region between 156 -180 ms and 210-  
429 336 ms, and three clusters in the parietal region (176-196 ms; 218-239 ms; and 355-438 ms).  
430 Descriptively, the first cluster in the frontocentral region was driven by a delay in the onset of an  
431 initial P200-like signal following an execution error, and the second cluster incorporated FRN  
432 deflections following selection and execution errors, along with subsequent positive deflections,  
433 likely reflecting the P3a subcomponent of the P300 signal (Polich, 2007). The early two clusters in  
434 the parietal region reflect shifts in the latency and amplitude of the execution error ERP, with the  
435 third cluster driven by the attenuation of the P3b subcomponent of the P300 following selection  
436 errors.



437

438 **Figure 2- Behavioral Responses and ERP Grand Averages.** (A) Switching rates following the three  
439 trial outcomes. Participants were more likely to repeat a choice (indexed by lower switch rates)  
440 following execution errors relative to selection error feedback. Error bars represent  $\pm 1$  SEM. Feedback-  
441 locked ERPs for each outcome type, recorded from (B) frontocentral and (C) parietal electrode clusters.  
442 Zero on the abscissa indicates feedback onset. The green shaded regions indicate the significant  
443 clusters identified in the mass univariate analysis. Pairwise differences in these clusters are visualized  
444 in Figures 3-5 through the comparison of difference waveforms.

445

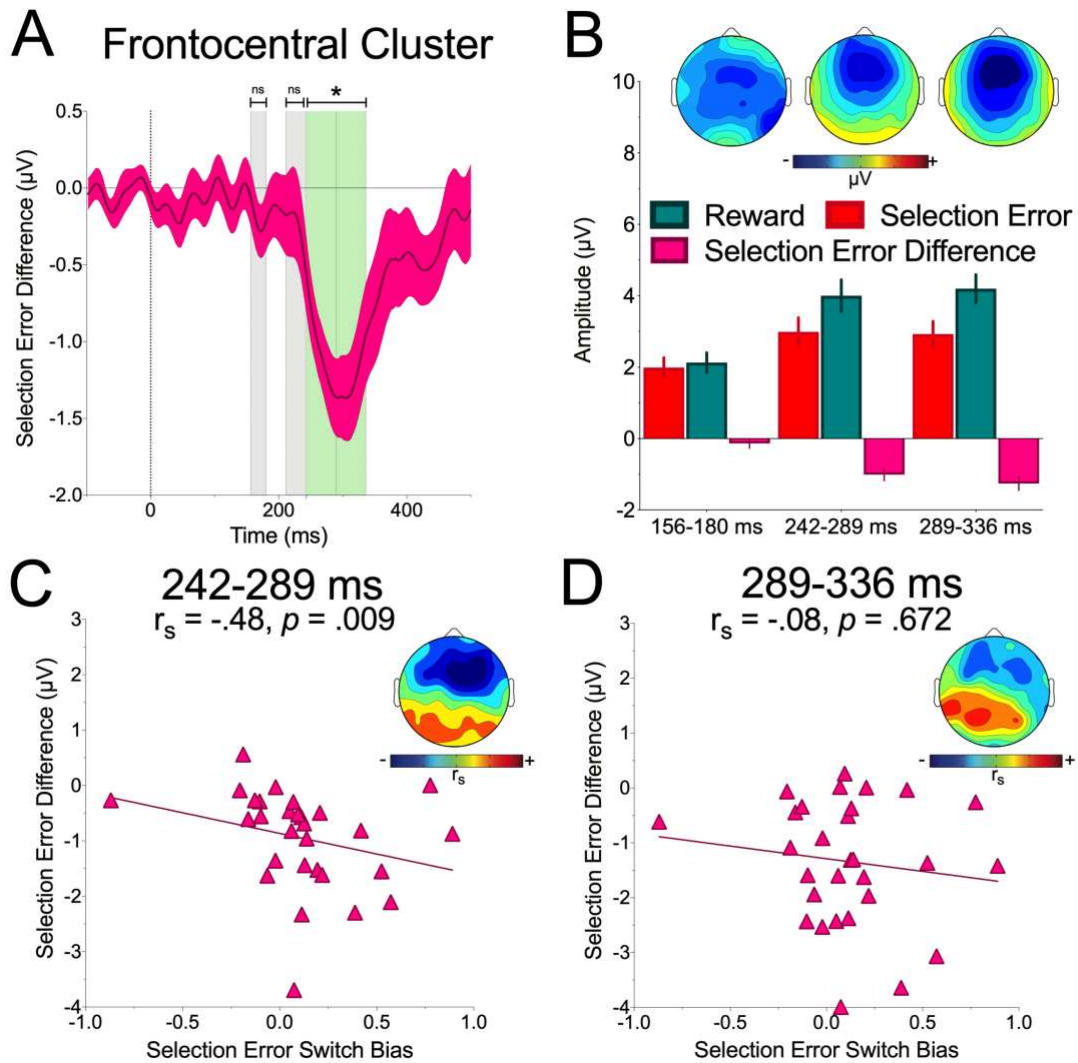
446 **Figure 3A** depicts the Selection Error difference waveform, derived by subtracting the  
447 Selection Error waveform from Reward ERPs for the frontocentral cluster (shown in **Figure 2B**)  
448 and shows a statistically significant cluster of time points between 242-336 ms (one-sample t-tests  
449 of the difference wave against zero). An examination of the scalp topography of the first (242-289  
450 ms) and second half of this window (289- 336 ms) indicated a clear frontocentral maximum in the  
451 early phase, followed by a shift towards centroparietal maximum in the later part of the window  
452 (**Figure 3B**).

453 In line with the reinforcement learning account of the FRN, there was a relationship  
454 between neural activity and behavior. Specifically, amplitude (mean:  $r_s = -.483$ ,  $p = .009$ ; peak:  $r_s =$   
455  $-0.36$ ,  $p = .052$ ; **Figure 3C**) from the early part of the cluster (capturing the FRN) negatively



456 correlated with behavioral adjustment: The larger the difference waveform (i.e., greater negative  
457 deflection for selection errors relative to rewards), the greater the bias for the participant to switch  
458 to a different bandit following a selection error outcome relative to a reward outcome. We note that  
459 one participant had a switch rate score of -0.87, which was 2.97 standard deviations away from the  
460 mean. Re-running the analysis without this participant showed a weaker relationship, but the  
461 pattern remained statistically significant (mean:  $r_s = -.39$ ,  $p = .042$ ; peak:  $r_s = -.34$ ,  $p = .074$ ).

462 The topographical map (**Figure 3C** inset) demonstrates that this effect was localized to the  
463 frontocentral region. We found no evidence for such a relationship in the later, P3a, part of the time  
464 window ( $r_s = -.08$ ,  $p = .672$ ; **Figure 3D**). The mean FRN and P3a correlations were marginally  
465 different from one another ( $z = 1.96$ ,  $p = .05$ ), providing support that the FRN, but not the P3a, is a  
466 reliable correlate of behavior change.



467

468 **Figure 3- Selection Error in the Frontocentral Cluster:** (A) The Selection Error waveform, defined as  
 469 the difference in the ERPs on trials resulting in selection errors and rewards. The green shaded regions  
 470 indicate significant clusters for this contrast and the grey shaded regions indicate where the clusters  
 471 identified in the original time-series analysis did not reach statistical significance for this difference  
 472 waveform. Zero on the abscissa indicates feedback onset. (B) Mean amplitudes for the early and late  
 473 phases of the statistically significant clusters, with insets showing scalp maps of the distribution of  
 474 differences across sites for each time interval. Selection Error difference waveform amplitude (shown  
 475 on the ordinate, where negative values indicate more negative amplitude for selection errors relative to  
 476 reward) correlated with an increase in the Switch Bias score (shown on the abscissa, where positive  
 477 values indicate more switching following selection errors relative to reward) at a time interval  
 478 corresponding to the FRN (C), but not the P3 (D). The insets show scalp maps of the distribution of  
 479 amplitude differences across sites, revealing a frontocentral maxima for the FRN correlation.

480

481 Execution Errors

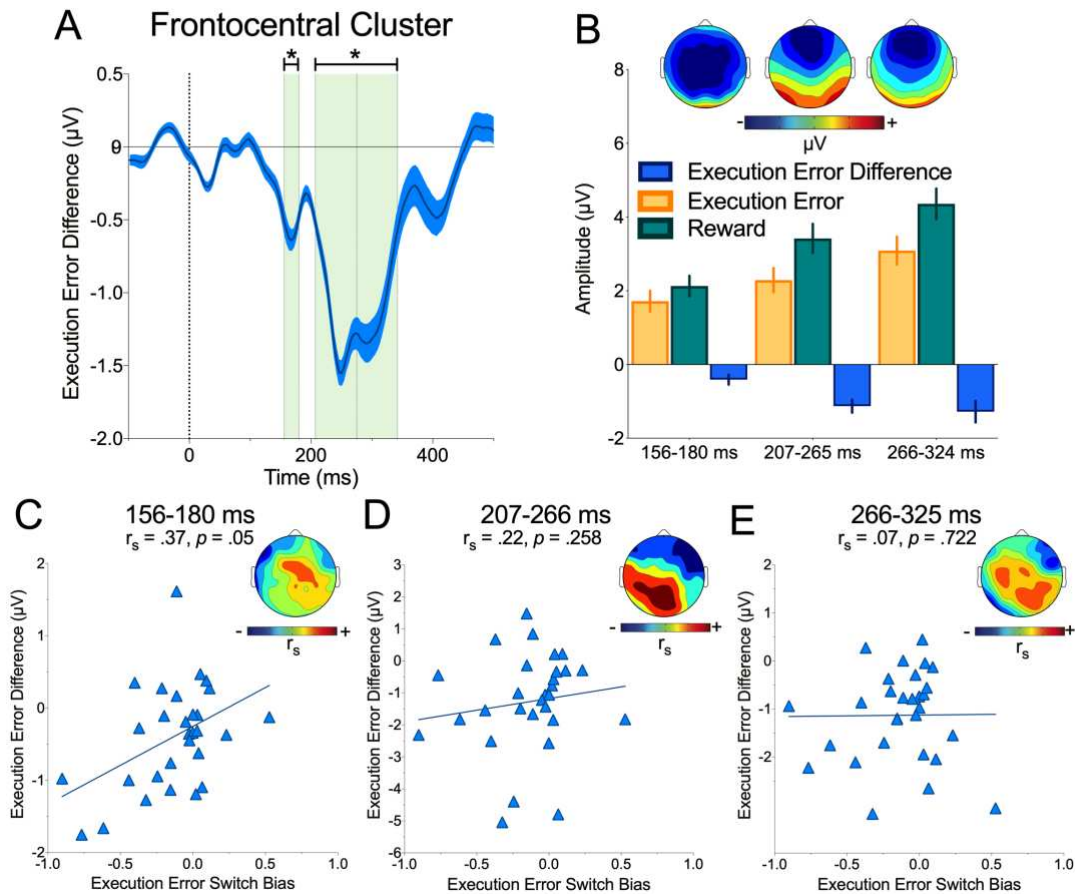
482 To examine the electrophysiological correlates associated with unrewarded outcomes attributed to  
 483 motor execution errors, we performed similar analyses, but now focus on the comparison between  
 484 execution error trials and reward trials (the Execution Error difference waveform- the result of  
 485 subtracting the Execution Error ERP from Reward ERPs in the frontocentral cluster shown in

486 **Figure 2B**). This comparison revealed two statistically significant clusters- one ranging from 156-  
487 180 ms and a second between 207-325 ms (**Figure 4A**).

488 The first cluster showed an amplitude reduction in response to Execution Errors relative to  
489 reward trials. Similar to the Selection Error waveform result, we expected the second cluster would  
490 be contaminated by a P3a signal. Thus, we followed the same protocol, splitting this cluster into  
491 two equal intervals – (i) an early phase marked by the time interval 207-266 ms; and (ii) a later  
492 phase for activity between 266-325 ms. There was a clear frontocentral distribution for the early  
493 phase, and in the later time window, a shift towards centroparietal electrodes (**Figure 4B**).

494 We next examined the relationship between these three epochs (156-180 ms; 207-266 ms;  
495 266-325 ms) and behavioral adjustment (**Figure 4C-E**). The peak amplitude difference in the  
496 earliest interval (156-180 ms) correlated positively ( $r_s = 0.37$ ,  $p = .05$ ) with switching rates following  
497 an execution error relative to reward. Following execution errors, smaller peaks in the 156-180 ms  
498 time window were associated with a lower tendency to switch. Note that this pattern is opposite to  
499 that observed between the amplitude of the FRN and behavioral adjustments following selection  
500 errors. The mean amplitude measure had a similar pattern of results, but was not significant ( $r_s =$   
501  $0.35$ ,  $p = .065$ ). An examination of topography revealed this correlation to be maximal in the  
502 frontocentral cluster, suggesting that smaller amplitudes in response to execution errors early in  
503 the feedback processing stream are associated with a higher tolerance to this outcome.

504 In contrast to the results for Selection Errors, the FRN captured in the 207-266 ms time  
505 window did not correlate with behavioral adjustment ( $r_s = .07$ ,  $p = .722$ ). We tested, and confirmed,  
506 that this correlation was reliably different to the correlation observed for Selection Errors in the  
507 FRN time interval ( $z = 2.40$ ,  $p = .016$ ). There was no correlation between the Execution Error  
508 waveform in the P3a time window (266-325 ms) and behavioral adjustment ( $r_s = -.22$ ,  $p = .258$ ).



509

510 **Figure 4- Execution Error in the Frontocentral Cluster:** (A) The Execution Error difference  
 511 waveform, defined as the difference amplitude for execution error and reward ERPs. The green shaded  
 512 regions indicate clusters showing statistically significant differences. Zero on the abscissa indicates  
 513 feedback onset. (B) Mean amplitudes for the early and late phases of the significant clusters. (C) The  
 514 Execution Error difference waveform amplitude (shown on the ordinate, where positive values indicate  
 515 larger amplitude for execution errors relative to reward) positively correlated with an increase in the  
 516 Switch Bias score (shown on the abscissa, where positive values indicate more switching following  
 517 execution errors relative to reward) in this early time window, but there were no correlations in the later  
 518 time windows (D & E).

519

520 We conducted the same analysis for the Execution Error waveform in the parietal cluster of  
 521 electrodes. Execution errors elicited smaller amplitude responses relative to rewards in an early  
 522 time window (176-196 ms) but elicited larger amplitude responses at 218-239 ms post feedback. In  
 523 the later time window, there was a positive correlation between amplitude and behavior ( $r_s = .47, p = .01$ ) in the posterior region, suggesting a shift from frontocentral to parietal regions in the  
 524 processes driving behavioral adjustment (Dhar & Pourtois, 2011; Overbeek et al., 2005).  
 525 Interestingly, and unexpectedly, the amplitude of the P3b subcomponent of the P300 signal—  
 526 proposed to reflect the revision of internal forward models in posterior parietal cortex (Krigolson &  
 527 Holroyd, 2007a) showed no difference in the processing execution errors and rewards (see **Figure**  
 528 **2C**) and there was no relationship with behavioral adjustment ( $r_s = -0.01, p = .946$ ).  
 529

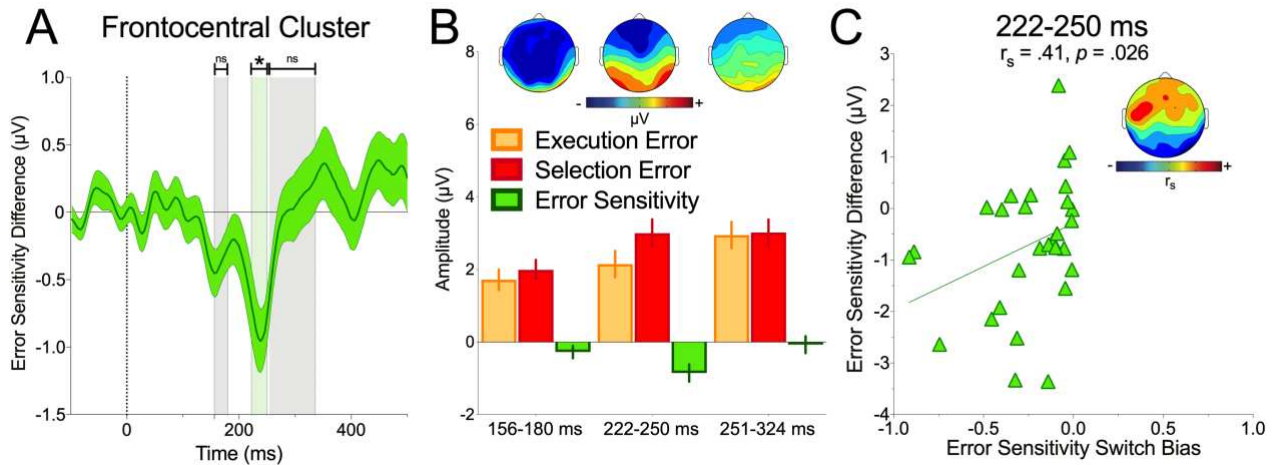
## 530 Error Sensitivity Difference Waveform

531 As described in the previous two sections, when using a common baseline (rewarded trials), we  
532 observed differences in both the ERP results and correlational analysis between unrewarded trials  
533 that were attributed to failures in movement execution or action selection. We performed a direct  
534 comparison between these two types of unrewarded outcomes by analyzing an Error Sensitivity  
535 difference waveform, subtracting the ERP for selection errors from the ERP for execution errors  
536 (see **Figure 2B** for the parent waveforms).

537 In the frontocentral cluster there was a significant difference in the range of the FRN (222-  
538 250 ms; **Figure 5 A, B**). We had anticipated that the amplitude of the FRN would be attenuated  
539 following execution errors, assuming a lower response would be reflective of reduced value  
540 updating (McDougle et al., 2019). However, the observed effect was in the opposite direction:  
541 Execution errors elicited a larger FRN deflection, relative to selection errors.

542 We also examined whether the magnitude of this difference correlated with the “Switch  
543 Bias” rate. For this measure, the proportion of switches following execution errors was subtracted  
544 from the number of switches made following selection errors. Note that these values range from 0  
545 to -0.91, due to the fact no participants produced more switches following execution errors relative  
546 to selection errors. Although the parent waveforms for this correlation are included in the previous  
547 analyses, the EEG activity in this analysis is specific to the range 220-250 ms, the window in which  
548 the error outcome ERPs differed significantly.

549 There was no relationship between mean amplitude in this window and Switch Bias ( $r_s =$   
550  $.23$ ,  $p = .23$ ). However, the peak negative amplitude revealed a positive correlation with Switch  
551 Bias ( $r_s = .41$ ,  $p = .026$ ; **Figure 5C**). Participants who had relatively similar switching rates to the  
552 two unrewarded outcomes had smaller FRN differences, while individuals with a large negative  
553 bias (i.e., less switching after execution errors) also exhibited larger FRN amplitudes for motor  
554 execution errors relative to selection errors. This correlation was maximal in frontocentral sites  
555 (**Figure 5C inset**).



556

557 **Figure 5- Error Processing Differences in the Frontocentral Cluster:** (A) The Error Sensitivity  
 558 difference waveform, calculated by subtracting ERPs for selection error from execution error ERPs. The  
 559 green shaded region indicates the single cluster in which there was a significant difference for this  
 560 contrast and the grey shaded regions indicate where the clusters identified in the original time-series  
 561 analysis did not reach statistical significance in this comparison. Zero on the abscissa indicates  
 562 feedback onset. (B) Mean amplitudes for the early and late clusters indicated by shaded regions in  
 563 panel A. Inset scalp maps show topographical distribution for each cluster. (C) Peak amplitude  
 564 difference in the FRN (shown on the ordinate, where negative values indicate a larger negative  
 565 deflection for execution errors relative to selection error) correlated with a larger Switch Bias score  
 566 (shown on the abscissa, where larger negative values indicate more switching following selection error  
 567 relative to execution error). Note that no participants showed higher rates of switching following  
 568 execution error relative to selection error. This correlation shows that as the similarity in the behavioral  
 569 response to execution and selection error increased, amplitude differences in the processing of  
 570 execution and selection error decreased.

571

572 Examining the parietal cluster revealed no differences in the earliest interval (176-196 ms).  
 573 However, differences emerged in the 218-239 ms and 359-445 ms epochs, with larger positive  
 574 amplitudes for execution errors relative to selection errors. The mean amplitude across each of  
 575 these clusters (218-239 ms and 359-445 ms) was not correlated with the behavioral adjustment  
 576 scores ( $r_s \leq .179$ ,  $p$ 's  $\geq .352$ ).

## 577 **Kinematic Analysis**

578 To gain a deeper understanding of the relationship between brain activity and task performance,  
579 we examined correlations between task kinematics and the statistically significant periods identified  
580 in the time series analysis in the frontocentral and parietal difference waveforms. We reasoned  
581 that, in contrast to Selection Errors, where there was a relationship between FRN amplitude and  
582 choice selection, the Execution Error FRN may instead be encoding information about cursor  
583 position and subsequent movement correction.

584 In the first analysis, we examined whether there was a relationship between cursor error  
585 (the presented position of the cursor shown to participants at the end of the movement) magnitude  
586 and ERP activity. There were no reliable correlations between the mean activity of the statistically  
587 significant clusters in the difference waveforms and corresponding differences in cursor error  
588 magnitude (Execution Error:  $r_s \leq 0.228$ ,  $p$ 's  $\geq 0.233$ ; Selection Error:  $r \leq 0.176$ ,  $p$ 's  $\geq .359$ ; Error  
589 Sensitivity:  $r_s \leq 0.152$ ,  $p$ 's  $\geq .429$ ).

590 In the second analysis, we asked whether ERP amplitude on the current trial would  
591 correlate with the degree of motor correction on subsequent trials. Here, we restricted analysis to  
592 the subset of trials in which participants chose the same target consecutively. The amount of motor  
593 correction in response to feedback (computed as the mean absolute change in end-point veridical  
594 hand position relative to the cursor position on the previous trial), varied as a function of Feedback  
595 ( $F(2, 56) = 75.37$ ,  $p < .001$ ,  $\eta^2_g = .66$ ). As both outcomes indicated a successful movement, we  
596 expected, and found, no difference ( $t(28) = 0.47$ ,  $p > .999$ ) in the subsequent degree of correction  
597 for Selection Error ( $M = 3.73^\circ$ ,  $SE = 0.15^\circ$ ) and Reward ( $M = 3.64^\circ$ ,  $SE = 0.17^\circ$ ) trials. In contrast,  
598 Execution Error, signaling a need to change one's motor response to hit the target ( $M = 6.53^\circ$ ,  $SE$   
599  $= 0.22^\circ$ ) had higher rates of correction relative to both Selection Error ( $t(28) = 8.95$ ,  $p < .001$ ) and  
600 Reward ( $t(28) = 8.95$ ,  $p < .001$ ) outcomes. Despite these behavioral differences, there were no  
601 correlations between mean activity of the statistically significant clusters in the difference  
602 waveforms and relative differences in the magnitude of subsequent motor corrections (Execution  
603 Error:  $r_s \leq -0.239$ ,  $p$ 's  $\geq 0.211$ ; Selection Error:  $r_s \leq -0.328$ ,  $p$ 's  $\geq 0.083$ ; Error Sensitivity:  $r_s \leq .152$ ;  
604  $p$ 's  $\geq 0.429$ ).

605 To ensure that we did not miss any potential sensitivity to task kinematics in other time  
606 ranges, we undertook an exploratory search of the full time series data by correlating cursor error  
607 and motor correction with mean amplitude from 150ms to 500ms.

608 We found no correlations between ERP difference waveforms and Cursor Error in the  
609 frontocentral ( $p$ 's  $\geq .45$ ) or parietal sites ( $p$ 's  $\geq .75$ ) following correction. We also note, with a  
610 degree of caution given the corrected  $p$  values were not significant, that there was one statistically  
611 significant pattern prior to correction- a positive correlation between the Error Sensitivity difference  
612 waveform and Cursor Error ( $r_s = .43$ , 406 ms). In correlating motor correction rates with ERP  
613 amplitude, we found no significant relationships in the frontocentral cluster ( $p$ 's  $\geq .454$ ). Here, we  
614 noted that the strongest relationship ( $r_s = .456$ ) was a positive one between motor correction and  
615 the Error Sensitivity difference waveform at 164 ms – a pattern that was sustained across 156- 174  
616 ms. As participants made larger degrees of correction following Execution Errors relative to  
617 Selection Errors, they also exhibited greater amplitude. In the parietal cluster, we found no reliable  
618 patterns of activity following ( $p$ 's  $\geq .97$ ) or prior to correction ( $p$ 's  $\geq .1$ ).

### 619 **Perturbation Awareness**

620 In a final set of explorations, we examined whether participants were sensitive to the feedback  
621 manipulation that had been applied to control the frequency of our three outcomes. In almost half  
622 the trials ( $M = 47.8\%$ ,  $SE = 0.01\%$ ) we delivered perturbed instead of veridical feedback ( $52.2\%$ ,  
623  $SE = 0.01\%$ ). We had taken measures to minimize the likelihood of participants becoming aware of  
624 these changes (e.g., no online movement feedback was provided, and end-point feedback was  
625 presented 1 s after the stylus had passed the bandit) and in a post-experiment survey, participants  
626 indicated that they believed execution error outcomes to be the result of poor reaches, suggesting  
627 no explicit awareness of the manipulation. Nevertheless, we did find differences in cursor error  
628 (**Figure 6A**), as revealed through a 3 (Outcome: Reward vs. Selection Error vs. Execution Error) X  
629 2 (Veracity: Veridical vs. Perturbed) interaction ( $F(2, 56) = 27.4$ ,  $p < .001$ ,  $\eta^2_g = .25$ ). In all cases,  
630 cursor error was largest in the Veridical trials, but the effect was greatest for Reward (Veridical  $M =$   
631  $1.68^\circ$ ,  $SE = 0.02^\circ$ , Perturbed  $M = 0.98^\circ$ ,  $SE = 0.01^\circ$ ;  $t(28) = 26.83$ ,  $p < .001$ ) and Selection Error  
632 (Veridical  $M = 1.72^\circ$ ,  $SE = 0.02^\circ$ , Perturbed  $M = 0.97^\circ$ ,  $SE = 0.02^\circ$ ;  $t(28) = 30.95$ ,  $p < .001$ )  
633 outcomes, with differences of  $0.7^\circ$  and  $0.75^\circ$  respectively. For Execution Error, there was a visual  
634 difference of  $0.27^\circ$  (Veridical  $5.99^\circ$ ,  $SE = 0.07^\circ$ , Perturbed  $M = 5.72^\circ$ ,  $SE = 0.04^\circ$ ;  $t(28) = 3.5$ ,  $p =$   
635  $.045$ ).

636 In examining hand error (position of the hand relative to the center of the target), we found  
637 a Veracity X Outcome interaction ( $F(2, 56) = 4770.99$ ,  $p < .001$ ,  $\eta^2_g = .981$ ; **Figure 6B**). Veridical  
638 Execution Error trials ( $M = 5.99^\circ$ ,  $SE = 0.07^\circ$ ) were not statistically significantly different to  
639 perturbed Selection Error ( $M = 5.90^\circ$ ,  $SE = 0.07^\circ$ ;  $t(28) = 1.08$ ,  $p = .886$ ) and perturbed Reward  
640 trials ( $M = 5.93^\circ$ ,  $SE = 0.07^\circ$ ;  $t(28) = 1.09$ ,  $p = .881$ ). Similarly, there was no difference in hand  
641 error for perturbed Execution Error trials ( $M = 1.75^\circ$ ,  $SE = 0.02^\circ$ ) compared to veridical Selection  
642 Error ( $M = 1.72^\circ$ ,  $SE = 0.02^\circ$ ;  $t(28) = 0.998$ ,  $p = .915$ ) and veridical Reward trials ( $M = 1.68^\circ$ ,  $SE =$   
643  $0.02^\circ$ ;  $t(28) = 2.41$ ,  $p = .188$ ).



644 Participants did not alter their behavioral strategy in response to feedback perturbations  
645 (Veracity:  $F(1, 28) = 0.899$ ,  $p = .351$ ,  $\eta^2_g = < .01$ ).; Veracity X Outcome:  $F(2, 56) = 1.42$ ,  $p = .251$ ,  
646  $\eta^2_g < .01$ ; **Figure 6C**). However, a suggestion that they might have been implicitly sensitive to  
647 these differences is indicated by the degree of motor correction following veridical and perturbed  
648 feedback (**Figure 6D**). One participant had no stay trials following perturbed feedback in this  
649 subset of data and was excluded from this analysis. In the remaining participants, we observed an  
650 Outcome X Veracity interaction ( $F(2, 54) = 4.49$ ,  $p = .016$ ,  $\eta^2_g = .04$ ). There were no differences in  
651 the degree of motor correction following Execution Error (Veridical  $M = 6.3^\circ$ ,  $SE = 0.19^\circ$ , Perturbed  
652  $M = 6.84^\circ$ ,  $SE = 0.32^\circ$ ;  $t(27) = 2.07$ ,  $p = .718$ ), but greater corrections (Reward: Veridical  $M = 2.92^\circ$ ,  
653  $SE = 0.13^\circ$ , Perturbed  $M = 4.28^\circ$ ,  $SE = 0.26^\circ$ ;  $t(27) = 4.56$ ,  $p < .001$ ; Selection Error: Veridical  $M =$   
654  $3.02^\circ$ ,  $SE = 0.20^\circ$ , Perturbed  $M = 4.62^\circ$ ,  $SE = 0.17^\circ$ ;  $t(27) = 6.30$ ,  $p < .001$ ) followed false hits trials.  
655 These positively surprising outcomes (real reaches had missed the target on these trials, hence  
656 the perturbation) may have prompted overcompensation as participants sought to calibrate their  
657 movements to task feedback.

658 Given these differences, we explored the extent to which the ERP signal was sensitive to  
659 the veracity of the feedback. We re-ran the ERP time-series analysis, performing a 3 (Outcome:  
660 Reward vs. Selection Error vs. Execution Error) X 2 (Veracity: Veridical vs. Perturbed) at each time  
661 point for the frontocentral and parietal clusters. There were no statistically significant main effects  
662 of Veracity ( $F$ 's  $\leq 6.99$ ,  $p$ 's  $\geq .397$ ) and no Outcome X Veracity interactions ( $F$ 's  $\leq 2.55$ ,  $p$ 's  $\geq .79$ ) in  
663 the frontocentral cluster and similarly, no main effects ( $F$ 's  $\leq 5.42$ ,  $p$ 's  $\geq .853$ ) or Veracity X  
664 Outcome interactions ( $F$ 's  $\leq 1.83$ ,  $p$ 's  $\geq .986$ ) in the parietal cluster.

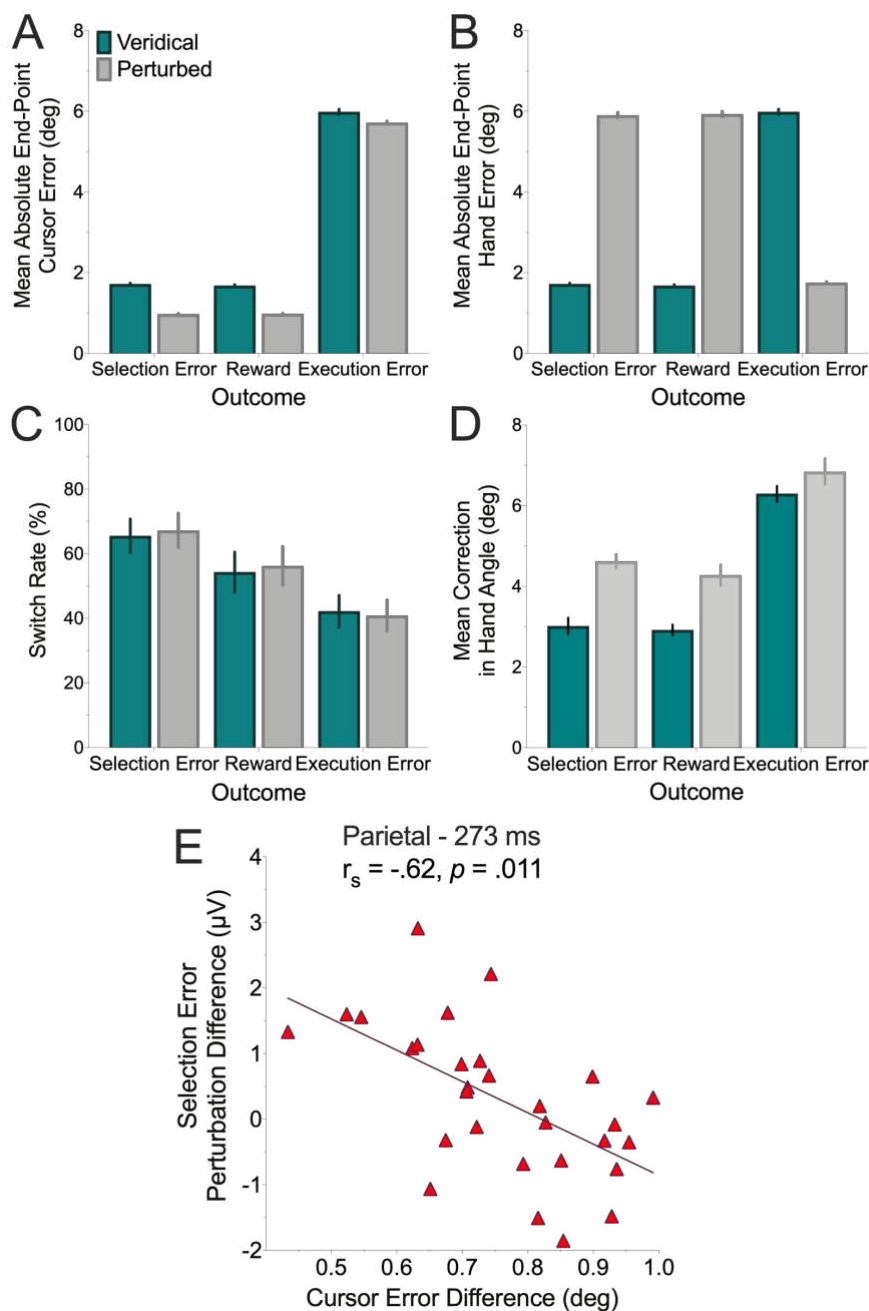
665 We then explored whether there were any differences in the relationship between ERP  
666 activity and kinematic adjustment as a function of Feedback Veracity. As perturbed feedback  
667 elicited larger corrective movements than veridical, we speculated that an ERP signal sensitive to  
668 positive surprise may scale in response to this behavior for Selection and Execution error trials. To  
669 explore this idea, a difference wave subtracting perturbed ERP amplitude from veridical was  
670 computed. The amplitude of this "Perturbation Difference" waveform was correlated with (i) the  
671 mean difference in cursor error for veridical and perturbed feedback per outcome; and (ii) the mean  
672 difference in degree of correction following veridical relative to perturbed feedback per outcome.

673 In analysing the relationship between the Perturbation Difference waveform and Cursor  
674 Error in the frontocentral cluster, we found no correlations that survived correction for multiple  
675 comparisons ( $p$ 's  $\geq .616$ ). However, in the parietal cluster, the Selection Error waveform strongly  
676 correlated with Perturbation Difference amplitude at 273 ms ( $r_s = -0.62$ ,  $p = .011$ ; **Figure 6E**),  
677 indicating a sensitivity to discrepancies between actual and presented hand position. Specifically,  
678 this correlation shows that for participants with larger veridical errors, perturbed feedback elicited  
679 larger positive amplitudes in a manner consistent with the P300 signaling surprise (Donchin, 1981;  
680 Nassar et al., 2019). The Error Sensitivity difference waveform showed a similar pattern but did not  
681 reach the significance threshold after correction ( $r_s = -.47$  at 343 ms). The pattern for Execution  
682 Error was reversed, with the strongest correlation observed later ( $r_s = .45$  at 492 ms)- with  
683 amplitude highest when both cursor error and amplitude were higher in the veridical condition  
684 relative to the perturbed condition. However, this too was not significant following correction.

685 In terms of the relationship between perturbation amplitude differences and the degree of  
686 motor correction, there were no significant effects in the frontocentral ( $p$ 's  $\geq .120$ ) or parietal  
687 clusters ( $p$ 's  $\geq .82$ ). With the same note of caution for non-significant correlations offered above,  
688 two patterns suggest a further dissociation in the processing of selection and execution error: In  
689 the time frame of the FRN, there was a relationship between frontocentral amplitude of the  
690 Perturbation Difference waveform and motor correction ( $r_s = -.542$  at 289 ms). Here, greater  
691 corrective movements in response to perturbed feedback correlated with larger differences in the  
692 FRN; and (ii) later in the window, the Perturbation Difference waveform for Execution Errors  
693 positively correlated ( $r_s = .52$  at 335 ms) with the degree of motor correction, indicating that larger  
694 cursor error corrections in response to perturbed feedback have correspondingly larger amplitudes  
695 for perturbed feedback in the time range of the P3a. Despite the finding that Selection Error, like  
696 Reward, resulted in adaptation following perturbed relative to veridical outcomes, no relationship  
697 was observed, with the strongest effect at 420 ms ( $r_s = -.299$ ).

698 Finally, as an alternative to averaging over perturbed and veridical trials, we correlated the  
699 degree of perturbation on a single trial, computed as the difference between hand error and cursor  
700 error (which was zero on veridical trials, a positive value on trials where the cursor was shown to  
701 be closer to the target than the hand position and a negative value when the cursor position was  
702 shown to be further away from the target relative to hand position) with amplitude in the  
703 frontocentral and parietal clusters at each time point in the ERP per outcome for every participant.  
704 We did not find any general patterns to indicate a sensitivity to perturbation magnitude. In the  
705 frontocentral cluster, one participant showed a positive correlation between perturbation and the  
706 processing of Reward (between 152-172 ms and 254-289 ms), another showed a correlation for  
707 Execution Error trials (between 70-86 ms, 110-137 ms, 188-204 and 289-500ms) and two  
708 participants showed positive correlations for Selection Error. The first had a positive correlation  
709 between 453-457 ms and the second had a positive correlation in multiple clusters across the  
710 whole time series (between 4-11 ms, 31-90 ms, 117-188 ms, 258-277 ms, and 460 -477 ms). In

711 the parietal cluster, no relationships emerged for Reward or Execution Error, with two participants  
 712 showing positive correlations between the degree of perturbation and the processing of Selection  
 713 Error: one between 340-356 ms and a second participant between 289-317 ms and 382-500 ms.  
 714



715

716 **Figure 6- Feedback Perturbation and Awareness:** (A) Cursor error was larger for veridical  
 717 feedback relative to perturbed; (B) There was no difference in the magnitude of hand error for  
 718 perturbed selection and reward error trials relative to veridical execution error trials and no  
 719 difference between perturbed Execution Error trials compared to veridical Selection Error and  
 720 Reward trials; (C) Despite smaller cursor error, participants made larger corrections in response to  
 721 perturbed feedback, with the pattern most pronounced for false hits; (D) Perturbed feedback did  
 722 not impact on the likelihood of switching bandits; (E) Amplitude differences between perturbed and  
 723 veridical feedback in the Parietal cluster for Selection Errors at 273 ms (shown on the ordinate,  
 724 where positive values indicate larger amplitude for veridical relative to perturbed outcomes)  
 725 correlated with magnitude of the difference in cursor error for these outcomes (shown on the  
 726 abscissa, where positive values indicate larger veridical cursor errors relative to perturbed).

## 727 **Discussion**

728 Adaptive behavior necessitates distinguishing between outcomes that fail to produce an expected  
729 reward due to either the selection of the wrong action plan or poor motor execution. Although the  
730 majority of decision-making research, in neuroscience as well as economics, have focused almost  
731 exclusively on the former, a few studies have shown that failed outcomes attributed to  
732 sensorimotor errors can markedly biases choice behavior (Green et al., 2010; McDougle et al.,  
733 2016, 2019). Here, we examined this issue by asking how an ERP signature of reinforcement  
734 learning, the Feedback-Related Negativity/Reward Positivity (FRN), varied in response to selection  
735 and motor errors. Predicated on the theory that the FRN is a scalp-related prediction error (Holroyd  
736 & Coles, 2002), we tested the hypothesis that errors attributed to failures in execution should lead  
737 to an attenuation in the FRN.

738 Consistent with our expectations, selection errors elicited a larger FRN relative to reward  
739 outcomes. Moreover, in line with a reinforcement learning account, the amplitude of the FRN  
740 following selection errors was negatively correlated with the probability that participants switched  
741 between the response options following feedback. Behaviorally, participants showed lower switch  
742 rates following execution errors, a pattern consistent with the hypothesis that the reinforcement  
743 learning system discounts these errors (McDougle et al., 2019). However, contrary to the  
744 prediction that FRN amplitude would be attenuated following execution errors, these errors actually  
745 produced the largest FRN. A striking difference between the ERPs in response to selection and  
746 execution error was that the amplitude of the FRN following selection errors was predictive of  
747 behavioral biases and learning, whereas this ERP response following execution errors did not  
748 correlate with these variables.

749 While almost all participants were more likely to switch after a selection error compared to  
750 an execution error, the differential response (i.e., difference in switch rates) to these two error  
751 outcomes varied considerably across participants. Moreover, this behavioral difference was  
752 correlated with the neural response to the two types of feedback: The more similarly participants  
753 treated the two outcomes at a behavioral level, the smaller the difference in FRN amplitude in  
754 response to these outcomes.

755 These findings could be reconciled by considering the top-down mechanisms that may  
756 modulate how execution errors are processed. Behavioral experiments have shown that a sense of  
757 agency related to the perceived ability to correct for motor errors biases choice behavior (Parvin et  
758 al., 2018). In the present experiment, the finding that participants persevered with a bandit  
759 following execution error but switched more often following selection errors also points towards  
760 differences in agency. Previous work on the FRN has shown that outcomes that can be controlled  
761 lead to a more negative FRN than those that cannot (Sidarus et al., 2017) and the FRN is  
762 attenuated in the absence of actively performed actions (Donkers et al., 2005; Donkers & van  
763 Boxtel, 2005). The finding that execution errors produced a larger FRN relative to selection error is  
764 consistent with the presumed greater sense of agency associated with this type of unrewarded

765 outcome.

766 A recent fMRI experiment using a 3-arm bandit task similar to that employed here, revealed  
767 an attenuation of the signal associated with negative reward prediction error in the striatum  
768 following execution failures (McDougle et al., 2019). Our observation of a larger negative deflection  
769 for execution error trials in the FRN may appear contrary to these previously reported striatal  
770 results. However, the fMRI investigation did show increased ACC activity in response to execution  
771 errors compared to selection errors, suggesting that the former have their own neural signature.  
772 With regards to the EEG response, there have been a number of studies reporting FRN deflections  
773 in response to execution error (Anguera et al., 2009; Krigolson et al., 2008; Torrecillos et al., 2014).  
774 These studies, in line with the Prediction-Response Outcome model of medial frontal cortex  
775 function (Alexander & Brown, 2011), point to the existence of a general monitoring system that  
776 responds to violation of expectations. However, an important aspect of these tasks is that errors in  
777 movement execution typically resulted in high level goal errors (e.g., failure to reach or remain on  
778 target in a manual tracking task) and/or involved the introductions of perturbations during the  
779 movement phase (Krigolson et al., 2008). This makes it difficult to rule out the contribution of  
780 cognitive control and response inhibition processes- which are known to generate an N200  
781 component that shares similar spatial and temporal characteristics to the FRN signal (Holroyd,  
782 2004; Holroyd et al., 2008). A recent study separating reward and sensory prediction errors in a  
783 motor adaptation task showed that the FRN responds to the former, but not the latter (Palidis et al.,  
784 2019). The present findings, indicating qualitatively different relationships between the two medial  
785 frontal negativities with behavioral modification, add weight to the possibility that execution error  
786 processing may be distinct from dopamine-related reinforcement learning processes.

787 We also observed two distinct patterns of activity in time windows preceding and following  
788 the FRN that provide further support for the claim of differential processing of execution and  
789 selection error. First, smaller amplitude responses were observed following execution errors  
790 relative to rewards in frontocentral sites 156-180 ms post-feedback, and the amplitude of this  
791 component correlated with switch rates. Second, in parietal sites (218-239 ms), larger amplitude  
792 responses occurred following execution errors relative to reward and this difference was also  
793 correlated with switch rates. Importantly, in a reversal of the FRN pattern, magnitude differences in  
794 these early frontocentral and late parietal signals correlated with behavioral adjustment linked to  
795 execution errors. This pattern points towards the existence of distinct error monitoring systems  
796 operating at different levels of behavioural control (Yordanova et al., 2004).

797 Exploratory analysis on the relationship between ERP amplitude and task showed that the  
798 degree of motor correction following execution errors relative to selection errors correlated with  
799 amplitude differences in an early frontocentral cluster (156-174 ms). The time course of this cluster  
800 closely mirrored that of the earliest difference between execution error and reward – where  
801 amplitude differences correlated with switch rates. Given that we had no a priori expectations for  
802 such a result and that this specific result did not survive correction for multiple comparisons,

803 interpretations must be treated with caution and require further robustly powered replication work  
804 to confirm. Should future work replicate this pattern it would add weight to the idea that the need to  
805 make a behavioural modification following an error in the motor system precedes the generation of  
806 the FRN.

807 A pertinent question of the present task and data is the extent to which participants were  
808 aware of the perturbations applied to the feedback to control outcome frequencies. Participants did  
809 not have access to online feedback and end-point cursor information was presented with a 1  
810 second delay to minimize the likelihood of participants becoming aware of the perturbations. In a  
811 post-experiment survey, participants indicated that they had attributed execution errors to poor  
812 motor control. Consistent with this we found that during the task, perturbed feedback did not alter  
813 choice strategy, nor did it result in any significant differences in the ERP. However, participants did  
814 on average make larger corrective movements following perturbed feedback- this was despite  
815 these outcomes showing smaller cursor errors than veridical feedback. In exploratory analysis, we  
816 did not find any relationships between amplitude and perturbation magnitude at a trial level for the  
817 majority of the participants, but we did find a correlation between amplitude differences and cursor  
818 error when averaging across perturbed and veridical trials. This correlation manifested in the  
819 parietal cluster at 273 ms, which likely reflected the onset of the P300. Here, the positive amplitude  
820 of this signal reduced as the amount of veridical error increased. That the P300 shows a sensitivity  
821 to discrepancies between actual and presented hand position is consistent with the theory that the  
822 signal is generated through the active updating of an internal model of the environment (Donchin &  
823 Coles, 1988). The P300 is also notable for being a putative marker of conscious perception (Rutiku  
824 et al., 2015). If participants did indeed have access to this information during the task, it may be  
825 that these perturbations were not sufficiently large enough to signal a need to change strategy.

826 These findings also raise a broader question of whether the present results might be  
827 specific to outcomes that are framed as execution errors, or extend to any endogenous or  
828 exogenous event that results in an unrewarded trial in which the outcome does not provide  
829 information about the reward probability associated with the selected object (Green et al., 2010).  
830 For example, if an unexpected gust of wind blew a tennis lob out-of-bounds, would that be treated  
831 as an “execution error”? Or, if after pulling the lever on a slot machine, a power failure caused the  
832 game to terminate without a payoff, would this affect how the choice is judged? A future study  
833 could test endogenous execution errors (e.g., reaching error) and exogenous errors (e.g., the task  
834 screen goes blank randomly before an outcome is delivered) more explicitly than the perturbations  
835 applied here. If similar results are found in both settings, elements of the early activity observed in  
836 frontocentral sites may indicate the establishment of a sensory “state”, representing that the  
837 intended action plan was not properly implemented, irrespective of whether this mismatch was due  
838 to endogenous or exogenous factors, even before the prediction error is evaluated. This echoes  
839 the sequential ordering in models of temporal difference learning, where first the agent perceives  
840 its state, and then computes reward prediction errors relevant to that state (Sutton & Barto, 1998).

841

## 842 **Limitations and Future Directions**

843           While we have hypothesized that execution errors impact choice behavior, either by  
844 attenuating the operation of reinforcement learning processes or via an enhanced sense of  
845 agency, it is also important to consider alternative hypotheses. In the behavioural data we  
846 observed a high base rate for switching between bandits. The highly probabilistic nature of the  
847 outcomes, coupled with the relatively low reward rate increased made the task of determining the  
848 optimal choice difficult (while each bandit different frequencies of execution and selection errors,  
849 they all had the same expected value). This may have biased participants towards an exploration  
850 strategy to reduce uncertainty by focusing on gathering more information about the reward  
851 likelihood of each bandit for later exploitation (Cohen et al., 2007; Daw et al., 2006). Viewed in this  
852 way, repetition of target selection following execution error might not be due to increased agency  
853 or RL discounting but may instead reflect a failure to acquire information on the reward probability  
854 of the chosen target on the previous trial and a drive to reduce uncertainty. Future work could  
855 disentangle these explanations by, for instance, assigning lower expected value to high  
856 execution/low selection error bandits and/or through the presentation of fictive outcomes for motor  
857 errors.

858

## 859 **Conclusion**

860 We observed a robust FRN in response to both selection and execution errors, but only the former  
861 correlated with behavioral adjustment. In contrast, the amplitude of a positive deflection in the  
862 ERP, both prior and after the FRN, correlated with choice behavior following execution errors.  
863 These results indicate a need for a more nuanced interpretation of what the FRN represents, and  
864 how it may be shaped by contextual information. More generally, the results provide insight into  
865 how the brain discriminates between different classes of error to determine future action.

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867

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