Performing a Motor Action Enhances Social Reward Processing and Modulates the Neural Processing of Predictive Cues

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Abstract

■ Associative learning affects many areas of human behavior. Recently, we showed that the neural response to monetary reward is enhanced by performing an action, suggesting interactions between neural systems controlling motor behavior and reward processing. Given that many psychiatric disorders are associated with social anhedonia, a key open question is whether such effects generalize to social rewards, and in how far they affect associative learning. We developed a novel task in which participants ($n = 66$) received social reward feedback and social punishment either by pressing a button or waiting. Predictive cues were linked to feedback valence with 80% accuracy. Using EEG, we measured the neural response to both predictive cues and social feedback. We found enhanced reward positivity for social reward preceded by an action, and an enhanced N2 for cues predicting negative feedback. Cue-locked P3 amplitude was reduced for cues associated with negative feedback in passive trials only, showing a modulation of outcome anticipation by performing a motor action. This was supported by connectivity analyses showing stronger directed theta synchronization, in line with increased top–down modulation of attention, in active compared with passive trials. These findings suggest that actively obtaining social feedback enhances reward sensitivity and modulates outcome anticipation. ■

INTRODUCTION

Predicting, processing, and learning from rewards are key components of motivated behavior. Associative learning is a central aspect of reward-based decision-making, with studies showing interactions between Pavlovian (stimulus–reward) and instrumental (action–reward) learning. Specifically, several studies in animals and humans have shown that existing Pavlovian associations can influence instrumental learning (Cartoni, Balleine, & Baldassarre, 2016), in that it is easier for participants to learn approach–reward and avoidance–nonpunishment associations, than the reverse (i.e., learning to make an approach response to avoid punishment, or an avoidance response to gain a reward [Guitart-Masip et al., 2012]).

Recently, we presented evidence that, in turn, performing a motor action (a central component of instrumental behavior) can influence reward processing, a key aspect of Pavlovian learning (Bikute, Di Bernardi Luft, & Beyer, 2022). Participants showed a stronger reward-related response to monetary rewards, when the reward presentation was immediately preceded by a button press, compared with a passive condition. Crucially, participants had no control over trial outcomes, precluding the need for instrumental learning. Furthermore, connectivity analyses showed that performing a motor action affected the directionality of information flow during the outcome anticipation stage: whereas we observed top–down directed connectivity (frontal to occipital) in active trials, in passive trials connectivity was reversed, in line with bottom–up, stimulus-driven processing (Bikute et al., 2022). This directed connectivity effect was observed in the theta frequency band, which has been linked to performance monitoring processes and cognitive control (Cooper et al., 2015; Luft, Nolte, & Bhattacharya, 2013; Van de Vijver, Ridderinkhof, & Cohen, 2011). Higher flow from frontal to posterior areas have been associated with increased top–down control for processing performance outcomes. In this study, we expect that performing an action will increase the top–down directed connectivity just before the social feedback in a similar way than it was observed in a monetary reward task. These findings suggest that activity in neural systems involved in motor control enhances reactivity in neural systems of reward processing, which has important implications for our understanding of several mental health disorders. For example, theories of addiction focus on the acquisition of incentive salience, that is, the ability of environmental stimuli to induce craving-type motivational tendencies (Robinson & Berridge, 2001). If neural systems of reward processing are sensitized by preceding motor actions, this could for example explain the enhanced addictiveness of slot-machine style games, compared with other forms of gambling that have a longer gap between motor actions and game outcomes (MacLaren, 2016; Bakken, Götestam, Gråwe, Wenzel, & Øren, 2009). Furthermore, depression

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is commonly characterized by symptoms of anhedonia (reduced sensitivity to, and/or motivation to obtain reward; Coccurello, 2019), as well as apathy (reduced levels of activity; Chase, 2011). On the basis of our findings (Bikute et al., 2022), one theory might be that apathy might in fact exacerbate symptoms of anhedonia, because of a lack of motor behavior reducing the sensitivity of neural reward systems.

However, before further exploring the implications of these findings for our understanding of mental health, it is important to distinguish between different types of rewards. In our previous study, we used monetary rewards, which have been shown to elicit robust and reliable neural responses (Kahnt, 2018). However, many psychiatric disorders are associated with particular deviations in the processing of social reward (Ait Oumeziane, Jones, & Foti, 2019). Thus, it is important to understand whether the link between motor actions and reward processing generalizes to social feedback. The current study investigated the effects of interest in healthy populations, to form the foundation for studies in clinical samples.

Previous studies have shown that monetary and social rewards are processed by overlapping, but partially distinct, neural systems (Gu et al., 2019; Levy & Glimcher, 2012; Rademacher et al., 2010). Many studies (e.g., Banica, Schell, Racine, & Weinberg, 2022; Pegg, Lytle, Arfer, & Kujawa, 2022; Pegg, Arfer, & Kujawa, 2021; Distefano et al., 2018) exploring the neural response to monetary and social reward in clinical and healthy populations have utilized EEG to measure ERPs. ERP components of particular interest are the Reward-related positivity (RewP) reflecting the neural response to reward (Holroyd, Pakzad-Vaezi, & Krigolson, 2008), and the feedback-related negativity (FRN), calculated as the difference in the neural response to negative (i.e., punishment) versus positive (reward) feedback (San Martín, 2012; Miltner, Braun, & Coles, 1997). Both components are measured between 200 and 350 msec post outcome onset, at fronto-central sites, and are believed to reflect sensitivity to feedback or action outcomes. In fact, although the FRN is traditionally seen as a neural response to negative feedback, its typical negative-going amplitude can be observed as a consequence of a positive deflection in response to reward, which is reduced in response to negative outcomes or nonreward (Foti, Weinberg, Dien, & Hajcak, 2011). As such, at least in some task setups, FRN (calculated as the punishment–reward difference) and RewP can reflect a joint, reward-driven neural process.

Another outcome-locked component of interest is the P3, which is thought to reflect motivational aspects of outcome processing (Glazer, Kelley, Pornpattananangkul, Mittal, & Nusslock, 2018; San Martín, 2012).

Although these ERP components are consistently observed for both monetary and social rewards, some studies find stronger neural responses to monetary than social reward feedback (Wang, Liu, & Shi, 2020; Ethridge et al., 2017). However, in line with specific deficits in social reward processing in mental health disorders, found reduced FRN and P3 amplitudes in participants with depression compared with controls for social, but not monetary, rewards. Similarly, adolescents who had experienced peer victimization—an important risk factor for later depression—showed reduced RewP in response to signals of social acceptance compared with control adolescents, but no difference in the neural response to monetary reward. In contrast, acute, mild forms of experimentally induced social exclusion enhanced the RewP in response to social (but not monetary) rewards.

Although at the group level in nonclinical populations neural responses to monetary and social reward tend to be similar (Distefano et al., 2018), individual differences in domain-specific (e.g., predominantly social) anhedonia are associated with corresponding domain-specific reductions in neural reward sensitivity (Banica et al., 2022). In line with this, research shows specifically reduced social reward sensitivity in participants with depression linked to the experience of social conflict (Hill et al., 2023). However, this relationship seems to be complex considering that depressive symptoms were found to be associated with an interaction between low reward responsiveness and high rejection sensitivity in a nonclinical population (Pegg et al., 2021).

These findings suggest that the distinction between monetary and social rewards is crucial when studying links between reward processing and mental health, as group differences can be specific to one reward type. Thus, in the current study, we aimed to explore whether our previous findings of motor behavior enhancing reward processing generalize to social rewards. This will be crucial for future models of links between action performance and outcome processing in general associative learning, as well as in the development and maintenance of mental health disorders. A potential added benefit when using social rather than monetary feedback in reward processing research is that issues of subjectivity associated with monetary value can be avoided. Monetary rewards will be of greater subjective value for participants with low or no income (as is often the case in studying student populations), compared with groups of interest with stable income (Ferdinand & Czernochowski, 2018). Where sensitivity to social feedback varies between populations, in many cases, this will be an effect of interest rather than a confound.

Besides its exclusive focus on monetary reward, a further limitation of our previous study was that cues signaling the likelihood of positive versus negative outcomes were conflated with cues signaling the need for a motor action. Thus, we could not study whether the neural response to reward cues differed for active versus passive trials, independently of the motor preparation seen in active trials. Thus, a secondary aim of the current study was to address this issue by separating outcome cues from action cues. This allowed us to study whether cue-locked

ERPs differed for cues predicting reward and punishment in active versus passive trials.

Several components of interest have been identified for predictive cues in reward learning tasks (Glazer et al., 2018): The early negative N2 component is commonly found to be sensitive to the valence of predictive cues, with more negative amplitudes found for cues predicting punishment compared with reward (Pornpattananangkul & Nusslock, 2015; Dunning & Hajcak, 2007). The cue-locked P3 component is believed to reflect attentional processes (Glazer et al., 2018) with evidence for enhanced amplitude in response to cues that predict either win or loss, compared with neutral cues (Novak & Foti, 2015), although effects can be stronger for reward cues than loss cues (Pfabigan et al., 2014).

Thus, to study the neural processing of both reward cues and outcomes for social rewards, we modified our previously developed task, such that participants experienced social reward feedback (a smiling face) or social punishment (an unhappy face). Two conditions were randomized on a trial-wise basis: an active condition, in which the outcome was immediately preceded by a button press, and a passive condition, in which the outcome was preceded by a short waiting period. This allowed us to test whether similarly to monetary reward, performing a motor action in the absence of instrumental choice enhances the neural sensitivity to social reward. Each trial was preceded by a cue, which deterministically predicted trial type (active vs. passive) and probabilistically predicted trial outcome. This allowed us to test whether participants formed stimulus–outcome associations (reflected in differential neural responses to positive vs. negative cues), and whether this differed for active versus passive trials.

On the basis of the above findings, we formed three hypotheses: H1: Outcome processing—reflected in RewP and FRN amplitudes—is enhanced for outcomes in active compared with passive trials. H2: As participants learn to associate predictive cues with outcome probabilities, cue-locked N2 amplitude is enhanced for negative compared with positive cues, with a stronger effect for active trials. H3: Cue-locked P3 amplitude is enhanced in response to cues associated with active trials, compared with passive trials, regardless of cue valence. H4: Theta phase synchronization from frontal to posterior areas (top–down) will increase preceding the presentation of social feedback in active compared with passive trials, whereas in passive trials, we will observe the reverse: a stronger flow from posterior to frontal areas (bottom–up modulation).

METHODS

Participants

Seventy-six participants took part in this study. The sample size was determined based on a separate study for which data were collected (see Procedures section below), which analyzed hyperscanning data, thus requiring a larger sample. Two data sets were incomplete because of technical failure during recording, and a further eight data sets were excluded based on artifact rejection criteria (see EEG processing below). Thus, 66 data sets were included in the analysis. On the basis of the effect size observed in our previous study ($d = .38$), a sample of $n = 56$ was required to achieve 80% power in a two-tailed t test with $\alpha < .05$.

Participants were recruited from local student populations via posters, email, and word of mouth. All participants were healthy adults (20 male participants, 56 female participants; age 18–33 years; because of experimenter error, age was only recorded for 39 participants, with a mean age of 22 years and a standard deviation of 2.55 years). No data on ethnicity were collected. The study was approved by the local ethics committee (PSY2022–33).

Unexpected Visitor Task

We used an adapted version of the task published in Bikute and colleagues (2022). As a narrative for this task, participants were instructed to imagine that they would be paying unannounced visits to the houses of four different friends. Upon arrival, they would either find the door to the house open, or closed; in the latter case, they should "ring the doorbell" by pressing the spacebar on a keyboard. Their friend would then "answer the door" and either be happy about their unexpected visit (i.e., smiling) or be unhappy. Participants were not instructed to imagine specific friends.

The trial outline is shown in Figure 1. At the beginning of each trial, participants saw the drawing of a house, marked by a squared fractal image. This was presented for 2 sec, followed by the presentation of the drawing of a door. Either an open door was shown for 1.5 sec or a closed door was shown, until participants pressed the spacebar of a standard computer keyboard. Following this, a blank screen was shown for 0.5–1 sec, followed by the outcome presentation for 1 sec. The outcome consisted of the drawing of a person standing in an open doorframe, either smiling or showing an unhappy expression. The intertrial interval was 1.5–2 sec.

The four trial types (active – happy friend, active – unhappy friend, passive – happy friend, and passive – unhappy friend) were mixed randomly. There were four different fractals presented on the houses: a fractal always shown in active trials, and in 80% of trials followed by a positive outcome ("active – happy"); a fractal always shown in active trials, and in 80% of trials followed by a negative outcome ("active – unhappy"); and the corresponding fractals for passive trials ("passive – happy"; "passive – unhappy"). Because of a programming error, allocation of the different fractals to the experimental conditions was not counterbalanced, which we controlled for in our cue-locked ERP analyses (see Results section for detail).

Participants completed 120 trials (30 trials per condition), split into two blocks with a short break in between.

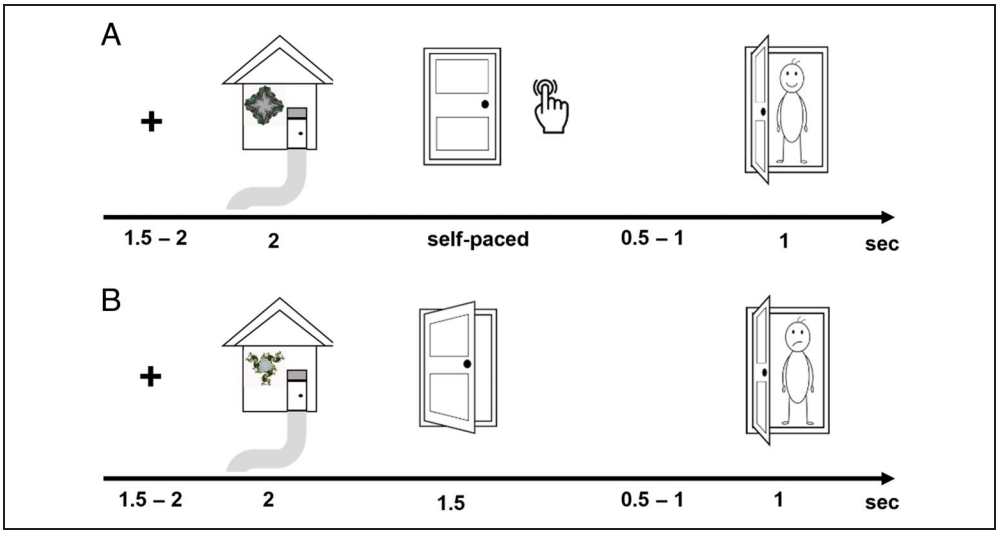

Figure 1. Task outline. Figure shows example trial outlines, with an active trial with positive outcome (A) and a passive trial with negative outcome (B).

Procedures

Participants took part in this study in pairs, as the session also involved collecting data for an unrelated hyperscanning study. After providing informed consent and setting up the EEG systems and caps, participants completed a task unrelated to this study. This involved participants completing socioeconomic decision-making tasks with and without eye contact, for about 20 min. Participants then received written instructions for the unexpected visitor task. This task was completed individually, and eye contact between participants was prevented by blocking the view between participants with their computer monitors. Thus, participants were not communicating during the task, and although they began the task at the same time, they moved through it at their individual pace. Therefore, we did not conduct pairwise analyses for this task.

After completing the unexpected visitor task, participants completed other tasks and questionnaires not reported here. At the end of the session, which in total lasted about 2 hr, participants were debriefed about the study aims and reimbursed for their participation with payment (£8 per hour).

EEG Recording and Signal Processing

EEG signal was recorded using an 20-channel Starstim system (Neuroelectrics) using saline-based conductive gel. Eighteen electrodes were positioned on the scalp based on the standard 10–20 positions and 2 electrodes were positioned on the earlobes using ear clips.

The EEG signal was rereferenced offline to the averaged signal of the two earlobes. The continuous signal was then highpass filtered at 0.5 Hz and lowpass filtered at 20 Hz. Epochs were created around the onsets of cues, that is, the house stimulus at the beginning of each trial (50 msec prestimulus – 1000 msec post stimulus) and the onset of the outcome, that is, the appearance of the friend (50 msec prestimulus –1000 msec post stimulus) and references to the prestimulus period. Independent component analysis was used to identify and remove eye blink and eye movement artifacts. Then, remaining artifacts were identified using a 100-mV threshold and epochs with artifacts excluded from analysis. Participants with > 20% of removed trials were excluded from further analysis (n = 8).

Planned ERP Analyses

Epochs for the cue processing were averaged according to the four cue types (active – "happy"; active – "unhappy"; passive – "happy"; passive – "unhappy"). As cue-based ERPs do not universally distinguish between reward- and punishment-associated cues, we averaged ERPs across all four task conditions (positive and negative valence, as well as active and passive trials) at electrode CZ, to determine ERP time windows (Figure 2A). Electrode CZ was chosen as we had no strong a priori hypotheses as to whether N2- or P3-type components would be more sensitive to task condition, and although cue-locked N2 is typically observed at fronto-central locations, P3 topography tends to be variable with centro-parietal distribution (Glazer et al., 2018). This showed three components of interest: a cue-based N2, which peaked at 282 msec and for which we analyzed the average amplitude between 250 and 330 msec; a cue-based P3, which peaked at 346 and for which we analyzed the average amplitude from 330 to 460 msec; and a second positive deflection peaking at 602 msec. This resembled a late positive potential (LPP) and was analyzed at 560–690 msec. We analyzed the three ERPs in 2 × 2 ANOVAs with the within-subject factors Condition (active vs. passive) and Associated Cue Value (good vs. bad).

To replicate and expand our ERP analyses from Bikute and colleagues (2022), epochs for outcome processing were averaged based on the four trial types (active – happy friend, active – unhappy friend, passive – happy friend, and

passive – unhappy friend). On the basis of our own and others' previous findings, we focused this analysis on electrode FZ, as FCZ was not included in the electrode grid. To establish the time window for FRN analysis, we computed the average FRN (unhappy – happy friend) at electrode FZ, averaged across task conditions (Figure 3A). This showed the maximum peak at 228 msec, and we averaged the amplitude between 210 and 270 msec. We then entered mean amplitudes for this time window into a 2 × 2 ANOVA with the within-subject factors Outcome (happy vs. unhappy) and Condition (active vs. passive).

Directed Connectivity Analysis

We compared the directed connectivity between passive and active trials based on the findings of our previous study (Bikute et al., 2022). First, we measured directed connectivity using the phase slope index (PSI), which is a robust measure of directed phase synchronization between two channels (Nolte et al., 2008) in the theta frequency band (4–8 Hz) in the period preceding the presentation of the social feedback, which is where we expected the strongest changes. Second, we extracted the PSI values for each condition (passive, active, negative, and positive feedback) in the time window before and after the feedback in the clusters we found in our previous study (Bikute et al., 2022). In the current study, we tested whether the same findings would replicate to social feedback: reverse phase synchronization direction, from front to back (top–down) for active trials, and back to front (bottom–up) for passive trials just before the feedback (−300 msec to feedback). Because we used a lower density system (18-channels), we selected the channels that were significant in each cluster. For Cluster 1 (C1, active cluster in our

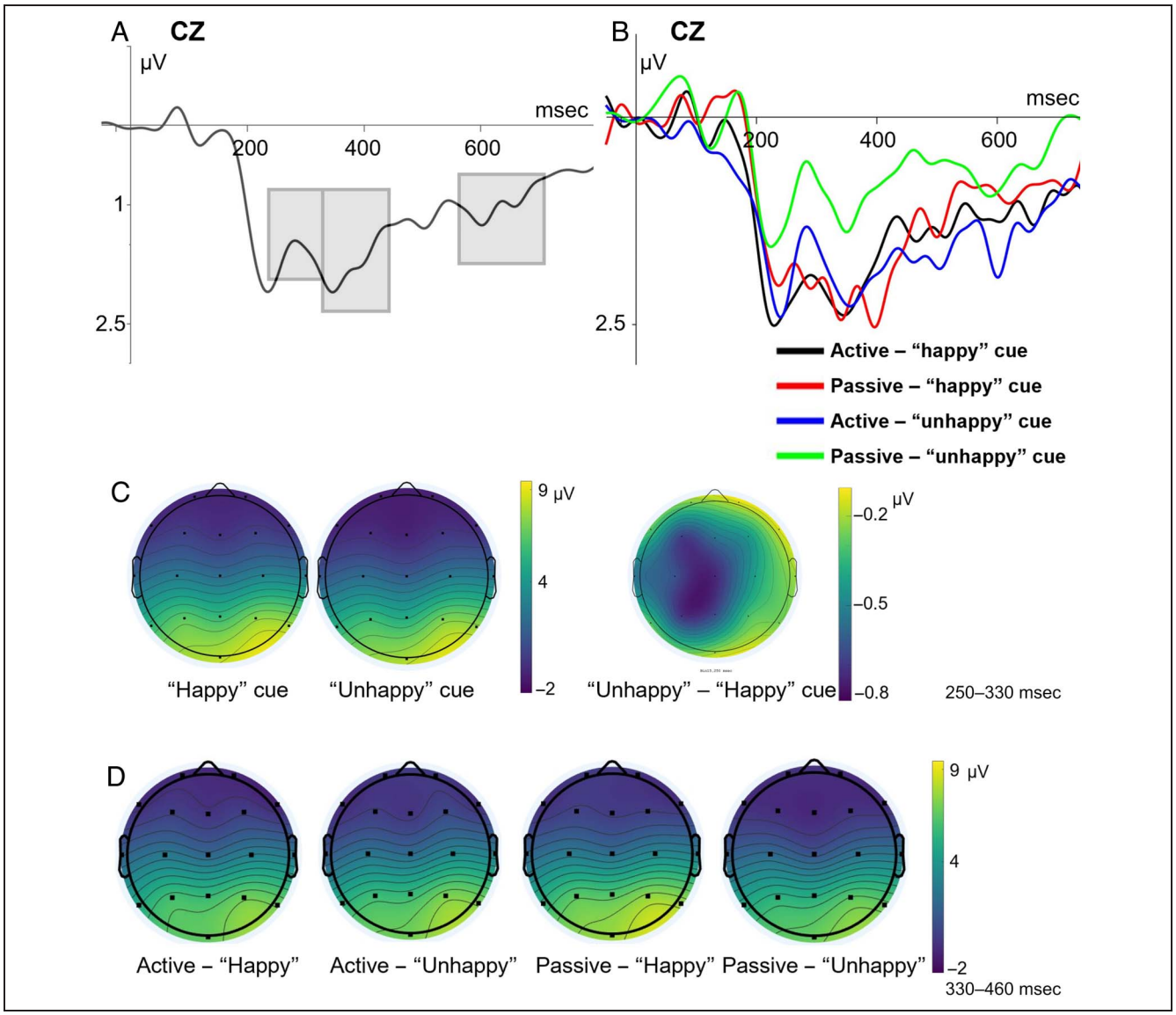

Figure 2. Cue-locked ERPs at electrode CZ. (A) Cue-locked average amplitude across all conditions. (B) Amplitudes shown separately for the four experimental conditions. Topographical maps are shown for the N2 time range (C) and the early P3 time range (D).

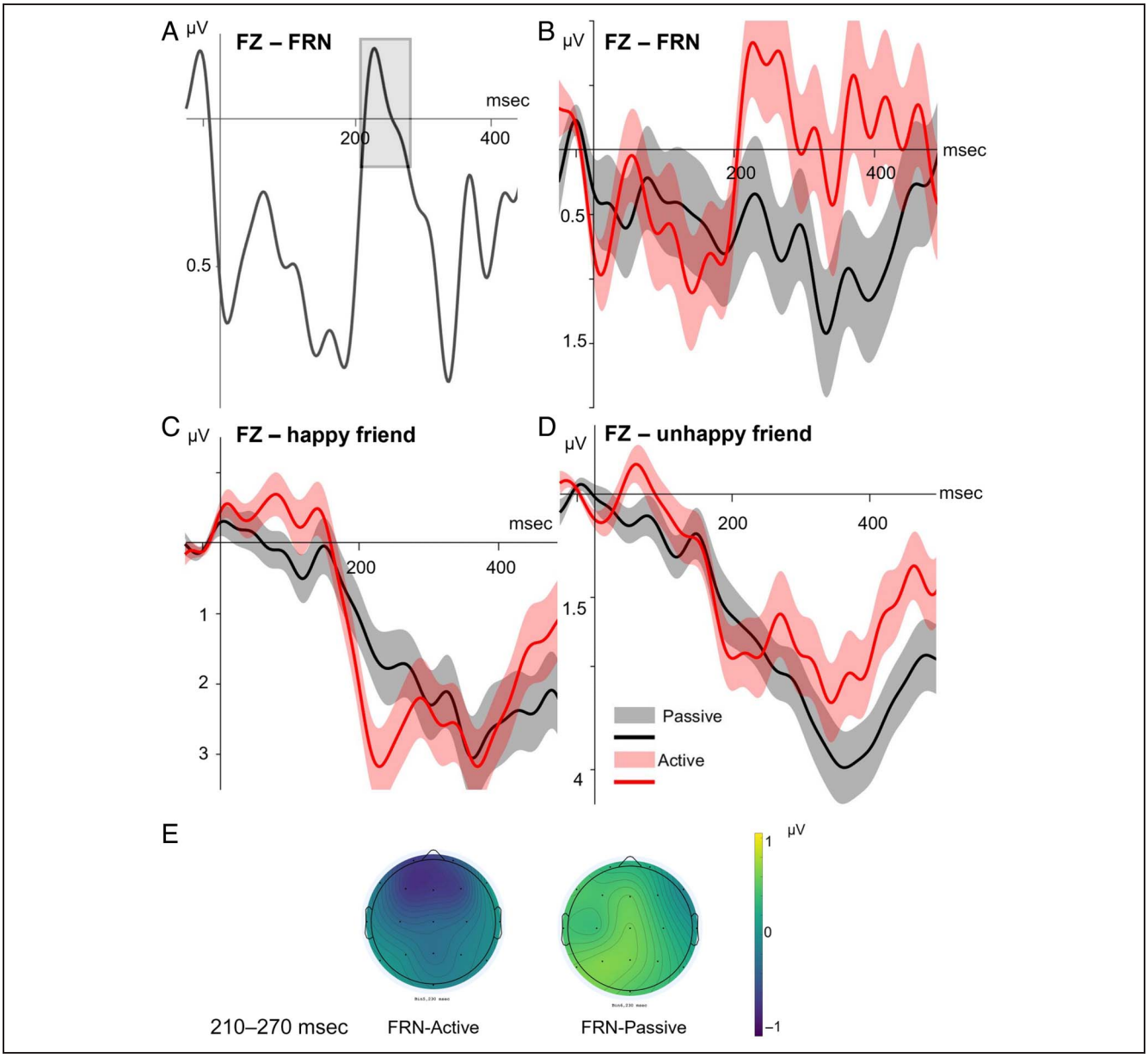

Figure 3. Outcome-locked ERPs at electrode FZ. (A) FRN amplitude (unhappy friend – happy friend amplitude) across active and passive trials. (B) FRN for active and passive conditions. (C) The average amplitude for positive outcomes (happy friend) for active and passive trials. (D) Amplitudes for negative outcomes (unhappy friend). (E) Topographical maps for the FRN amplitudes (unhappy – happy friend ERPs).

previous article), we calculated the average PSI from all the frontal electrodes significant in the previous cluster (F3, F7, Fz, F4, F8, Fp1, Fp2) to the lateral posterior areas (T7, T8, P3, P4, P8). We did not select specific significant electrode pairs, but we simply averaged all the frontal to lateral posterior connections in these electrodes (mainly because of the slightly different electrode montages). We did the same for Cluster 2 (C2) in our article (passive cluster); we calculated the connectivity from mid-posterior (Oz, Pz, P4) to frontal (Fz, F3, F4, F7). This approach of averaging across multiple electrodes was chosen to allow for a direct comparison of results to our previous findings, and to avoid issues of multiple comparison. We then entered them in a 2 (Outcome: happy vs. unhappy friend) × 2 (Condition: active vs. passive) ANOVA for each cluster separately. On the basis of our previous findings, we expected a main effect of Condition but no interaction with Outcome, for both clusters.

RESULTS

Cue-locked ERPs

We analyzed three components of interest at electrode CZ: a cue-based N2 between 250 and 330 msec, an early P3 (330–460 msec), and a late P3 component (560–690 msec;

Figure 2A). We analyzed the three ERPs in 2 × 2 ANOVAs with the within-subject factors Valence (positive vs. negative) and Condition (active vs. passive; Table 1).

For the N2, we found a significant effect of Valence, but no effect of Condition, and no Valence × Condition interaction (Table 1). Across conditions, the N2 amplitude was more negative for stimuli associated with negative outcomes ($M = 1.25$, $SD = 4.21$) than for stimuli associated with positive outcomes, $M = 2.02$, $SD = 4.16$; $t(65) = 2.46$, $p = .017$ (Figure 2B).

For the P3, we found no main effect of Valence and no main effect of Condition, but a significant Valence × Condition interaction (Table 1). Post hoc analyses (Table 2) showed a reduced P3 amplitude for passive cues associated with negative outcomes ($M = .90$, $SD = 4.14$), compared with the other stimuli (active – "unhappy" $M = 1.93$, $SD = 4.83$; passive – "happy" $M = 2.09$, $SD = 4.57$; active – "happy" $M = 1.79$, $SD = 4.34$; Figure 2B).

Electrode CZ was chosen a priori, but P3 and LPP components are observed with topographies varying between centro-parietal locations. Thus, we conducted post hoc t tests comparing P3 and LPP amplitudes between CZ and PZ. This showed a stronger P3 amplitude at PZ ($M = 5.64$, $SD = 4.24$) than CZ ($M = 1.68$, $SD = 3.01$), $t(65) =$

Table 1. Test Statistics for Planned ERP Analyses

	df	*F value*	*p Value*	*Partial Eta Square*
Cue-locked at CZ				
N2, 250–330 msec				
Valence	1, 65	6.04	.017	.085
Condition	1, 65	2.18	.145	.032
Valence × Condition	1, 65	2.17	.146	.032
P3, 330–460 msec				
Valence	1, 65	2.81	.098	.041
Condition	1, 65	1.41	.239	.021
Valence × Condition	1, 65	4.56	.036	.066
Late PP, 560–690 msec				
Valence	1, 65	0.02	.902	<.001
Action	1, 65	2.04	.158	.030
Valence × Condition	1, 65	0.52	.473	.008
Cue-locked at PZ				
P3, 330–460 msec				
Valence	1, 65	5.11	.027	.073
Condition	1, 65	<0.01	.996	<.001
Valence × Condition	1, 65	3.82	.055	.056
Late PP, 560–690 msec				
Valence	1, 65	<0.01	.984	<.001
Action	1, 65	0.57	.451	.009
Valence × Condition	1, 65	0.05	.832	.001
Outcome-locked at FZ				
FRN, 210–270 msec				
Condition	1, 65	2.40	.127	.036
Outcome	1, 65	.07	.791	.001
Condition × Outcome	1, 65	4.74	.033	.068

Table 2. Post Hoc Comparison Test Statistics for Cue-locked ERPs

Comparison	*df*	*t Value*	*p Value*
Passive "unhappy" vs. Active "unhappy"	65	−2.62	.011
Passive "unhappy" vs. Passive "happy"	65	−2.90	.006
Passive "unhappy" vs. Active "happy"	65	−2.08	.042

12.11, $p < .001$. We thus repeated the same 2 × 2 ANOVA as above for electrode PZ, showing a main effect of Valence, no effect of Condition, and the Valence × Condition interaction approaching significance (Table 1). For the LPP, there was also a significant difference with a more positive amplitude at PZ ($M = 2.97$, $SD = 3.0$) than CZ ($M = 1.04$, $SD = 2.81$), $t(65) = 9.28$, $p < .001$. The corresponding ANOVA for PZ showed no significant effects (Table 1).

For the LPP, we found no significant effect for Valence or Condition, nor a significant Valence × Condition interaction.

Control Analyses

As the cue stimuli had not been randomized across conditions, we ran a check whether stimulus properties themselves could have elicited differing N2 amplitudes. To test this, we calculated N2 amplitudes for "happy" and "unhappy" cues (collapsed across active and passive conditions) for the first half of the task only, when participants had had less opportunity to learn the associated stimulus values. This showed no significant difference in amplitude between "happy" ($M = 1.75$, $SD = 4.79$) and "unhappy" ($M = 1.53$, $SD = 4.79$) cues, $t(65) = 0.53$, $p = .600$.

In contrast, analyzing the second half of the task, only, showed the expected difference in amplitude between "happy" ($M = 2.23$, $SD = 4.32$) and "unhappy" ($M = 0.93$, $SD = 4.28$) cues, $t(65) = 2.82$, $p = .006$.

Outcome-locked ERPs

For the FRN time window of 210–270 msec, the 2 × 2 ANOVA with the within-subject factors Outcome (happy vs. unhappy friend) and Condition (active vs. passive) showed no significant effect for Outcome, nor Condition, but a significant Condition × Outcome interaction (Table 1). As can be seen in Figure 3, this interaction was because of a pronounced RewP signal that was present in the active, but not the passive, condition, reflected in a significantly more positive signal for positive (happy friend) outcomes (Figure 3C) in active ($M = 2.88$, $SD = 4.24$) compared with passive trials ($M = 1.67$, $SD = 3.65$), $t(65) = 2.52$, $p = .014$, but no difference between active ($M = 2.18$, $SD = 4.45$) and passive ($M = 2.23$, $SD = 3.05$) conditions for negative (unhappy friend) outcomes, $t(65) = -0.11$, $p = .913$ (Figure 3D). Post hoc power analysis for the

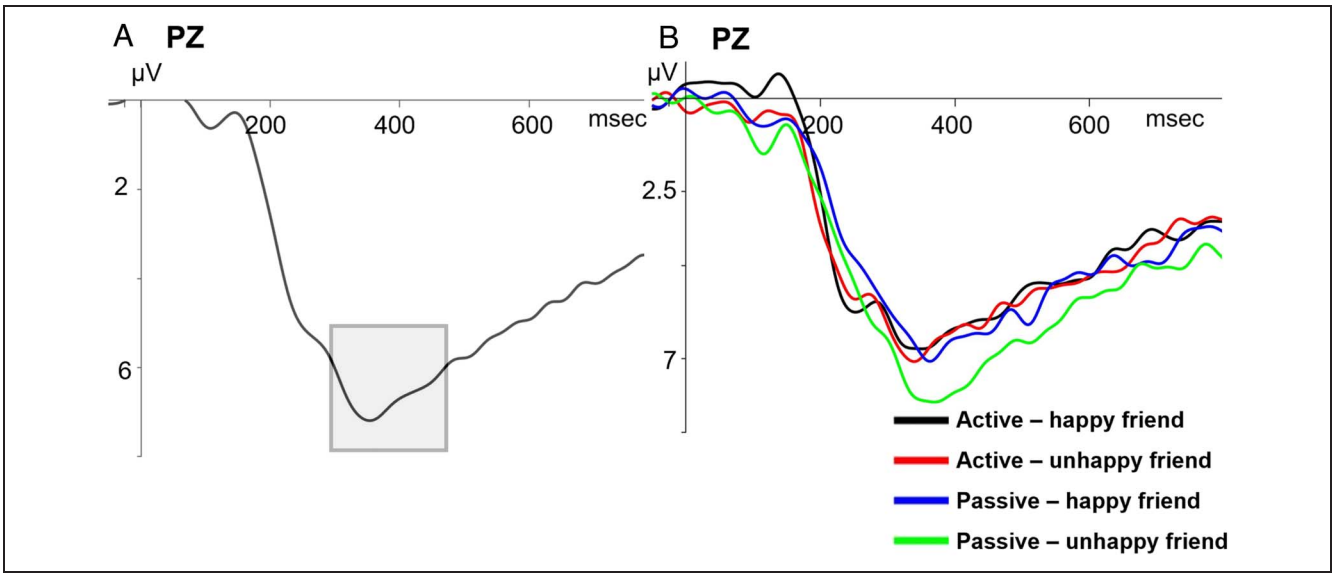

Figure 4. Outcome-locked ERPs at electrode PZ. (A) Average amplitude across all conditions. (B) Outcome-locked amplitudes for the four conditions.

Table 3. Test Statistics for Outcome-locked Exploratory Analyses

Outcome-locked at PZ	*df*	*F value*	*p Value*	*Partial Eta Square*
P3, 290–480 msec				
Condition	1, 65	4.26	.043	.062
Outcome	1, 65	4.03	.049	.058
Condition × Action	1, 65	3.64	.061	.053

main comparison of interest (active-positive vs. passive-positive; Cohen's $d = 0.311$) showed a critical t value of $t = 1.67$ and achieved a power of $1 - \beta = .804$ for a one-sided t test with $p < .05$.

Exploratory Analyses

To explore ERPs of interest beyond the FRN, we averaged the outcome-locked signal across all task conditions and inspected the signal at electrodes FZ, Cz, and PZ, which showed primarily a P3-like component that was strongest at PZ (Figure 4A). On the basis of the ERP shown for electrode PZ, we selected the time window of 290–480 msec for the primary P3 ERP. We then entered the average amplitudes for this time-window into a 2 × 2 repeated measures ANOVA, as for the FRN analysis (Table 3).

This showed a main effect of Condition and a main effect of Outcome. Although the Condition × Outcome

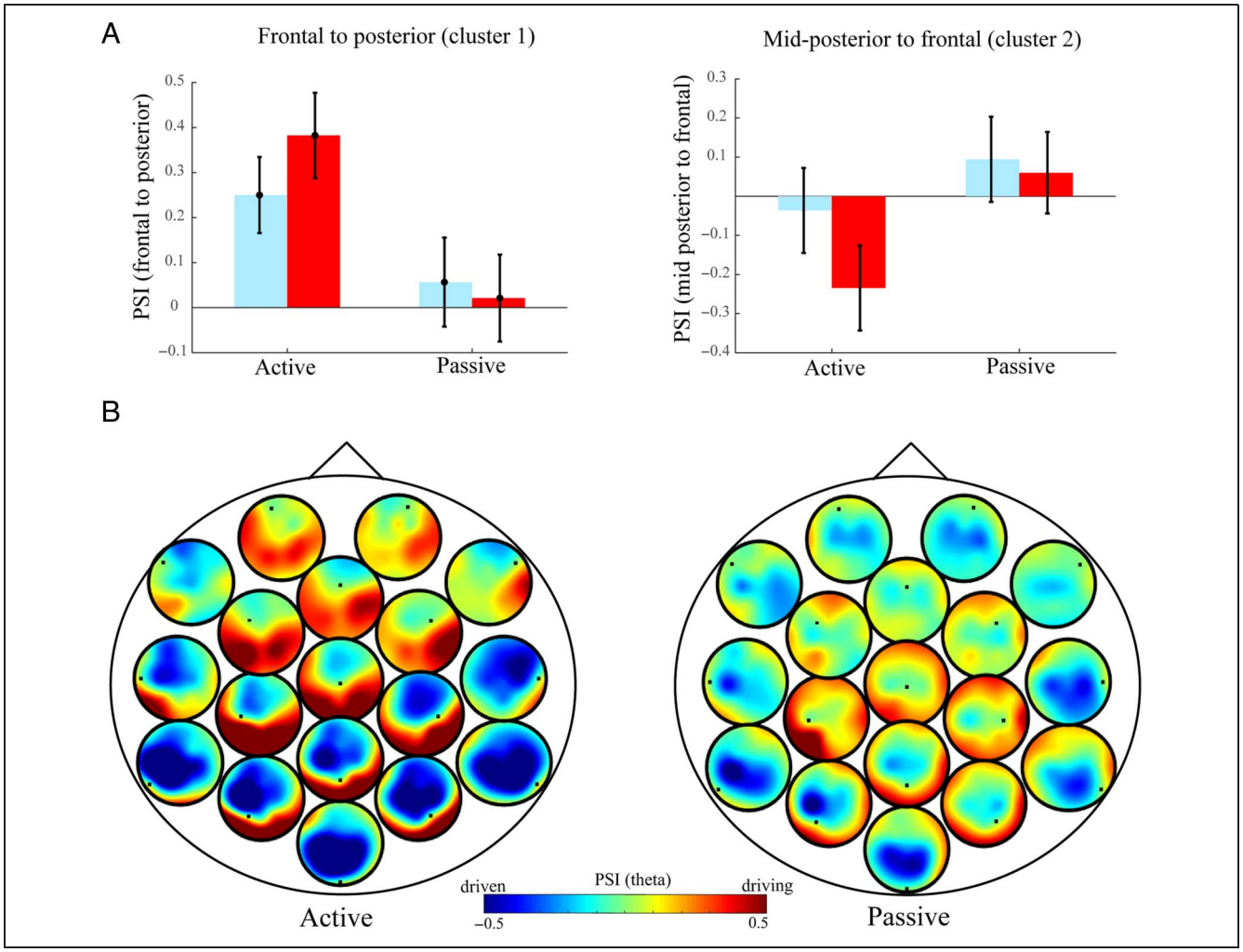

Figure 5. Directed connectivity in the theta frequency range (4–8 Hz). (A) Mean PSI values from frontal to posterior regions (C1: higher values mean higher top–down flux) and from mid-posterior to frontal regions (C2: higher values mean higher bottom–up flux). (B) Topographical distribution of the directed synchronization values (all-to-all) in active (left-hand side) and passive (right-hand side) trials (−300 msec to feedback). Each individual topoplot display the synchronization between that particular electrode (displayed as a dot) and all the others, whereas red colors represent the regions where this electrode is driving, whereas blue colors represent areas which this electrode is being driven by.

interaction was not significant, as is evident in Figure 4B, the main effects were primarily driven by an increased P3 amplitude in the passive–unhappy friend condition.

Directed Connectivity Analyses

We entered the theta PSI values for C1 (from frontal to posterior) in a 2 (Condition: active vs. passive) × 2 (Outcome: happy vs. unhappy friend) ANOVA to replicate our previous findings showing that active trials are associated with the opposite direction of theta synchronization compared with passive trials. We expected higher flow from frontal to posterior areas in the active compared with the passive feedback trials. For C1, we observed a significant main effect of Condition, $F(1, 65) = 7.81$, $p = .007$, $\eta_p^2 = .107$, but no effect of Outcome, $F(1, 65) = .73$, $p = .395$, $\eta_p^2 = .011$, nor interaction, $F(1, 65) = 1.52$, $p = .222$, $\eta_p^2 = .023$. On Figure 5A, it is clear that this effect can be explained by a higher phase synchronization (theta PSI) from frontal to posterior areas in the active compared with the passive conditions.

For C2, we also observed a significant main effect of Condition, $F(1, 65) = 4.53$, $p = .037$, $\eta_p^2 = .065$, but no effect of Outcome, $F(1, 65) = 1.49$, $p = .227$, $\eta_p^2 = .022$, nor interaction, $F(1, 65) = 0.72$, $p = .398$, $\eta_p^2 = .011$. On Figure 5B, it is possible to see that these effects might not being driven by strong bottom–up connectivity in the passive trials, but by the difference in flow direction between the two (as the highest value is negative, for active negative trials), because there is a partial overlap in the electrode pairs.

DISCUSSION

In this study, we investigated whether performing a motor action enhances the neural processing of social reward and whether this in turn affects the processing of predictive cues. In line with previous findings on the processing of monetary rewards, we found that after performing a button press, compared with a passive waiting period, the reward positivity (RewP) signal in response to positive social feedback was enhanced. We further found a stronger N2 component in response to predictive cues associated with negative feedback, compared with positive cues, and a reduced P3 component in response to passive cues associated with negative feedback. Finally, we found that active trials were associated with higher phase synchronization from the frontal to the posterior areas (top–down modulation) just before the presentation of the social feedback, which replicates the findings from our previous study using monetary rewards.

Performing a Motor Action Enhances the Neural Sensitivity to Social Feedback

Our core finding of an enhanced RewP in active trials is in line with our previous findings for monetary win outcomes (Bikute et al., 2022). Thus, at the neural level, participants appeared to be more sensitive to social feedback when they had brought about that response through their own motor behavior. As in our previous study, participants had no active control over the outcome in a given trial, as they only had one button to press. Thus, performing a motor action enhances the neural processing of social feedback above and beyond any effects of active choice or instrumental learning. We replicated our previous findings showing that performing a motor action increases theta synchronization from frontal to posterior areas, which could suggest a stronger level of top–down modulation just before the outcome is presented. This increase in top–down control might increase people's attention to the outcomes and therefore modulate the neural responses to them. However, in passive trials, we did not observe the same bottom–up (posterior to frontal) cluster as in our previous study. The direction of the theta synchronization preceding feedback was not reversed in passive trials during the social feedback task. This could suggest that perhaps social feedback is associated with higher top–down modulation preceding feedback, although this requires a further study directly comparing social and monetary feedback.

Previous studies have similarly shown a reduced reward positivity for task conditions in which participants made no overt actions (Stewardson & Sambrook, 2021; Hassall, Hajcak, & Krigolson, 2019; Yeung, Holroyd, & Cohen, 2005). However, in these studies, blocked designs were used. In such designs, attentional processes arguably would be expected to greatly affect participants' outcome monitoring, as they would be aware that no response is required for several minutes. In Hassall and colleagues' study, there was also no learning incentive as cues did not predict outcomes, thus likely further reducing attention in passive blocks. In line with this, this study showed overall reduced ERP amplitudes to outcome presentation, including P300 (Hassall et al., 2019). In contrast, using a trial-wise design, we find a specific reduction in reward positivity in response to passively presented rewarding stimuli.

Links between motor behavior and neural sensitivity to social reward could have important implications for our understanding of mental health disorders associated with social anhedonia (Yang, Guo, Harrison, & Liu, 2022; Feng, Jiang, Li, Liu, & Wu, 2020; Kupferberg, Bicks, & Hasler, 2016; Rey, Jouvent, & Dubal, 2009). Future studies should explore whether reduced sense of agency—that is, reduced feelings of action control—observed in depression are associated with a reduced impact of motor behavior on social reward processing, opening up new avenues for understanding causes and potential treatments for depression-related symptoms of social anhedonia, a key transdiagnostic symptom of mental health disorders (Porcelli et al., 2019).

In an exploratory analysis, we further found an enhanced P3 amplitude for passive trials, which appeared most pronounced for negative outcomes. Given the observation of reduced P3 amplitude in response to passive-negative predictive cues, a possible explanation

for this finding is that a lack of associative learning for this condition leads to more unpredicted outcomes, as discussed below.

Predictive Cues Acquire Associated Valence

In line with previous research (Glazer et al., 2018), we found that predictive cues presented ahead of the action or waiting period were processed differently depending on their associated value. Specifically, we found an enhanced N2 amplitude for cues predicting negative social feedback with 80% accuracy. Most importantly, this finding suggests that despite outcomes being uncontrollable and of no real-life consequence to participants, participants learned associations between predictive cues and social feedback. This was the case for both active and passive trials, suggesting that participants did not disengage attentionally from passive trials.

Yet, for the early P3 component, we found an interaction of condition and valence, in that amplitude was reduced for passive cues associated with negative feedback, compared with all other conditions. This finding is in line with our observation of enhanced P3 amplitude in response to negative feedback in passive trials: As participants showed a reduced response to predictive cues, the actual outcome may have been more surprising, eliciting a larger P3. It is possible that cues associated with the passive waiting period elicited a transient disengagement from the task, which could be at least partially counteracted by the anticipation of positive social feedback. However, given these findings were based on post hoc analyses and not predicted in our hypotheses, they require replication before strong conclusions can be drawn.

Feedback Processing and Reward Learning

A question of theoretical relevance is whether positive feedback in the absence of a motor action can be considered a reward. This depends on whether reward is defined as an affective state or the ability of a stimulus to enhance the likelihood of a behavior, thus requiring the occurrence of a preceding action. The current research is predominantly concerned with the formation of stimulus–outcome associations. Thus, although a positive stimulus following a neutral cue might not be classified as a reward in passive trials according to reinforcement-based definitions of reward, we do find that participants form stimulus–outcome associations in this condition. As such, the neural processing of positive feedback serves similar functions in active and passive trials but appears to be enhanced by preceding motor behavior.

Limitations and Outlook

The stimuli we used in this study were non-naturalistic, and highly simplified line drawings. While this excluded potential confounds of naturalistic stimuli, such as gender, ethnicity, and perceived attractiveness of presented faces, it reduces the external validity of the task. Nevertheless, our findings show that even minimalistic social feedback is sufficient for associative learning and that motor behavior enhanced the processing of symbolized social reward. It remains to be show whether this effect is preserved, enhanced, or attenuated for more naturalistic stimuli.

Furthermore, the mapping of predictive cues onto conditions was not randomized because of a programming error. Thus, cue-locked findings need to be interpreted with caution. However, post hoc N2 analysis showed that valence-based effects only emerged during later task stages, suggesting that they were driven by associated value, rather than inherent stimulus properties.

Future studies should aim to replicate these findings with more varied and natural feedback stimuli, as well as investigating the role of sense of agency in effects of motor action on reward processing. Furthermore, the development of paradigms to test differences in associated value on a behavioral level will be needed to assess real-life implications of our findings for our understanding of social anhedonia.

Future studies should further test the link between depressive symptoms or anhedonia and social reward sensitivity. As the current study was not sufficiently powered to test for interindividual differences, we did not assess participants' depression or anhedonia symptoms. Thus, although all participants were generally healthy according to self-report, we cannot exclude the possibility of existing symptoms affecting our findings.

Conclusions

We found that performing a motor action enhances the neural response to social reward, suggesting that actively bringing about positive social outcomes might be more impactful than incidentally encountering them. Furthermore, we found P3 amplitude to be reduced for cues associated with negative feedback in passive trials, but enhanced for passively obtained negative outcomes. Together, our findings suggest a tight link between motor control and reward processing, with implications for associative learning based on social feedback.

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Data Availability Statement

Fully anonymized ERP data are available on OSF (https://osf.io/2734d/). Raw data are available upon request.

Author Contributions

Caroline Di Bernardi Luft: Conceptualization; Formal analysis; Methodology; Supervision; Writing—Original draft; Writing—Review & editing. Iman Atchoum: Data curation; Formal analysis; Writing—Review & editing. Frederike Beyer: Conceptualization; Formal analysis; Methodology; Supervision; Writing—Original draft; Writing—Review & editing.

Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. The authors of this article report its proportions of citations by gender category to be: M/M = .564; W/M = .154; M/W = .051; W/W = .231.

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