

Electrocortical components of anticipation and consumption in a monetary incentive delay task

Douglas J. Angus¹ | Andrew J. Latham^{2,3} | Eddie Harmon-Jones¹  | Matthias Deliano⁴ | Bernard Balleine¹ | David Braddon-Mitchell²

¹School of Psychology, University of New South Wales, Sydney, Australia

²School of Philosophy, University of Sydney, Sydney, Australia

³Brain & Mind Research Institute, University of Sydney, Sydney, Australia

⁴Department Systemphysiology, Leibniz Institute for Neurobiology, Magdeburg, Germany

Correspondence

Douglas Jozef Angus, School of Psychology, University of New South Wales, 2052, Sydney, Australia.
Email: dang9080@gmail.com

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Abstract

In order to improve our understanding of the components that reflect functionally important processes during reward anticipation and consumption, we used principle components analyses (PCA) to separate and quantify averaged ERP data obtained from each stage of a modified monetary incentive delay (MID) task. Although a small number of recent ERP studies have reported that reward and loss cues potentiate ERPs during anticipation, action preparation, and consummatory stages of reward processing, these findings are inconsistent due to temporal and spatial overlap between the relevant electrophysiological components. Our results show three components following cue presentation are sensitive to incentive cues (N1, P3a, P3b). In contrast to previous research, reward-related enhancement occurred only in the P3b, with earlier components more sensitive to break-even and loss cues. During feedback anticipation, we observed a lateralized centroparietal negativity that was sensitive to response hand but not cue type. We also show that use of PCA on ERPs reflecting reward consumption successfully separates the reward positivity from the independently modulated feedback-P3. Last, we observe for the first time a new reward consumption component: a late negativity distributed over the left frontal pole. This component appears to be sensitive to response hand, especially in the context of monetary gain. These results illustrate that the time course and sensitivities of electrophysiological activity that follows incentive cues do not follow a simple heuristic in which reward incentive cues produce enhanced activity at all stages and substages.

KEYWORDS

ERP, MID, N1, PCA, P3, reward, reward positivity

1 | INTRODUCTION

Two vital aspects of reward processing, the anticipatory and consummatory stages, have been frequently investigated using variations of the monetary incentive delay (MID) task (Knutson, Westdorp, Kaiser, & Hommer, 2000). Each experimental trial in the MID task begins with the presentation of an incentive cue indicating the possible outcome for that trial: reward, loss, or break-even. After a brief anticipatory

period, a target stimulus is presented that requires a behavioral response. If participants respond successfully to the target, they are rewarded with money; otherwise, they break-even or are penalized.

Research using fMRI has found that anticipation of rewards and losses in the MID task are associated with an increased BOLD signal in the dorsal anterior cingulate (dACC) and supplementary motor region (Knutson & Greer, 2008; Knutson et al., 2000). Anticipation of reward has also been associated with a selective increase in activity in the nucleus accumbens (NAcc; Knutson, Taylor, Kaufman, Peterson, & Glover, 2005), a striatal structure implicated in

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assigning values to predictive stimuli (Berridge, 2007; Berridge, Robinson, & Aldridge, 2009; Haber & Knutson, 2009). Reward consumption, on the other hand, has been associated with activity in ventromedial frontal cortex structures (Knutson, Fong, Adams, Varner, & Hommer, 2001).

Understanding reward anticipation and consumption requires not just the assessment of spatial anatomical correlates revealed by fMRI but also its temporal dynamics using ERPs. While there is extensive research on ERPs associated with reward consumption and feedback processing (Bellebaum & Daum, 2008; Bellebaum, Kobza, Thiele, & Daum, 2010; Foti, Weinberg, Bernat, & Proudfit, 2015; Hajcak, Moser, Holroyd, & Simons, 2006; Proudfit, 2014), very few studies have investigated ERPs associated with reward anticipation *and* consumption in MID-type tasks. Those that have present inconsistent findings with respect to reward- and loss-related ERP modulation. As Novak and Foti (2015) have pointed out, electrophysiological components important for reward anticipation and consumption are susceptible to spatial and temporal overlap. This limitation could explain why consistent results in the context of MID-type tasks continue to remain elusive.

1.1 | Reward cue

While only a small number of studies have investigated ERPs in the MID task, a wide range of components are reported to be sensitive to reward, loss, and break-even cues. Given the motivational and affective significance of these cues as secondary reinforcers, their capacity to modulate ERPs is to be expected. What is unclear is which components reflect *functionally* important processes in response to incentive cues in the MID task. It is important to note that the surface deflections we observe and that constitute ERPs are not in themselves components. Moreover, components are not isomorphic to discrete brain processes. Rather, ERPs and components that are assigned particular labels (e.g., N1, P3) reflect systematic variation in neural activity (Luck, 2014).

Several studies have reported that early components associated with low-level vision, postperceptual processing, cognitive control, and template updating are sensitive to reward and loss cues relative to break-even cues. Results, however, are inconsistent, with null and entirely opposite effects commonly reported. For example, greater N1 amplitudes have been observed following reward cues relative to break-even cues in some studies (Doñamayor, Schoenfeld, & Münte, 2012), while other studies have observed no effect (e.g., Goldstein et al., 2006; Santesso et al., 2012). Greater P2 amplitudes have been observed for loss cues relative to reward (Santesso et al., 2012), but not in all studies (Goldstein et al., 2006). Modulation of N2 by cue type provides a particularly salient illustration of this inconsistency. While Novak and Foti (2015) observed greater N2

amplitudes for reward cues relative to loss and break-even cues, others have observed greater amplitudes for break-even cues relative to reward cues (Doñamayor et al., 2012; Pornpattananangkul & Nusslock, 2015) and for loss cues relative to reward cues (Yu & Zhou, 2006).

P3 effects in the context of the MID have been interpreted to reflect attentional allocation to motivational stimuli, irrespective of whether they are appetitive or aversive (Novak & Foti, 2015; Pfabigan et al., 2014). Again the results are inconsistent suggesting that processes associated with the P3 may not be consistent across studies. Greater P3 amplitudes have been observed in response to (1) reward cues relative to break-even cues (Broyd et al., 2012; Goldstein et al., 2006; Novak & Foti, 2015; Pfabigan et al., 2014; Pornpattananangkul & Nusslock, 2015; Vignapiano et al., 2017); (2) loss cues relative to break-even cues (Broyd et al., 2012 for null result; Novak & Foti, 2015; Vignapiano et al., 2017); (3) reward cues relative to loss cues (Broyd et al., 2012 for null result; Novak & Foti, 2015; Pfabigan et al., 2014; Santesso et al., 2012); and (4) loss cues relative to reward cues (Vignapiano et al., 2017).

ERPs involved in action anticipation and preparation have also been inconsistent. Some studies have observed a greater contingent negative variation (CNV) following reward and loss cues relative to break-even cues (Novak & Foti, 2015; Plichta et al., 2013), but once again, other studies have not (Goldstein et al., 2006; Sobotka, Davidson, & Senulis, 1992; Vignapiano et al., 2017). If there is reward-related modulation of the CNV it appears to be restricted to late-stages, in the 200 ms preceding behavioral response. Research also suggests the enhancement of preparatory activity for self-timed actions. Pornpattananangkul and Nusslock (2015) observed a significantly larger readiness potential (RP) when participants were preparing to respond to a reward-cued temporal-estimation task.

1.2 | Target

The prospect of receiving reward has been found to modulate ERPs associated with the presentation of target stimuli in MID tasks. Recently, the target-P3 was found to be greater to target stimuli following reward cues (Broyd et al., 2012), consistent with earlier research showing greater P3 amplitudes to target stimuli associated with receiving reward (Homberg, Grunewald, & Grunewald-Zuberbier, 1981; Otten, Gaillard, & Wientjes, 1995; Ramsey & Finn, 1997). Moreover, the target-P3 has also been found to be enhanced for target stimuli following loss cues (Broyd et al., 2012).

1.3 | Anticipation of results

Incentive cue effects can also occur when anticipating feedback stimuli. Stimulus preceding negativity (SPN)

amplitudes are modulated whenever a reward or punishment is possible. The SPN presents as a sustained slow negativity that is most pronounced over the right hemisphere and has been found to be reliably enhanced by reward and punishment expectancies. Across several studies, larger SPN amplitudes have been observed when participants are anticipating feedback that indicates they will receive a reward or avoid punishment, relative to when they are anticipating feedback that has no extrinsic motivational value (e.g., they can be neither rewarded nor punished; Brunia, Hackley, van Boxtel, Kotani, & Ohgami, 2011; Ohgami, Kotani, Hiraku, Aihara, & Ishii, 2004; Ohgami et al., 2006).

In one study, the SPN has also been found to be modulated as a function of incentive cue in a variation of the MID task, with larger SPN amplitudes on trials where a reward is possible relative to those where no reward is possible (Pornpattananangkul & Nusslock, 2015).

1.4 | Consumption

MID tasks have operationalized reward consumption through presenting feedback stimuli. Feedback stimuli indicate the accuracy and consequently the outcome of target detection and self-paced actions. Although this use of the term *reward consumption* is prevalent in the reinforcement learning and MID literature (Baskin-Sommers & Foti, 2015), reward consumption likely encompasses additional processes that *follow* the receipt of visual or auditory feedback, and constitute the delivery and consumption of an actual physical reward (e.g., sucrose solution in animal studies; Castro & Berridge, 2014). While the issue of which ERPs reflect these different aspects of reward consumption is important, it is outside the scope of the present study, which is restricted to feedback-locked ERPs. Within this class of stimulus, reward consumption has been associated with two distinct ERPs: reward positivity (RewP) and feedback-P3 (fb-P3).

The RewP is positive frontocentral deflection occurring 200 to 300ms that is strongest following reward feedback (Bellebaum, Polezzi, & Daum, 2010; Hajcak, Moser, Holroyd, & Simons, 2006; Proudfit, 2014). Multiple neuronal generators are associated with the RewP, including the anterior cingulate cortex (ACC; Gehring & Willoughby, 2002; Hauser et al., 2014) and regions implicated in reward processing (Haber & Knutson, 2009) such as the ventral striatum and subregions of the medial prefrontal cortex (PFC; Becker, Nitsch, Miltner, & Straube, 2014; Carlson, Foti, Harmon-Jones, & Proudfit, 2015; Carlson, Foti, Mujica-Parodi, Harmon-Jones, & Hajcak, 2011).

The RewP is also referred to as the feedback-related negativity (FRN). From a measurement standpoint, one is simply the inverse transformation of the other. Although the RewP and FRN are argued to be synonymous (Proudfit, 2014),

with the core measurement difference being their polarity in difference waves, there are differences in interpretation. The FRN research literature has typically focused on the reinforcement learning functions that the component reflects, with dominant theoretical models proposing that it signifies either absolute prediction errors (e.g., the outcome differs from expected), or reward prediction errors (e.g., the outcome is worse than expected) specifically (Holroyd & Yeung, 2012). These models have received broad support from a range of empirical studies showing that FRN (or RewP) amplitudes are larger when outcomes are unexpectedly better or worse (e.g., Holroyd, Krigolson, & Lee, 2011; Ichikawa, Siegle, Dombrowski, & Ohira, 2010; Pfabigan, Alexopoulos, Bauer, & Sailer, 2011).

Despite its ubiquitous presentation in equiprobable gambling tasks (e.g., Angus, Kemkes, Schutter, & Harmon-Jones, 2015; Foti & Hajcak, 2010; Hajcak et al., 2006, 2007; Holroyd et al., 2011) and expectancy violation tasks (Holroyd et al., 2011; Ichikawa et al., 2010; Pfabigan et al., 2011), only four MID studies have reliably observed greater RewP amplitudes following reward feedback than following loss or break-even feedback (Novak & Foti, 2015; Pfabigan et al., 2015; Santesso et al., 2012; Yu & Zhou, 2006). Other MID studies have either observed RewPs in response to reward, loss, and break-even feedback (Broyd et al., 2012; Pornpattananangkul & Nusslock, 2015) or no clear RewP at all (Doñamayor et al., 2012).

Overlapping with the RewP is the fb-P3, which is sensitive to expectancy violation (Bellebaum & Daum, 2008) and reward magnitude (Yeung & Sanfey, 2004). Greater fb-P3 amplitudes have been observed in MID tasks following feedback when participants expected to win or lose money relative to expecting to break even (Doñamayor et al., 2012; Novak & Foti, 2015; Pornpattananangkul & Nusslock, 2015). The fb-P3 has also been observed when participants successfully won or avoided losing money relative to only receiving performance feedback (Broyd et al., 2012).

Last, the presentation of feedback stimuli in the MID task has occasionally been found to modulate centroparietal slow waves such the late positive potential (LPP), with enhanced amplitudes in response to feedback indicating poor performance regardless of whether this resulted in financial loss or not (Pornpattananangkul & Nusslock, 2015).

1.5 | The present study

While a variety of electrophysiological components are elicited by the MID task, the effect of reward and loss anticipation and consumption on these components has been inconsistent. A likely explanation for this inconsistency is the spatial and temporal overlap of electrophysiological components. For example, the substantial scalp and temporal

distribution of the P3 means it overlaps with other ERP components modulated by motivational and affective variables such as the early posterior negativity and P3a. Similarly, the RewP and fb-P3 are present over similar time scales making the identification and quantification of one or both components difficult (Novak & Foti, 2015). The spatial and temporal overlap of ERPs confounds the measurement and interpretation of ERP results obtained in the MID task. Although several previous studies (Broyd et al., 2012; Novak & Foti, 2015; Pornpattananangkul & Nusslock, 2015) have examined ERPs that occur during the MID task, these studies have used quantification approaches that require a priori assumptions about which electrocortical activity will reflect functionally important processes. Only one study (Doñamayor et al., 2012) has used data-driven exploratory approaches, and the permutation methods used in that study do not allow for the decomposition of overlapping components.

To overcome these issues and accurately assess what electrophysiological activity reflects *functionally* important processes during reward anticipation and consumption in the MID task, we used exploratory temporospatial principle components analysis (PCA) to quantify ERPs. Specifically, we applied PCA to ERPs generated at each stage of the MID task: cue, target, response preparation, and feedback. Temporospatial PCA has several advantages over typical approaches to ERP quantification. First, temporospatial PCA is well suited to exploratory analysis of ERPs as it allows for the extraction of variance across time (e.g., samples) and space (e.g., electrodes), which decomposes an ERP wave form into its constituent components. This decomposition approach does not require a priori assumptions regarding the specific time points or location that measurements will be taken from. Second, temporospatial PCA allows for the identification of components that are obfuscated by temporal and spatial overlap, and prove difficult to measure using traditional ERP analyses (Dien & Frishkoff, 2005).

Although this study was exploratory, we did have general predictions regarding which factor combinations would likely be identified as functionally relevant. First, we anticipated that factor combinations reflecting the P3 and CNV following incentive cues would be modulated by cue type, with greater amplitudes for gain rather than loss or break-even cues. Second, we anticipated that a factor combination reflecting the readiness potential preceding responses would be modulated by response hand and incentive cue, such that amplitudes would be larger for the contra-lateral hand and following gain incentives than following loss or break-even. Third, we anticipated that a factor combination reflecting the SPN prior to feedback would be enhanced by incentive cues related to expected gains or losses. Last, we anticipated that the factor combinations that reflect the RewP and fb-P3

following feedback presentation would be enhanced for trials where participants received positive rather than negative feedback.

2 | METHOD

2.1 | Participants

Twenty males (Mean age = 23.6, $SD = 4.0$) participated in exchange for monetary compensation (AU\$15/hr). Participants also received an additional AU\$15 “bonus money” at the end of the experiment. All participants were right handed and without past or current diagnoses of an affective disorder. This study was approved by the University of Sydney Human Research Ethics Committee and all participants provided informed written consent. Electrophysiological data from one participant were excluded from analyses due to insufficient usable trials.

2.2 | Procedure

Upon arrival, participants were provided with a brief overview of the study and consent form. Participants were not informed they could receive “bonus money” until after they had provided written consent. Participants then completed a brief demographic questionnaire. Electroencephalography (EEG) and EOG electrodes were attached to the participant, and they were seated in a darkened soundproofed testing chamber. The MID task was explained to the participant, and they were guided through at least 10 practice trials. Once the experimenter was satisfied the participant understood the task, the experiment began. At the end of the task, participants completed a series of post-task questions. After these questions were completed, the electrodes were removed and the participant was debriefed. Experimental materials were displayed on a 24-inch LCD computer screen with a refresh rate of 100 Hz. Stimulus display and timings were controlled using the Psychophysics Toolbox for MATLAB (version 2013b).

2.3 | Design

The task consisted of 360 trials divided into two 180 trial blocks. Each block was comprised of 60 “probable gain,” 60 “probable loss,” and 60 “break-even” trials. Each trial consisted of four key stages designed to produce different facets of reward- and nonreward-related processes. First, to examine reward anticipation-related processes, we presented participants with an incentive cue. Then, to examine incentive-related modulation of target processing, we presented participants with a target stimulus. To examine response preparation modulation, we asked participants to complete a simple

temporal estimation task. Participants were instructed that to complete the estimation task, they had to press a key when they thought 1,000 ms had elapsed from the appearance of the target. Participants were informed that successful performance on the temporal estimation task would increase the probability of winning money rather than losing money. Finally, to examine consummatory processes, we presented participants with feedback regarding their performance.

Each trial began with a fixation-cross in the center of the screen. After a variable interval of approximately 1,200 ms, the fixation cross was replaced with a leftward- or rightward-pointing arrow for 200 ms, serving as the incentive cue. On probable gain, probable loss, and break-even trials, the arrow was green, red, or black, respectively. Participants were informed of the contingency between the arrow color and probable outcome. Because we wished to tease apart activity related to motor preparation from activity related to incentive cue type, we instructed participants to use either their left or right hand on the temporal estimation. Moreover, if there were an interaction between these response hand and cue type, it would suggest that the incentive-based modulation of electrocortical activity involved in, for example, the potentiation of response preparation is specific to response hand.

The direction of the arrow indicated which hand participants would need to use on the temporal estimation task on that trial. When the arrow (regardless of color) faced left, participants had to press the “z” key using the index finger of their left hand. When the arrow faced right, participants had to press the “/” key with the index finger of their right hand. Probable gain and probable loss trials were mapped to opposite hands within each block, with the hand used alternating between blocks (e.g., left-hand response on probable gain, right-hand response on probable loss). Break-even trials were made with the left or right hand, in equal proportions within each block.

In order to distinguish activity associated with anticipation of the target stimulus from activity associated with motor preparation, we embedded a temporal estimation task within the MID task (see Pornpattananangkul & Nusslock, 2015). In this version of the MID, the target stimulus indicates the point from which participants are required to judge

1,000 ms passing. A black square was used as the target stimulus. The target stimulus was presented 2,000 ms after the onset of an arrow and remained on screen for 200 ms.

Last, the outcome of each trial was signaled by feedback stimulus presented 1,000 ms after a response, or after 4,000 ms had passed from target onset (i.e., the latest possible time a participant would be allowed to make a response on that trial). Feedback stimulus remained onscreen for 1,000 ms. Gains were signaled by a green upward-pointing arrow and losses by a red downward-pointing arrow. On break-even trials, an equals sign was presented, even when an incorrect response or no response was made. Probable gain and probable loss trials were further subdivided on the basis of the actual outcome. On 39 trials, outcomes were congruent (e.g., winning money on probable gain trial) and on the remaining 21 trials outcomes were incongruent (e.g., losing money probable gain trial). The actual response made by participants affected only the outcome of probable gain and probable loss trials when (1) they made a response with the incorrect hand (e.g., left-hand response on a right-hand response trial); (2) they responded too quickly, which was defined as 250 ms following the presentation of the target stimulus; or (3) they failed to make a response. We chose to do this as we wished to have a fixed ratio of trials in which participants received win/loss feedback. Because performance could have varied between expected win and expected loss conditions, we were concerned that this performance mismatch could have led to systematic imbalances in the number of trials available for feedback-locked analysis. An example trial is depicted in Figure 1.

Participants were informed that they start on \$10 and that on every successful gain-outcome trial, they would gain \$0.25, while on every loss-outcome trial, they would lose \$0.25.

2.4. | Physiological recording and data reduction

EEG was recorded from 60 active Ag/AgCl electrodes (Acti-Cap, Brain Products, Gilching, Germany) located according to the International 10–20 system. EOG was recorded from

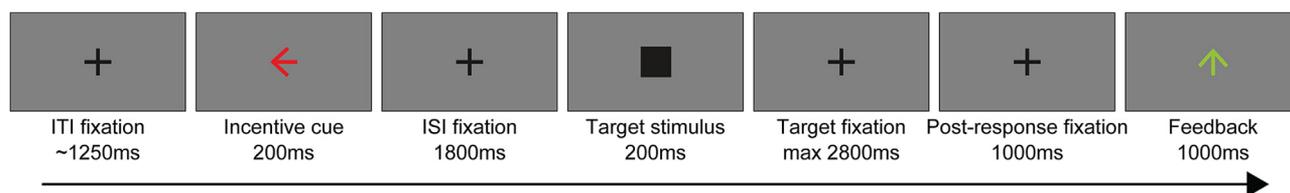


FIGURE 1 In this trial, the participant was required to form the intention to press the “z” key using their left hand, doing so in a context where they will probably lose—rather than gain—money. Participants were instructed that executing this action as close to 1,000 ms following the onset of the target stimulus increased the likelihood of winning money rather than losing it. At the end of the trial, the participant receives feedback signaling that they had won money

two electrodes placed 1 cm lateral to the outer canthi of each eye (for horizontal EOG) and from one electrode placed on the suborbital region of the right eye (for vertical EOG, e.g., Hofmann, Kuchinke, Tamm, Vö, & Jacobs, 2009). Raw data were amplified and sampled at 1000 Hz by a Brain Products QuickAmp72, referenced to a common average with a ground electrode located at AFz and recorded using Brain Vision Recorder (version 1.20, Brain Products, Gilching, Germany).

Raw EEG data were preprocessed offline using native EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014) functions. Continuous EEG data were down sampled to 256 Hz, re-referenced to the average of TP9 and TP10, bandpass filtered between .01–30 Hz (IIR Butterworth, 25 db roll-off), and residual line noise was reduced using a 50 Hz Parks-McClellan notch filter. Sections of continuous data containing gross movement artefacts were removed and independent components analysis (ICA) was used to remove electrophysiological artefacts introduced by eye movements (Jung et al., 2000).

Separate segments were created for each “stage” of reward processing. For incentive cue segments the period 200 ms prior through to 2,000 ms after cue presentation was selected. For target segments, the period 200 ms prior through to 500 ms after the target presentation was selected.¹ For response segments, the period 1,000 ms prior through to 200 ms after participant’s responses was selected. To examine responses that occur in anticipation of feedback, a period 1,000 ms prior to feedback presentation was selected. Finally, feedback segments were created using the period 200 ms prior through to the 1,000 ms after feedback presentation. Cue, target, and feedback segments were baseline corrected to their 200 ms prestimulus periods. Response-locked activity was baseline corrected to the period 200 ms prior to target stimulus presentation, while feedback anticipation activity was baseline corrected to the period 200 ms following responses. Segments from trials in which participants made an incorrect response (e.g., used the incorrect key, failed to respond, or responded in < 250 ms) were excluded from analyses. Retained segments were submitted to artefact rejection processes implemented in ERPLAB (Lopez-Calderon & Luck, 2014). Segments were rejected if on any electrode (1) the voltage difference was greater than 200 μV , (2) the voltage changed by more than 50 μV within a 200 ms sliding window across the entire segment, or (3) the voltage changed by more than 50 μV between samples.

¹Although 16 factor combinations each accounted for greater than 1% of variance in target ERPs, and several of these factor combinations appeared to reflect ubiquitous components previously found to be effected by reward and loss incentives (e.g., the P3), these were not significantly modulated in the current task by cue type (all $p > .047$), response hand (all $p > .023$), or an interaction between the two (all $p > .072$; adjusted critical $p = .003125$).

Subject averages for cue, target, response, and feedback anticipation ERPs were binned according to the cue type (probable gain, probable loss, break-even) and response hand (left, right). Feedback activity was binned according to cue type (probable gain, probable loss), response hand (left, right), and feedback type (positive, negative). Break-even trials were not included in the analysis of feedback ERPs as only a single outcome was ever possible. Participants were excluded from the analysis of a task stage if there were not at least 10 trials in the bin. One participant was excluded from feedback analysis due to having nine usable trials in one bin. Descriptive statistics for available and retained trials are presented in Table 1. Grand averages for all bins and segment types are presented in Figures S1 (Cue), S2 (Target), S3 (Response), S4 (Feedback Anticipation), and S5 (Feedback).

2.5 | Statistical analysis

Quantification of ERP components was conducted using the PCA Toolkit (Dien, 2010a). PCA is a factor analytic method that identifies and separates linear combinations of data points across temporal and spatial domains, allowing identification of overlapping electrocortical activity. All PCA analyses followed an identical process. First, temporal PCA was applied using samples as variables, and conditions, participants, and electrodes as observations. Consistent with previous recommendations, we used a Promax rotation with Kaiser normalization (Dien, 2010b). The number of temporal factors extracted for rotation in each PCA was determined using the parallel test (Cattell, 1966). Second, temporal factors were submitted to a spatial PCA using Infomax rotation (Dien, 2010b; Dien, Khoe, & Mangun, 2007) with electrodes as variables, and conditions, participants, and temporal factor loadings as observations. Factors extracted for rotation were again determined using the parallel test (Cattell, 1966). Grand averages of example data submitted to PCA are presented in Figure 2. More comprehensive grand averages for each stage of reward processing are included in supplementary information 1, 2, 3, 4, and 5.

To aid interpretation, peak factor loadings were converted into microvolts. For all task stages, factor combinations were retained for subsequent analyses if they accounted for more than 1% of variance (e.g., Foti, Hajcak, & Dien, 2009). For each set of analyses, we report the total number of extracted factors and total number of retained factors that met the 1% threshold. The latter were subjected to robust ANOVA in accordance with published recommendations (Dien, Franklin, & May, 2006; Keselman, Wilcox, & Lix, 2003), and as implemented in the PCA Toolkit (Dien, 2010a). This approach to null hypothesis testing has been shown to be robust to violations of homogeneity and non-normal distributions, and reduces type 1 error rate (Keselman

TABLE 1 Mean trials retained for analysis in each condition

	Cue	Response	Feedback anticipation	Feedback
Probable gain, left hand	53.6	55.3	55.7	
Probable gain, right hand	52.8	54.4	55.2	
Probable loss, left hand	52.4	53.2	54.3	
Probable loss, right hand	52.7	54.5	55.5	
Break-even, left hand	52.4	53.0	54.1	
Break-even, right hand	51.0	52.2	54.0	
Probable gain, left hand, win				36.2
Probable gain, left hand, loss				19.6
Probable gain, right hand, win				36.1
Probable gain, right hand, loss				18.8
Probable loss, left hand, win				19.1
Probable loss, left hand, loss				35.7
Probable loss, right hand, win				20.1
Probable loss, right hand, loss				36.3

et al., 2003). Each ANOVA used a starting seed of 100, was bootstrapped 5,000 times, and 5% upper and lower means trimming. Robust ANOVA tests are indicated by “ $T_{WJ/c}$,” and the interpretation of this statistic and resulting p values are identical to a conventional ANOVA. Significance thresholds for omnibus tests were corrected for multiple comparisons using the Bonferroni method, with the number of extracted factors subjected to the ANOVA determining the magnitude of the correction. Significance thresholds for pairwise comparisons were also corrected for multiple comparisons. Descriptions of factor combinations that were sensitive to manipulations in the MID task are presented in Table 2.

Regarding behavioral data, mean response times on correct trials (e.g., participants pressed the instructed key 250–3,000 ms following target onset) first underwent a linear transform, where 1,000 ms was subtracted from each response, providing a more easily interpretable measure of performance. The resulting values were then subjected to a repeated measures ANOVA as implemented in SPSS (IBM, V20), with partial eta squared is provided as a measure of effect size.

3 | RESULTS

3.1 | Behavioral data

Response time values were submitted to a three (cue type: probable gain, probable loss, break-even) by two (response hand:

left, right) factor ANOVA. Consistent with previous research indicating improved accuracy on incentivized trials, there was a main effect of cue type ($F(2,36) = 3.65, p = .036, \eta_p^2 = .17$). Post hoc tests indicated that this effect was driven by a more accurate response times on probable gain trials ($M = 232.39, SD = 402.52$) than on break-even trials ($M = 262.78, SD = 412.21; p = .018$). There was no difference between probable loss trials ($M = 241.30, SD = 410.29$) and probable gain trials ($p = 1.00$) or break-even trials ($p = .377$). There was no effect of response hand on response times ($F(1,18) = 1.57, p = .226, \eta_p^2 = .08$), or an interaction between incentive cue and response hand ($F(2,36) = .81, p = .398, \eta_p^2 = .043$).

3.2 | Cue activity

A total of 18 temporal and 4 spatial factors were extracted for cue-locked ERPs. Of these 72 factor combinations, 16 explained at least 1% of variance and were submitted to a three (cue type: probable gain, probable loss, break-even) by two (response hand: left, right) factor ANOVA with a Bonferroni corrected significance threshold of $p < .0031$. Three factor combinations were sensitive to cue type; their wave forms and scalp maps are presented in Figure 3.

The earliest factor combination, TF8/SF1 (Temporal Factor 8/Spatial Factor 1), was maximal over P2 between 132–136 ms, and appears to reflect a parietal N1, $T_{WJ/c}(2.0,16.0) = 9.85, p = .0014$. Pairwise comparisons between

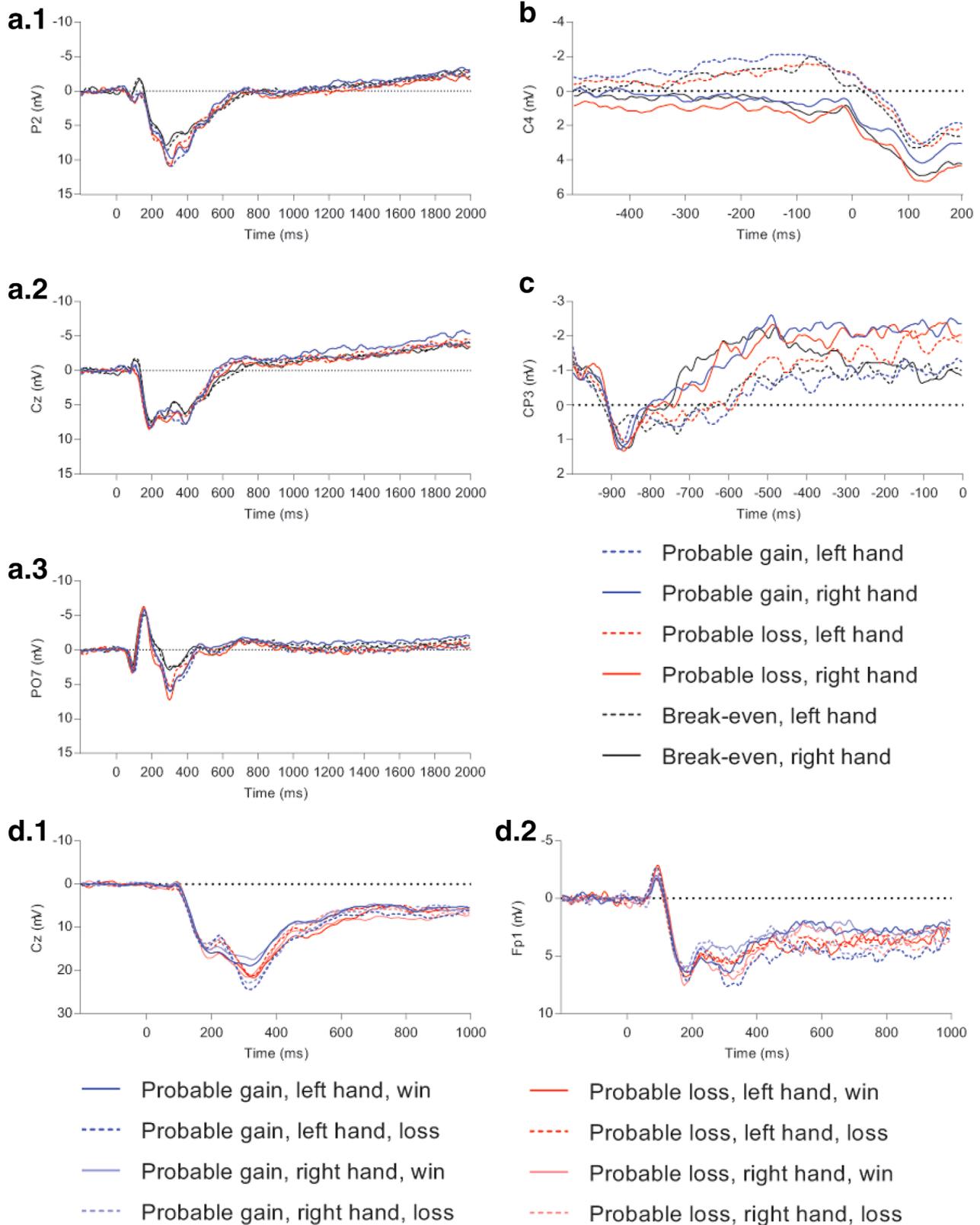


FIGURE 2 Grand average ERPs prior to PCA for cue-locked (A.1, A.2, A.3), response-locked (B), feedback anticipation (C), and feedback-locked (D.1, D.2) activity. Sites presented were those identified as being the spatial peak of relevant temporospatial factor combinations

cue types indicate the negativity is stronger for break-even cues than probable gain cues ($T_{WJ/c}(1.0,18.0) = 7.28, p = .015$) and probable loss cues ($T_{WJ/c}(1.0,18.0) = 20.41,$

$p = .00020$). Factor loadings did not differ significantly between probable gain and probable loss cues, $T_{WJ/c}(1.0,18.0) = 0.50, p = .50$.

TABLE 2 Descriptions of temporospatial factor combinations found to be sensitive to experimental manipulations

	Temporal loading peak (ms)	Spatial distribution of effect	Experimental effects	ERP deflection
Cue				
TF8/SF1	132–136	Parietal negativity	Break-even > Probable gain & Probable loss	N1
TF6/SF1	267–280	Central positivity	Break-even & Probable loss > Probable gain	P3a
TF2/SF2	360–364	Left parietal positivity	Probable gain > Probable loss > Break-even	P3b
Response				
TF1/SF3	132–128	Lateralized central negativity	Left hand > Right hand	RP
Feedback anticipation				
TF2/SF3	600–596	Lateralized centroparietal negativity	Right hand > Left hand	
Feedback				
TF4/SF1	224–228	Central positivity	Gain > Loss	RewP
TF1/SF1	380–384	Central positivity	Probable gain, loss > Probable gain, win; Probable loss, win > Probable loss, loss; Probable gain, loss > Probable loss, loss	fb-P3
TF2/SF3	880–884	Left lateralized frontopolar negativity	Right hand, win > Left hand, win	

The next factor combination to be affected by cue type, TF6/SF1, had a scalp distribution and latency similar to the P3a and was maximal over Cz between 276–280 ms, $T_{WJ/c}(2.0,16.0) = 15.34$, $p = .00060$. Follow-up pair-wise comparisons indicate that the loadings for probable gain cue were significantly smaller than probable loss ($T_{WJ/c}(1.0,18.0) = 22.67$, $p = .00080$) and break-even cues ($T_{WJ/c}(1.0,18.0) = 21.31$, $p = .00020$), which did not differ significantly from one another ($T_{WJ/c}(1.0,18.0) = 0.89$, $p = .36$).

Last, TF2/SF2, a P3b like factor combination, was maximal over PO7 between 360–364 ms ($T_{WJ/c}(2.0,16.0) = 20.95$, $p = .00020$). Consistent with previous research indicating enhanced P3 amplitudes to incentive cues (Novak & Foti, 2015), factor loadings for TF2/SF2 were significantly greater for probable gain ($T_{WJ/c}(1.0,18.0) = 40.73$, $p < .00000001$) and probable loss cues ($T_{WJ/c}(1.0,18.0) = 14.48$, $p = .0020$) than break-even cues. TF2/SF2 amplitudes were also significantly greater for probable gain cues than probable loss cues ($T_{WJ/c}(1.0,18.0) = 11.95$, $p = .0040$). Although one factor combination appeared to reflect the CNV, this was insensitive to any of the experimental manipulations (see Appendix A). No other factor combinations were

significantly affected by cue type, response hand, or their interactions.²

3.3 | Response activity

Response locked ERPs yielded 5 temporal and 4 spatial factors, with 17 of the 20 factor combinations accounting for at least 1% of variance. These factors combinations were submitted to a three (cue type: probable gain, probable loss, break-even) by two (response hand: left, right) factor ANOVA with a Bonferroni corrected threshold of $p < .0029$.

Only one factor combination, TF1/SF3, was sensitive to any of the experimental manipulations. TF1/SF3 was a sustained right hemisphere negativity maximal over C4 132–128 ms prior to responses and it likely reflects a readiness

²While there was reliable modulation of these factor combinations by cue type, they were insensitive to response hand (TF8/SF1: $T_{WJ/c}(1.0,18.0) = 0.03$, $p = .87$, TF6/SF1: $T_{WJ/c}(1.0,18.0) = 0.00$, $p = .99$, TF2/SF2: $T_{WJ/c}(1.0,18.0) = 1.63$, $p = .23$), or the interaction between response hand and cue type (TF8/SF1: $T_{WJ/c}(2.0,16.0) = 3.66$, $p = .071$, TF6/SF1: $T_{WJ/c}(2.0,16.0) = 1.10$, $p = .39$, TF2/SF2: $T_{WJ/c}(2.0,16.0) = 1.85$, $p = .21$).

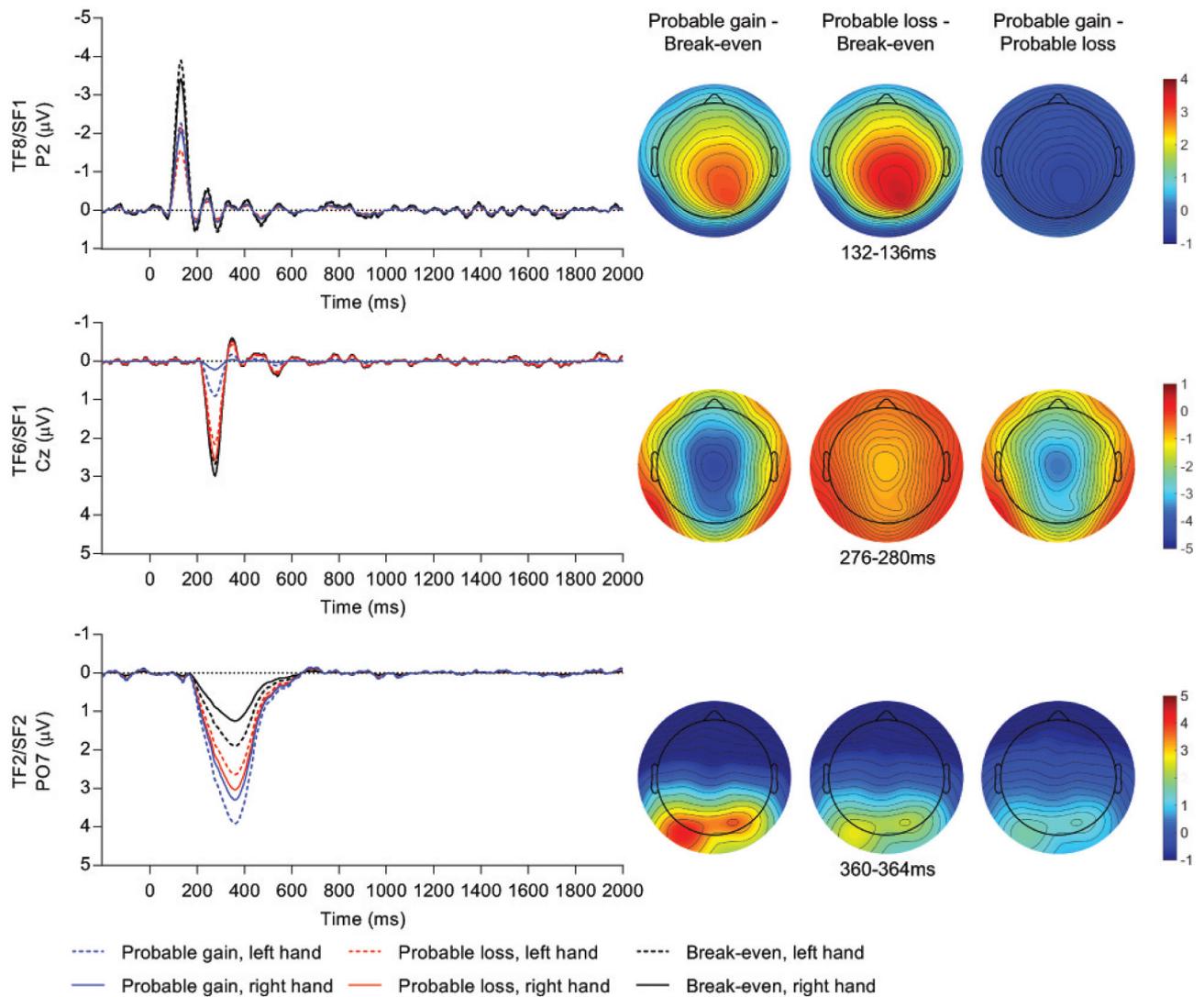


FIGURE 3 Cue locked wave forms and topographic maps for factor combinations reflecting the N1 (upper row), P3a (middle row), and P3b (bottom row). Wave forms and topographic maps are presented in microvolt scale. Topographic maps present the difference between cue types at the peak latency of each temporospatial factor combination

potential (RP). As shown in Figure 4, TF1/SF3 is modulated by response hand ($T_{WJ/c}(1.0,18.0) = 46.98, p < .00000001$). Consistent with basic research on motor preparation ERPs (Brunia, 1988), amplitudes were significantly more negative for left-hand responses than right-hand responses. Moreover, the direction of this effect was reversed when amplitudes were measured from C3.

While TF1/SF3 appears to reflect a readiness potential, contrary to some recent research, it was not significantly affected by cue type ($T_{WJ/c}(2.0,16.0) = 0.75, p = .48$). Nor was there an interaction between cue type and response hand, $T_{WJ/c}(2.0,16.0) = 0.75, p = .48$.

3.4 | Feedback anticipation activity

For activity that occurred prior to feedback presentation, 11 temporal factors were extracted, with 3 spatial factors each.

Nine of these 33 factor combinations explained at least 1% of variance and were subjected to a three (cue type: probable gain, probable loss, break-even) by two (response hand: left, right) factor ANOVA, with a Bonferroni corrected threshold of $p < .0056$. A single factor combination was sensitive to any of the experimental manipulations used in the present task, which is presented in Figure 5.

This factor combination, TF2/SF3, was centroparietal negativity that peaked over CP3 600–596 ms prior to the presentation of feedback. TF2/SF3 was reliably modulated by the response hand that participants had used, with more negative voltages over CP3 following right-hand responses than left-hand responses, $T_{WJ/c}(1.0,18.0) = 14.25, p = .0020$. As was also observed for the factor combination preceding actual motor responses (TF1/SF3), the direction of this effect was reversed when measured over CP4. Although the topology and sensitivity of this factor combination superficially

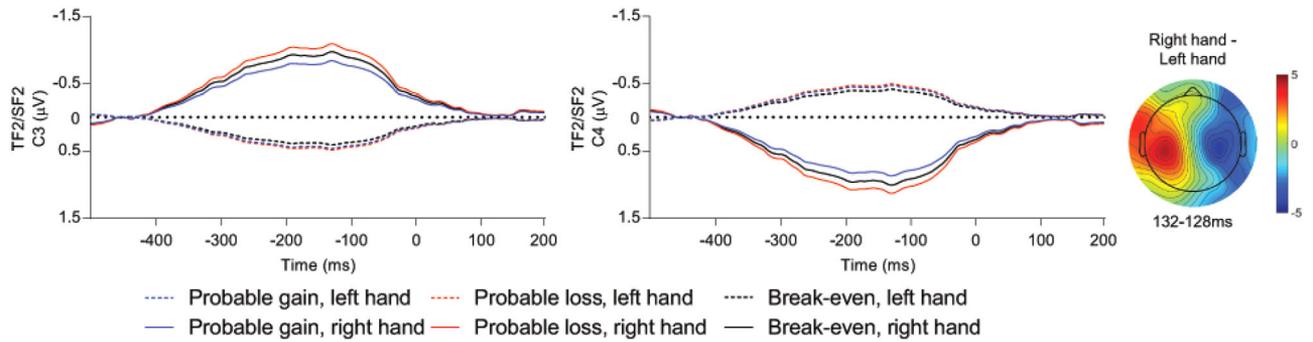


FIGURE 4 Response locked wave forms and topographic map for the factor combination that reflects the readiness potential. The wave forms and topographic map are presented in microvolt scale. The topographic map presents the difference between response hands at the peak latency of the temporospatial factor combination. Although this factor combination peaked over C4, the contralateral site, C3, is provided to illustrate the inversion of the waveform. Because this factor combination was maximal over C4 and for left-hand responses, the topographic map is most negative over the right hemisphere

resembles that of preparatory motor activity, it is important to emphasize that it occurred in anticipation of receiving feedback (i.e., 400–500 ms following responses).

A factor combination that had a similar time course and scalp topology to the SPN was also extracted but was not affected by any of the experimental manipulations (see Appendix B).

3.5 | Feedback activity

For feedback-locked averages, a total of 10 temporal factors and 4 spatial factors were extracted. Of these 40 factor combinations, 14 explained at least 1% of variance. These 14 factors were subjected to a two (cue type: probable gain, probable loss) by two (response hand: left, right) by two (outcome: gain, loss) factor ANOVA with a Bonferroni corrected threshold of $p < .0035$. This ANOVA yielded three factor combinations that were sensitive to different aspects of the task. The wave forms of which are displayed in Figure 6.

The earliest factor combination, TF4/SF1, was a fronto-central positivity that peaked over Cz between 224–228 ms. TF4/SF1 was modulated by feedback outcome with more

positive voltages observed in response to gain feedback than loss feedback, $T_{WJ/c}(1.0,17.0) = 15.20$, $p = .0034$. The topology and latency of this TF4/SF1 suggest it represents the RewP. This replicates a previous application of PCA to reward-consumption ERPs (Foti & Hajcak, 2009), confirming that the RewP can be observed in response to feedback stimuli in the MID task.

While TF4/SF1 was only modulated by outcome and not expected outcome or response hand, an overlapping factor, TF1/SF1, was sensitive to the interaction between cue type and feedback type, $T_{WJ/c}(1.0,17.0) = 22.82$, $p = .0014$. TF1/SF1 had a centroparietal distribution peaking over Cz, 380–384 ms following feedback presentation, suggesting it corresponds to the fb-P3 observed in other studies (Balconi & Crivelli, 2010; Novak & Foti, 2015). Pair-wise comparisons of the interaction between cue type and outcome, with a corrected significance threshold of $p < .0125$, revealed three significant contrasts. First, TF1/SF1 was significantly more positive on probable gain trials when participants received loss feedback relative to when they received gain feedback ($p = .0002$). Second, more positive amplitudes were observed in response to win feedback on probable loss trials

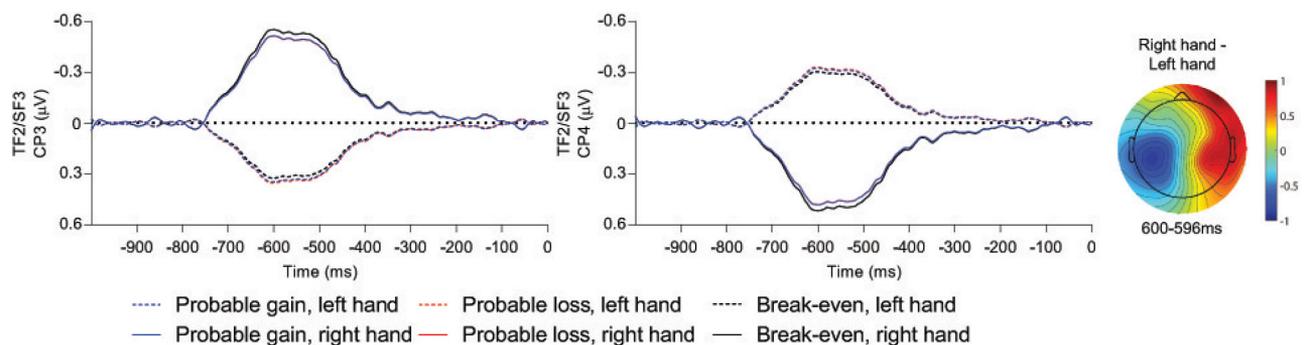


FIGURE 5 Feedback anticipation wave forms and topographic map for TF2/SF3. The wave forms and topographic map are presented in microvolt scale. The topographic map presents the difference between response hands at the peak latency of the temporospatial factor combination. Although this factor combination peaked over CP3, the contralateral site, CP4, is provided to illustrate the inversion of the waveform. Because this factor combination was maximal over CP3 and for right-hand responses, the topographic map is most negative over the left hemisphere

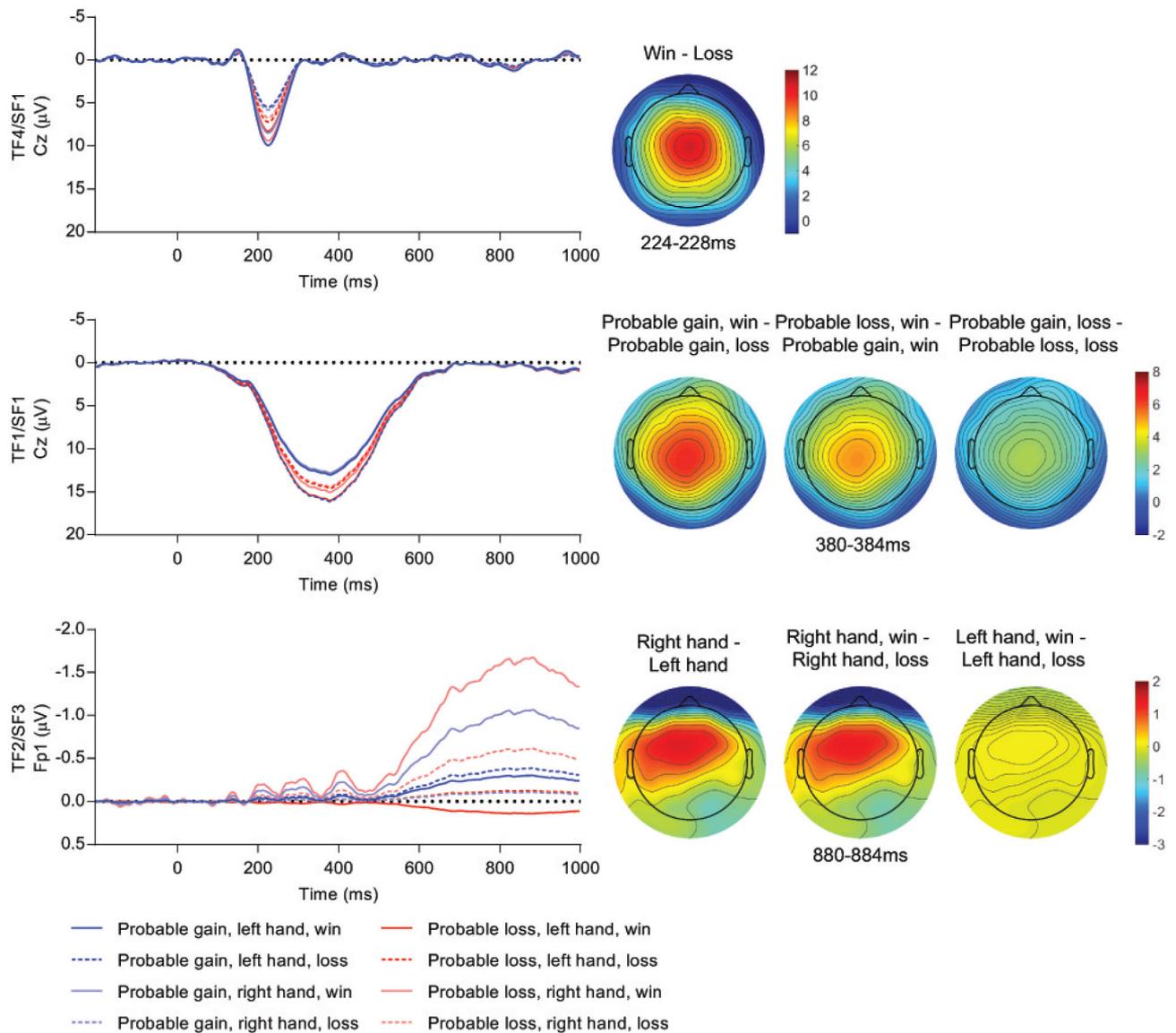


FIGURE 6 Feedback locked waveforms and topographic maps for factor combinations reflecting the reward positivity (upper row), feedback-P3 (middle row), and late frontopolar negativity (bottom row). Wave forms and topographic maps are presented in microvolt scale. Topographic maps present the difference between feedback valence (upper row), cue type and feedback valence (middle row), and feedback valence and response hand (bottom row) at the peak latency of each temporospatial factor combination

relative to probable gain trials ($p = .007$). Third, the opposite pattern was observed in response to loss feedback, with significantly more positive amplitudes on probable gain trials relative to probable loss trials ($p = .009$). Taken together, these comparisons indicate that TF1/SF1 amplitudes were enhanced when the outcome of a given trial violated the expectation established by the cue.

Last, a factor combination, TF2/SF3, representing a late frontopolar negativity was modulated by the response hand used by participants on each trial, $T_{WJ/c}(1.0,17.0) = 22.06$, $p = .0010$. TF2/SF3 peaked between 880–884 ms following feedback over Fp1 and was more negative for right-hand than left-hand responses. There was also a significant interaction between response hand and feedback type, $T_{WJ/c}(1.0,17.0) = 12.28$, $p = .0022$. Pairwise comparisons indicate

that gain feedback for right-hand responses elicited significantly more negative amplitudes than gain feedback for left-hand responses, $T_{WJ/c}(1.0,17.0) = 38.00$, $p < .00000001$. Amplitudes did not differ as a function of response hand for loss feedback, $T_{WJ/c}(1.0,17.0) = 0.19$, $p = .67$.

4 | DISCUSSION

In this study we applied temporospatial PCA to data from a modified MID task. This novel approach was used in order to identify electrophysiological components important for reward anticipation and consumption in the MID task. PCA successfully extracted several components differentially modulated by stimuli cuing anticipation of probable gain,

probable loss, and breaking-even. When applied to feedback anticipation, PCA was able to extract a factor combination that resembled the SPN. However, this factor combination was not reliably modulated by incentive cue or response hand. Instead, we observed a lateralized centroparietal factor combination that was acutely sensitive to the hand participants had *just* used to make a response. The application of PCA to reward consumption also extracted well-established feedback processing ERPs in the RewP and fb-P3, components that have proved difficult to observe in the MID task. In addition, a new component was revealed in the late stages of feedback processing. This component is a late negativity distributed over the left frontal pole that appears to be sensitive to response hand, especially in the context of monetary gain. While a component reflecting the RP was identified preceding responses, it appeared to be insensitive to the prospect of gains, losses, and breaking-even. Target components as well appeared to be insensitive to cue type.

4.1 | Incentive Cues

This study provides important insight into the modulation of ERPs by incentive cues in the MID task. Specifically, it provides evidence that the ERP components modulated by probable gain, probable loss, and break-even cues reflect distinct processes. There is no simple heuristic where reward incentive cues produce greater activity than loss and break-even cues. Furthermore, reward enhancement may not be present until relatively late in stimulus processing.

The early parietal factor combination, reflecting the N1, was enhanced for break-even cues relative to probable gain and probable loss. As the N1 is associated with early processes related to selective attention, this observation suggests “neutral” incentive cues may receive some preferential processing relative to reward and loss cues. This finding is inconsistent with the results of one previous study where N1 amplitudes were enhanced for reward cues relative to break-even (Doñamayor et al., 2012). However, grand averages from other MID studies also appear to show a greater N1 to break-even cues, but these effects have not been directly reported (e.g., Study 1; Novak & Foti, 2015).

This early negativity was distinct from two subsequent, independently modulated centroparietal and parietal positivities, which typically overlap to form the P3 (Polich, 2007). The first positivity had a latency and centroparietal distribution consistent with the P3a. The P3a is enhanced by stimuli requiring the automatic attentional switching or the initiation of inhibitory processes. Interestingly, P3a amplitudes were smaller for probable gain cues than probable loss or break-even cues, a finding broadly consistent with the observation that P3a amplitudes are enhanced by stimuli of negative

affect (Delplanque, Silvert, Hot, Rigoulot, & Sequeira, 2006).

The second positivity reflects the P3b and has a predominantly parietal distribution. Consistent with previous research, P3b amplitudes were larger for probable gain cues relative to probable loss and break-even cues (Broyd et al., 2012; Goldstein et al., 2006; Novak & Foti, 2015; Pfabigan et al., 2014; Pompattananangkul & Nusslock, 2015; Santesso et al., 2012). The topology of the P3b that we observe was considerably left lateralized in contrast to the more central distributions observed in other studies. While it is difficult to identify a clear explanation for this lateralization, several studies have noted that object/color recognition and action processes may be more prevalent over the left hemisphere (Johnson-Frey, Newman-Norlund, & Grafton, 2005; Proverbio, Burco, del Zotto, & Zani, 2004). Aspects of these processes could conceivably be enhanced when an incentive cue indicates a possible reward. However, given the ubiquity of the P3b across multiple contexts, and considerable problems that reverse inference creates, we are reluctant to ascribe any particular psychological process as causative of this lateralization.

These data suggest that electrophysiological activity discriminates between different incentive cues and have distinct time courses. First, an initial parietal negativity occurs that is more sensitive to break-even cues than probable gain or loss cues. Second, a centroparietal positivity occurs that is more sensitive to probable loss and break-even cues than gain cues. Finally, a slow parietal positivity occurs that is more sensitive to probable gain cues than loss or break-even cues. Importantly, while these results replicate the common finding that the P3b/P3 is greater to reward incentive cues, it also suggests this enhancement is not present until relatively late in processing. In sum, while earlier components reflect capture by motivationally salient stimuli that signal increased probability of losses, the later positivity corresponding to the P3b/P3 reflects capture by motivationally salient stimuli that signal increased probability of gains.

In the context of incentive cues, earlier components (e.g., N1, P3a) may reflect the automatic capture and allocation of attention to stimuli signaling future events that may be disadvantageous: this includes both probable loss and break-even cues. Break-even cues require participants to expend physical and cognitive effort with no possibility of reward, representing a net loss to participants. This conjecture is broadly supported by findings that nonreward feedback produce identical RewP amplitudes to loss feedback (Hajcak et al., 2006). This finding is also consistent with recent perspectives on the nature of incentive salience and incentive cue processing. Berridge and Kringelbach (2015) argue that even though an incentive cue may produce approach-related feelings of “wanting” in anticipation of a reward, this is not

intrinsically a positive state. When the incentive cue—or features of the environment—simultaneously signals that a reward will not be forthcoming, this can produce a form of negative incentive salience, which is borne out as a feeling of frustration (Harmon-Jones, Harmon-Jones, & Price, 2013). Conversely, the presentation of a break-even cue could be also appraised as a relief from the possibility of loss that is associated with both probable loss and probable gain trials. We speculate that whether break-even cue stimuli are interpreted as net losses or the relief from potential loss may be dependent on participants' perceptions that they can influence the outcome of each trial, and the development of expectations on this basis. Because blunted RewP amplitudes are observed when participants have limited perceived agency or sense of control over action-outcome contingencies (Angus et al., 2015; Bellebaum, Kobza, et al., 2010; Mühlberger, Angus, Jonas, Harmon-Jones, & Harmon-Jones, 2017), this speculation could be tested using experimental designs that directly manipulate perceived control, in conjunction with examination of RewP amplitudes.

In this study, we do not observe reliable incentive cue modulation of anticipatory slow waves such as the CNV. These effects have proved difficult to measure in ERP versions of the MID task with inconsistency both in the presence of modulation and the effects of probable gain, loss, and breaking-even cues. Nevertheless, recent research has reported a semiconsistent enhancement to later stages of the CNV by reward cues relative to break-even cues (Novak & Foti, 2015; Pfabigan et al., 2014). While further research is required to confirm this effect, it is possible that methodological differences are responsible for our null effect. Typical MID tasks involve an incentive cue followed by a target stimulus signaling for an immediate response. The slow wave that precedes the target is therefore a combination of anticipatory processes (e.g., the early CNV) and action preparation (e.g., the late CNV). In our version of the task, participants were not required to make a response to the target stimulus but instead begin the temporal estimation task. It is unsurprising, then, that a component involved in action preparation is unaffected.

4.2 | Responses

Unlike previous research we failed to observe any enhancement of the RP in response to incentive cues (Pornpattananangkul & Nusslock, 2015). There are a number of possible reasons for this null effect. First, when reported, the effect size of RP modulation—as with the CNV—by incentive cue is weak relative to the effect size of the anticipatory ERPs that follow cue presentation. While we may simply have required significantly more statistical power to detect these effects, it is possible these effects may not be robust.

Second, two key methodological differences may have influenced our result. First, unlike Pornpattananangkul and Nusslock (2015), the contingencies in our study were probabilistic. When participants received a probable gain cue, they were only more likely to gain money, whereas when they received a probable loss cue, they were only more likely to lose. In contrast, in Pornpattananangkul and Nusslock (2015), incentive cues of various forms indicated with certainty what the outcome would be, provided that participants' responses were accurate. In our task, despite being told otherwise, the timing of participants' responses never actually guaranteed the reward outcome.³ It is possible that RP modulation is sensitive to the efficacy of participant responses to secure the monetary gains or avoid the monetary losses indicated by the incentive cue. When accurate responses only *increase* rather than guarantee the possibility of reward, RP modulation may be reduced, if not entirely absent.

Third, it is also possible that while RP modulation is enhanced by incentive cues, it does not distinguish between motivations to secure monetary gain or avoid monetary loss. Unlike Pornpattananangkul and Nusslock (2015) who had an equal amount of reward and break-even trials, our study had an equal amount of probable gain, probable loss, and break-even trials. The failure to observe RP modulation may be due to the fact that the vast majority of our trials involved incentivized performance. Note that this could still occur even if the RP is not being modulated by the anticipatory cue as our results suggest. All that it requires is the experiment to be designed to emphasize incentivized performance.

4.3 | Feedback anticipation

While we did observe a factor combination that reflects the SPN in topology and time course, it was not modulated by any of the experimental manipulations. One reason for the absence of incentive cue modulation may be that participants' perception of control did not differ between probable gain, probable loss, and neutral cue conditions. In the present study, the outcome of each trial was predetermined, and participants' responses could only alter this outcome if they failed to respond or responded using the incorrect hand. This element of the task design may have reduced participants' perceived control and contributed to an absence of cue-related modulation. Consistent with this explanation, research has shown that SPN amplitudes are smaller when participants believe they have limited control over outcomes than when they believe they have greater control (Mühlberger et al., 2017; see also Kotani, Ohgami, Yoshida, Kiryu, & Inoue, 2017; Masaki, Yamazaki, & Hackley, 2010).

³Aside from failing to perform at all.

We did, however, find a factor combination that was robustly modulated by the response hand that participants had just used. This factor combination was superficially similar to typical preparatory motor responses (e.g., RP, LRP) in its topology and lateralization as a function of response hand. Importantly, however, it occurred at least 400 ms *after* a response had been made, presenting 600 ms prior the receipt of feedback regarding the success or failure of that action. A conservative interpretation is that this factor combination reflects the residual motor activity that follows responses (e.g., a slow motor potential; Müller et al., 1994). The broader implications of this factor combination within the context of the MID task and reinforcement learning is unclear; however, we note that the particular context in which it has evoked is broadly consistent with the notion of an “eligibility trace,” which is thought to be produced following an action and serves as a form of working memory regarding the behavior that will—or will not—be reinforced by feedback (Doya, 2008). Alternatively, this component may reflect activity associated with hand movements following participants’ responses in the temporal estimation task. Specifically, following their response on each trial, participants likely returned their hand to a resting position, producing tactile and kinesthetic activity. This tactile and kinesthetic activity produces reafferent activity in the somatosensory cortex (Keysers, Kaas, & Gazzola, 2010). However, in the present study, we did not collect surface electromyography (EMG) from participants’ arms, and as such, it is impossible to determine whether outcome anticipation or reafference better explains the results. Moreover, the omission of EMG measurements also limits our ability to address different explanations for CNV and RP modulation.

The limited modulation of SPN amplitudes by incentive cues and the presence of a postmotor component may also be due to the duration of the interval between motor responses and feedback onset. Previous studies have reported that postmovement activity can be observed contralateral to the response hand up to 2 s following responses (Damen & Brunia, 1994). Consequently, this activity may mask SPN modulation. However, the application of PCA in our study has allowed us to disentangle postmovement activity from the SPN itself. Indeed, one of the factor combinations we observed reflected this postmovement activity and was more negative contralateral to the response hand, while the factor combination that we argue reflects the SPN was maximal over the right hemisphere and did not reliably differ as a function of response hand.

4.4 | Reward consumption

Previous MID research has had issues observing reward consumption ERPs. Even when these ERPs are observed, their modulation is inconsistent with the wide literature on reward consumption (e.g., Broyd et al., 2012; Novak & Foti, 2015).

In this study, the novel application of PCA to feedback-locked ERPs in the MID task successfully separated and quantified the RewP and fb-P3. This is despite the substantial temporal and spatial overlap that has contributed to equivocal effects reported in the past. Consistent with research applying PCA to a non-MID task (Foti & Hajcak, 2009), the RewP had a frontocentral distribution and was greater to feedback signaling gains than losses. RewP amplitudes were not influenced by whether participants expected a gain or loss. In other words, incentive cues did not influence the RewP; only feedback cues did.

The RewP’s independence from incentive and expectation effects is important given the results of previous MID research. As pointed out by Novak and Foti (2015), loss and break-even feedback on MID tasks are typically less frequent than reward. This element of their design confounds the effects of feedback type with stimulus probability making quantification of the RewP difficult. Importantly, in the present study, probable gain and probable loss trials had opposite feedback probabilities (e.g., wins were obtained on 60% of probable gain trials and on 40% of probable loss trials. Losses were obtained on 40% of probable gain trials and on 60% of probable loss trials) and produced, as expected, identical RewP amplitudes.

This finding is inconsistent with some studies that have examined feedback processing from a reinforcement learning perspective (Holroyd et al., 2011; Ichikawa et al., 2010; Pfabigan et al., 2011). In these studies, the RewP (or FRN) has typically been investigated as an electrocortical manifestation of reward prediction errors, with more negative amplitudes being observed for loss feedback than for gain feedback, and the difference between feedback valences being enhanced by greater reward expectancies (Bellebaum & Daum, 2008; Bellebaum, Poleschi, et al., 2010), and when outcomes differ from expectations (Pfabigan et al., 2015). However, these effects have not always been consistently observed, with several studies finding that the FRN is sensitive to binary differences in outcome (e.g., reward vs. nonreward) and not expectancy and expectancy violation (Highsmith, Wuensch, Tran, Stephenson, & Everhart, 2017). The findings of the present study are in broad agreement with research that interprets the RewP as a binary index of desired versus undesired outcomes, rather than a measure of expectancy violation and prediction error per se. If a prediction error or expectancy violation effect was observed, then RewP amplitudes would be larger on trials where participants had viewed incentive cues that indicated a likely counterfactual outcome. It is important to note that because we did not vary reward probabilities throughout our task on a block-by-block or trial-by-trial basis, it is difficult to draw any definitive conclusions with respect to which model of the RewP is best supported.

In contrast to the RewP, the fb-P3 tracked expectancy violation. Greater amplitudes were observed when feedback

signaled losses on probable gain trials and gains on probable loss trials. This pattern of results is consistent with the effects reported in previous studies where feedback events that are seen as infrequent or important are associated with greater fb-P3 amplitudes. Importantly, our results suggest that application of PCA to reward consumption ERPs in the MID task can measure both the valence aspects of the RewP, and expectation and salience aspects of the fb-P3.

We also observed for the first time a very late negativity distributed over the left frontal pole. There is currently no existing explanation for this effect in the literature on reward consumption. While this component could potentially reflect an SPN to the offset of feedback stimuli, there is limited evidence that this is the case. First, while the time course and polarity of the factor combination is consistent with the SPN, its topology is not. Second, there is limited evidence of the SPN being produced prior to feedback offset in other studies using the MID task or in studies using gambling tasks (e.g., Foti & Hajack, 2012). As the negativity is sensitive to the participant's response hand, especially in the context of reward feedback, we speculate this component may be associated with encoding and updating some form of successful response prototype. The greater negativity observed for right-hand responses might be a function of hand dominance as all the participants in our sample were right handed. Similar frontopolar negativities have been observed in prospective memory tasks when individuals successfully encode the intention to act in the near future, although these effects have only been observed following viewing instruction stimuli, rather than following feedback stimuli (West, 2011; West & Moore, 2002). An alternative explanation could be that this factor combination also reflects processes similar to an eligibility trace, albeit at a different stage of processing (Doya, 2008). Further research is required to reproduce the presentation of this component and establish the feature(s) of reward consumption with which it is associated.

Last, while some studies (e.g., Pornpattananangkul & Nusslock, 2015) have reported LPP modulation to feedback stimuli in the MID task, we did not observe this in the present study.

5 | CONCLUSION

The MID task offers a promising experimental approach to assessing and modeling reward processing and consumption. Results from our study show that the dynamics of reward anticipation can be parsed into discriminable stages that are differentially modulated by probable gain, probable loss, and break-even cues. In addition, use of PCA on feedback-locked ERPs can allow researchers to assess both the RewP and fb-P3 independently in the MID task. We also observe for the first time a late negativity distributed over the left frontal pole in response to task feedback. This new reward

consumption component appears to be sensitive to response hand, especially in the context of monetary gain. Further investigation is required to understand the exact functions that these components signify in the context of reward anticipation and consumption.

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SUPPORTING INFORMATION

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

Figure S1
 Figure S2
 Figure S3
 Figure S4
 Figure S5

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APPENDIX A

One factor combination appeared to reflect the CNV. This combination, TF1/SF4 had a frontocentral distribution and peaked between 1,840 and 1,844 ms following the onset of cue stimuli (Figure A1). While the topology and latency of this factor combination is consistent with previous reports of CNV modulation by incentive cues (Novak & Foti, 2015; Plichta et al., 2013), we did not observe reliable differences between probable gain, probable loss, and break-even cues. A robust ANOVA using a Bonferroni adjusted p value threshold of .003125 indicated that there was no significant effect of incentive cue ($T_{WJ}/c(2.0,16.0) = 3.07$, $p = .082$), cued response hand ($T_{WJ}/c(1.0,18.0) = 12.53$, $p = .0044$), or an interaction between the two, $T_{WJ}/c(2.0,16.0) = 0.01$, $p = .98$.

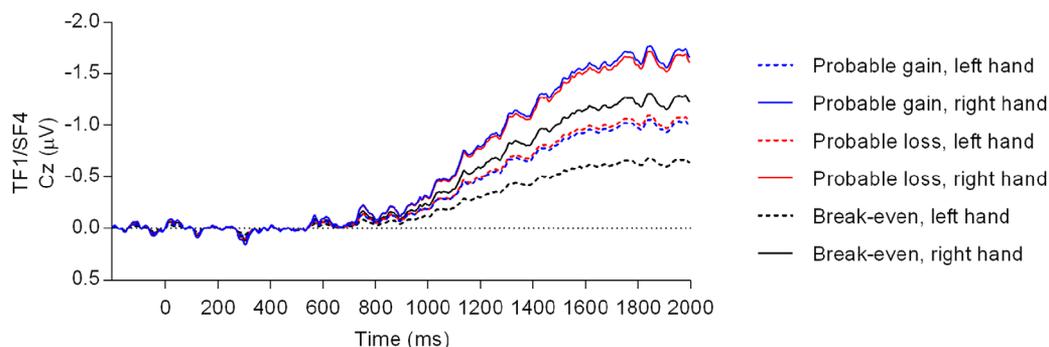


FIGURE A1 Cue locked wave forms for factor combination reflecting the CNV. Wave forms are presented in microvolt scale

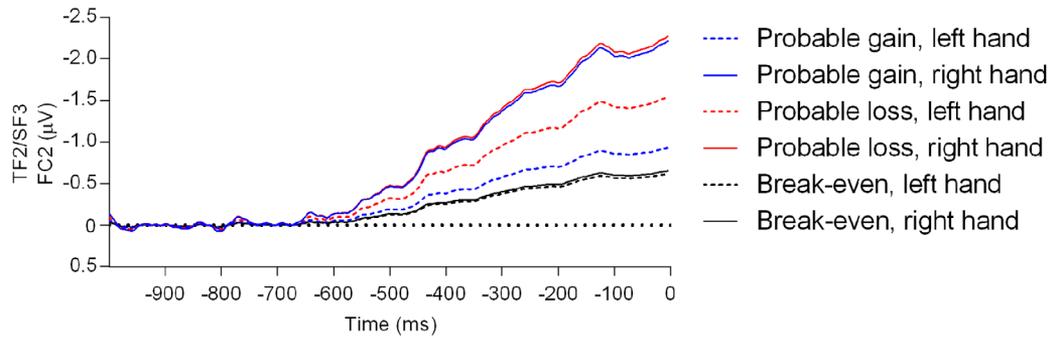


FIGURE A2 Feedback anticipation wave forms for factor combination reflecting the SPN. Wave forms are presented in microvolt scale

APPENDIX B

One factor combination appeared to reflect the SPN. This combination, TF1/SF1 had a frontocentral distribution and peaked between 4 ms before the onset of feedback stimuli (Figure A2). Although the topology and latency of this factor combination is consistent with previous reports of SPN modulation by reward expectancy (Brunia et al., 2011; Ohgami et al., 2004; Ohgami et al., 2006; Pornpattananangkul &

Nusslock, 2015), there were no reliable differences between probable gain, probable loss, and break-even cues. A robust ANOVA using a Bonferroni adjusted p value threshold of .0055556 indicated that there was no significant effect of incentive cue ($T_{WJ}/c(2.0,16.0) = 1.85$, $p = .20$), cued response hand ($T_{WJ}/c(1.0,18.0) = 4.68$, $p = .048$), or an interaction between the two, $T_{WJ}/c(2.0,16.0) = 2.00$, $p = .20$.