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Performing a motor action enhances social reward processing and modulates the neural processing of predictive cues

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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 behaviour. Recently, we showed that the neural response to monetary reward is enhanced by performing an action, suggesting interactions between neural systems controlling motor behaviour and reward processing. Given many psychiatric disorders are associated with social anhedonia, a key open question is whether such effects generalise 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 to passive trials. These findings suggest that actively obtaining social feedback enhances reward sensitivity and modulates outcome anticipation.

Predicting, processing, and learning from rewards are key components of motivated

behaviour. 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 et al., 2016), in that it is easier for subjects to learn approach-

reward and avoidance-non-punishment associations, than the reverse (i.e. learning

to make an approach response in order 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 behaviour) can influence reward processing, a key aspect

of pavlovian learning (Bikute et al., 2022). Participants showed a stronger reward-

related response to monetary rewards, when the reward presentation was

immediately preceded by a button press, compared to a passive condition. Crucially,

participants had no control over trial outcomes, precluding the need for instrumental

learning. Further, 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 et al., 2013;

Van de Vijver et al., 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, i.e. 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 to other forms of gambling

which have a longer gap between motor actions and game outcomes (Bakken et al.,

2009; MacLaren, 2016). Further, depression 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).

Based on our findings (Bikute et al., 2022) one theory might be that apathy might in

fact exacerbate symptoms of anhedonia, due to a lack of motor behaviour 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 et al., 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.

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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 et al., 2022; Distefano et al., 2018; Pegg et al., 2021, 2022) exploring the neural response to monetary and social reward in clinical and healthy populations have utilised EEG to measure event-related potentials (ERPs). ERP components of particular interest are the Reward-related positivity (RewP) reflecting the neural response to reward (Holroyd et al., 2008), and the feedback-related negativity (FRN), calculated as the difference in the neural response to negative (i.e. punishment) vs. positive (reward) feedback (Miltner et al., 1997; San Martín, 2012). Both components are measured between 200-350ms post outcome onset, at fronto-central sites, and are believed to reflect sensitivity to feedback or action outcomes. In fact, while 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 non-reward (Foti et al., 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 et al., 2018; San Martín, 2012).

While these ERP components are consistently observed for both monetary and social rewards, some studies find stronger neural responses to monetary than social reward feedback (Ethridge et al., 2017; Wang et al., 2020). However, in line with specific deficits in social reward processing in mental health disorders, Zhang et al. (2020) found reduced FRN and P3 amplitudes in participants with depression compared to 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 to control adolescents, but no difference in the neural response to monetary reward (Rappaport et al., 2019). In contrast, acute, mild forms of experimentally induced social exclusion enhanced the RewP in response to social (but not monetary) rewards (Xu et al., 2022).

While at the group level in non-clinical 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 non-clinical 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 behaviour 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 to 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 signalling the likelihood of positive vs. negative outcomes were conflated with cues signalling the need for a motor action. Thus, we could not study whether the neural response to reward cues differed for active vs. 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 vs. 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 to reward (Dunning & Hajcak, 2007; Pornpattananangkul & Nusslock, 2015). 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 to neutral cues (Novak & Foti, 2015), though 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 randomised 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 vs. passive trials.

Based on the above findings, we formed three hypotheses: H1: Outcome processing – reflected in RewP and FRN amplitudes – is enhanced for outcomes in active compared to passive trials. H2: As participants learn to associated predictive cues with outcome probabilities, cue-locked N2 amplitude is enhanced for negative compared to 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 to 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 to passive trials whereas in passive trials, we will observe the reverse: a stronger flow from posterior to frontal areas (bottom-up modulation).

Methods

Participants

76 participants took part in this study. The sample size was determined based a separate study for which data was collected (see procedures below), which analysed hyperscanning data, thus requiring a larger sample. Two datasets were incomplete due to technical failure during recording, and a further 8 datasets were excluded based on artefact rejection criteria (see EEG processing below). Thus, 66 datasets were included in the analysis. Based on 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, 56 female; age 18-33; due to experimenter error, age was only recorded for 39 participants, with a mean age of 22 and a standard deviation of 2.55). No data on ethnicity was 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 et al., 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 unhappy. Participants were not instructed to imagine specific friends.
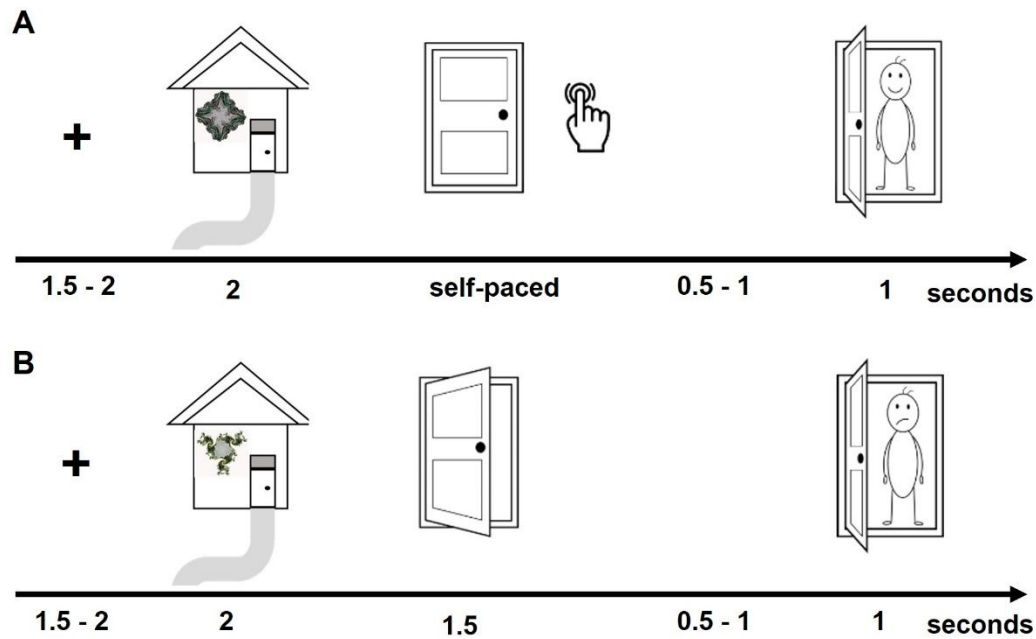
Figure 1: task outline. Figure shows example trial outlines, with an active trial with positive outcome in 1A, and a passive trial with negative outcome in 1B.

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 seconds, followed by the presentation of the drawing of a door. Either, an open door was shown for 1.5 seconds, 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 seconds, followed by the outcome presentation for 1 seconds. The outcome consisted of the drawing of a person standing in an open doorframe, either smiling or showing an unhappy expression. The inter trial interval was 1.5-2 seconds.

The four trial types (active-happy friend; active-unhappy friend; passive-happy friend; passive-unhappy friend) were mixed randomly. There were 4 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'). Due to

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 a total of 120 trials (30 trials per condition), split up into two

blocks with a short break in between.

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 socio-economic decision-making tasks

with and without eye contact, for about 20 minutes. 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 while 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 hours, 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 using saline based conductive gel. Eighteen electrodes were positioned on the scalp based on the standard 10-20 positions while 2 electrodes were positioned on the earlobes using ear clips.

The EEG signal was re-referenced offline to the averaged signal of the two earlobes. The continuous signal was then highpass filtered at 0.5Hz and lowpass filtered at 20Hz. Epochs were created around the onsets of cues, i.e. the house stimulus at the beginning of each trial (50ms pre stimulus – 1000ms post stimulus) and the onset of the outcome, i.e. the appearance of the friend (50ms pre stimulus – 1000ms post stimulus), and references to the pre-stimulus period. Independent component analysis was used to identify and remove eye blink and eye movement artefacts. Then, remaining artefacts were identified using a 100mV threshold, and epochs with artefacts 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 4 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 4 task conditions (positive & negative valence, as well as active & 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 while cue-locked N2 is typically observed at fronto-central locations, P3 topography tends to be

variable with centro-parietal distribution (Grazer et al., 2018). This showed three

components of interest: a cue-based N2 which peaked at 282ms, and for which we

analysed the average amplitude between 250-330ms; a cue-based P3, which

peaked at 346 and for which we analysed the average amplitude from 330-460ms;

and a second positive deflection peaking at 602ms. This resembled a Late Positive

Potential (LPP) and was analysed at 560-690ms. We analysed the three ERPs in

2x2 ANOVAs with the within-subject factors Condition (active vs. passive) vs

associated cue value (good vs bad).

To replicate and expand our ERP analyses from (Bikute et al., 2022), epochs for

outcome processing were averaged based on the four trial types (active-happy

friend; active-unhappy friend; passive-happy friend; passive-unhappy friend). Based

on 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

228ms, and we averaged the amplitude between 210-270ms. We then entered mean

amplitudes for this time window into a 2x2 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 (4-8Hz) 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 (-300ms to feedback). Since we used a lower density system (18-channels) we selected the channels which were significant in each cluster. For cluster one (C1, active cluster in our previous paper), 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 the all frontal to lateral posterior connections in these electrodes (mainly due to the slightly different electrode montages). We did the same for cluster two in our paper (C2, 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*) x 2 (*condition: active vs. passive*) ANOVA for each cluster separately. Based on our previous findings, we expected a main effect of condition but no interaction with outcome, for both clusters.

Results

Cue-locked ERPs

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We analysed three components of interest at electrode CZ: a cue-based N2 between 250-330ms, an early P3 (330-460ms) and a late P3 component (560-690ms; figure 2A). We analysed the three ERPs in 2x2 ANOVAs with the within-subject factors Valence (positive vs. negative) and Condition (active vs. passive; *table 1*).

Table 1: test statistics for planned ERP analyses

Cue-Locked at CZ	df	F-Value	p-value	Partial Eta-sq
N2, 250-330ms				
Valence	1,65	6.04	.017	.085
Condition	1,65	2.18	.145	.032
Valence*Condition	1,65	2.17	.146	.032
P3, 330-460ms				
Valence	1,65	2.81	.098	.041
Condition	1,65	1.41	.239	.021
Valence*Condition	1,65	4.56	.036	.066
Late PP, 560-690ms				
Valence	1,65	.02	.902	<.001
Action	1,65	2.04	.158	.030
Valence*Condition	1,65	0.52	.473	.008
Cue-Locked at PZ				
P3, 330-460ms				
Valence	1,65	5.11	.027	.073
Condition	1,65	<.01	.996	<.001
Valence*Condition	1,65	3.82	.055	.056
Late PP, 560-690ms				
Valence	1,65	<.01	.984	<.001
Action	1,65	0.57	.451	.009
Valence*Condition	1,65	0.05	.832	.001
Outcome-locked at FZ	df	F-Value	p-value	
FRN, 210-270ms				
Condition	1,65	2.40	.127	.036
Outcome	1,65	.07	.791	.001
Condition*Outcome	1,65	4.74	.033	.068

For the N2, we found a significant effect of Valence, but no effect of Condition, and no Valence x 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).
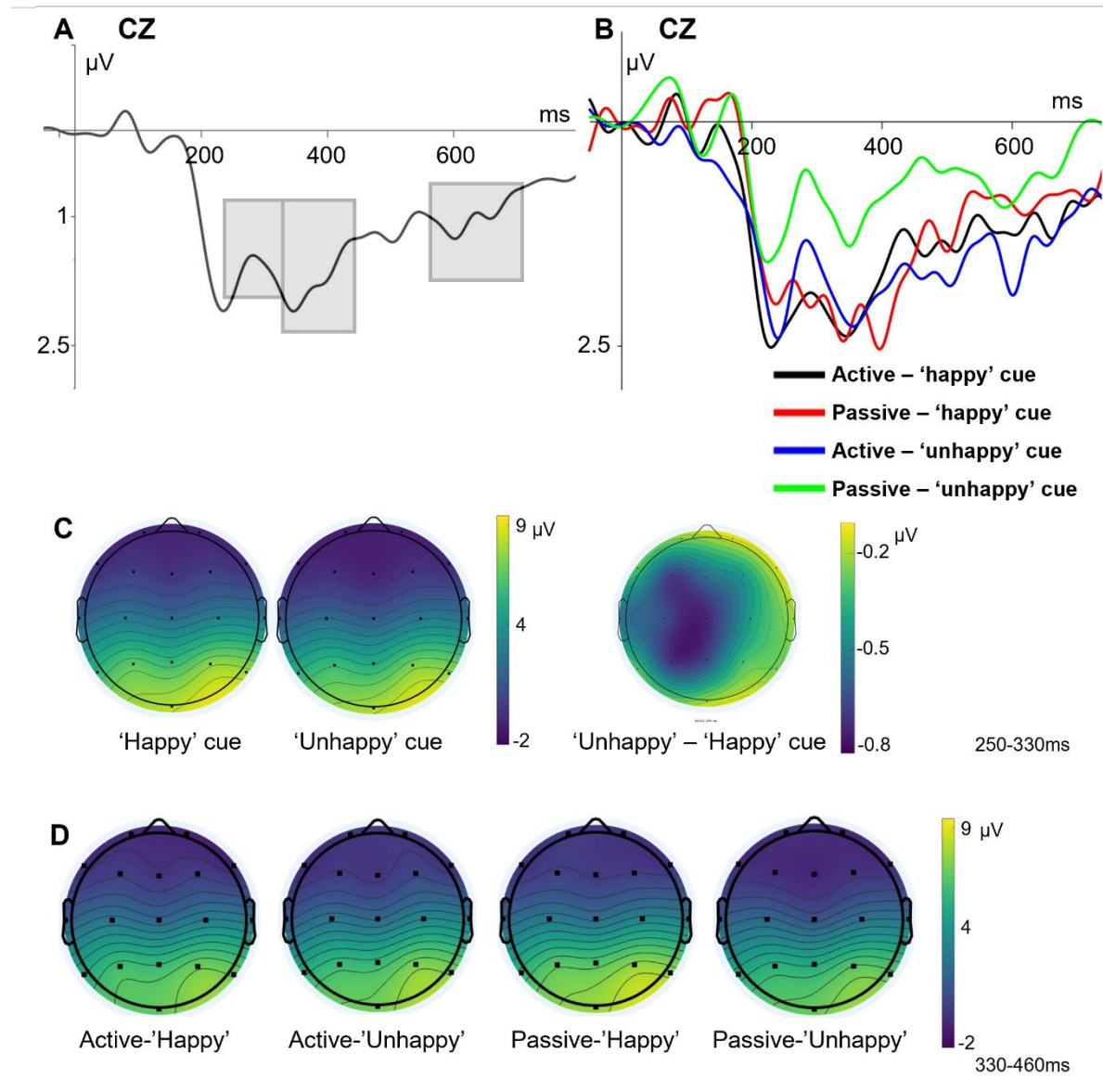

Figure 2: Cue-locked ERPs at electrode CZ. 2A shows cue-locked average amplitude across all conditions. 2B shows amplitudes separately for the 4 experimental conditions. Topographical maps are shown for the N2 time range (2C) and the early P3 time range (2D).

For the P3, we found no main effect of Valence and no main effect of Condition, but a significant Valence x 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 to 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} = 12.11, p < .001). We thus repeated the same 2x2 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**).

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

For the LPP, we found no significant effect for Valence or Condition, nor a significant Valence x 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, analysing 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 210-270ms, the 2x2 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 x Outcome interaction (**table 1**). As can be seen in *figure 3*, this interaction was due to 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 to 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} = -.11, p = .913; figure 3D). Post-hoc power analysis for the main comparison of interest (active-positive vs. passive-positive; cohen's d =.311) showed a critical t-value of t=1.67 and achieved power of 1-ß=.804 for a one-sided t-test with p<.05.
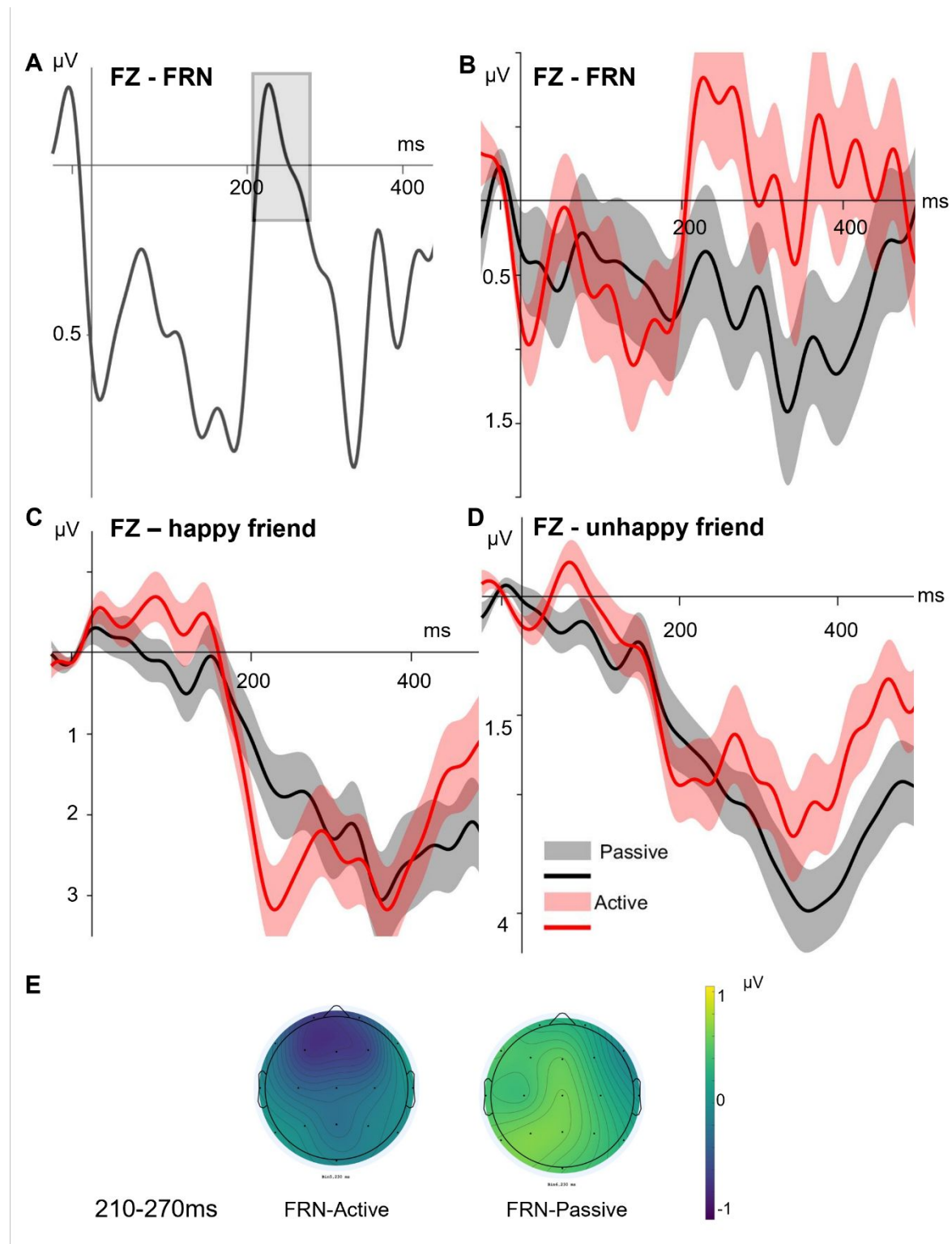
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Figure 3: Outcome-locked ERPs at electrode FZ. 3A shows FRN amplitude

(unhappy friend – happy friend amplitude) across active and passive trials, FRN for

active and passive conditions is shown in 3B. 3C shows the average amplitude for

positive outcomes (happy friend) for active and passive trials, amplitudes for

negative outcomes (unhappy friend) are shown in 3D. 3E shows the topographical

maps for the FRN amplitudes (unhappy – happy friend ERPs).

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 which was strongest at PZ (figure

4A). Based on the ERP shown for electrode PZ, we selected the time window of 290-

480ms for the primary P3 ERP. We then entered the average amplitudes for this

time-window into a 2x2 repeated measures ANOVA, as for the FRN analysis (table

3).
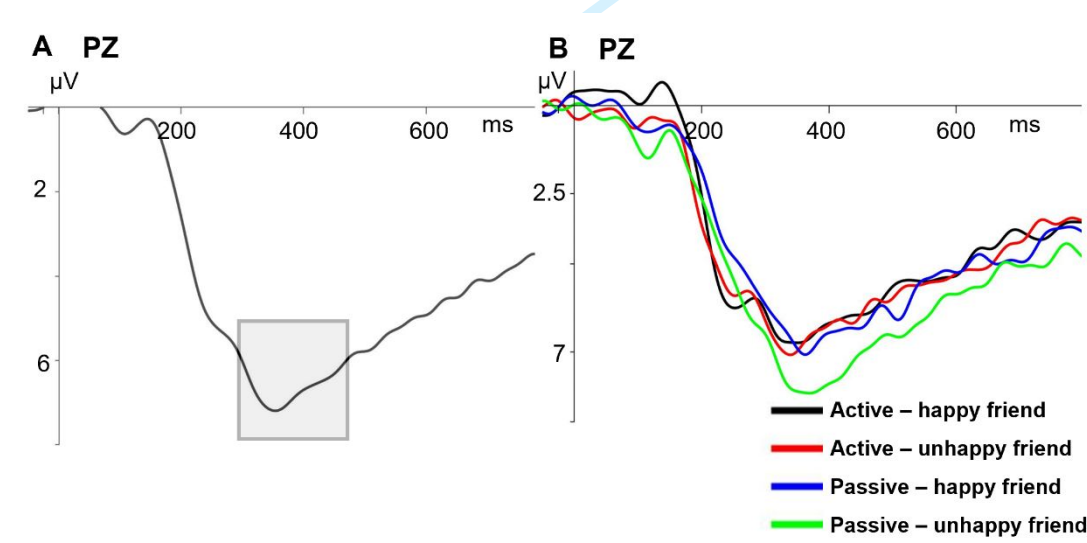
Figure 4: Outcome-locked ERPs at electrode PZ. 4A shows average amplitude

across all conditions. 4B shows outcome-locked amplitudes for the 4 conditions.

This showed a main effect of Condition and a main effect of Outcome. While the Condition*Outcome 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.

Table 3: test statistics for outcome-locked exploratory analyses

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

Directed Connectivity analyses

We entered the theta PSI values for cluster 1 (from frontal to posterior) in a 2 (condition: active vs. passive) x 2 (outcome: happy vs. unhappy friend) ANOVA in order to replicate our previous findings showing that active trials are associated with the opposite direction of theta synchronization compared to passive trials. We expected higher flow from frontal to posterior areas in the active compared to the passive feedback trials. For cluster 1, we observed a significant main effect of condition ($F(1,65) = 7.81$, $p = .007$, *partial eta squared* = .107) but no effect of outcome ($F(1,65) =.73$, $p = .395$, *partial eta squared* = .011) nor interaction ($F(1,65)$ = 1.52, $p = .222$, *partial eta squared* = .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 to the passive conditions.

For cluster 2, we also observed a significant main effect of condition ($F(1,65) = 4.53$, $p = .037$, *partial eta squared* = .065), but no effect of outcome ($F(1,65) = 1.49$, $p = .227$, *partial eta squared* = .022) nor interaction ($F(1,65) =.72$, $p = .398$, *partial eta*

squared = .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), since there is a partial overlap in the electrode pairs.
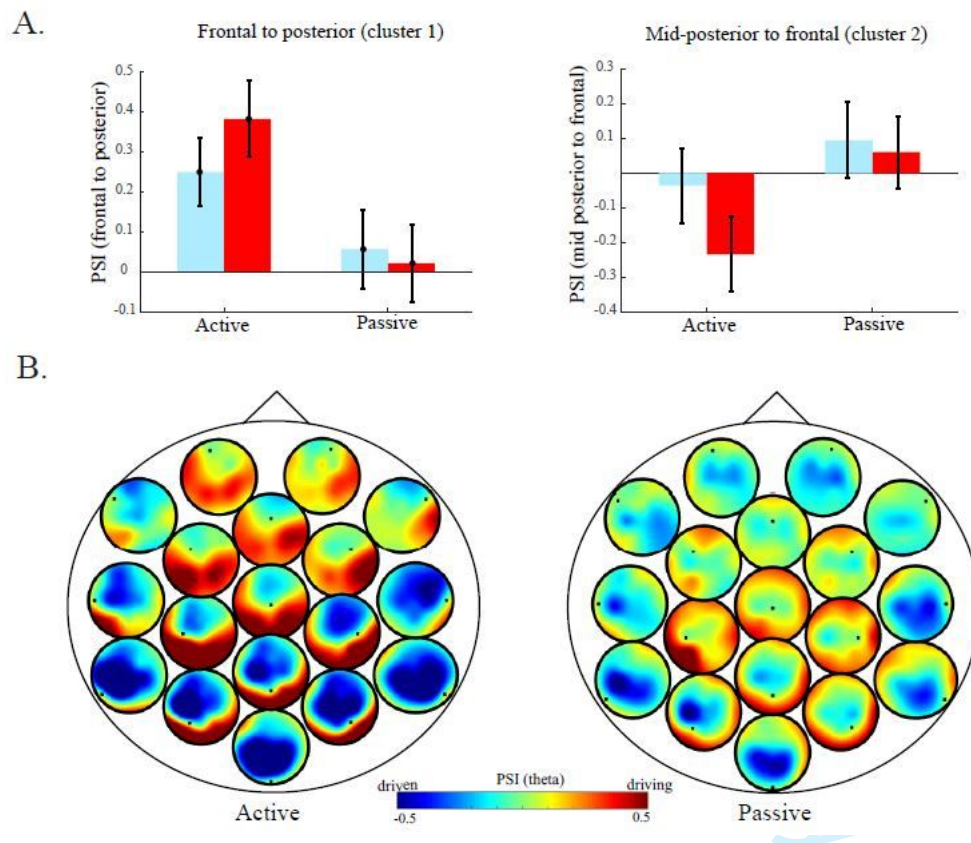

Figure 5. Directed connectivity in the theta frequency range (4-8Hz). A. Mean PSI values from frontal to posterior regions (cluster 1: higher values mean higher top-down flux) and from mid-posterior to frontal regions (cluster 2: higher values mean higher bottom-up flux). B. Topographical distribution of the directed synchronization values (all-to-all) in active (left-hand side) and passive (right-hand side) trials (-300msecs to feedback). Each individual topoplot display the synchronization between that particular electrode (displayed as a dot) and all the

others, whilst red colours represent the regions where this electrode is driving,

whereas blue colours represent areas which this electrode is being driven by.

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 to 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 to 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 behaviour. 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 (Hassall et al., 2019; Stewardson & Sambrook, 2021; Yeung et al., 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'd be aware that no response is required for several minutes. In Hassall et al.'s 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 behaviour and neural sensitivity to social reward could have important implications for our understanding of mental health disorders associated

with social anhedonia (Feng et al., 2020; Kupferberg et al., 2016; Rey et al., 2009; Yang et al., 2022). Future studies should explore whether reduced sense of agency – i.e. reduced feelings of action control – observed in depression are associated with a reduced impact of motor behaviour 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 lead 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 to 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 behaviour (Schultz, 2017; White, 2011), thus requiring the occurrence of a preceding action. The current research is predominantly concerned with the formation of stimulus-outcome associations. Thus, while 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 behaviour.

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 behaviour enhanced the processing of symbolised social reward. It remains to be show whether this effect is preserved, enhanced, or attenuated for more naturalistic stimuli.

Further, the mapping of predictive cues onto conditions was not randomized due to 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. Further, the development of paradigms to test differences in associated value on a behavioural 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, while 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. Further, 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.

Author contributions

CDBL: designed study, analysed data, wrote manuscript; IA: collected data, analysed data, revised manuscript; FB: designed study, analysed data, wrote manuscript.

Data availability

Fully anonymised ERP data will be made available on OSF upon publication. Raw data are available upon request.

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Figure 1: task outline. Figure shows example trial outlines, with an active trial with positive outcome in 1A, and a passive trial with negative outcome in 1B.
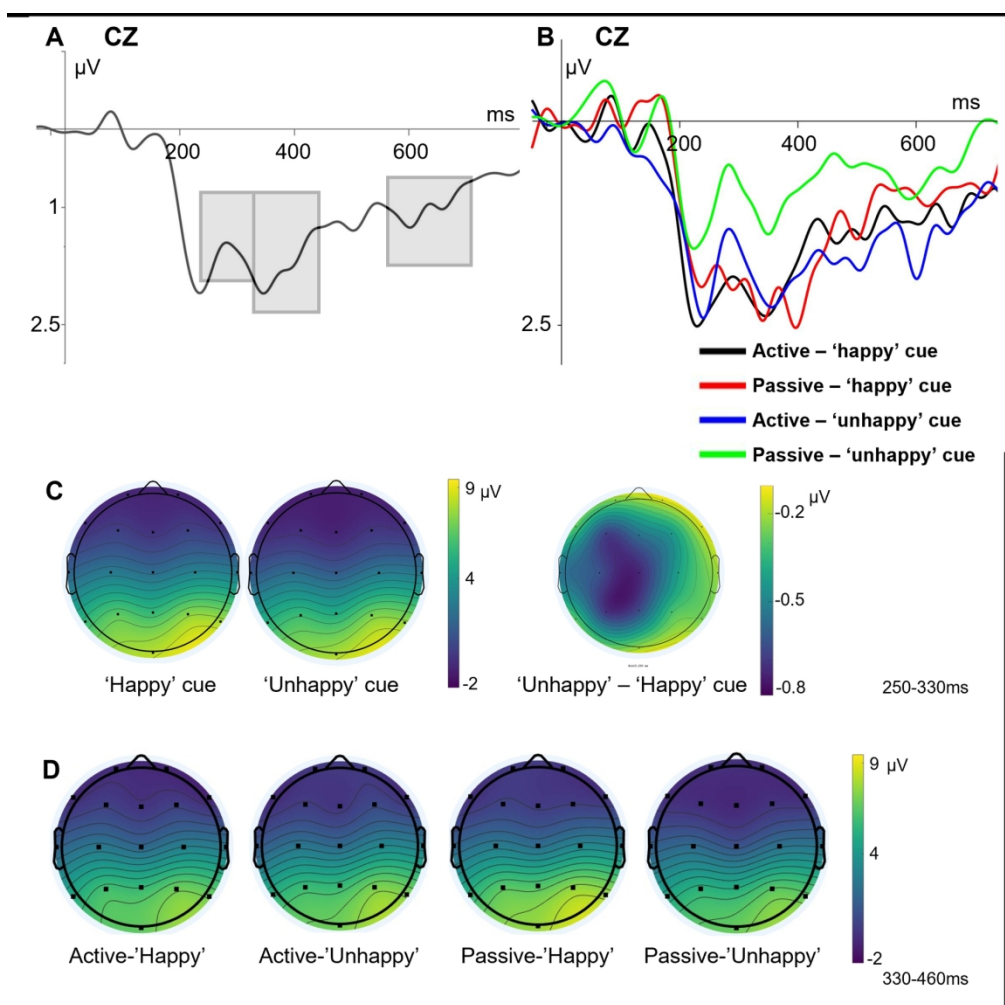
160x88mm (330 x 330 DPI)

Figure 2: Cue-locked ERPs at electrode CZ. 2A shows cue-locked average amplitude across all conditions. 2B shows amplitudes separately for the 4 experimental conditions. Topographical maps are shown for the N2 time range (2C) and the early P3 time range (2D).
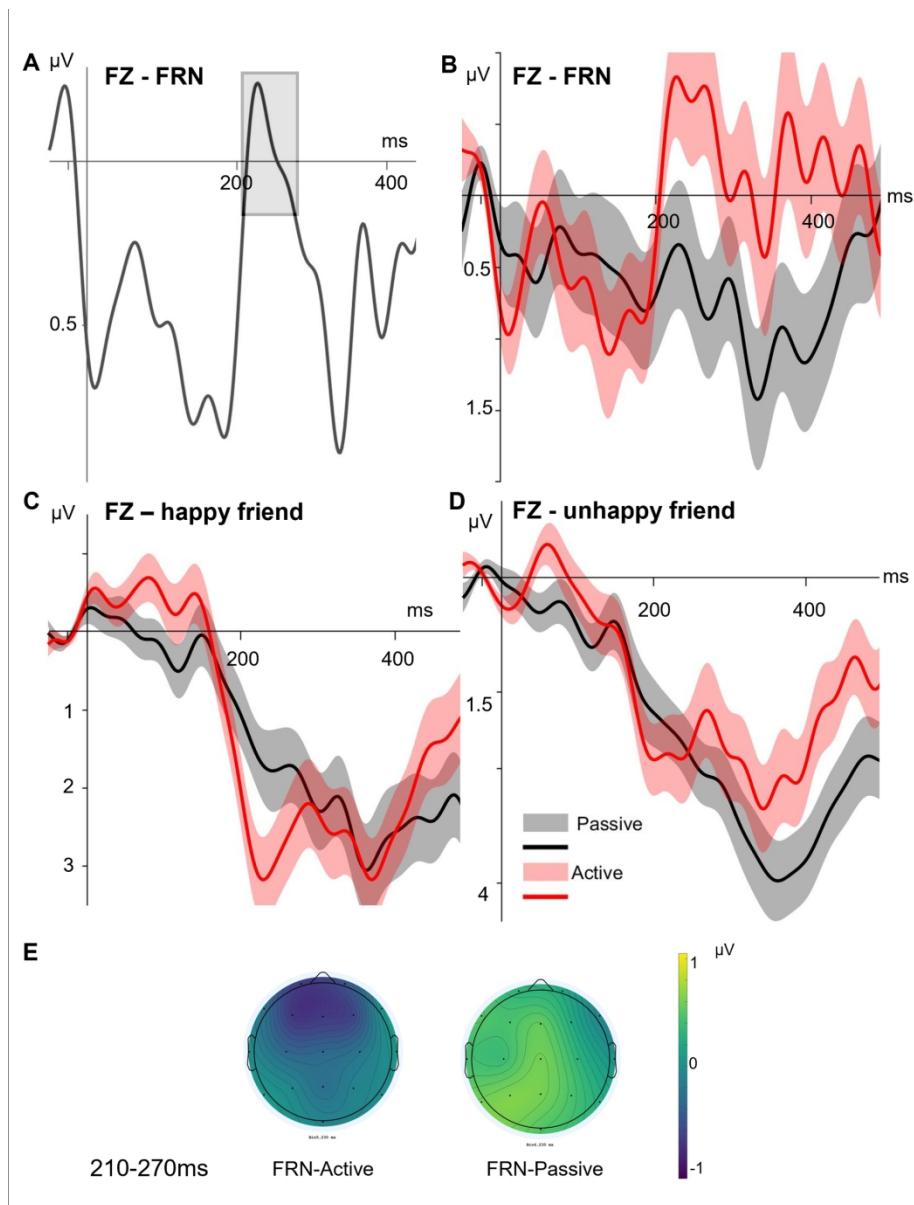
164x163mm (300 x 300 DPI)

Figure 3: Outcome-locked ERPs at electrode FZ. 3A shows FRN amplitude (unhappy friend – happy friend amplitude) across active and passive trials, FRN for active and passive conditions is shown in 3B. 3C shows the average amplitude for positive outcomes (happy friend) for active and passive trials, amplitudes for negative outcomes (unhappy friend) are shown in 3D. 3E shows the topographical maps for the FRN amplitudes (unhappy – happy friend ERPs).
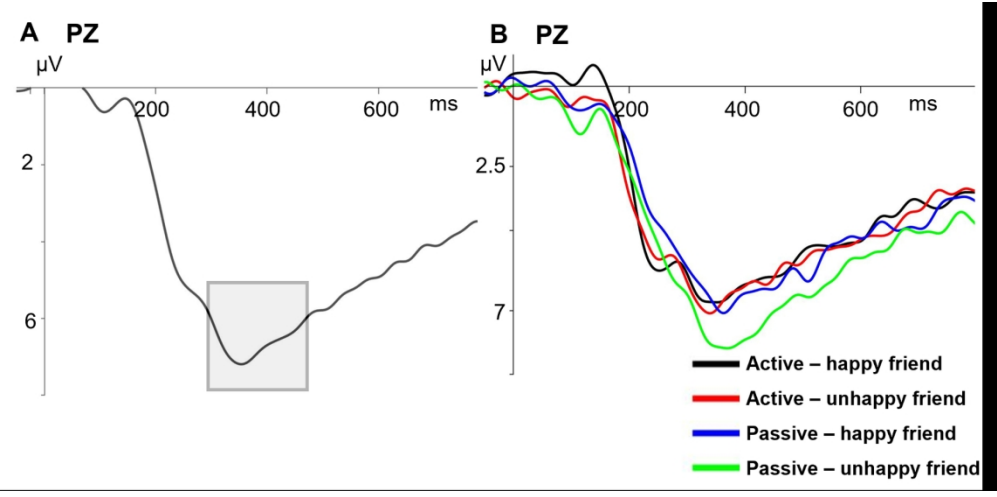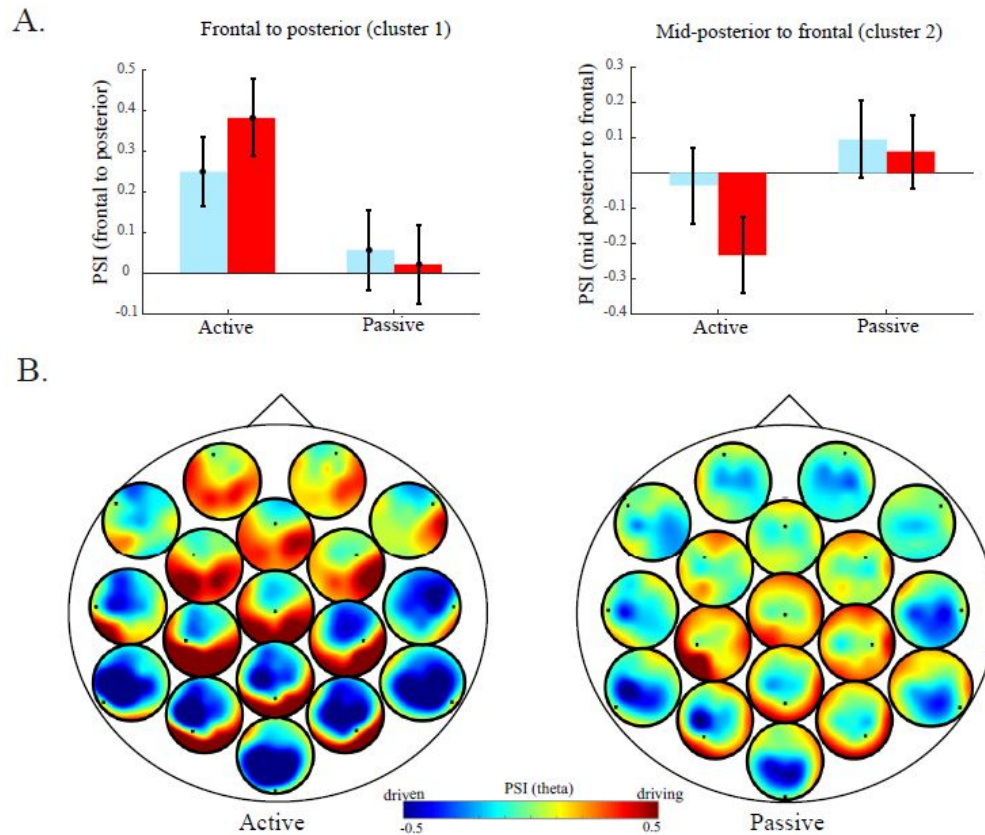
165x212mm (300 x 300 DPI)

Figure 4: Outcome-locked ERPs at electrode PZ. 4A shows average amplitude across all conditions. 4B shows outcome-locked amplitudes for the 4 conditions.

162x79mm (300 x 300 DPI)

Figure 5. Directed connectivity in the theta frequency range (4-8Hz). A. Mean PSI values from frontal to posterior regions (cluster 1: higher values mean higher top-down flux) and from mid-posterior to frontal regions (cluster 2: 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 (-300msecs to feedback). Each individual topoplot display the synchronization between that particular electrode (displayed as a dot) and all the others, whilst red colours represent the regions where this electrode is driving, whereas blue colours represent areas which this electrode is being driven by.

129x110mm (144 x 144 DPI)