

Frontal cortical effects on feedback processing and reinforcement learning: Relation of EEG asymmetry with the feedback-related negativity and behavior

Petra C. Schmid¹ | Leor M. Hackel² | Lee Jasperse³ | David M. Amodio^{3,4}

¹Swiss Federal Institute of Technology (ETH) Zurich, Zurich, Switzerland

²Stanford University, Palo Alto, California

³New York University, New York, New York

⁴University of Amsterdam, Amsterdam, the Netherlands

Correspondence

David M. Amodio, Department of Psychology, New York University, 6 Washington Place, Room 782, New York, NY 10003.

Email: david.amodio@gmail.com

Abstract

Reinforcement learning refers to the acquisition of approach or avoidance action tendencies through repeated reward/nonreward feedback. Although much research on reinforcement learning has focused on the striatum, the prefrontal cortex likely modulates this process. Given prior research demonstrating a consistent pattern of lateralized frontal cortical activity in affective responses and approach/avoidance tendencies in the EEG literature, we aimed to elucidate the role of frontal EEG asymmetry in reinforcement learning. Thirty-two participants completed a probabilistic selection task in which they learned to select some targets and avoid others though correct/incorrect feedback. EEG indices of frontal cortical asymmetry were computed from alpha power recorded at baseline and during task completion. We also examined the feedback-related negativity ERP component to assess feedback processing associated with activity in the dorsal anterior cingulate cortex. Results revealed that greater right-lateralized frontal cortical activity during learning was associated with better avoidance learning, but neither left- nor right-sided asymmetry reliably related to approach learning. Results also suggested that left frontal activity may relate to reinforcement feedback processing, as indicated by the feedback-related negativity (FRN). These findings offer preliminary evidence regarding the role of frontal cortical activity in reinforcement learning while integrating classic and contemporary research on lateralized frontal cortical functions.

KEYWORDS

asymmetry, EEG, FRN, frontal cortex, learning

1 | INTRODUCTION

In everyday life, people make choices to approach some things and avoid others based on their previous experiences. This form of learning, in which one's actions are reinforced with positive or negative feedback across multiple experiences, characterizes the process of reinforcement learning. To date, reinforcement learning has been associated most directly with activity in the striatum, which is believed to represent and update the value associated with an action (e.g., Frank, Moustafa, Haughey, Curran, & Hutchison, 2007; O'Doherty et al., 2004). However, recent

theoretical accounts suggest that the prefrontal cortex (PFC) may play a role in guiding goal-directed behaviors and in processing reinforcement feedback (Doll, Jacobs, Sanfey, & Frank, 2009; Fellows & Farah, 2005; O'Reilly & Frank, 2006). This suggestion aligns with nearly 40 years of research on frontal EEG asymmetry, which has associated greater relative left-sided frontal cortical activity with more positive affective responses (Davidson, Ekman, Saron, Senulis, & Friesen, 1990), stronger approach motivation (Harmon-Jones & Allen, 1998), and greater readiness to act and implement control (Amodio, 2010; Harmon-Jones, Harmon-Jones, Fearn, Sigelman, & Johnson, 2008).

Given the role of frontal asymmetry in responding to positive and negative feedback and coordinating approach and avoidance actions, we proposed that frontal asymmetry may also relate to the processing of reinforcement feedback when learning to approach or avoid novel objects. Hence, the present research investigated the link between frontal cortical asymmetry and feedback-based reinforcement learning, using an EEG approach that permitted us to examine changes in PFC activity, neural processing of reinforcement, and behavior-based indices of learning and performance.

1.1 | Reinforcement learning and approach/avoidance

In reinforcement learning, one learns to execute or avoid actions through repeated positive or negative feedback. This process has been examined using tasks in which participants learn through trial and error based on feedback that is probabilistically reinforcing. In a well-studied probabilistic selection task (Frank, Woroch, & Curran, 2005), participants view pairs of unfamiliar Japanese figures and, on each trial, must select one. After selection, participants receive either “correct” or “wrong” feedback, such that they learn, through trial and error, which figure to approach and which to avoid (Figure 1). However, this feedback is not deterministic; unbeknown to participants, the probability of correct/incorrect feedback varies between the three object pairs. In one pair, choosing object A over B is rewarded with “correct” feedback 80% of the time (and “wrong” 20% of the time). In a second pair, choosing object C over D is rewarded 70% of the time. And in the third pair, choosing object E over F is rewarded 60% of the time. Thus, participants learn to approach objects A, C, and E and to avoid B, D, and F with varying certainty. The overall degree of approach and avoidance learning can then be assessed in a test phase in which each possible combination of objects is presented for choice. By determining the probability that a participant chooses object A over all other options in novel pairings and avoids object B over all other options in novel pairings, estimates of overall approach and avoidance learning rates may be obtained.

The processing of positive and negative feedback in probabilistic reinforcement tasks may be indexed by the feedback-related negativity (FRN), a medial frontal ERP component that emerges in response to feedback. The FRN is an expression of the class of medial negativity waveforms, which includes the N2 and error-related negativity, and it may be interpreted as reflecting a general process of expectancy violation or conflict processing. Consistent with this view, the FRN is typically larger in response to negative (or loss) feedback in comparison with positive (or gain) feedback, though both forms of feedback may elicit an FRN

relative to baseline activity (Frank et al., 2005; Nieuwenhuis, Holroyd, Mol, & Coles, 2004; Yeung & Sanfey, 2004). The FRN is believed to represent anterior cingulate cortex (ACC) signaling to the striatum to aid its encoding and updating, as well as to the PFC to engage regulatory processing to guide future choices.

Following each instance of feedback, the strength (i.e., *value*) of a learned response is updated—a process instantiated in the striatum via midbrain dopaminergic signaling (Doll & Frank, 2009; O’Doherty et al., 2004; Schultz, Dayan, & Montague, 1997). However, more recent work has suggested that the PFC may play a role in modulating striatal activity during reinforcement learning (Doll et al., 2009; O’Reilly & Frank, 2006), a hypothesis that corresponds with known reciprocal anatomical connections between the PFC and striatum (Alexander, DeLong, & Strick, 1986). Thus, it would be informative to examine the relation of frontal cortical activity as it relates to the processing of feedback in a reinforcement context.

1.2 | Frontal cortical asymmetry and reinforcement learning processes

The two major components of reinforcement learning described above—the coordination of approach/avoidance action and the processing of reward/nonreward feedback—correspond to the two major processes associated with asymmetrical frontal cortical activity in the EEG literature. Early research on frontal EEG asymmetry effects emphasized its sensitivity to positive versus negative affective cues, such that greater left frontal asymmetry was associated with positive affect and responses to appetitive stimuli, whereas greater right-sided asymmetry was associated with negative affect and responses to aversive stimuli (e.g., Coan & Allen, 2003; Davidson, 1984, 1988, 1992; Davidson et al., 1990; Harmon-Jones & Allen, 1997; Sutton & Davidson, 1997). Similar patterns were observed in the relation between baseline resting frontal asymmetry and a variety of individual differences linked to positive and negative dispositions, such as depression and anxiety (Davidson & Fox, 1982; Davidson, Schwartz, Saron, Bennett, & Goleman, 1979; Tucker, 1981; Tucker, Stenslie, Roth, & Shearer, 1981), reward sensitivity (Pizzagalli, Sherwood, Henriques, & Davidson, 2005), and promotion-prevention focus (Amodio, Shah, Sigelman, Brazy, & Harmon-Jones, 2004). This body of work would suggest that frontal cortical asymmetry should be responsive to the valence of reinforcement feedback, with stronger left-sided asymmetry in response to positive (i.e., correct) feedback and right-sided asymmetry in response to negative (i.e., incorrect) feedback.

Although frontal cortical asymmetry has been consistently associated with positive or negative affect, researchers

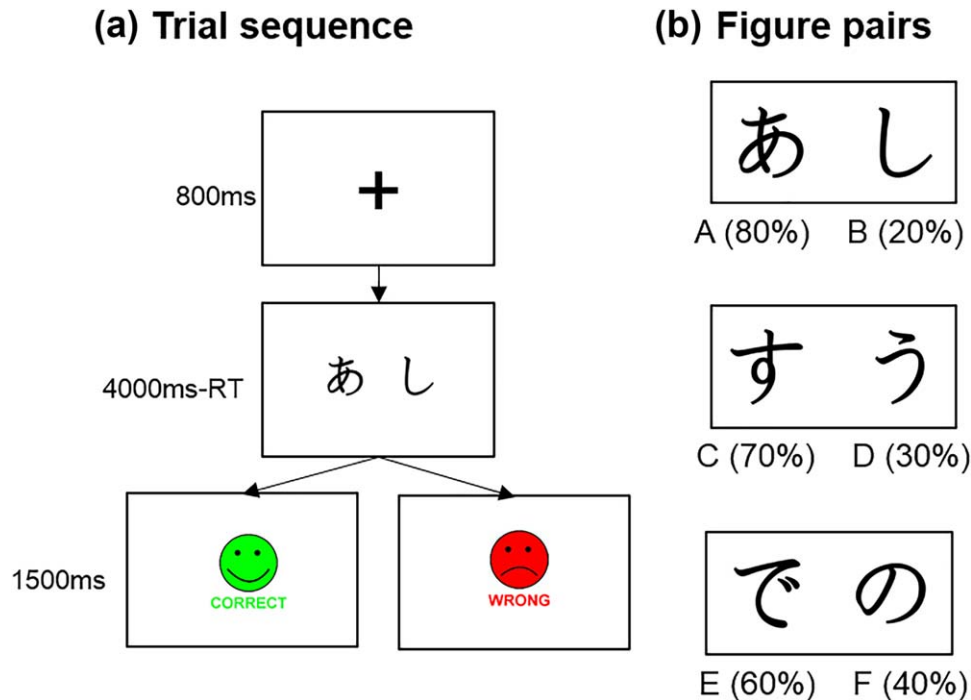


FIGURE 1 Panel A depicts a trial sequence in the reinforcement learning task and Panel B the Japanese figures that participants learned about. The correspondence between each figure and its reward probability was counterbalanced across participants

noted that instead of representing affective valence, frontal asymmetry effects may instead relate to approach or withdrawal motivational orientations and action tendencies (Harmon-Jones & Allen, 1998; Reuter-Lorenz & Davidson, 1981). Harmon-Jones and Allen (1998) observed that the valence and motivational orientation of most emotions are highly conflated (e.g., disgust is both negative and withdrawal related), but that anger may be an important exception—an approach-related response that is typically considered to be objectively negative. Indeed, anger inductions have been shown to increase reported anger and approach-related states (e.g., active, determined), and these responses were inversely related to happiness (Harmon-Jones, Harmon-Jones, Abramson, & Peterson, 2009). Consistent with a motivational account, several studies have shown anger to be associated with greater left-frontal cortical activity (Harmon-Jones, 2003; Harmon-Jones & Allen, 1998; Harmon-Jones & Sigelman, 2001). Much subsequent research has further shown frontal asymmetry to relate to approach or withdrawal orientations, often independent of the valence or intensity of experienced emotion (e.g., Amodio, Devine, & Harmon-Jones, 2007; Harmon-Jones & Harmon-Jones, 2002; Harmon-Jones et al., 2008; Harmon-Jones, Sigelman, Bohlig, & Harmon-Jones, 2003; Master et al., 2009), as well as with trait measures of approach-avoidance action tendencies (Amodio, Master, Yee, & Taylor, 2008; Gable, Mechin, Hicks, & Adams, 2015; Harmon-Jones & Allen, 1998).

The motivation-based model suggests that frontal asymmetry could affect reinforcement learning in two ways. First,

it predicts an overall effect of motivational orientation toward the learning task as a whole, such that greater left-frontal activity would relate to greater overall engagement in the learning task, which should promote feedback processing (e.g., FRN amplitudes) and both approach and avoidance learning. A second, alternative prediction is that greater left asymmetry would predict better learning of approach responses, whereas greater right asymmetry would predict better learning of avoidance responses.

More recent research on PFC function, based largely on fMRI and neurological studies, has significantly advanced our understanding of more specific processes that relate to frontal asymmetries observed in EEG studies (Miller, Crocker, Spielberg, Infantolino, & Heller, 2013). These findings highlight the role of the PFC in the planning and implementation of action, including both the engagement and inhibition of goal-directed responses. In particular, left dorso-lateral PFC and inferior frontal gyrus activity has been associated in much research with working memory processes, and some evidence suggests it pertains most directly to task-set representation and preparation for goal-directed action. These regions include BA 8, 44, 45, and 47, and they may correspond most closely with EEG activity recorded from left lateral and medial frontal sites (e.g., F3 and F7 in the 10–20 coordinate system; Siltan et al., 2010; Woolgar, Thompson, Bor, & Duncan, 2011). By contrast, the right inferior frontal gyrus has been associated with the controlled inhibition of action, in both fMRI and brain lesion patient studies (Aron, 2011; Aron, Robbins, & Poldrack, 2004).

This focus on the role of PFC in guiding actions is evident in recent EEG asymmetry research, which has linked greater left frontal activity during task performance to enhanced action control (Amodio, 2010; Schmid, Kleiman, & Amodio, 2015). Furthermore, increased left frontal EEG at baseline has been found to predict larger error-related negativity amplitudes in response to nonreward feedback in a cognitive control task (described in Allen, Trujillo, & Dikman, 2004), suggesting that frontal asymmetry may also influence how instrumental feedback is processed.

These findings highlight the important connection between frontal cortical activity and the regulation of action—a psychological function closely related to the process of learning through reinforcement. This connection is consistent with brain tractography findings: dorsolateral PFC and inferior frontal gyrus both receive input from common areas of the striatum (Jarbo & Verstynen, 2015). These corticostriatal projections permit the bidirectional interaction of PFC and striatum, which may support the learning of task rules from feedback. Reinforcement learning research suggests that PFC representations of context provide top-down constraint of striatal sensitivity to features of the environment presumed to be valuable for behavior, and striatal activity provides bottom-up refinement of value representations based on decision outcomes (Frank & Badre, 2012; Niv et al., 2015).

Considered together, frontal EEG asymmetry research on emotion, motivation, and action, along with contemporary models of PFC function, suggests that lateralized frontal cortical activity should relate to reinforcement learning processes. Specifically, greater task-related left frontal activity during learning may be functionally linked to updating representations about what stimuli to orient toward (i.e., approach learning), whereas greater task-related right frontal activity may support disengagement from nonrewarding stimuli (i.e., avoidance learning). Thus, we hypothesized that greater left frontal activity would be related to approach learning, whereas greater right frontal activity would relate to avoidance learning. Although our hypotheses concern separate functions of left and right PFC regions, we expected these effects to be evident in degree of asymmetry in left- versus right-sided EEG alpha power.

1.3 | The present study

The goal of this research was to illuminate the role of frontal cortical activity in reinforcement learning. To this end, we tested the associations of left and right frontal cortical activity during reinforcement with (1) an FRN index of feedback processing and (2) approach/avoidance learning outcomes. Effects of left and right cortical activity were examined using a traditional left-right difference score approach, as well as site-

specific tests of alpha power (with and without covarying activity in the homologous site). Although these approaches were expected to produce comparable results, their inclusion permitted a more comprehensive understanding of the data and provided links to both classic and contemporary EEG research.

2 | METHOD

2.1 | Participants

Thirty-two undergraduate students at New York University participated in exchange for partial course credit. The mean age was 19.91 years ($SD = 1.66$), 66% were female, and all were right-handed (Chapman & Chapman, 1987).¹

2.2 | Procedure

After providing consent, participants were prepared for EEG recording. Prior to the main task, 4 separate minutes of baseline EEG were recorded; 2 minutes with eyes open and 2 minutes with eyes closed, in counterbalanced order. Participants then received instructions for the main task and completed up to six blocks of trials until learning criteria were met (see below). Next, participants completed a test phase. If time remained in the session, participants learned a second stimulus set and performed a second application task in order to increase the number of trials (as in Frank et al., 2005). Finally, they completed questionnaires and provided demographics.²

2.3 | Materials

2.3.1 | Learning phase

Learning blocks included 60 trials presented in randomized order. On each trial, a fixation cross was presented for 800 ms, followed by two Japanese figures presented side-by-side onscreen (Figure 1). Participants were asked to choose one of these figures. Once chosen, positive or negative feedback on the response was presented for 1500 ms. Positive feedback comprised an image of a smiling green cartoon face above the word “correct,” and negative feedback comprised an image of a frowning red cartoon face above the word “wrong.” If no response was given within 4s, a “Too slow” message appeared. Inter-trial

¹Data of four participants were missing for the handedness questionnaire. These four participants, however, reported being right-handed.

²Participants completed a questionnaire that was not analyzed for the present report. The questionnaire included scales of current affective states and feelings, as well as three trait measures: the Ten-Item Personality Inventory (Gosling, Rentfrow, & Swann, 2003), the mini-Social Phobia Inventory (Connor, Kobak, Churchill, Katzelnick, & Davidson, 2001), and the Generalized Sense of Power Scale (Anderson, John, & Keltner, 2012).

intervals varied between 2,000 and 3,000 ms. During intertrial intervals, an ampersand (“&”) was shown in the center of the screen to retain participants’ gaze.

The task included three different trial types, each consisting of a pair of Japanese figures. During training (i.e., the learning phase), figures were always presented in the same pairs with their placement (right vs. left) counterbalanced across trials. That is, figures A and B were always paired together, as were figures C and D, and E and F. Importantly, the reward/nonreward feedback probabilities varied as a function of pair type. On AB trials, the reward probability was 80% for A and 20% for B. On CD trials, the reward probability was 70% for C and 30% for D. On EF trials, the reward probability was 60% for E and 40% for F. Participants were told that they would see these pairs of figures repeatedly and that their task was to learn which figures were more likely to be correct than the others. Thus, participants were aware that there was no absolute correct answer in this task, but that some figures had a higher probability of being correct than others. Figure 1 illustrates a sample trial sequence (panel A) and the Japanese figures along with their probabilities of being correct (panel B). Participants were asked at the end of the experiment whether they could read the Japanese letters; none could.

Participants completed training blocks until predefined learning criteria were met. Following Frank et al. (2005), criteria for correct responses were 65% for AB trials, 60% for CD trials, and 55% for EF trials. The number of blocks completed prior to reaching learning criteria ranged from one to six across participants. If criteria were not met after six blocks, participants automatically advanced to the testing phase (but were coded as nonlearners, and assigned the score “7” on the number of learning blocks measure). Time permitting, participants learned a second stimulus set with different figures, following same procedure. However, nine participants were only able to complete the first iteration in the 2 hr allotted for the entire experimental session. Therefore, analyses were restricted to data from the first iteration of the task.

2.3.2 | Test phase

The test phase was designed to assess learned representations of each target’s reward value after the opportunity for learning has ceased. The test phase included 90 trials, presented in randomized order. Each trial began with the presentation of a fixation cross for 800 ms, which was followed by a pair of Japanese figures. Pairs of figures included all fifteen possible combinations of the six figures from the learning phase. Participants’ task was again to choose the figure that they believed had a higher probability of being correct. This test measures fine-grained differences in value representations for choosing positive and negative targets, such as knowing that

object A (80% correct) is better than object C (70% correct) or object B (20% correct) is worse than object D (30% correct). Pairs of figures remained onscreen until a response was given, or, if no response was given within 4 s, a “Too Slow” message appeared. No accuracy feedback was given. During intertrial intervals, the symbol “&” was again presented for 2,000–3,000 ms, with jittered latencies. Participants were instructed to apply what they had learned from the previous learning blocks and, if they were unsure, to go with their gut feelings.

Three performance indices were computed from this task. “Approach learning” scores reflected hit rates in choosing A over all other figures in novel pairs, and the “avoidance learning” scores reflected hit rates in avoiding B over all other figures in novel pairs. A composite measure of approach and avoidance learning, labeled “overall accuracy,” was also computed.

2.4 | EEG recording and processing

EEG was recorded from F7, F3, Fz, F4, F8, FCz, Cz, CPz, P7, P3, Pz, P4, P8, and Oz, using tin electrodes embedded in a nylon cap (ElectroCap, Eaton, OH), with left earlobe reference ($\Omega < 5k$). This array was guided by our specific interest in frontal alpha activity and midline ERP components, with lateral parietal sites included for comparison with frontal sites. Vertical and horizontal electrooculograms (EOG) were recorded for use in artifact correction. Signal was amplified using Neuroscan Synamps2 (El Paso, TX) with AC coupling, digitized at 1,000 Hz and passed through a 0.15–100 Hz online filter. Offline, EEG was submitted to regression-based blink correction and re-referenced to average earlobes. It is notable that reference is a point of much discussion in the EEG asymmetry literature (Allen, Coan, & Nazarian, 2004; Davidson, Jackson, & Larson, 2000). The average earlobes reference was chosen because it is a relatively inactive reference, which permits observed EEG to be attributed to the “active” site of interest (Allen et al., 2004). By comparison, a whole-head reference was inappropriate given our selective array, and a vertex (or common Cz) reference was inappropriate because its proximity to FCz would diminish its sensitivity to the FRN (scored at FCz).

2.4.1 | Frontal EEG scoring

Baseline EEG was quantified from eyes-open and eyes-closed resting activity. Following Towers and Allen’s (2009) recommendation in favor of short epochs, 2-s epochs were extracted and submitted to a fast-Fourier transformation using a 50%-overlapping Hamming window; alpha power was extracted (8–13 Hz) and all scores were then natural log-transformed (Harmon-Jones & Amodio, 2012). Alpha activity was examined as a function of single electrode scores as well

TABLE 1 Zero-order correlation coefficients (r) between learning outcomes, EEG frontal asymmetry difference scores (F8–F7), and FRN amplitudes (FCz)

	1	2	3	4	5	6	7	8	9	10
Learning outcome										
1 Approach learning										
2 Avoidance learning	-.03									
3 Overall accuracy	.59**	.79**								
4 # of learning blocks	.20	-.17	-.02							
EEG asymmetry difference scores at F8–F7										
5 Baseline	-.18	-.17	-.25	.04						
6 During learning all	.07	-.39*	-.27	-.14	.56**					
7 During learning, after neg fb	.04	-.31	-.23	-.13	.46**	.84**				
8 During learning, before neg fb	.15	-.26	-.12	-.08	.53**	.83**	.76**			
9 During test	-.10	-.03	-.09	-.00	.58**	.75**	.75**	.73**		
FRN amplitudes, FCz										
10 FRN to negative feedback	-.01	-.05	-.04	.35*	-.30†	-.31†	-.27	-.37*	-.17	
<i>M</i>	.74	.70	.72	3.00	.60	.70	.68	.68	.72	-6.68
<i>SD</i>	.18	.24	.15	1.59	.22	.20	.17	.20	.18	4.79

^aNotes. † $p < .10$. * $p < .05$. ** $p < .01$.

as the more traditional difference scores, whereby left-sided alpha power was subtracted from right-sided alpha power (i.e., F8–F7, F4–F3, P8–P7, and P4–P3), such that higher values indicate greater left-sided cortical activity (e.g., Davidson, Coe, Dolski, & Donzella, 1999; Lindsley & Wicke, 1974; Pizzagalli et al., 2005; Wheeler, Davidson, & Tomarken, 1993). Because the effects of eyes-open and eyes-closed resting activity were nearly identical in our analyses, these were combined into a single index of resting asymmetry.

To compute task-related frontal EEG during learning, 2-s epochs were extracted from intertrial intervals beginning at feedback offset, during which participants viewed a fixation point (as in Amodio, 2010; Schmid et al., 2015). The main task-related EEG index included activity from all intertrial intervals.

2.4.2 | ERPs

To compute the ERPs of interest, re-referenced raw EEG signal was submitted to a 30 Hz lowpass filter, and then 800 ms feedback-locked epochs were extracted beginning 200 ms before feedback onset. Average voltage during the baseline period (200 ms prior to stimulus onset) was subtracted from the entire epoch, and epochs associated with positive “correct” feedback and negative “wrong” feedback were averaged separately. Visual inspection of the wave form indicated that the FRN was strongest at FCz, consistent with previous research (e.g., Frank et al., 2005; Holroyd, Hajcak, & Larsen, 2006). Following past research (e.g., Frank et al.,

2005; Holroyd & Coles, 2002), the FRN was scored at FCz as the peak-to-peak voltage difference between the negative FRN peak (within 190 and 300 ms after feedback onset) and the preceding positive peak (within 140–230 ms).

3 | RESULTS

Descriptive statistics and intercorrelations pertaining to key variables are reported in Table 1 (additional descriptives and analyses are presented in the Supplement). In what follows, we report preliminary analyses aimed at establishing the validity of key measures and then present results pertaining to our central questions concerning the role of frontal EEG asymmetry in reinforcement learning.

3.1 | Preliminary analyses

3.1.1 | Task behavior

On average, participants required three blocks of learning trials to reach criterion ($SD = 1.59$). Two participants did not reach criterion after six blocks. Moreover, participants were able to transfer their acquired knowledge to the test phase: one-sample t tests showed that participants performed well above chance (.50) for both approach learning ($M_{accuracy} = .74$, $SD = .18$), $t(31) = 7.47$, $p < .001$, and avoidance learning ($M_{accuracy} = .70$, $SD = .24$), $t(31) = 4.66$, $p < .001$, and that both aspects of learning were evident to a similar degree,

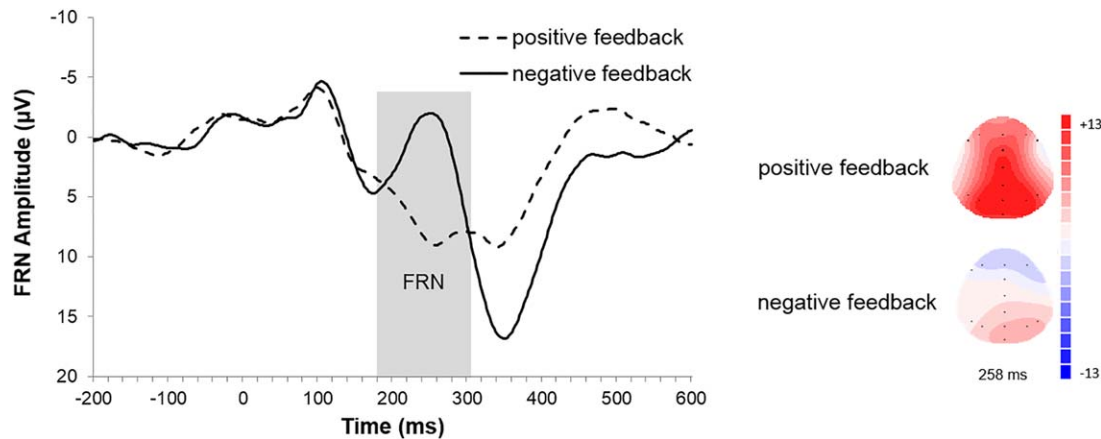


FIGURE 2 FRN amplitudes at FCz were larger to negative feedback than to positive feedback

$t(31) = 0.81, p = .422$. Thus, the task was effective in inducing learning.

3.1.2 | EEG asymmetry

An examination of EEG asymmetry scores indicated significant left-sided asymmetry at baseline and during task completion at both F8–F7 and F4–F3, $t_s > 14.03, p_s < .001$ (see Table 1 for Means and *SD*). Additionally, task-related EEG elicited increased left asymmetry relative to baseline: during learning task at F8–F7, $t(31) = 2.75, p = .010$, and at F4–F3, $t(31) = 1.82, p = .078$; during test at F8–F7: $t(31) = 3.48, p = .002$, and at F4–F3, $t(31) = 2.33, p = .027$. This finding was consistent with past research showing greater left frontal asymmetry associated with engagement in an experimental task, relative to baseline (Amodio et al., 2007).

3.1.3 | Feedback-related negativity

In line with previous research, participants' FRN responses were significantly larger (i.e., more negative) to negative feedback ($M = -6.68, SD = 4.79$) than to positive feedback ($M = -1.39, SD = 1.87$), $t(31) = 6.58, p < .001$ (Figure 2). In this sample, positive feedback did not elicit a discernable FRN.

3.2 | Relation between frontal asymmetry and reinforcement learning

Our primary question concerned the relationship between frontal EEG asymmetry during the learning process and test-phase assessments of approach and avoidance learning. We first examined whether approach and avoidance learning were associated with an asymmetric pattern of frontal cortical activity, based on single electrode scores and traditional difference scores involving dorso- and ventrolateral PFC sites (F7, F8, F3, and F4). Correlations among the key variables are presented in Table 1 (see also Tables S1–S3 in the Supplement).

Furthermore, unique effects of frontal sites were examined by adjusting for any effects of homologous parietal sites.

3.2.1 | Baseline EEG

First, associations between baseline alpha power and learning outcomes were computed. Interestingly, although approach learning was not associated with alpha activity at any frontal site (i.e., F8, F7, F4, and F3), $r_s = .06$ to $.16, p_s > .37$, avoidance learning was correlated with alpha power at all frontal electrodes, $r_s = -.38$ to $-.44, p_s < .032$ (see Tables S1 and S3 in the Supplement). A similar pattern was evident in parietal electrode sites (i.e., P8, P7, P4, and P3; see Tables S5–S6), indicating that, across sites, greater alpha power was associated with worse avoidance learning. These results suggest a link between baseline whole-head alpha and learning that was specific to instrumental avoidance, suggesting that lower overall cortical activity (i.e., inverse alpha) during baseline recording was associated with worse avoidance learning but was unrelated to approach learning.

However, frontal asymmetry in baseline EEG was not significantly associated with either approach or avoidance learning, based on both single channel analyses (i.e., regressions that included the site of interest as the predictor along with the homologous site as a covariate) and difference score analyses, $p_s > .128$.

3.2.2 | Learning-phase EEG effects on learning

Correlations between alpha power at frontal sites (F3, F4, F7, and F8) and learning outcomes are presented in Tables S1 and S3 in the Supplement. Our core questions concerned the effects of frontal EEG asymmetry during learning (across all trials) on behavioral indicators of learning. First, regressions were computed which tested whether the relationship between alpha power at one site (e.g., F8) and avoidance learning holds when controlling for the other site (e.g., F7).

This analysis revealed unique effects of both left- and right-sided frontal EEG and avoidance learning when examining activity at lateral frontal sites (F7: $\beta = 1.24$, $t = 2.16$, $p = .039$; F8: $\beta = -1.69$, $t = 2.94$, $p = .006$). Similar, but weaker, effects emerged for medial frontal sites (F3: $\beta = 1.90$, $t = 1.62$, $p = .115$; F4: $\beta = -2.35$, $t = 2.02$, $p = .053$). In light of the putative inverse relationship between alpha power and cortical activity, this pattern suggests that instrumental avoidance learning was associated with increased right frontal cortical activity and decreased left frontal cortical activity, particularly in lateral frontal regions.

Difference score analyses revealed similar results. Approach learning was not associated with difference scores at either lateral frontal (F8–F7: $r(32) = .07$, $p = .688$; Figure 3, panel A) or medial frontal (F4–F3: $r(32) = -.16$, $p = .383$) sites. By contrast, avoidance learning was significantly associated with lower relative right-sided alpha power at lateral (F8–F7: $r(32) = -.39$, $p = .026$; Figure 3, panel B) and medial (F4–F3: $r(32) = -.36$, $p = .046$) sites, again suggesting that greater relative right-sided frontal cortical activity was associated with better instrumental avoidance learning.

The pattern of association between frontal EEG asymmetry and learning persisted in supplemental covariate analyses that adjusted for parietal asymmetry difference scores (see Supplement). Moreover, similar results were found when looking at EEG activity associated with positive versus negative feedback (Table 1 and Tables S1–S3).³

³To further isolate the effect of task-related frontal alpha power on learning, supplementary analyses were conducted that adjusted for baseline frontal asymmetry (eyes open, to match task behavior) in individual electrode sites. Results showed that alpha power across sites during the learning phase predicted worse approach learning, whereas baseline alpha predicted better approach learning. These effects were significant at F7, F4, and F3 (for alpha power during learning, $t_s > -2.43$, and $p_s < .022$, and during baseline, $t_s > 2.29$, and $p_s < .029$). This effect was only marginally significant at F8, for alpha power during learning, $\beta = -0.83$, $t = 1.95$, $p = .060$ and during baseline, $\beta = 0.84$, $t = 1.97$, $p = .058$. When focusing on avoidance learning, no significant correlations were found with single electrode alpha power, $t_s < 1.55$, $p_s > .133$. Effects of task-related frontal EEG asymmetry difference scores (i.e., F8–F7) remained similar to results presented in the main text when adjusting for baseline EEG asymmetry, with a null effect on approach learning (for F8–F7: $\beta = .19$, $t = 0.99$, $p = .332$; for F4–F3: $\beta = -.12$, $t = 0.53$, $p = .599$), and a significant effect on avoidance learning (for F8–F7: $\beta = -.40$, $t = 2.12$, $p = .042$; for F4–F3: $\beta = -0.41$, $t = 1.95$, $p = .062$). In addition, difference scores were computed that subtracted baseline EEG asymmetry from task-related frontal asymmetry during learning. These difference scores did not significantly correlate with any of the learning outcomes measures (for F8–F7 asymmetry scores, $r_s < .28$, $p_s > .123$ and for F4–F3 asymmetry scores, $r_s < -.22$, $p_s > .224$).

3.3 | Frontal asymmetry and the feedback-related negativity

To probe the mechanism underlying the effect of frontal activity on learning outcomes, we examined the relationship between EEG asymmetry and FRN amplitudes. As in past work, and given the lack of FRN responses to positive feedback, analysis focused on FRN responses to negative feedback only. We hypothesized that frontal cortical activity during learning would modulate sensitivity to task feedback, as indicated by the FRN, which in turn might relate to task performance.

3.3.1 | Baseline EEG effects on FRN

Correlations between alpha power at frontal sites (i.e., F8, F7, F4, and F3) and FRN responses to negative feedback were all nonsignificant (see Tables S1 and S3). To examine effects of baseline frontal asymmetry on the FRN, left- and right-sided single channel scores were included in a regression simultaneously (e.g., F7 and F8, F3 and F4) predicting FRN responses to negative feedback. Alpha power at F7 was marginally related to reduced FRN responses to negative feedback when controlling for F8, $\beta = 1.03$, $t = 1.84$, $p = .076$. No other site predicted FRN responses significantly, $\beta_s < 0.84$, $t_s < 1.50$, $p_s > .144$. Consistent with the F7 result, a trend emerged when looking at the F8–F7 asymmetry difference score. That is, greater lateral left-frontal EEG asymmetry at baseline was marginally associated with larger FRN amplitudes to negative feedback, $r(32) = -.30$, $p = .090$. However, medial frontal asymmetry (F4–F3) during baseline did not significantly correlate with FRN to negative feedback (Table 1). When adjusting for parietal scores in supplementary analyses, frontal EEG effects on the FRN were nonsignificant (see Supplement). Thus, these results did not reveal a reliable relationship between frontal asymmetry at baseline and FRN amplitudes.

3.3.2 | Learning phase EEG effects on FRN

Preliminary analysis revealed that learning phase alpha power from individual sites was not directly associated with FRN amplitude (Tables S1 and S3). Next, we examined the association between EEG asymmetry recorded during learning and the FRN. Regression analysis revealed a marginal association between left lateral alpha and FRN amplitude (F7: $\beta = 1.27$, $t = 1.93$, $p = .064$, while adjusting for F8), indicating that greater left frontal cortical activity was related to stronger negative feedback processing (given the negative scoring of the FRN). No effects at other frontal EEG sites reached even marginal significance, $\beta_s < 1.10$, $t_s < 1.66$, $p_s > .107$.

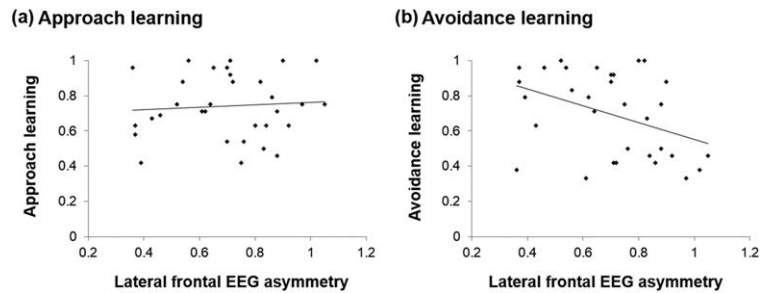


FIGURE 3 Scatterplots illustrating the relationships between frontal EEG asymmetry (F8 minus F7 alpha power) and approach learning performance (Panel A) and avoidance learning performance (Panel B). Learning performance is indicated in accuracy rates (i.e., values range between 0–1). Higher EEG asymmetry scores reflect greater left-sided cortical activity (i.e., inverse alpha power)

Difference score analyses revealed a similar pattern, such that greater relative left lateral frontal cortical activity was marginally related to larger FRN amplitudes, $r(32) = -.31$, $p = .083$ (Figure 4), and these effects persisted when parietal asymmetry scores were covaried (see Supplement). No relationship was observed between medial frontal EEG asymmetry and FRN amplitude (Tables 1 and S2). Importantly, however, the marginal association between learning phase EEG and FRN amplitude was reduced to nonsignificance when baseline EEG was included in the regression as a covariate, $\beta = -.21$, $t = 0.98$, $p = .336$. This overall pattern could suggest a potential relationship between left frontal PFC activity and the FRN, but it may instead reflect EEG activity associated with engagement in the overall experimental session as opposed to activity specific to learning task trials.

Because the FRN index appeared to be valid only in response to negative feedback, we conducted additional analyses that focused specifically on the relationship of EEG asymmetry and FRN amplitudes on trials associated with negative feedback. Furthermore, given our theoretical interest in how frontal asymmetry may correspond to an orientation or readiness (e.g., to approach or avoid) during learning, we tested whether frontal asymmetry just prior to a learning experience related to the FRN. To this end, regression

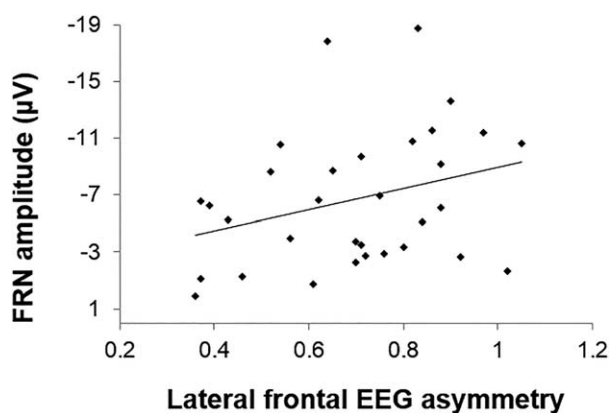


FIGURE 4 Relative greater left frontal activity in the EEG (F8 minus F7 alpha power) was associated by trend with larger FRN amplitudes to negative feedback at FCz

analysis revealed that left-lateral alpha power prior to the learning trial was significantly associated with smaller (more positive) FRN amplitudes (F7: $\beta = 1.58$, $t = 2.25$, $p = .032$), whereas right lateral frontal alpha power was associated with larger FRNs (F8: $\beta = -1.37$, $t = 1.69$, $p = .059$). A regression analysis examining medial frontal effects revealed a similar pattern (F3: $\beta = 2.56$, $t = 2.01$, $p = .054$; F4: $\beta = -2.32$, $t = 1.82$, $p = .080$). These results indicated that left-sided frontal cortical activity was associated with increased processing of negative feedback. As expected, similar results emerged from difference score analyses (F8–F7: $r(32) = -.37$, $p = .038$; F4–F3: $r(32) = -.34$, $p = .059$), and all effects remained when further adjusting for parietal activity (see Supplement). However, when corresponding baseline EEG activity was covaried, these effects were weakened to nonsignificance (F8–F7: $\beta = -0.29$, $t = 1.42$, $p = .165$, and F4–F3: $\beta = -0.31$, $t = 1.38$, $p = .178$), again suggesting that the EEG asymmetry effect may represent a more general psychological orientation to the task that was not specific to the learning phase.

This general pattern suggests that greater left frontal activity just prior to a learning experience was associated with stronger feedback-related processing, putatively in the ACC. By contrast, FRN amplitudes were not significantly related to frontal activity *after* negative feedback, for both single channel and difference score tests, $\beta s < 1.92$, $t s < 1.61$, $p s > .105$.

3.4 | FRN effects on learning outcomes

To test whether FRN responses to negative feedback related to learning, we examined correlations between FRN amplitude and both approach and avoidance learning scores obtained in the test phase. No significant associations were observed (see Table 1).

In addition, we computed an alternative index of learning that comprised the number of blocks required to reach criteria during the learning phase. Because the FRN was also derived from learning phase trials, this measure of learning represented an index that was more psychologically proximal

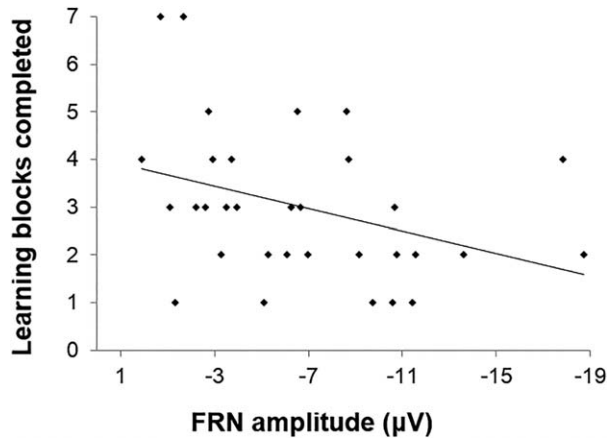


FIGURE 5 Larger FRN amplitudes to negative feedback at FCz were related to faster learning (i.e., a smaller number of learning blocks needed to reach performance criteria in the learning phase)

and might correspond more directly to FRN responses. Indeed, participants with larger FRN amplitudes to negative feedback learned faster—that is, they required fewer blocks of trials to reach criterion, $r(32) = .35$, $p = .047$ (Figure 5).⁴

4 | DISCUSSION

Frontal cortical asymmetry has long been associated with motivational and emotional processes, but relatively little is known about its role in learning. Here, we examined associations between frontal asymmetry and reinforcement learning in the context of a probabilistic selection task, with the goal of illuminating the role of PFC activity in learning while linking these processes to existing models of emotion and motivation. In doing so, our research further informs the functional significance of frontal EEG asymmetry, relating it to contemporary models of lateralized PFC function and, most importantly, to learning.

4.1 | Frontal asymmetry and reinforcement learning

The central goal of this research was to examine the association between frontal EEG asymmetry and reinforcement learning processes. We found that frontal asymmetry assessed during the learning process predicted the strength of participants' avoidance-based learning, as revealed at test. That is, greater right frontal cortical activity during the learning process was associated with stronger acquisition of

avoidance learning; at the same time, greater left frontal cortical activity was associated with reduced avoidance learning. These results were observed at both lateral and medial frontal electrode sites (F7, F8, F3, and F4). By contrast, frontal asymmetry was not associated with approach-based learning. This overall pattern was specific to frontal asymmetry during the learning process; that is, these results held when controlling for baseline EEG activity as well as parietal asymmetry. These findings provide evidence of a link between frontal cortical alpha asymmetry and reinforcement learning, such that greater relative right-sided activity was associated with learned instrumental avoidance.

Given previous research linking left frontal activity to approach motivation and action tendencies, we also expected that left frontal activity would be associated with approach learning. Although an obvious hypothesis, it was not supported by our data. We can offer some speculation for this null result. One possibility is that participants were simply less variable in the approach learning, which may have limited our ability to detect an association; indeed, test-phase indices of approach learning were numerically higher and less variable than avoidance learning. Moreover, the task was highly engaging, such that the task may have promoted approach-related responses and learning beyond any individual differences in frontal cortical asymmetry. For this reason, as well, the task may have been more sensitive to individual differences in avoidance processing, which in turn are theoretically related to right frontal activity. Although virtually all experimental paradigms used to assess learning involve active task engagement (i.e., they require a response to be delivered on each trial), it is possible that a link between frontal asymmetry and approach learning might become apparent using tasks that place less emphasis on continuous active engagement. Of course, it is also possible that no relation exists between frontal cortical activity and instrumental approach learning. Because our findings represent an initial test of this association, additional data from other labs will be required before strong conclusions can be made.

4.2 | Frontal asymmetry and feedback processing

The second major finding of our study was that frontal asymmetry was also associated with FRN amplitudes in response to negative feedback. Specifically, greater cortical activity at left frontal sites (i.e., decreased alpha power at F7 and F3) was associated with larger FRN amplitudes, whereas reduced activity at right frontal sites (i.e., greater alpha power at F8 and F4) was associated with smaller FRN responses. This pattern of results was especially evident for alpha power corresponding to negative feedback trials (i.e., trials producing a valid FRN) and when EEG was assessed during a period

⁴We conducted additional analyses using a computational modeling approach in which behavioral data were modeled in the learning and test phase in order to compute estimates of learning rates from positive feedback and from negative feedback, as well as an exploration factor. However, the computational models produced poor fits to the data and are thus not reported.

prior to receiving negative feedback. By comparison, frontal asymmetry *following* negative feedback was unrelated to the FRN. All findings remained stable when controlling for parietal alpha power, indicating that effects were specific to frontal asymmetry. However, because adjustment for baseline EEG asymmetry reduced this effect, it is possible that the association between frontal asymmetry and the FRN reflected a more general orientation to the experimental session (e.g., an approach or avoidance orientation) that may not have been specific to the learning experience. That is, it is possible that participants' degree of frontal cortical asymmetry while engaged in learning was very similar to their degree of asymmetry during the baseline task (e.g., the baseline recording task in which they followed eyes open/eyes closed instructions), such that adjusting for baseline activity masks a real association between learning-phase frontal asymmetry and the FRN.

Nevertheless, this pattern is consistent with an approach/withdrawal model of frontal asymmetry, such that greater approach-related engagement toward the upcoming trial was associated with a stronger response to feedback. It is notable that this correlational effect does not necessarily indicate direct signaling between the PFC and ACC. Rather, it may reflect a simpler process whereby the greater left PFC activity produced increased attention to the task, which in turn led to stronger ACC response when negative expectancy-violating feedback was encountered. Additionally, according to recent theories, behavior in the training phase reflects both striatal learning and working memory processes mediated by PFC, whereas performance in the test phase is thought to primarily reflect striatal value signaling (Collins & Frank, 2012; Frank et al., 2007). In line with these ideas, we found that the FRN predicted a behavioral measure of learning in the training phase (number of blocks to reach criterion), which may indicate that participants were more attentive to the negative feedback and thus learned faster. However, FRN responses were unrelated to performance in the test phase (accuracy), suggesting that FRNs did not reflect the process of integrating the acquired knowledge and its application to novel pairs in the test phase. Thus, it is possible that the enhanced FRN during learning was due to working memory processes, whereas enhanced avoidance learning as revealed in the test phase was due to striatal learning processes.

4.3 | Implications for interpretations of frontal asymmetry

Considered together, our findings offer two main contributions to the frontal asymmetry literature. First, our results provide evidence that frontal asymmetry is associated with reinforcement learning, such that relatively stronger right-sided asymmetry during the learning task was associated

with enhanced avoidance learning. Hence, we demonstrated that frontal asymmetry has implications for how information is processed and deployed in future behaviors, at least in the context of feedback-based learning.

Second, our results shed light on the psychological processes represented by frontal EEG asymmetry. Broadly, our findings are consistent with an approach-withdrawal model of frontal EEG asymmetry. However, a consideration of contemporary models of PFC function suggests more specific roles of left and right frontal activation. According to these models, left dorsolateral PFC supports working memory processes that should guide goal-directed attention and action tendencies (e.g., Siltan et al., 2010; Woolgar et al., 2011). By contrast, right lateral PFC activity has been associated with response inhibition (Aron et al., 2004). Our findings are generally consistent with this model: during the learning task, greater left frontal activity was associated with larger FRN amplitudes in response to negative feedback, which characterizes greater attentional engagement during learning and greater processing of expectancy-violating feedback. However, right-sided EEG was associated with avoidance learning assessed during the test phase in which avoidance learning indexed the ability to inhibit the behavioral choice of low-value targets. This result is consistent with the proposed role of right inferior frontal gyrus in the controlled inhibition of action. In other words, left frontal activity was associated with stronger engagement in the learning process, but right frontal activity was associated with behavioral expression of learning (i.e., for avoid responses).

When applied to classic models of frontal EEG asymmetry, our findings suggest that left and right frontal asymmetries may not represent opposite ends of a psychological dimension (e.g., positive-negative, approach-avoidance) but instead reflect more specific cognitive and motor functions that generally correspond with affective valence or motivational orientation. This analysis pertains most directly to task-related or state assessments of frontal EEG, but it may also inform results of baseline "resting" EEG studies. More broadly, these results integrate ideas from contemporary cognitive neuroscience models with the extensive EEG literature to illuminate the functional significance of frontal asymmetry effects.

4.4 | Limitations

Two limitations are notable. First, the sample size in this experiment was relatively small ($N = 32$)—a factor that affects statistical power and, thus, the ability to detect small effects and the robustness of the obtained effects. Thus, the marginal and null effects reported in our study must be interpreted in the light of potential type I and type II errors. Although our interpretations are bolstered by the use of a

within-subjects design, an established experimental task, and the sensitivity of electrophysiological measures, it remains possible that the reliability of some observed effects may be undermined by insufficient power. For example, the relationship between EEG asymmetry and FRN amplitude was relatively small. Yet this effect held when controlling for parietal sites, and it was strengthened when the analysis focused on EEG and FRN variables derived from the same set of negative-feedback trials. Thus, although the effect was small, it appeared stable and consistent across multiple analyses. It is also notable that while the present effects were observed with $N = 32$, prior studies examining the FRN in reinforcement learning observed effects with considerably smaller samples (Cohen, Elger, & Ranganath, 2007; Hajcak, Moser, Holroyd, & Simons, 2006; Ichikawa, Siegle, Dombrovski, & O'Hira, 2010; Santesso et al., 2009; Santesso et al., 2008; van der Helden, Boksem, & Blom, 2010). Going forward, it will be useful to replicate such effects with adequate power and to examine them in the context of meta-analysis.

A second issue is that EEG was recorded from a relatively restricted electrode array. This may present a limitation depending on one's question. Our primary question concerned general frontal asymmetry effects, and our use of F3–F4 and F7–F8 was chosen based on our theoretical question and previous literature. Moreover, given the spatial smoothing caused by the skull and scalp, it is difficult to gain significantly greater spatial resolution with denser frontal electrode arrays. Nevertheless, this array limits the use of source analysis. Future research on the specific structures underlying the asymmetry effects observed here would thus benefit from additional electrode coverage.

5 | CONCLUSIONS

Reinforcement learning involves the formation of approach or avoidance responses through repeated experiences with positive or negative feedback. Building on the long-standing association between frontal EEG alpha asymmetry and both affective processing and approach/avoidance responses, the present research demonstrated links between frontal EEG asymmetry, the processing of reinforcement feedback, and behavioral expressions of instrumental learning. In doing so, these findings provide evidence for the role of PFC in reinforcement learning processes. Furthermore, by interpreting our findings in terms of both the classic EEG literature and contemporary cognitive neuroscience models of PFC function, this research further illuminates the functional significance of frontal EEG asymmetry and broadens its purview to include learning.

REFERENCES

- Alexander, G. E., DeLong, M. R., & Strick, P. L. (1986). Parallel organization of functionally segregated circuits linking basal ganglia and cortex. *Annual Review of Neuroscience*, *9*, 357–381. doi:10.1146/annurev.ne.09.030186.002041
- Allen, J. J. B., Coan, J. A., & Nazarian, M. (2004). Issues and assumptions on the road from raw signals to metrics of frontal EEG asymmetry in emotion. *Biological Psychology*, *67*, 183–218. doi:10.1016/j.biopsycho.2004.03.007
- Allen, J. J. B., Trujillo, L., & Dikman, Z. V. (2004). Assessing moderators and mediators of error-monitoring. In M. Ullsperger & M. Falkenstein (Eds.), *Errors, conflicts, and the brain: Current opinions on performance monitoring* (pp. 164–171). Leipzig: Max-Planck-Institut für Kognitions- und Neurowissenschaften.
- Amodio, D. M. (2010). Coordinated roles of motivation and perception in the regulation of intergroup responses: Frontal cortical asymmetry effects on the P2 event-related potential and behavior. *Journal of Cognitive Neuroscience*, *22*, 2609–2617. doi:10.1162/jocn.2009.21395
- Amodio, D. M., Devine, P. G., & Harmon-Jones, E. (2007). A dynamic model of guilt: Implications for motivation and self-regulation in the context of prejudice. *Psychological Science*, *18*, 524–530. doi:10.1111/j.1467-9280.2007.01933.x
- Amodio, D. M., Master, S. L., Yee, C. M., & Taylor, S. E. (2008). Neurocognitive components of the behavioral inhibition and activation systems: Implications for theories of self-regulation. *Psychophysiology*, *44*, 1–9. doi:10.1111/j.1469-8986.2007.00609.x
- Amodio, D. M., Shah, J. Y., Sigelman, J., Brazy, P. C., & Harmon-Jones, E. (2004). Implicit regulatory focus associated with asymmetrical frontal cortical activity. *Journal of Experimental Social Psychology*, *40*, 225–232. doi:10.1016/S0022-1031(03)00100-8
- Anderson, C., John, O. P., & Keltner, D. (2012). The personal sense of power. *Journal of Personality*, *80*, 313–344. doi:10.1111/j.1467-6494.2011.00734.x
- Aron, A. R. (2011). From reactive to proactive and selective control: Developing a richer model for stopping inappropriate responses. *Biological Psychiatry*, *69*, e55–e68. doi:10.1016/j.biopsycho.2010.07.024
- Aron, A. R., Robbins, T. W., & Poldrack, R. A. (2004). Inhibition and the right inferior frontal cortex. *Trends in Cognitive Sciences*, *8*, 170–177. doi:10.1016/j.tics.2004.02.010
- Chapman, L. J., & Chapman, J. P. (1987). The measurement of handedness. *Brain and Cognition*, *6*, 175–183. doi:10.1016/0278-2626(87)90118-7
- Coan, J. A., & Allen, J. J. B. (2003). Frontal EEG asymmetry and the behavioral activation and inhibition systems. *Psychophysiology*, *40*, 106–114. doi:10.1111/1469-8986.00011
- Cohen, M. X., Elger, C. E., & Ranganath, C. (2007). Reward expectation modulates feedback-related negativity and EEG spectra. *NeuroImage*, *35*, 968–978. doi:10.1016/j.neuroimage.2006.11.056
- Collins, A. G. E., & Frank, M. J. (2012). How much of reinforcement learning is working memory, not reinforcement learning? A behavioral, computational, and neurogenetic analysis. *European Journal of Neuroscience*, *35*, 1024–1035. doi:10.1111/j.1460-9568.2011.07980.x
- Connor, K. M., Kobak, K. A., Churchill, L. E., Katzelnick, D., & Davidson, J. R. T. (2001). Mini-SPIN: A brief screening

- assessment for generalized social anxiety disorder. *Depression and Anxiety*, *14*, 137–140. doi:10.1002/da.1055
- Davidson, R. J. (1984). Affect, cognition and hemispheric specialization. In C. E. Izard, J. Kagan, & R. Zajonc (Eds.), *Emotion, cognition and behavior* (pp. 320–365). New York, NY: Cambridge University Press.
- Davidson, R. J. (1988). EEG measures of cerebral asymmetry: Conceptual and methodological issues. *International Journal of Neuroscience*, *39*, 71–89. doi:10.3109/00207458808985694
- Davidson, R. J. (1992). Anterior cerebral asymmetry and the nature of emotion. *Brain and Cognition*, *20*, 125–151. doi:10.1016/0278-2626(92)90065-T
- Davidson, R. J., Coe, C. C., Dolski, I., & Donzella, B. (1999). Individual differences in prefrontal activation asymmetry predict natural killer cell activity at rest and in response to challenge. *Brain, Behavior, and Immunity*, *13*, 93–108. doi:10.1006/brbi.1999.0557
- Davidson, R. J., Ekman, P., Saron, C. D., Senulis, J. A., & Friesen, W. V. (1990). Approach-withdrawal and cerebral asymmetry: Emotional expression and brain physiology. *Journal of Personality and Social Psychology*, *58*, 330–341. doi:10.1037/0022-3514.58.2.330
- Davidson, R. J., & Fox, N. A. (1982). Asymmetrical brain activity discriminates between positive and negative affective stimuli in human infants. *Science*, *218*, 1235–1237. doi:10.1126/science.7146906
- Davidson, R. J., Jackson, D. C., & Larson, C. L. (2000). Human electroencephalography. In J. T. Cacioppo, L. G. Tassinary, & G. G. Berntson (Eds.), *Handbook of psychophysiology*, (Vol. 2, pp. 27–52). Cambridge, UK: Cambridge University Press.
- Davidson, R. J., Schwartz, G. E., Saron, C., Bennett, J., & Goleman, D. (1979). Frontal versus parietal EEG asymmetry during positive and negative affect. *Psychophysiology*, *16*, 202–203.
- Doll, B. B., & Frank, M. J. (2009). The basal ganglia in reward and decision making: Computational models and empirical studies. In J.-C. Dreher & L. Tremblay (Eds.), *Handbook of reward and decision making* (pp. 399–425). Oxford, UK: Academic Press.
- Doll, B. B., Jacobs, W. J., Sanfey, A. G., & Frank, M. J. (2009). Instructional control of reinforcement learning: A behavioral and neurocomputational investigation. *Brain Research*, *1299*, 74–94. doi:10.1016/j.brainres.2009.07.007
- Fellows, L. K., & Farah, M. J. (2005). Different underlying impairments in decision-making following ventromedial and dorsolateral frontal lobe damage in humans. *Cerebral Cortex*, *15*, 58–63. doi:10.1093/cercor/bhh108
- Frank, M. J., & Badre, D. (2012). Mechanisms of hierarchical reinforcement learning in corticostriatal circuits 1: Computational analysis. *Cerebral Cortex*, *22*, 509–526. doi:10.1093/cercor/bhr114
- Frank, M. J., Moustafa, A. A., Haughey, H. M., Curran, T., & Hutchison, K. E. (2007). Genetic triple dissociation reveals multiple roles for dopamine in reinforcement learning. *Proceedings of the National Academy of Sciences*, *104*, 16311–16316. doi:10.1073/pnas.0706111104
- Frank, M. J., Worocho, B. S., & Curran, T. (2005). Error-related negativity predicts reinforcement learning and conflict biases. *Neuron*, *47*, 495–501. doi:10.1016/j.neuron.2005.06.020
- Gable, P. A., Mechin, N. C., Hicks, J. A., & Adams, D. L. (2015). Supervisory control system and frontal asymmetry: Neurophysiological traits of emotion-based impulsivity. *Social Cognitive and Affective Neuroscience*, *10*, 1310–1315. doi:10.1093/scan/nsv017
- Gosling, S. D., Rentfrow, P. J., & Swann, W. B. Jr. (2003). A very brief measure of the big five personality domains. *Journal of Research in Personality*, *37*, 504–528. doi:10.1016/S0092-6566(03)00046-1
- Hajcak, G., Moser, J. S., Holroyd, C. B., & Simons, R. F. (2006). The feedback-related negativity reflects the binary evaluation of good versus bad outcomes. *Biological Psychology*, *71*, 148–154. doi:10.1016/j.biopsycho.2005.04.001
- Harmon-Jones, E. (2003). Clarifying the emotive functions of asymmetrical frontal cortical activity. *Psychophysiology*, *40*, 838–848. doi:10.1111/1469-8986.00121
- Harmon-Jones, E., & Allen, J. J. B. (1997). Behavioral activation sensitivity and resting frontal EEG asymmetry: Covariation of putative indicators related to risk for mood disorders. *Journal of Abnormal Psychology*, *106*, 159–163. doi:10.1037/0021-843X.106.1.159
- Harmon-Jones, E., & Allen, J. J. B. (1998). Anger and frontal brain activity: EEG asymmetry consistent with approach motivation despite negative affective valence. *Journal of Personality and Social Psychology*, *74*, 1310–1316. doi:10.1037/0022-3514.74.5.1310
- Harmon-Jones, E., & Amodio, D. M. (2012). Electroencephalographic methods in psychology. In H. Cooper, P. M. Camic, D. L. Long, A. T. Panter, D. Rindskopf, & K. J. Sher (Eds.), *APA handbook of research methods in psychology* (pp. 503–522). Washington, DC: American Psychological Association.
- Harmon-Jones, E., & Harmon-Jones, C. (2002). Testing the action-based model of cognitive dissonance: The effect of action orientation on postdecisional attitudes. *Personality and Social Psychology Bulletin*, *28*, 711–723. doi:10.1177/0146167202289001
- Harmon-Jones, E., Harmon-Jones, C., Abramson, L., & Peterson, C. K. (2009). PANAS positive activation is associated with anger. *Emotion*, *9*, 183–196. doi:10.1037/a0014959
- Harmon-Jones, E., Harmon-Jones, C., Fearn, M., Sigelman, J. D., & Johnson, P. (2008). Left frontal cortical activation and spreading of alternatives: Tests of the action-based model of dissonance. *Journal of Personality and Social Psychology*, *94*, 1–15. doi:10.1037/0022-3514.94.1.1
- Harmon-Jones, E., & Sigelman, J. (2001). State anger and prefrontal brain activity: Evidence that insult-related relative left-prefrontal activation is associated with experienced anger and aggression. *Journal of Personality and Social Psychology*, *80*, 797–803. doi:10.1037/0022-3514.80.5.797
- Harmon-Jones, E., Sigelman, J. D., Bohlig, A., & Harmon-Jones, C. (2003). Anger, coping, and frontal cortical activity: The effect of coping potential on anger-induced left frontal activity. *Cognition and Emotion*, *17*, 1–24. doi:10.1080/026999303022278
- Holroyd, C. B., & Coles, M. G. H. (2002). The neural basis of human error processing: Reinforcement learning, dopamine, and the error-related negativity. *Psychological Review*, *109*, 679–709. doi:10.1037/0033-295X.109.4.679
- Holroyd, C. B., Hajcak, G., & Larsen, J. T. (2006). The good, the bad and the neutral: Electrophysiological responses to feedback stimuli. *Brain Research*, *1105*, 93–101. doi:10.1016/j.brainres.2005.12.015
- Ichikawa, N., Siegle, G. J., Dombrovski, A. Y., & O'Hira, H. (2010). Subjective and model-estimated reward prediction: Association with the feedback-related negativity (FRN) and reward prediction error in a reinforcement learning task. *International Journal of Psychophysiology*, *78*, 273–283. doi:10.1016/j.ijpsycho.2010.09.001

- Jarbo, K., & Verstynen, T. D. (2015). Converging structural and functional connectivity of orbitofrontal, dorsolateral prefrontal, and posterior parietal cortex in the human striatum. *Journal of Neuroscience*, *35*, 3865–3878. doi:10.1523/JNEUROSCI.2636-14.2015
- Lindsley, D. B., & Wicke, J. D. (1974). The encephalogram: Autonomous electrical activity in man and animals. In R. Thompson & M. N. Patterson (Eds.), *Bioelectric recording techniques* (pp. 3–79). New York, NY: Academic Press.
- Master, S. L., Amodio, D. M., Stanton, A. L., Yee, C. M., Hilmert, C. J., & Taylor, C. (2009). Neurobiological correlates of coping through emotional approach. *Brain, Behavior, and Immunity*, *23*, 27–35. doi:10.1016/j.bbi.2008.04.007
- Miller, G. A., Crocker, L. D., Spielberg, J. M., Infantolino, Z. P., & Heller, W. (2013). Issues in localization of brain function: The case of lateralized frontal cortex in cognition, emotion, and psychopathology. *Frontiers in Integrative Neuroscience*, *7*, 1–9. doi:10.3389/fnint.2013.00002
- Nieuwenhuis, S., Holroyd, C. B., Mol, N., & Coles, M. G. H. (2004). Reinforcement-related brain potentials from medial frontal cortex: Origins and functional significance. *Neuroscience and Biobehavioral Reviews*, *28*, 441–448. doi:10.1016/j.neubiorev.2004.05.003
- Niv, Y., Daniel, R., Geana, A., Gershman, S. J., Leong, Y. C., Radulescu, A., & Wilson, R. C. (2015). Reinforcement learning in multidimensional environment relies on attention mechanisms. *Journal of Neuroscience*, *35*, 8145–8157. doi:10.1523/JNEUROSCI.2978-14.2015
- O'Doherty, J., Dayan, P., Schultz, J., Deichmann, R., Friston, K. J., & Dolan, R. J. (2004). Dissociable roles of ventral and dorsal striatum in instrumental conditioning. *Science*, *304*, 452–454. doi:10.1126/science.1094285
- O'Reilly, R. C., & Frank, M. J. (2006). Making working memory work: A computational model of learning in the prefrontal cortex and basal ganglia. *Neural Computation*, *18*, 283–328. doi:10.1162/089976606775093909
- Pizzagalli, D. A., Sherwood, R., Henriques, J. B., & Davidson, R. J. (2005). Frontal brain asymmetry and reward responsiveness: A source localization study. *Psychological Science*, *16*, 805–813. doi:10.1111/j.1467-9280.2005.01618.x
- Reuter-Lorenz, P., & Davidson, R. J. (1981). Differential contributions of the two cerebral hemispheres to the perception of happy and sad faces. *Neuropsychologia*, *19*, 609–613. doi:10.1016/0028-3932(81)90030-0
- Santesso, D. L., Evins, A. E., Frank, M. J., Cowman Schetter, E. M., Bogdan, R., & Pizzagalli, D. A. (2009). Single dose of a dopamine agonist impairs reinforcement learning in humans: Evidence from event-related potentials and computational modeling of striatal-cortical function. *Human Brain Mapping*, *30*, 1963–1976. doi:10.1002/hbm.20642
- Santesso, D. L., Steele, K. T., Bogdan, R., Holmes, A. J., Deveney, C. M., Meites, T. M., & Pizzagalli, D. A. (2008). Enhanced negative feedback responses in remitted depression. *NeuroReport*, *19*, 1045–1048. doi:10.1097/WNR.0b013e3283036e73
- Schmid, P. C., Kleiman, T., & Amodio, D. M. (2015). Neural mechanisms of proactive and reactive cognitive control in social anxiety. *Cortex*, *70*, 137–145. doi:10.1016/j.cortex.2015.05.030
- Schultz, W., Dayan, P., & Montague, P. R. (1997). A neural substrate of prediction and reward. *Science*, *275*, 1593–1599. doi:10.1126/science.275.5306.1593
- Silton, R. L., Heller, W., Towers, D. N., Engels, A. S., Spielberg, J. M., Edgar, J. C., ... Miller, G. A. (2010). The time course of activity in dorsolateral prefrontal cortex and anterior cingulate cortex during top-down attentional control. *NeuroImage*, *50*, 1292–1302. doi:10.1016/j.neuroimage.2009.12.061
- Sutton, S. K., & Davidson, R. J. (1997). Prefrontal brain asymmetry: A biological substrate of the behavioral approach and inhibition systems. *Psychological Science*, *8*, 204–210. doi:10.1111/j.1467-9280.1997.tb00413.x
- Towers, D. N., & Allen, J. J. B. (2009). A better estimate of the internal consistency reliability of frontal EEG asymmetry scores. *Psychophysiology*, *46*, 132–142. doi:10.1111/j.1469-8986.2008.00759.x
- Tucker, D. M. (1981). Lateral brain function, emotion, and conceptualization. *Psychological Bulletin*, *89*, 19–46. doi:10.1037/0033-2909.89.1.19
- Tucker, D. M., Stenslie, C. E., Roth, R. S., & Shearer, S. L. (1981). Right frontal lobe activation and right hemisphere performance: Decrement during a depressed mood. *Archives of General Psychiatry*, *38*, 169–174. doi:10.1001/archpsyc.1981.01780270055007
- van der Helden, J., Boksem, M. A. S., & Blom, J. H. G. (2010). The importance of failure: Feedback-related negativity predicts motor learning efficiency. *Cerebral Cortex*, *20*, 1596–1603. doi:10.1093/cercor/bhp224
- Wheeler, R. E., Davidson, R. J., & Tomarken, A. J. (1993). Frontal brain asymmetry and emotional reactivity: A biological substrate of affective style. *Psychophysiology*, *30*, 82–89. doi:10.1111/j.1469-8986.1993.tb03207.x
- Woolgar, A., Thompson, R., Bor, D., & Duncan, J. (2011). Multi-voxel coding of stimuli, rules, and responses in human frontoparietal cortex. *NeuroImage*, *56*, 744–752. doi:10.1016/j.neuroimage.2010.04.035
- Yeung, N., & Sanfey, A. G. (2004). Independent coding of reward magnitude and valence in the human brain. *The Journal of Neuroscience*, *24*, 6258–6264. doi:10.1523/JNEUROSCI.4537-03.2004

SUPPORTING INFORMATION

Additional supporting information may be found online in the supporting information tab for this article.

Table S1

Table S2

Table S3

Table S4

Table S5

Table S6

How to cite this article: Schmid PC, Hackel LM, Jasperse L, Amodio DM. Frontal cortical effects on feedback processing and reinforcement learning: Relation of EEG asymmetry with the feedback-related negativity and behavior. *Psychophysiology*. 2017;00:000–000. <https://doi.org/10.1111/psyp.12911>