1

Distinct Neural Signatures of Outcome Monitoring following Selection and Execution Errors

Faisal Mushtaq*[1], Samuel D. McDougle[2], Matt P. Craddock[3], Darius E. Parvin[4,5], Jack Brookes[1], Alexandre Schaefer[6], Mark Mon-Williams[1], Jordan A. Taylor[7,8] & Richard B. Ivry[4,5]

[1]School of Psychology, University of Leeds, Leeds, West Yorkshire, United Kingdom
[2]Department of Psychology, Yale University, New Haven, CT, USA
[3]School of Psychology, University of Lincoln, Lincoln, United Kingdom
[4]Department of Psychology, University of California, Berkeley, CA, USA
[5]Helen Wills Neuroscience Institute, University of California, Berkeley, CA, USA
[6]Department of Psychology, Jeffrey Cheah School of Medicine and Health Sciences, Monash University Malaysia, Malaysia
[7]Department of Psychology, Princeton University, Princeton, NJ, USA
[8]Princeton Neuroscience Institute, Princeton University, Princeton, NJ, USA

*Correspondence can be addressed to Faisal Mushtaq, School of Psychology, Faculty of Medicine and Health, University of Leeds, Leeds, LS2 9JT, UK; email: f.mushtaq@leeds.ac.uk

Abbreviated Title: ERP Correlates of Execution and Selection Error
Number of Pages: 39
Number of Figures: 6

Conflicts of Interest: The authors declare no competing financial interests.

Abstract

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

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

Introduction

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

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

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

A window into the processes that underlie outcome monitoring is offered through the discovery of the Feedback-Related Negativity (FRN), a negative deflection in the EEG first identified following the presentation of feedback indicating incorrect responses (Miltner et al., 1997). After its identification, the component quickly became the subject of intense investigation as a marker signaling gains and losses (Gehring & Willoughby, 2002) and outcomes that are worse than expected (Holroyd et al., 2006). The most prominent explanation of its significance, the "reinforcement learning theory of the error-related negativity" (RL-ERN; Holroyd & Coles, 2002) holds that the component indexes the activity of signals from the midbrain dopamine that are conveyed to the anterior cingulate cortex for adaptive modification of behaviour (Holroyd & Coles, 2002; Holroyd & Umemoto, 2016). Recent developments reveal that much of the variation in this

94   component is driven 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 (referred to as the "FRN/RewP" from here onwards) is framed as

97   a feedback negativity or reward positivity, there is a consensus (as indicated by a meta-analysis of

98   55 datasets; Sambrook & Goslin, 2015), that it is sensitive to reward prediction error.

99   The FRN/RewP's sensitivity to errors of action is more contentious. A series of experiments

100   (Krigolson et al., 2008; Krigolson & Holroyd, 2006, 2007a) contrasting high level (goal-attainment)

101   errors, variously operationalized as a failure to reach a target (Krigolson et al., 2008; Krigolson &

102   Holroyd, 2007a), avoid a collision (Krigolson & Holroyd, 2006, 2007b), and the erroneous selection

103   of the wrong hand or force (de Bruijn et al., 2003) with low-level errors (i.e. mismatch between

104   actual and intended motor command), concluded that the latter do not elicit a FRN/RewP. Instead,

105   reflecting a hierarchical error processing system (Krigolson & Holroyd, 2006), these motor errors

106   are proposed to be mediated within posterior parietal cortex (Desmurget et al., 1999, 2001;

107   Diedrichsen, 2005). Further elaborations indicated that the FRN/RewP may only be generated for

108   action errors that cannot be corrected (Krigolson et al., 2008; Krigolson & Holroyd, 2007a),

109   indicating a binary high level coding of outcomes in the FRN/RewP (i.e. signaling whether the goal

110   was achieved or not). In line with this, a recent experiment isolating reward-based and sensory

111   error-based motor adaptation reported a FRN/RewP in response to binary reward feedback, but

112   not sensory error feedback- which instead generated a P300 (Palidis et al., 2019). Previous work

113   on the P300's sensitivity to "low level" motor execution errors led to the proposal that this later

114   parietally distributed component might reflect the revision of an internal forward model in posterior

115   parietal cortex (Krigolson & Holroyd, 2007a).

116   A contrasting set of results suggest that the FRN/RewP (and its response-locked variant,

117   the ERN) may in fact be sensitive to motor errors and reflect more than binary coding of outcomes,

118   with evidence showing that it scales with the magnitude of error during sensorimotor adaptation

119   (Anguera et al., 2009) and correlates with the size of hand-path deviations following externally

120   perturbation to target reaches (Torrecillos et al., 2014). These findings are more in line with a

121   growing body of work suggesting that the FRN/RewP indexes a general salience prediction error

122   (Oliveira et al., 2007; Torrecillos et al., 2014). A computational model attempting to unify a broad

123   range of findings on medial prefrontal cortex function (Alexander & Brown, 2011) proposes that this

124   region is responsible for tracking discrepancies between expectations and outcomes, which are

125   reflected in the FRN/RewP. Viewed in this way, the processing of execution and selection error

126   may share a common neural network that signals a mismatch between the outcome and

127   expectations in the service of behavioural adaptation (Cavanagh et al., 2012; Torrecillos et al.,

128   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/RewP response. If this medial frontal monitoring system also tracks general

136   action-outcome discrepancies, then we should expect a deflection following errors of action

137   execution too. However, should the recently proposed movement-dependent account of RL hold,

138   the FRN/RewP response should be attenuated when errors can be ascribed to the motor system.

139   We would expect P300 amplitude, as a putative index of internal forward model revision (Krigolson

140   & Holroyd, 2007a), should be largest for execution errors.

141   In addition to these predictions, we also examined the relationship between the FRN/RewP

142   and behavioral modification. Specifically, we predicted that participants who exhibited a larger

143   change in the FRN/RewP would be more likely to switch between the different options. Notably, we

144   expected this brain-behavior relationship would hold for selection errors, but not for execution

145   errors. Reasoning that action errors may instead be encoding information about the size of the

146   execution error, with this feedback used to correct discrepancies between the planned and actual

147   outcome, we explored the possibility that these signals may be correlated with the magnitude of

148   error and subsequent change in motor response.

Materials and Methods

Participants

Using an effect size estimate derived from our previously published work on the FRN/RewP ($\eta2p$ = .167; Mushtaq et al., 2016), with a desired statistical power of 0.8 and alpha criterion set at 0.05, we set a minimum sample size of 28 participants. In total we tested thirty-two right-handed participants (EHI > 40; Oldfield, 1971). Two participants were excluded due to excessive EEG artifacts, and a technical error during data collection rendered one participant's dataset unusable. All analyses were performed on the resulting sample of 29 participants (19 females, 10 males, μ age = 26.75 years, ±9.51 years).

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

Design and Procedure

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

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

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

Following McDougle et al. (McDougle et al., 2019), each bandit had its own fixed probabilities for the three trial outcomes. All bandits had a 40% reward outcome, and thus, the 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 ($\pm 6.24°$, 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° 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°

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 post-experiment survey where

237   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.
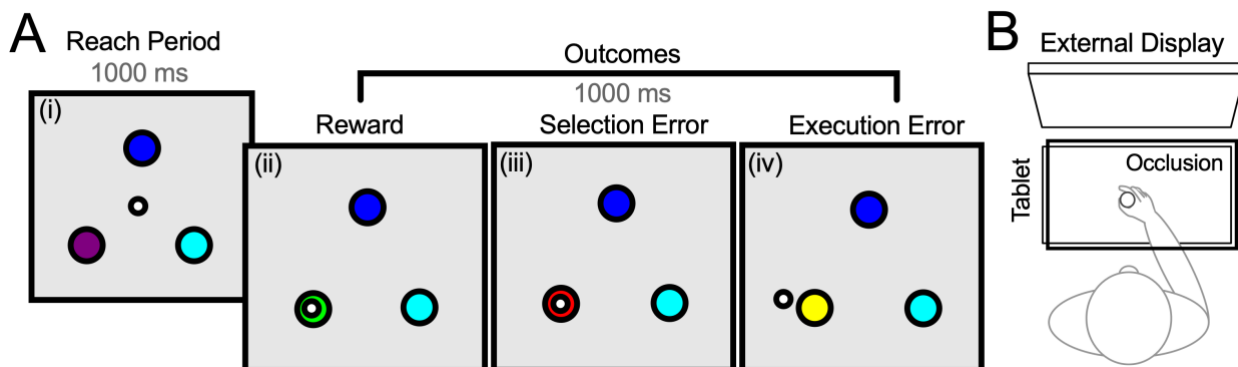
246
247   **Figure 1**- **Experimental Task:** (A) Participants moved a stylus on a tablet to make rapid shooting
248   movements (i) through one of 3 bandits (large circles) at 90°, 210° and 330° degrees relative to the
249   home position (small circle). Following a 1000 ms delay (not pictured), pseudo-veridical 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 across the conditions ($F_{(2, 56)} = 85.2$, $p < .001$), with more reward trials ($\mu = 150$, ±9)

287 available for analysis relative to execution error ($\mu = 114$, ±12; $t(28) = 12.21$, $p < .001$) and

288 selection error trials ($\mu = 110$, ±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,

297 meta-analyses (Sambrook & Goslin, 2015; Walsh & Anderson, 2012) have shown the feedback-

298 locked FRN/RewP effect to be maximal over the frontocentral region of the scalp. As such, we

299 averaged activity across three frontocentral electrodes FC1, FCz, and FC2. Second, given that the

300 P300 (specifically, the P3b sub-component) is commonly present in feedback-locked ERPs and

301 typically maximal over parietal electrodes (Polich, 2007), we averaged over electrodes P1, Pz, and

302 P2. 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 frontal analysis and Pz for parietal); and (iv) grand averaged activity from

310   bootstrapped means extracted from a single electrode. An intraclass correlation coefficient

311   indicated a high level of agreement between all four approaches (Frontal ICC = .995, 95% CI

312   0.989- 0.997; Parietal ICC: = .996, 95% CI 0.994- 0.997). Clustered bootstrapped averaged ERP

313   waveforms are reported here.

314   With growing evidence that most of the variation in the FRN/RewP is driven by a reward

315   positivity, we decided to make use of difference waveforms for our analysis to detect differences

316   irrespective of whether they were driven by positive or negative deflections in the ERP (Krigolson,

317   2018). A difference waveform procedure has the added benefit of more easily isolating the

318   FRN/RewP from components that precede (P2) and follow (a large P3 component comprising a

319   frontal P3a and parietal P3b), eliminating activity in common between two conditions (Kappenman

320   & Luck, 2017). The majority of research on the FRN/RewP has typically computed "reward

321   prediction error" (RPE) difference waveforms, derived by subtracting error/loss trials from reward

322   trials (Sambrook & Goslin, 2015). Here, we created a "Selection Error" difference waveform by

323   subtracting the average activity associated with Selection Error trials from the average activity

324   related to all Reward trials, and an "Execution Error" difference waveform by subtracting the

325   average activity associated with Execution Error trials from the average activity associated with

326   Reward trials. Finally, we directly contrasted Execution and Selection Error ERPs by subtracting

327   the Execution Error waveform from the Selection Error waveform to create an "Error Sensitivity"

328   difference waveform. For statistical analysis, the parent waveform outcome trials were subjected to

329   a one-way ANOVA and where main effects emerged, one-sample t tests were conducted to

330   identify 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/RewP

333   and P3 ERPs) was analysed. For each analysis, p values were corrected by applying a false

334   discovery rate (FDR) control algorithm (Benjamini & Hochberg, 1995; Lage-Castellanos et al.,

335   2010). The Benjamin-Hochberg correction approach was adopted as previous studies have shown

336   it to reliably control the FDR when data are correlated, even when the number of comparisons are

337   relatively small (Hemmelmann et al., 2005). This method is also ideally suited for the exploration of

338   focally 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/RewP 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/RewP (Holroyd and Coles, 2002), we would

351   expect the amplitude of the FRN/RewP to scale with the degree of behavioral adjustment: large

352   differences in the FRN/RewP should be more likely to lead to changes in choice behavior

353   compared to small differences in the FRN/RewP. Here we can ask this question with respect to

354   both selection and 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. The degree of motor correction was examined on a subset of data where

365   participants selected the same target on consecutive trials and quantified as the degree of angular

366   change in hand position relative to cursor position on the previous outcome. Mean cursor error and

367   motor correction scores were correlated with mean amplitudes from the previously identified

368   statistically significant clusters of EEG activity.

369

370 Statistical Analysis

371   For reporting purposes, time points are rounded to the nearest millisecond, amplitude (in

372 microvolts; μV) to two decimal places and p values to three decimal places. The range for the

373 scalp maps was time-interval specific and determined by the 1st and 99th percentile values across

374 all electrodes. Spearman's rho (r_s) was used to examine correlations between amplitude and

375 behavior. For correlations between behavior and neural activity, peak and mean amplitudes were

376 extracted. Both are reported and the strongest correlations are visualized. Where appropriate,

377 pairs of correlations were directly compared with Hittner, May, and Silver's (2003) modification of

378 Dunn and Clark's (1969) approach, using a back-transformed average Fisher's Z procedure as

379 implemented in the R package Cocor v. 1.1-3 (Diedenhofen & Musch, 2015). The statistical

380 significance threshold was set at $p < .05$. Generalized eta squared (η_G^2) is used as a measure of

381 effect size for repeated measures ANOVAs. This measure was selected over eta squared and

382 partial eta squared because it provides comparability across between- and within-subjects designs

383 (Bakeman, 2005; Olejnik & Algina, 2003); we considered $\eta_G^2 = 0.02$ to be small, $\eta_G^2 = 0.13$ medium

384 and $\eta_G^2 = 0.26$ to be a large effect size. All statistical analyses were performed using R (R Core

385 Team, 2015).

386 ## Results

387 **Behavioral Responses**

388 A one-way ANOVA revealed a significant difference in bandit preference (F [2, 56] = 8.27, p

389 < .001, η^2_g = .23), with participants exhibiting bias towards the High Execution/Low Selection Error

390 bandit. Overall, this bandit was chosen on average on 39% (SE = 2%) of the trials, which was

391 significantly greater than the Low Execution/High Selection error bandit (M = 29%; SE = 1%; t(28)

392 = 4.03, p = .001) and Neutral bandit (M = 32%; SE = 2%; t(28) = 2.58, p = .046), with no difference

393 for the latter two (t(28) = 1.07, p = .877). Consistent with previous work, when expected value is

394 equal, the data show that participants prefer choices in which unrewarded trials are attributed to

395 errors in movement execution rather than errors in action selection (Parvin et al., 2018; Green et

396 al., 2010; Wu et al., 2009).

397 We then examined the effect of the different outcomes on the subsequent choice, asking

398 how they influenced switching behavior (**Figure 2**A). Participants exhibited high switching rates

399 overall (54%), but the rate differed according to outcome type (F [2, 56] = 10.23, p < .001, η^2_g =

400 .11). Switching was highest following selection errors (M = 66%; SE = 5%) and markedly lower

401 following execution errors (M = 42%, SE = 5%; t(28) = 5.22, p < .001). This difference is consistent

402 with the hypothesis that motor errors attenuate value updating, perhaps because participants

403 believe they have more control to correct for execution errors (Parvin et al., 2018).

404 Interestingly, switch rates following rewarded trials fell between the other two outcome

405 types (M = 55%, SE = 6%). There was no difference between switch rates following reward relative

406 to selection errors (t(28) = 1.85, p = .227) or execution errors, although the latter approached

407 significance (t(28) = 2.46, p = .062, following Bonferroni correction). The fact that many participants

408 (18 of 29) were so prone to switching after a rewarded outcome and even more so (numerically)

409 than after an execution error was unexpected. The high switching rates would suggest a bias

410 towards exploratory behavior in this task- which might have been promoted by the relatively low

411 rewards and/or the highly probabilistic nature of the outcomes (Cohen et al., 2007; Daw et al.,

412 2006). Notably, there were very large individual differences in the treatment of the outcomes:

413 Switch rates ranged from 3% to 98% following rewards, 7%-99% following selection errors and
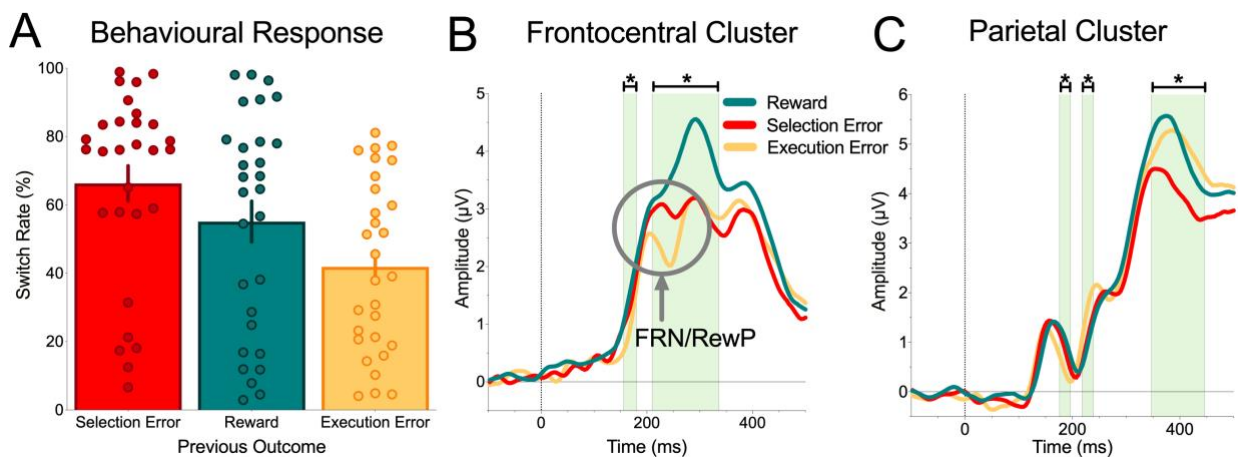
414 4%-81% following execution errors.

415

416 ## ERP Responses

417 Our primary aim was to examine whether selection and execution errors could be reliably

418 distinguished in outcome-locked ERPs. To start, we ran an exploratory 3 (Bandit Type: High

419 Execution/Low Selection Error vs. Low Execution/High Selection Error vs. Neutral) X 3 (Outcome:

420 Reward vs. Selection Error vs. Execution Error) ANOVA at each time point for the frontocentral and

421 parietal clusters. The main effect of Bandit Type was not significant (p's ≥ .702) and there was no

422 Bandit Type X Outcome interaction (p's ≥ .671). Thus, we collapsed across the three bandits in

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

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

435

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

443

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

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

454   correlated with behavioral adjustment: The larger the difference waveform (i.e., greater negative

455   deflection for selection errors relative to rewards), the greater the bias for the participant to switch

456   to a different bandit following a selection error outcome relative to a reward outcome. We note that

457   one participant had a switch rate score of -0.87, which was 2.97 standard deviations away from the

458   mean. Re-running the analysis without this participant showed a weaker relationship, but the

459   pattern remained statistically significant (mean: r_s = -.39, p = .042; peak: r_s = -.34, p = .074).

460   The topographical map (**Figure 3**C inset) demonstrates that this effect was localized to the

461   frontocentral region. We found no evidence for such a relationship in the later, P3a, part of the time

462   window (r_s = -.08, p = .672; **Figure 3**D). The mean FRN/RewP and P3a correlations were

463   marginally different from one another (z = 1.96, p = .05), providing support that the FRN/RewP, but

464   not the P3a, is a reliable correlate of behavior change.
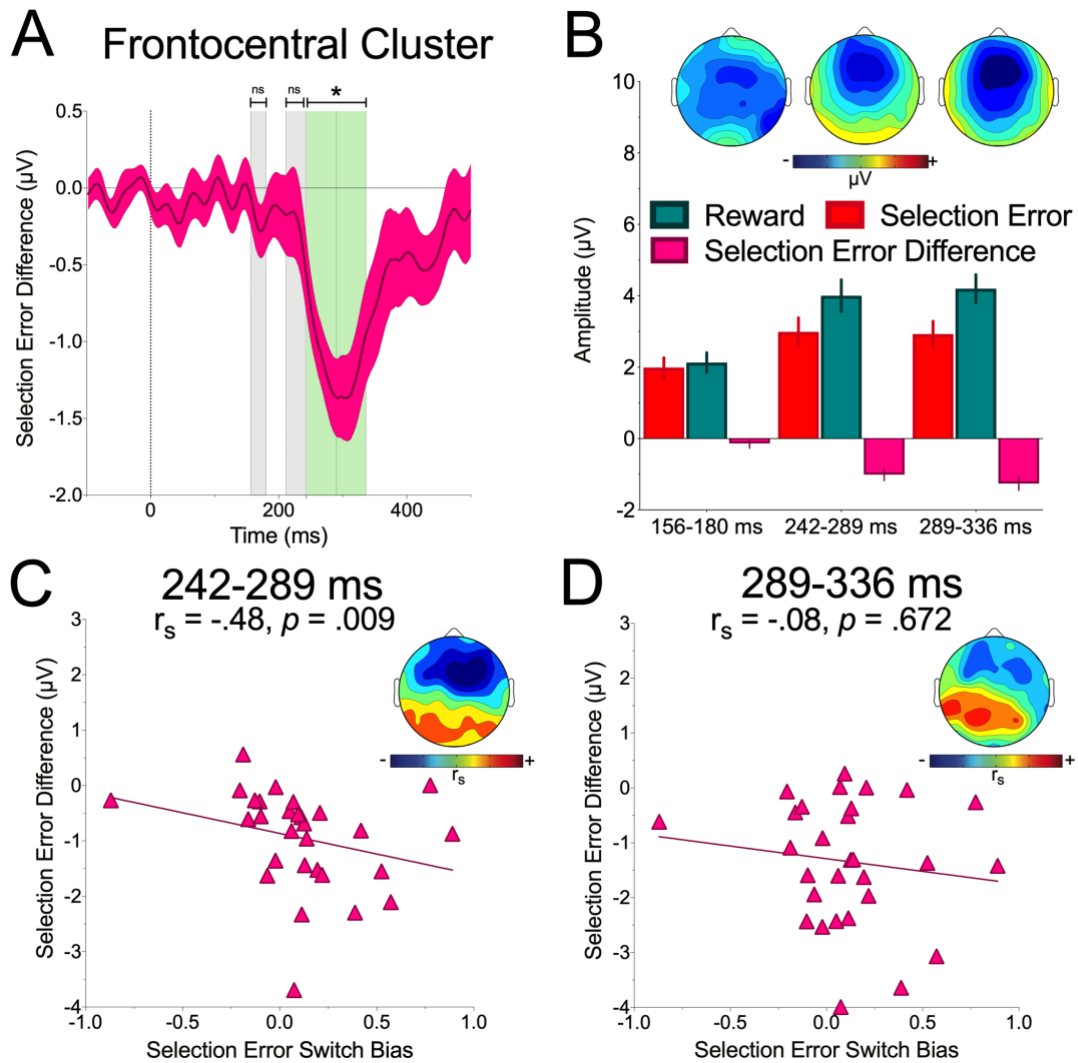
Figure 3- Selection Error in the Frontocentral Cluster: (A) The Selection Error waveform, defined as the difference in the ERPs on trials resulting in selection errors and rewards. The green shaded regions indicate significant clusters for this contrast and the grey shaded regions indicate where the clusters identified in the original time-series analysis did not reach statistical significance for this difference waveform. Zero on the abscissa indicates feedback onset. (B) Mean amplitudes for the early and late phases of the statistically significant clusters, with insets showing scalp maps of the distribution of differences across sites for each time interval. Selection Error difference waveform amplitude (shown on the ordinate, where negative values indicate more negative amplitude for selection errors relative to reward) correlated with an increase in the Switch Bias score (shown on the abscissa, where positive values indicate more switching following selection errors relative to reward) at a time interval corresponding to the FRN/RewP (C), but not the P3 (D). The insets show scalp maps of the distribution of amplitude differences across sites, revealing a frontocentral maxima for the FRN/RewP correlation.
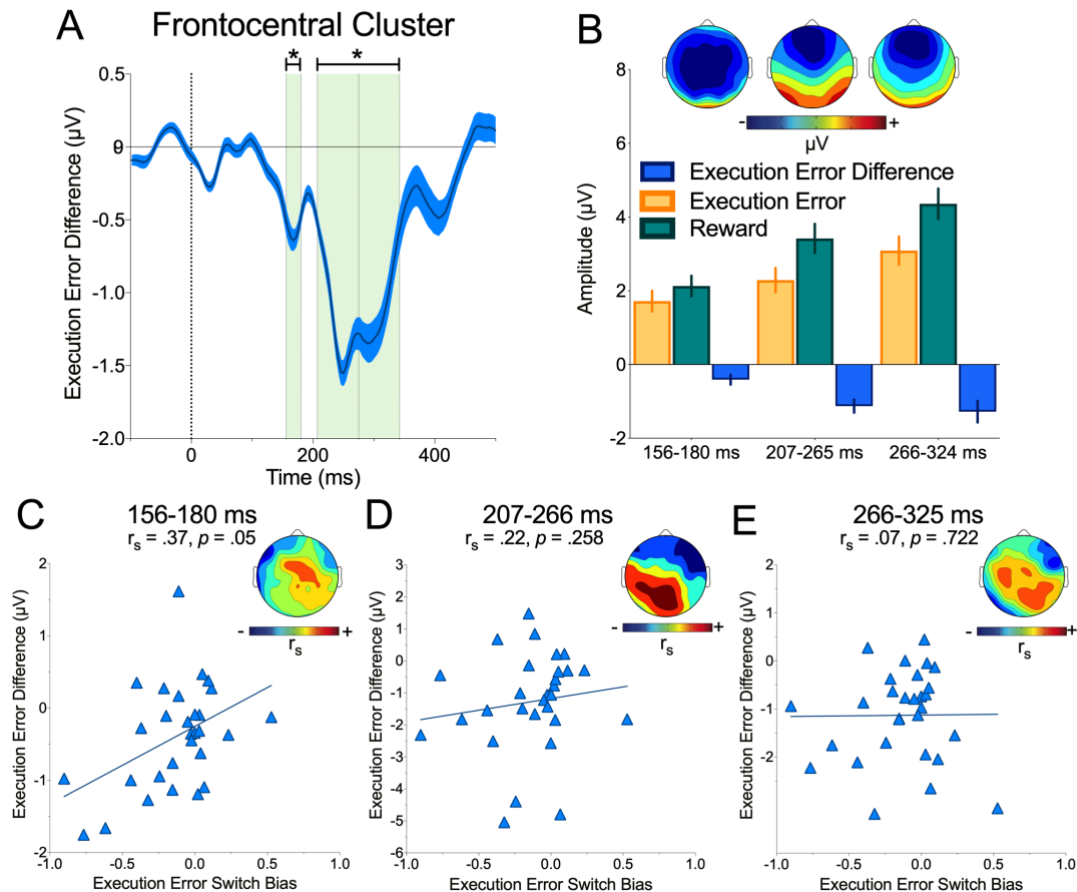

Execution Errors

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

484   frontocentral cluster shown in **Figure 2B**). This comparison revealed two statistically significant

485   clusters- one ranging from 156-180 ms and a second between 207-325 ms (**Figure 4**A).

486   The first cluster showed an amplitude reduction in response to Execution Errors relative to

487   reward trials. Similar to the Selection Error waveform result, we expected the second cluster would

488   be contaminated by a P3a signal. Thus, we followed the same protocol, splitting this cluster into

489   two equal intervals – (i) an early phase marked by the time interval 207-266 ms; and (ii) a later

490   phase for activity between 266-325 ms. There was a clear frontocentral distribution for the early

491   phase, and in the later time window, a shift towards centroparietal electrodes (**Figure 4**B).

492   We next examined the relationship between these three epochs (156-180 ms; 207-266 ms;

493   266-325 ms) and behavioral adjustment (**Figure 4**C-E). The peak amplitude difference in the

494   earliest interval (156-180 ms) correlated positively (r_s = 0.37, p = .05) with switching rates following

495   an execution error relative to reward. Following execution errors, smaller peaks in the 156-180 ms

496   time window were associated with a lower tendency to switch. Note that this pattern is opposite to

497   that observed between the amplitude of the FRN/RewP and behavioral adjustments following

498   selection errors. The mean amplitude measure had a similar pattern of results, but was not

499   significant (r_s = 0.35, p = .065). An examination of topography revealed this correlation to be

500   maximal in the frontocentral cluster, suggesting that smaller amplitudes in response to execution

501   errors early in the feedback processing stream are associated with a higher tolerance to this

502   outcome.

503   In contrast to the results for Selection Errors, the FRN/RewP captured in the 207-266 ms

504   time window did not correlate with behavioral adjustment (r_s = .07, p = .722). We tested, and

505   confirmed, that this correlation was reliably different to the correlation observed for Selection Errors

506   in the FRN/RewP time interval (z = 2.40, p = .016). There was no correlation between the

507   Execution Error waveform in the P3a time window (266-325 ms) and behavioral adjustment (r_s =-

508   .22, p = .258).

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

We conducted the same analysis for the Execution Error waveform in the parietal cluster of electrodes. Execution errors elicited smaller amplitude responses relative to rewards in an early time window (176-196 ms) but elicited larger amplitude responses at 218-239 ms post feedback. In 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 processes driving behavioral adjustment (Dhar & Pourtois, 2011; Overbeek et al., 2005). Interestingly, and unexpectedly, the amplitude of the P3b subcomponent of the P300 signal— proposed to reflect the revision of internal forward models in posterior parietal cortex (Krigolson & Holroyd, 2007a) showed no difference in the processing execution errors and rewards (see **Figure 2**C) and there was no relationship with behavioral adjustment (r_s = -0.01, p = .946).
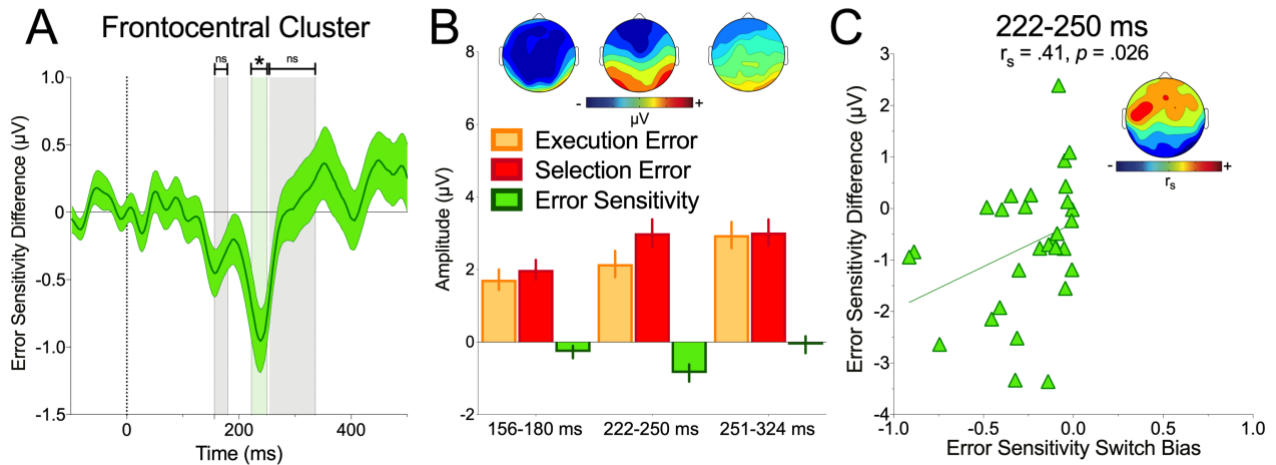
530   Error Sensitivity Difference Waveform

531   As described in the previous two sections, when using a common baseline (rewarded

532   trials), we observed differences in both the ERP results and correlational analysis between

533   unrewarded trials that were attributed to failures in movement execution or action selection. We

534   performed a direct comparison between these two types of unrewarded outcomes by analyzing an

535   Error Sensitivity difference waveform, subtracting the ERP for selection errors from the ERP for

536   execution errors (see **Figure 2B** for the parent waveforms).

537   In the frontocentral cluster there was a significant difference in the range of the FRN/RewP

538   (222-250 ms; **Figure 5** A, B). We had anticipated that the amplitude of the FRN/RewP would be

539   attenuated following execution errors, assuming a lower response would be reflective of reduced

540   value updating (McDougle et al., 2019). However, the observed effect was in the opposite

541   direction: Execution errors elicited a larger FRN/RewP 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 5**C). Participants who had relatively similar switching rates to the

552   two unrewarded outcomes had smaller FRN/RewP differences, while individuals with a large

553   negative bias (i.e., less switching after execution errors) also exhibited larger FRN/RewP

554   amplitudes for motor execution errors relative to selection errors. This correlation was maximal in

555   frontocentral sites (**Figure 5**C inset).

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

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

Kinematic Analysis

577

578   To gain a deeper understanding of the relationship between brain activity and task

579   performance, we examined correlations between task kinematics and the statistically significant

580   periods identified in the time series analysis in the frontocentral and parietal difference waveforms.

581   We reasoned that, in contrast to Selection Errors, where there was a relationship between

582   FRN/RewP amplitude and choice selection, the Execution Error FRN/RewP may instead be

583   encoding information about cursor position and subsequent movement correction.

584   In the first analysis, we examined whether there was a relationship between cursor error

585   magnitude and ERP activity. As expected from the task manipulation, the kinematic data revealed

586   a significant difference in mean absolute end-point cursor error as a function of Outcome ($F(2, 56)$

587   $= 8209$, $p < .001$, $\eta^2_g > .99$). There were no differences ($t(28) = 1.26$, $p = .655$) between Rewards

588   ($M = 1.37°$, $SE = 0.01°$) and Selection Errors ($M = 1.4°$, $SE = 0.01°$), both of which presented the

589   cursor within the boundaries of the target, but Execution Errors ($M = 5.87°$, $SE = 0.22°$) elicited

590   more error relative Selection Error ($t(28) = 91.68$, $p < .001$) and Reward ($t(28) = 99.57$, $p < .001$).

591   Despite this, there were no statistically significant correlations between the mean activity of the

592   statistically significant clusters in the difference waveforms and corresponding differences in cursor

593   error magnitude (Selection Error Difference Waveforms: $r \leq 0.176$, p's $\geq .359$; Execution Error

594   Difference Waveforms: $r_s \leq 0.228$, p's ≥ 0.233; Error Difference waveform: $r_s \leq 0.152$, p's $\geq .429$).

595   In the second analysis, we asked whether ERP amplitude on the current trial would

596   correlate with the degree of change in cursor position on subsequent trials. Here, we restricted

597   analysis to the subset of trials in which participants chose the same target consecutively. The

598   amount of motor correction in response to feedback (computed as the mean absolute change in

599   end-point position relative to the cursor position on the previous trial), varied as a function of

600   Feedback ($F (2, 56) = 75.37$, $p < .001$, $\eta^2_g = .66$). As both outcomes indicated a successful

601   movement, we expected, and found, no difference ($t(28) = 0.47$, $p > .999$) in the subsequent

602   degree of correction for Selection Error ($M = 3.73°$, $SE = 0.15°$) and Reward ($M = 3.64°$, $SE =$

603   $0.17°$) trials. In contrast, Execution Error, signaling a need to change one's motor response to hit

604   the target ($M = 6.53°$, $SE = 0.22°$) had higher rates of correction relative to both Selection Error

605   ($t(28) = 8.95$, $p < .001$) and Reward ($t(28) = 8.95$, $p < .001$) outcomes. Despite these behavioral

606   differences, there were no correlations between mean activity of the statistically significant clusters

607   in the difference waveforms and the magnitude of subsequent corrections (Execution Error: $r_s \leq -$

608   0.239, p's ≥ 0.211; Selection Error: $r_s \leq -0.328$, p's ≥ 0.083; Error Sensitivity: $r_s \leq .152$; p's ≥ 0.429).

609   To ensure that we did not miss any potential sensitivity to task kinematics in other time

610   ranges, we undertook an exploratory search of the full time series data by correlating cursor error

611   and motor correction with mean amplitude from 150ms to 500ms.

612   We found no correlations between ERP difference waveforms and Cursor Error in the

613   frontal (p's ≥ .45) or parietal sites (p's ≥ .75) following correction. We also note, with a degree of

614   caution given the corrected p values were not significant, that there was one statistically significant

615   pattern prior to correction- a positive correlation between the Error Sensitivity difference waveform

616   and Cursor Error (r_s = .43, 406 ms). In correlating motor correction rates with ERP amplitude, we

617   found no significant relationships in the frontocentral cluster (p's ≥ .454). Here, we noted that the

618   strongest relationship (r_s = .456) was a positive one between motor correction and the Error

619   Sensitivity difference waveform at 164 ms – a pattern that was sustained across 156- 174 ms. As

620   participants made larger degrees of correction following Execution Errors relative to Selection

621   Errors, they also exhibited greater amplitude. In the parietal cluster, we found no reliable patterns

622   of activity following (p's ≥ .97) or prior to correction (p's ≥ .1).

623   **Perturbation Awareness**

624   In a final set of explorations, we examined whether participants were sensitive to the

625   feedback manipulation that had been applied to control the frequency of our three outcomes. In

626   almost half the trials (M = 47.8%, SE = 0.01%) we delivered perturbed instead of veridical

627   feedback (52.2%, SE= 0.01%). We had taken measures to minimize the likelihood of participants

628   booming aware of these changes (e.g., no online movement feedback was provided, and end-point

629   feedback was presented 1 s after the stylus had passed the bandit) and in a post-experiment

630   survey, participants indicated that they believed execution error outcomes to be the result of poor

631   reaches, suggesting no explicit awareness of the manipulation. Nevertheless, we did find

632   differences in cursor error (**Figure 6**A), as revealed through a 3 (Outcome: Reward vs. Selection

633   Error vs. Execution Error) X 2 (Veracity: Veridical vs. Perturbed) interaction (F (2, 56) = 27.4, p <

634   .001, η^2_g = .25). In all cases, Veridical cursor error was largest in the Perturbed trials, but the effect

635   was greatest for Reward (Veridical M = 1.68°, SE = 0.02°, Perturbed M = 0.98°, SE = 0.01°; t(28) =

636   26.83, p < .001) and Selection Error (Veridical M = 1.72°, SE = 0.02°, Perturbed M = 0.97°, SE =

637   0.02°; t(28) = 30.95, p < .001) outcomes, with differences of 0.7° and 0.75° respectively. For

638   Execution Error, there was a visual difference of 0.27° (Veridical 5.99°, SE = 0.07°, Perturbed M =

639   5.72°, SE = 0.04°; t(28) = 3.5, p = .045).

640   Participants did not alter their behavioral strategy in response to feedback perturbations
641   (Veracity: $F(1, 28) = 0.899$, $p = .351$, $\eta^2_g = < .01$).; Veracity X Outcome: $F(2, 56) = 1.42$, $p = .251$,
642    $\eta^2_g < .01$; **Figure 6**B). However, a suggestion that they might have been implicitly sensitive to
643   these differences is indicated by the degree of motor correction following veridical and perturbed
644   feedback (**Figure 6**C). One participant had no stay trials following perturbed feedback in this
645   subset of data and was excluded from this analysis. In the remaining participants, we observed an
646   Outcome X Veracity interaction ($F (2, 54) = 4.49$, $p = .016$, $\eta^2_g = .04$). There were no differences in
647   the degree of motor correction following Execution Error (Veridical M= 6.3°, SE = 0.19°, Perturbed
648   M = 6.84°, SE = 0.32°; $t(27) = 2.07$, $p = .718$), but greater corrections (Reward: Veridical M= 2.92°,
649   SE = 0.13°, Perturbed M = 4.28°, SE = 0.26°; $t(27) = 4.56$, $p <.001$; Selection Error: Veridical M=
650   3.02°, SE = 0.20°, Perturbed M = 4.62°, SE = 0.17°; $t(27) = 6.30$, $p <.001$) followed false hits trials.
651   These positively surprising outcomes (real reaches had missed the target on these trials, hence
652   the perturbation) may have prompted overcompensation as participants sought to calibrate their
653   movements to task feedback.
654   Given these differences, we explored the extent to which the ERP signal was sensitive to
655   the veracity of the feedback. We re-ran the ERP time-series analysis, performing a 3 (Outcome:
656   Reward vs. Selection Error vs. Execution Error) X 2 (Veracity: Veridical vs. Perturbed) at each time
657   point for the frontocentral and parietal clusters. There were no statistically significant main effects
658   of Veracity (F's ≤ 6.99, p's ≥ .397) and no Outcome X Veracity interactions (F's ≤ 2.55, p's ≥ .79) in
659   the frontocentral cluster and similarly, no main effects (F's ≤ 5.42, p's ≥ .853) or Veracity X
660   Outcome interactions (F's ≤ 1.83, p's ≥ .986) in the parietal cluster.
661   We then explored whether there were any differences in the relationship between ERP
662   activity and kinematic adjustment as a function of Feedback Veracity. As perturbed feedback
663   elicited larger corrective movements than veridical, we speculated that an ERP signal sensitive to
664   positive surprise may scale in response to this behavior for Selection and Execution error trials. To
665   explore this idea, a difference wave subtracting perturbed ERP amplitude from veridical was
666   computed. The amplitude of this "Perturbation Difference" waveform was correlated with (i) the
667   mean difference in cursor error for veridical and perturbed feedback per outcome; and (ii) the mean
668   difference in degree of correction following veridical relative to perturbed feedback per outcome.

669   In analysing the relationship between the Perturbation Difference waveform and Cursor

670   Error in the frontocentral cluster, we found no correlations that survived correction for multiple

671   comparisons (p's ≥ .616). However, in the parietal cluster, the Selection Error waveform strongly

672   correlated with Perturbation Difference amplitude at 273 ms (r_s = -0.62, p = .011; **Figure 6**D),

673   indicating a sensitivity to discrepancies between actual and presented hand position. Specifically,

674   this correlation shows that for participants with larger veridical errors, perturbed feedback elicited

675   larger positive amplitudes in a manner consistent with the P300 signaling surprise (Donchin, 1981;

676   Nassar et al., 2019). The Error Sensitivity difference waveform showed a similar pattern but did not

677   reach the significance threshold after correction (r_s = -.47 at 343 ms). The pattern for Execution

678   Error was reversed, with the strongest correlation observed later (r_s = .45 at 492 ms)- with

679   amplitude highest when both cursor error and amplitude were higher in the veridical condition

680   relative to the perturbed condition. However, this too was not significant following correction.

681   Finally, in terms of the relationship between perturbation amplitude differences and the

682   degree of motor correction, there were no significant effects in the frontocentral (p's ≥ .120) or

683   parietal clusters (p's ≥ .82). With the same note of caution for non-significant correlations offered

684   above, two patterns suggest a further dissociation in the processing of selection and execution

685   error: In the time frame of the FRN/RewP, there was a relationship between frontocentral

686   amplitude of the Perturbation Difference waveform and motor correction (r_s = -.542 at 289 ms).

687   Here, greater corrective movements in response to perturbed feedback correlated with larger

688   differences in the FRN/RewP; and (ii) later in the window, the Perturbation Difference waveform for

689   Execution Errors positively correlated (r_s = .52 at 335 ms) with the degree of motor correction,

690   indicating that larger cursor error corrections in response to perturbed feedback have

691   correspondingly larger amplitudes for perturbed feedback in the time range of the P3a. Despite the

692   finding that Selection Error, like Reward, resulted in adaptation following perturbed relative to

693   veridical outcomes, no relationship was observed, with the strongest effect at 420 ms (r_s = -.299).
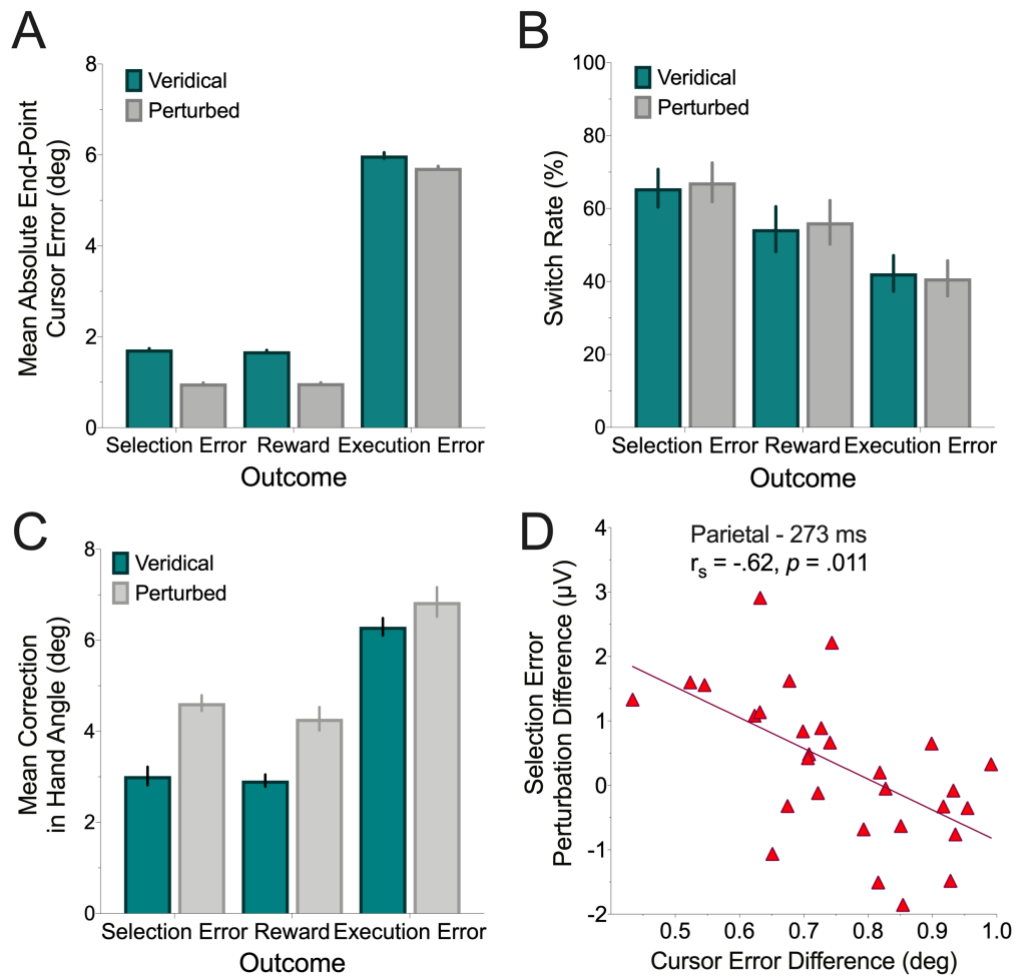
Figure 6- Feedback Perturbation and Awareness: (A) Cursor error was larger for veridical feedback relative to perturbed; (B) Despite smaller cursor error, participants made larger corrections in response to perturbed feedback, with the pattern most pronounced for false hits; (C) Perturbed feedback did not impact on the likelihood of switching bandits; (D) Amplitude differences between perturbed and veridical feedback in the Parietal cluster for Selection Errors at 273 ms (shown on the ordinate, where positive values indicate larger amplitude for veridical relative to perturbed outcomes) correlated with magnitude of the difference in cursor error for these outcomes (shown on the abscissa, where positive values indicate larger veridical cursor errors relative to perturbed).

Discussion

704

705   Adaptive behavior necessitates distinguishing between outcomes that fail to produce an

706   expected reward due to either the selection of the wrong action plan or poor motor execution.

707   Although the majority of decision-making research, in neuroscience as well as economics, have

708   focused almost exclusively on the former, a few studies have shown that failed outcomes attributed

709   to sensorimotor errors can markedly biases choice behavior (Green et al., 2010; McDougle et al.,

710   2016, 2019). Here, we examined this issue by asking how an ERP signature of reinforcement

711   learning, the Feedback-Related Negativity/Reward Positivity (FRN/RewP), varied in response to

712   selection and motor errors. Predicated on the theory that the FRN/RewP is a scalp-related

713   prediction error (Holroyd & Coles, 2002), we tested the hypothesis that errors attributed to failures

714   in execution should lead to an attenuation in the FRN/RewP.

715   Consistent with our expectations, selection errors elicited a larger FRN/RewP relative to

716   reward outcomes. Moreover, in line with a reinforcement learning account, the amplitude of the

717   FRN/RewP following selection errors was negatively correlated with the probability that participants

718   switched between the response options following feedback. Behaviorally, participants showed

719   lower switch rates following execution errors, a pattern consistent with the hypothesis that the

720   reinforcement learning system discounts these errors (McDougle et al., 2019). However, contrary

721   to the prediction that FRN/RewP amplitude would be attenuated following execution errors, these

722   errors actually produced the largest FRN/RewP. A striking difference between the ERPs in

723   response to selection and execution error was that the amplitude of the FRN/RewP following

724   selection errors was predictive of behavioral biases and learning, whereas this ERP response

725   following execution errors did not correlate with these variables.

726   While almost all participants were more likely to switch after a selection error compared to

727   an execution error, the differential response to these two error outcomes varied considerably

728   across participants. Moreover, this behavioral difference was correlated with the neural response

729   to the two types of feedback: The more similarly participants treated the two outcomes at a

730   behavioral level, the smaller the difference in FRN/RewP amplitude in response to these

731   outcomes.

732   These findings could be reconciled by considering the top-down mechanisms that may

733   modulate how execution errors are processed. Behavioral experiments have shown that a sense of

734   agency related to the perceived ability to correct for motor errors biases choice behavior (Parvin et

735   al., 2018). In the present experiment, the finding that participants persevered with a bandit

736   following execution error but switched more often following selection errors also points towards

737   differences in agency. Previous work on the FRN/RewP has shown that outcomes that can be

738   controlled lead to a more negative FRN/RewP than those that cannot (Sidarus et al., 2017) and the

739   FRN/RewP is attenuated in the absence of actively performed actions (Donkers et al., 2005;

740   Donkers & van Boxtel, 2005). The finding that execution errors produced a larger FRN/RewP

741   relative to selection error is consistent with the presumed greater sense of agency associated with

742   this type of unrewarded outcome.

743   A recent fMRI experiment using a 3-arm bandit task similar to that employed here, revealed

744   an attenuation of the signal associated with negative reward prediction error in the striatum

745   following execution failures (McDougle et al., 2019). Our observation of a larger negative deflection

746   for execution error trials in the FRN/RewP may appear contrary to these previously reported striatal

747   results. However, the fMRI investigation did show increased ACC activity in response to execution

748   errors compared to selection errors, suggesting that the former have their own neural signature.

749   With regards to the EEG response, there have been a number of studies reporting FRN/RewP

750   deflections in response to execution error (Anguera et al., 2009; Krigolson et al., 2008; Torrecillos

751   et al., 2014). These studies, in line with the Prediction-Response Outcome model of medial frontal

752   cortex function (Alexander & Brown, 2011), point to the existence of a general monitoring system

753   that responds to violation of expectations. However, an important aspect of these tasks is that

754   errors in movement execution typically resulted in high level goal errors (e.g., failure to reach or

755   remain on target in a manual tracking task) and/or involved the introductions of perturbations

756   during the movement phase (Krigolson et al., 2008). This makes it difficult to rule out the

757   contribution of cognitive control and response inhibition processes- which are known to generate

758   an N200 component that shares similar spatial and temporal characteristics to the FRN/RewP

759   signal (Holroyd, 2004; Holroyd et al., 2008). A recent study separating reward and sensory

760   prediction errors in a motor adaptation task showed that the FRN/RewP responds to the former,

761   but not the latter (Palidis et al., 2019). The present findings, indicating qualitatively different

762   relationships between the two medial frontal negativities with behavioral modification, add weight to

763   the possibility that execution error processing may be distinct from dopamine-related reinforcement

764   learning processes.

765   We also observed two distinct patterns of activity in time windows preceding and following

766   the FRN/RewP that provide further support for the claim of differential processing of execution and

767   selection error. First, smaller amplitude responses were observed following execution errors

768   relative to rewards in frontocentral sites 156-180 ms post-feedback, and the amplitude of this

769   component correlated with switch rates. Second, in parietal sites (218-239 ms), larger amplitude

770   responses occurred following execution errors relative to reward and this difference was also

771   correlated with switch rates. Importantly, in a reversal of the FRN/RewP pattern, magnitude

772   differences in these early frontal and late parietal signals correlated with behavioral adjustment

773   linked to execution errors. This pattern points towards the existence of distinct error monitoring

774   systems operating at different levels of behavioural control (Yordanova et al., 2004).

775   Exploratory analysis on the relationship between ERP amplitude and task showed that the

776   degree of motor correction following execution errors relative to selection errors correlated with

777   amplitude differences in an early frontal cluster (156-174 ms). The time course of this cluster

778   closely mirrored that of the earliest difference between execution error and reward – where

779   amplitude differences correlated with switch rates. Given that we had no a priori expectations for

780   such a result and that this specific result did not survive correction for multiple comparisons,

781   interpretations must be treated with caution and require further robustly powered replication work

782   to confirm. Should future work replicate this pattern it would add weight to the idea that the need to

783   make a behavioural modification following an error in the motor system precedes the generation of

784   the FRN/RewP.

785   A pertinent question of the present task and data is the extent to which participants were

786   aware of the perturbations applied to the feedback to control outcome frequencies. Participants did

787   not have access to online feedback and end-point cursor information was presented with a 1

788   second delay to minimize the likelihood of participants becoming aware of the perturbations. In a

789   post-experiment survey, participants indicated that they had attributed execution errors to poor

790   motor control. Consistent with this we found that during the task, perturbed feedback did not alter

791   choice strategy, nor did it result in any significant differences in the ERP. However, participants did

792   make larger corrective movements following perturbed feedback- this was despite these outcomes

793   showing smaller cursor errors than veridical feedback. In an exploratory search we also found a

794   correlation between the degree of cursor error in veridical and perturbed outcomes and amplitude

795   differences at 273 ms, likely reflecting the onset of the P300. Here, amplification of the signal

796   following perturbed feedback reduced as the amount of veridical error increased. That the P300

797   shows a sensitivity to discrepancies between actual and presented hand position is consistent with

798   the theory that the signal is generated through the active updating of an internal model of the

799   environment (Donchin & Coles, 1988). The P300 is also notable for being a putative marker of

800   conscious perception (Rutiku et al., 2015). If participants did indeed have access to this information

801   during the task, it may be that these perturbations were not sufficiently large enough to signal a

802   need to change strategy.

803   These findings also raise a broader question of whether the present results might be

804   specific to outcomes that are framed as execution errors, or extend to any endogenous or

805   exogenous event that results in an unrewarded trial in which the outcome does not provide

806   information about the reward probability associated with the selected object (Green et al., 2010).

807   For example, if an unexpected gust of wind blew a tennis lob out-of-bounds, would that be treated

808   as an "execution error"? Or, if after pulling the lever on a slot machine, a power failure caused the

809   game to terminate without a payoff, would this affect how the choice is judged? A future study

810   could test endogenous execution errors (e.g., reaching error) and exogenous errors (e.g., the task

811   screen goes blank randomly before an outcome is delivered) more explicitly than the perturbations

812   applied here. If similar results are found in both settings, elements of the early activity observed in

813   frontocentral sites may indicate the establishment of a sensory "state", representing that the

814   intended action plan was not properly implemented, irrespective of whether this mismatch was due

815   to endogenous or exogenous factors, even before the prediction error is evaluated. This echoes

816   the sequential ordering in models of temporal difference learning, where first the agent perceives

817   its state, and then computes reward prediction errors relevant to that state (Sutton & Barto, 1998).

Limitations and Future Directions

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

Conclusion

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

References

Alexander, W. H., & Brown, J. W. (2011). Medial prefrontal cortex as an action-outcome predictor. *Nature Neuroscience*, *14*(10), 1338–1344. https://doi.org/10.1038/nn.2921

Anguera, J. A., Seidler, R. D., & Gehring, W. J. (2009). Changes in Performance Monitoring During Sensorimotor Adaptation. *Journal of Neurophysiology*, *102*(3), 1868–1879. https://doi.org/10.1152/jn.00063.2009

Bakeman, R. (2005). Recommended effect size statistics for repeated measures designs. *Behavior Research Methods*, *37*(3), 379–384. https://doi.org/10.3758/BF03192707

Benjamini, Y., & Hochberg, Y. (1995). Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *Source Journal of the Royal Statistical Society. Series B (Methodological) Journal of the Royal Statistical Society. Series B J. R. Statist. Soc. B*, *57*(1), 289–300. https://doi.org/10.2307/2346101

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436. https://doi.org/10.1163/156856897X00357

Cavanagh, J. F., Zambrano-Vazquez, L., & Allen, J. J. B. (2012). Theta lingua franca: A common mid-frontal substrate for action monitoring processes. *Psychophysiology*, *49*(2), 220–238. https://doi.org/10.1111/j.1469-8986.2011.01293.x

Chaumon, M., Bishop, D. V. M., & Busch, N. A. (2015). A practical guide to the selection of independent components of the electroencephalogram for artifact correction. *Journal of Neuroscience Methods*, *250*, 47–63. https://doi.org/10.1016/j.jneumeth.2015.02.025

Cohen, J. D., McClure, S. M., & Yu, A. J. (2007). Should I stay or should I go? How the human brain manages the trade-off between exploitation and exploration. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1481), 933–942. https://doi.org/10.1098/rstb.2007.2098

Daw, N. D., O'Doherty, J. P., Dayan, P., Dolan, R. J., & Seymour, B. (2006). Cortical substrates for exploratory decisions in humans. *Nature*, *441*(7095), 876–879. https://doi.org/10.1038/nature04766

de Bruijn, E. R. A., Hulstijn, W., Meulenbroek, R. G. J., & Van Galen, G. P. (2003). Action monitoring in motor control: ERPs following selection and execution errors in a force production task. *Psychophysiology*, *40*(5), 786–795. https://doi.org/10.1111/1469-8986.00079

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*(1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009

Desmurget, M., Epstein, C. M., Turner, R. S., Prablanc, C., Alexander, G. E., & Grafton, S. T. (1999). Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nature Neuroscience*, *2*(6), 563–567. https://doi.org/10.1038/9219

881 Desmurget, M., Gréa, H., Grethe, J. S., Prablanc, C., Alexander, G. E., & Grafton, S. T. (2001).
882   Functional anatomy of nonvisual feedback loops during reaching: A positron emission
883   tomography study. *Journal of Neuroscience*, *21*(8), 2919–2928.

884 Dhar, M., & Pourtois, G. (2011). Early error detection is generic, but subsequent adaption to errors
885   is not: Evidence from ERPs. *Neuropsychologia*, *49*(5), 1236–1245.
886   https://doi.org/10.1016/j.neuropsychologia.2011.01.006

887 Diedenhofen, B., & Musch, J. (2015). Cocor: A comprehensive solution for the statistical
888   comparison of correlations. *PLoS ONE*, *10*(4), 1–12.
889   https://doi.org/10.1371/journal.pone.0121945

890 Diedrichsen, J. (2005). Neural Correlates of Reach Errors. *Journal of Neuroscience*, *25*(43), 9919–
891   9931. https://doi.org/10.1523/JNEUROSCI.1874-05.2005

892 Donchin, E. (1981). Surprise!… Surprise? *Psychophysiology*, *18*(5), 493–513.
893   https://doi.org/10.1111/j.1469-8986.1981.tb01815.x

894 Donchin, E., & Coles, M. G. (1988). Is the P300 component a manifestation of context updating?
895   *Behavioral and Brain Sciences*, *11*(3), 357–427.
896   https://doi.org/10.1017/S0140525X00058027

897 Donkers, F. C., Nieuwenhuis, S., & van Boxtel, G. J. (2005). Mediofrontal negativities in the
898   absence of responding. *Cognitive Brain Research*, *25*(3), 777–787.
899   https://doi.org/10.1016/j.cogbrainres.2005.09.007

900 Donkers, F. C., & van Boxtel, G. J. (2005). Mediofrontal negativities to averted gains and losses in
901   the slot-machine task—A further investigation. *Journal of Psychophysiology*, *19*(4), 256–
902   262. https://doi.org/10.1027/0269-8803.19.4.256

903 Dunn, O. J., & Clark, V. (1969). Correlation coefficients on the same sets of data. *Journal of the
904   American Statistical Association*, *64*(325), 366–377.

905 Foti, D., Weinberg, A., Dien, J., & Hajcak, G. (2011). Event-related potential activity in the basal
906   ganglia differentiates rewards from nonrewards: Temporospatial principal components
907   analysis and source localization of the feedback negativity. *Human Brain Mapping*, *32*(12),
908   2207–2216. https://doi.org/10.1002/hbm.21182

909 Gehring, W. J., & Willoughby, A. R. (2002). The medial frontal cortex and the rapid processing of
910   monetary gains and losses. *Science*, *295*(5563), 2279–2282.
911   https://doi.org/10.1126/science.1066893

912 Green, C. S., Benson, C., Kersten, D., & Schrater, P. (2010). Alterations in choice behavior by
913   manipulations of world model. *Proceedings of the National Academy of Sciences*, *107*(37),
914   16401–16406. https://doi.org/10.1073/pnas.1001709107

915 Groppe, D. M., Urbach, T. P., & Kutas, M. (2011). Mass univariate analysis of event-related brain
916   potentials/fields I: A critical tutorial review. *Psychophysiology*, *48*(12), 1711–1725.
917   https://doi.org/10.1111/j.1469-8986.2011.01273.x

918   Hemmelmann, C., Horn, M., Süsse, T., Vollandt, R., & Weiss, S. (2005). New concepts of multiple
919   tests and their use for evaluating high-dimensional EEG data. *Journal of Neuroscience*
920   *Methods*, *142*(2), 209–217. https://doi.org/10.1016/j.jneumeth.2004.08.008

921   Hittner, J. B., May, K., & Silver, N. C. (2003). A monte carlo evaluation of tests for comparing
922   dependent correlations. *Journal of General Psychology*, *130*(2), 149–168.
923   https://doi.org/10.1080/00221300309601282

924   Holroyd, C. B. (2004). A note on the oddball N200 and the feedback ERN. In *Errors, conflicts, and*
925   *the brain: Current opinions on performance monitoring*. MPI of Cognitive Neuroscience.

926   Holroyd, C. B., & Coles. (2002). The neural basis of human error processing: Reinforcement
927   learning, dopamine, and the error-related negativity. *Psychological Review*, *109*(4), 679–
928   709. https://doi.org/10.1037/0033-295X.109.4.679

929   Holroyd, C. B., Hajcak, G., & Larsen, J. T. (2006). The good, the bad and the neutral:
930   Electrophysiological responses to feedback stimuli. *Brain Research*, *1105*(1), 93–101.
931   https://doi.org/10.1016/j.brainres.2005.12.015

932   Holroyd, C. B., & Krigolson, O. E. (2007). Reward prediction error signals associated with a
933   modified time estimation task. *Psychophysiology*, *44*(6), 913–917.
934   https://doi.org/10.1111/j.1469-8986.2007.00561.x

935   Holroyd, C. B., Pakzad-Vaezi, K. L., & Krigolson, O. E. (2008). The feedback correct-related
936   positivity: Sensitivity of the event-related brain potential to unexpected positive feedback.
937   *Psychophysiology*, *45*(5), 688–697. https://doi.org/10.1111/j.1469-8986.2008.00668.x

938   Holroyd, C. B., & Umemoto, A. (2016). The research domain criteria framework: The case for
939   anterior cingulate cortex. *Neuroscience & Biobehavioral Reviews*, *71*, 418–443.
940   https://doi.org/10.1016/j.neubiorev.2016.09.021

941   Kappenman, E. S., & Luck, S. J. (2017). Best Practices for Event-Related Potential Research in
942   Clinical Populations. *Biol Psychiatry Cogn Neurosci Neuroimaging*, *4425*, 1–13.
943   https://doi.org/10.1016/j.bpsc.2015.11.007.Best

944   Kleiner, M., Brainard, D. H., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007). What's new in
945   Psychtoolbox-3. *Perception*, *36*, 1–16. https://doi.org/10.1068/v070821

946   Krigolson, O. E. (2018). Event-related brain potentials and the study of reward processing:
947   Methodological considerations. *International Journal of Psychophysiology*, *132*, 175–183.
948   https://doi.org/10.1016/j.ijpsycho.2017.11.007

949   Krigolson, O. E., & Holroyd, C. B. (2006). Evidence for hierarchical error processing in the human
950   brain. *Neuroscience*, *137*(1), 13–17. https://doi.org/10.1016/j.neuroscience.2005.10.064

951   Krigolson, O. E., & Holroyd, C. B. (2007a). Hierarchical error processing: Different errors, different
952   systems. *Brain Research*, *1155*, 70–80. https://doi.org/10.1016/j.brainres.2007.04.024

953   Krigolson, O. E., & Holroyd, C. B. (2007b). Predictive information and error processing: The role of
954   medial-frontal cortex during motor control. *Psychophysiology*, *44*(4), 586–595.
955   https://doi.org/10.1111/j.1469-8986.2007.00523.x

956 Krigolson, O. E., Holroyd, C. B., Van Gyn, G., & Heath, M. (2008). Electroencephalographic
957   correlates of target and outcome errors. *Experimental Brain Research*, *190*(4), 401–411.
958   https://doi.org/10.1007/s00221-008-1482-x

959 Lage-Castellanos, A., Martínez-Montes, E., Hernández-Cabrera, J. a, & Galán, L. (2010). False
960   discovery rate and permutation test: An evaluation in ERP data analysis. *Statistics in*
961   *Medicine*, *29*(1), 63–74. https://doi.org/10.1002/sim.3784

962 Luck, S. J., & Gaspelin, N. (2017). How to get statistically significant effects in any ERP experiment
963   (and why you shouldn't). *Psychophysiology*, *54*(1), 146–157.
964   https://doi.org/10.1111/psyp.12639

965 McDougle, S. D., Boggess, M. J., Crossley, M. J., Parvin, D., Ivry, R. B., & Taylor, J. A. (2016).
966   Credit assignment in movement-dependent reinforcement learning. *Proceedings of the*
967   *National Academy of Sciences*, *113*(24), 6797–6802.
968   https://doi.org/10.1073/pnas.1523669113

969 McDougle, S. D., Butcher, P. A., Parvin, D. E., Mushtaq, F., Niv, Y., Ivry, R. B., & Taylor, J. A.
970   (2019). Neural Signatures of Prediction Errors in a Decision-Making Task Are Modulated by
971   Action Execution Failures. *Current Biology*, *29*(10), 1606-1613.e5.
972   https://doi.org/10.1016/j.cub.2019.04.011

973 Miltner, W. H., Braun, C. H., & Coles, M. G. (1997). Event-related brain potentials following
974   incorrect feedback in a time-estimation task: Evidence for a 'generic' neural system for error
975   detection. *Journal of Cognitive Neuroscience*, *9*(6), 788–798.
976   https://doi.org/10.1162/jocn.1997.9.6.788

977 Mushtaq, F., Wilkie, R. M., Mon-Williams, M. A., & Schaefer, A. (2016). Randomised prior
978   feedback modulates neural signals of outcome monitoring. *NeuroImage*, *125*, 868–879.
979   https://doi.org/10.1016/j.neuroimage.2015.10.046

980 Nassar, M. R., Bruckner, R., & Frank, M. J. (2019). Statistical context dictates the relationship
981   between feedback-related EEG signals and learning. *ELife*, *8*, e46975.
982   https://doi.org/10.7554/eLife.46975

983 Nolan, H., Whelan, R., & Reilly, R. B. (2010). FASTER: Fully Automated Statistical Thresholding
984   for EEG artifact Rejection. *Journal of Neuroscience Methods*, *192*(1), 152–162.
985   https://doi.org/10.1016/j.jneumeth.2010.07.015

986 Oken, B. S., & Chiappa, K. H. (1986). Statistical issues concerning computerized analysis of
987   brainwave topography. *Annals of Neurology*, *19*(5), 493–497.
988   https://doi.org/10.1002/ana.410190511

989 Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory.
990   *Neuropsychologia*, *9*(1), 97–113. http://dx.doi.org/10.1016/0028-3932(71)90067-4

991 Olejnik, S., & Algina, J. (2003). Generalized Eta and Omega Squared Statistics: Measures of Effect
992   Size for Some Common Research Designs. *Psychological Methods*, *8*(4), 434–447.
993   https://doi.org/10.1037/1082-989X.8.4.434

994   Oliveira, F. T. P., McDonald, J. J., & Goodman, D. (2007). Performance monitoring in the anterior
995   cingulate is not all error related: Expectancy deviation and the representation of action-
996   outcome associations. *Journal of Cognitive Neuroscience*, *19*(12), 1994–2004.
997   https://doi.org/10.1162/jocn.2007.19.12.1994

998   Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for
999   advanced analysis of MEG, EEG, and invasive electrophysiological data. *Intell.*
1000   *Neuroscience*, *2011*, 1:1-1:9. https://doi.org/10.1155/2011/156869

1001   Overbeek, T. J. M., Nieuwenhuis, S., & Ridderinkhof, K. R. (2005). Dissociable components of
1002   error processing—On the functional significance of the Pe Vis-a-vis the ERN/Ne. *Journal of*
1003   *Psychophysiology*, *19*(4), 319–329. https://doi.org/10.1027/0269-8803.19.4.319

1004   Palidis, D. J., Cashaback, J., & Gribble, P. (2019). Neural Signatures of Reward and Sensory
1005   Prediction Error in Motor Learning. *Journal of Neurophysiology*, 262576.
1006   https://doi.org/10.1152/jn.00792.2018

1007   Parvin, D. E., McDougle, S. D., Taylor, J. A., & Ivry, R. B. (2018). Credit assignment in a motor
1008   decision making task is influenced by agency and not sensorimotor prediction errors. *The*
1009   *Journal of Neuroscience*, *38*(19), 3601–3617. https://doi.org/10.1523/JNEUROSCI.3601-
1010   17.2018

1011   Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*,
1012   *118*(10), 2128–2148. https://doi.org/10.1016/j.clinph.2007.04.019

1013   Proudfit, G. H. (2015). The reward positivity: From basic research on reward to a biomarker for
1014   depression: The reward positivity. *Psychophysiology*, *52*(4), 449–459.
1015   https://doi.org/10.1111/psyp.12370

1016   R Core Team. (2015). *R: A language and environment for statistical computing.* R Foundation for
1017   Statistical Computing.

1018   Rutiku, R., Martin, M., Bachmann, T., & Aru, J. (2015). Does the P300 reflect conscious perception
1019   or its consequences? *Neuroscience*, *298*, 180–189.
1020   https://doi.org/10.1016/j.neuroscience.2015.04.029

1021   Sambrook, T. D., & Goslin, J. (2015). A Neural reward prediction error revealed by a meta-analysis
1022   of ERPs using great grand averages. *Psychological Bulletin*, *141*(1), 213–235.
1023   https://doi.org/10.1037/bul0000006

1024   San Martín, R. (2012). Event-related potential studies of outcome processing and feedback-guided
1025   learning. *Frontiers in Human Neuroscience*, *6*. https://doi.org/10.3389/fnhum.2012.00304

1026   Sidarus, N., Vuorre, M., & Haggard, P. (2017). How action selection influences the sense of
1027   agency: An ERP study. *NeuroImage*, *150*, 1–13.
1028   https://doi.org/10.1016/j.neuroimage.2017.02.015

1029   Sutton, R. S., & Barto, A. G. (1998). *Reinforcement Learning: An Introduction*. MIT Press.

1030 Torrecillos, F., Albouy, P., Brochier, T., & Malfait, N. (2014). Does the Processing of Sensory and

1031 Reward-Prediction Errors Involve Common Neural Resources? Evidence from a

1032 Frontocentral Negative Potential Modulated by Movement Execution Errors. *Journal of*

1033 *Neuroscience*, *34*(14), 4845–4856. https://doi.org/10.1523/JNEUROSCI.4390-13.2014

1034 Walsh, M. M., & Anderson, J. R. (2012). Learning from experience: Event-related potential

1035 correlates of reward processing, neural adaptation, and behavioral choice. *Neuroscience*

1036 *and Biobehavioral Reviews*, *36*(8), 1870–1884.

1037 https://doi.org/10.1016/j.neubiorev.2012.05.008

1038 Winkler, I., Debener, S., Muller, K. R., & Tangermann, M. (2015). On the influence of high-pass

1039 filtering on ICA-based artifact reduction in EEG-ERP. *Proceedings of the Annual*

1040 *International Conference of the IEEE Engineering in Medicine and Biology Society, EMBS*,

1041 *2015-Novem*, 4101–4105. https://doi.org/10.1109/EMBC.2015.7319296

1042 Wu, S.-W., Delgado, M. R., & Maloney, L. T. (2009). Economic decision-making compared with an

1043 equivalent motor task. *Proceedings of the National Academy of Sciences of the United*

1044 *States of America*, *106*(15), 6088–6093. https://doi.org/10.1073/pnas.0900102106

1045 Yordanova, J., Falkenstein, M., Hohnsbein, J., & Kolev, V. (2004). Parallel systems of error

1046 processing in the brain. *NeuroImage*, *22*(2), 590–602.

1047 https://doi.org/10.1016/j.neuroimage.2004.01.040

1048