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Reward Contingencies and the Recalibration of Task Monitoring and Reward Systems: A high-density electrical mapping study

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Abstract

Task execution almost always occurs in the context of reward-seeking or punishment-avoiding behavior. As such, ongoing task monitoring systems are influenced by reward anticipation systems. In turn, when a task has been executed either successfully or unsuccessfully, future iterations of that task will be re-titrated on the basis of the task outcome. Here, we examined the neural underpinnings of the task-monitoring and reward-evaluation systems to better understand how they govern reward seeking behavior. Twenty-three healthy adult participants performed a task where they accrued points that equated to real world value (gift cards) by responding as rapidly as possible within an allotted timeframe, while success rate was titrated online by changing the duration of the timeframe dependent on participant performance. Informative cues initiated each trial, indicating the probability of potential reward or loss (four levels from very low to very high). We manipulated feedback by first informing participants of task success/failure, after which a second feedback signal indicated actual magnitude of reward/loss. High-density EEG recordings allowed for examination of event-related potentials (ERPs) to the informative cues and in turn, to both feedback signals. Distinct ERP components associated with reward cues, task preparatory and task monitoring processes, and reward feedback processes were identified. Unsurprisingly,

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participants displayed increased ERP amplitudes associated with task preparatory processes following cues that predicted higher chances of reward. They also rapidly updated reward and loss prediction information dependent on task performance after the first feedback signal. Finally, upon reward receipt, initial reward probability was no longer taken into account. Rather, ERP measures suggested that only the magnitude of actual reward or loss was now processed. Reward and task monitoring processes are clearly dissociable, but interact across very fast timescales to update reward predictions as information about task success or failure is accrued. Careful delineation of these processes will be useful in future investigations in clinical groups where such processes are suspected of having gone awry.

Keywords

Reward; Punishment; Task Monitoring; EEG; ERP; Motivation

INTRODUCTION

It could reasonably be argued that all activity undertaken by an organism is in the service of achieving reward, either in the short or long term. Organisms must determine the potential value of a reward and develop and adjust reward expectations depending on environmental contingencies, and monitoring of ongoing activity and calibration of task effort and preparation occur in the context of these reward expectations and are adjusted based on outcomes (Ryan, 1983, Deci et al., 1999). There has been great interest in the neural underpinnings of both reward processing and task monitoring and how these processes and their underlying brain circuitry interact to govern reward seeking behavior.

Functional Magnetic Resonance Imaging (fMRI) has demonstrated the presence of at least partially distinct brain mechanisms for task monitoring and reward processing. Work has implicated the orbitofrontal and prefrontal cortices in the representation of rewarding items and reward prediction while participants performed gambling tasks (Dreher et al., 2006, Preuschoff et al., 2006) or delayed reward tasks (Kable and Glimcher, 2007). Meanwhile, the ventral striatum and anterior cingulate cortex have been implicated in task monitoring when participants made errors while bidding for rewards (Hare et al., 2008), when participants evaluate task effort needed to obtain primary rewards (Prevost et al., 2010), and when evaluating conflict between high risk or low risk choices (Kuhnen and Knutson, 2005).

Neuroimaging, however, is not ideal for examining the interaction of processes that may occur over very fast timescales. To this end, researchers have examined various components of the Event Related Potential (ERP), which provide temporally precise measures of information processing well-suited for the examination of reward processing and task monitoring. Work by Pedroni et al., (2011), which examined the timing and topography of reward responses, has put forth the suggestion that early processing of reward feedback results in a binary, "Good/bad" evaluation, while later processes take into account more detailed information. Further, their work identified different topographies for rewards and losses, suggesting a need to examine these processes in more detail. ERP components

associated with reward processing include the so-called "Correct Related Positivity," which arises as early as 200 to 250 ms after cues predicting reward (Holroyd et al., 2011, Yu, 2011), and the P300, a component that arises later between 300–600 ms and is usually associated with arousal and attention to task (Polich and Kok, 1995). The P300 is also sensitive to elements of reward processing, such as the magnitude and valence of the reward (Hajcak et al., 2005, Sato et al., 2005, Wu and Zhou, 2009). However, there remain open questions in this literature about these components. Work by (Yeung and Sanfey, 2004) suggested that the P300 is sensitive to reward magnitude alone. By investigating reward and monitoring in separate stages, we are well positioned to shed light on this question.

ERP research of task monitoring in the context of reward has focused on a component often referred to as the Feedback Related Negativity (FRN), a negative-going deflection in the ERP occurring approximately 200–300 ms after the receipt of external feedback (Miltner et al., 1997). Task monitoring and cognitive control in non-reward contexts has also been measured using the Error Related Negativity (ERN), which is believed to reflect internally generated error monitoring signals as opposed to responses to external feedback like the FRN. However, it has been suggested that both the ERN and FRN reflect the same anterior cingulate mechanisms (Gehring and Willoughby, 2002, Holroyd and Coles, 2002, Nieuwenhuis et al., 2004). Further, a sustained negativity called the Contingent Negative Variation (CNV) precedes the onset of a predicted stimulus that requires a response (Walter et al., 1964). The CNV can be affected by motor or cognitive processes (Leynes et al., 1998) and the probability of having to make a specific response (Dias, 2003). Source analysis of the CNV has implicated not only premotor and sensory areas, but also aspects of the fronto-parietal network that may underlie evaluation of task effort (Gomez et al., 2007).

Interactions between reward processing and task monitoring have also been investigated during performance of a spatial incompatibility task, wherein participants responded using vertically oriented response keys to stimuli that appeared above or below a fixation cross. This created both spatially compatible trials and more difficult spatially incompatible trials, in a manner similar to the well known Simon task (Simon, 1963). When reward was contingent upon performance, the ERN and FRN amplitudes differed compared to blocks of trials when reward was not contingent upon performance (Sturmer et al., 2011). However, there is conflict in the literature about whether the FRN is purely related to monitoring of good or bad task outcomes regardless of reward. Some have suggested that it reflects only the salience of an unexpected response (Ferdinand et al., 2012) while others have suggested it reflects prediction errors in the context of reward (Cohen et al., 2007) and is dependent on monitoring related to details about reward (Yeung and Sanfey, 2004, Hajcak et al., 2006). Research focused upon the FRN is not alone in raising questions about the interaction of reward and monitoring. While some research has suggested that the CNV is insensitive to reward (Goldstein et al., 2006), other work has demonstrated an influence of monetary incentives (Hughes et al., 2012).

The goal of the current study was to examine reward processing and task monitoring in depth, as well as the interactions between these processes. Much of the previous work investigating these mechanisms presented the reward outcome simultaneously with task performance feedback. This potentially conflates task monitoring with aspects of reward

processing. To our knowledge, no studies have expressly divided task and performance feedback in an ERP paradigm designed to examine reward and monitoring separately. Here, we designed a task to at least partially dissociate feedback about received reward from feedback about task execution. Our paradigm took the form of a speeded reaction time task wherein the presentation of a symbolic cue provided information to the participant about the upcoming probability of monetary gains or losses based upon performance. The unique manipulation of our task was that participants received immediate feedback when they responded, informing them only if they had successfully executed their response within an allotted timeframe. This allowed them to make a second prediction about the magnitude of the reward they were likely to receive. In turn, participants received a second instance of feedback informing them of the actual magnitude of their losses or gains. By systematically varying reward expectation and reward outcome, we set out to explore the interface of task monitoring and reward processing, and how the mechanisms that underlie these processes are altered as a function of differing reward contingencies. We recorded high-density EEG from a 168-channel montage, which allowed us to investigate not only the ERP components associated with reward motivation and task monitoring but to also perform source analysis in order to model the underlying neural sources.

METHODS

Participants

Twenty-four participants were recruited using advertisements on Craigslist and through word of mouth. All potential participants were administered the Structured Clinical Interview (SCID-I) for the DSM-IV and responded to screening questionnaires related to their overall physical and mental health. Exclusion criteria were as follows: 1) Any DSM-IV Axis 1 diagnosis; 2) Head trauma resulting in loss of consciousness for longer than 30 minutes; 3) Presence of any past or current brain pathology; 4) A diagnosis of HIV; 5) Age above 55 years and below 18 years; 6) Any evidence of an alcohol/drug dependence diagnosis, including nicotine dependence, or if any biologically-related family members had an alcohol/drug dependence diagnosis. One participant performed a pilot version of the task and their data was not usable, leaving twenty-three participants total. Participants were paid for their participation in the form of one \$12 gift card to a local department store per hour of experiment time. All participants also received approximately the same amount of extra money, which was dependent on their performance in our reward task and was awarded in extra gift cards. All participants signed an informed consent document administered by HIPAA-certified staff (as per the U.S. Health Insurance Portability and Accountability Act). All procedures were approved by the Institutional Review Board of the Albert Einstein College of Medicine and the City College of the City University of New York. The study conformed to the principles outlined in the Declaration of Helsinki. EEG recordings for the reaction time task were completed on all 23 participants. Participants had an average age of 39 years with a range between 25 and 53 years, and an average of 12 years of education with a range between 11 and 16 years. Seven participants were female and 2 participants were left-handed.

Task and Recording Procedures

For the electrophysiological portion of the study, participants were seated in a dimly lit, doublewalled, sound-attenuated, electrically shielded room (Industrial Acoustics, Bronx, NY). They were seated 80 cm from a LCD monitor (Viewsonic VP2655WP, 55 x 65 cm). Each block consisted of 100 trials. Participants completed one mandatory practice block before the main experiment began. If needed, additional practice blocks were allowed. Twenty experimental blocks were run, each lasting approximately 5 minutes, for a total of 2000 trials. Participants took 30 second breaks between blocks and were permitted to take longer breaks when needed to reduce fatigue and concentration lapses. There was a succession of visual and auditory stimuli presented in a fixed sequence on each trial during this experiment. Participants were required to maintain central fixation through the experiment. Visual stimuli were generated and edited in Microsoft Paint and auditory stimuli were generated and edited using Matlab version 2007b (The MathWorks Inc., Natick, Massachusetts). Visual stimuli were presented on a Dell PC using Presentation version 14 (Neurobehavioral Systems, Albany, CA). Visual cue and feedback stimuli were presented centrally and subtended 1.7° horizontally by 1.5° vertically. Auditory stimuli were presented from a set of BOSE companion series II speakers, placed 80 cm from the participant at either corner of the computer monitor (65 cm apart).

Figure 1 illustrates the order of stimuli and what one succession of trials consisted of for one of four possible conditions. The first screen of any trial displayed one out of a possible set of four stimuli (purple, red, blue or yellow discs) in the center of the screen. These discs served as a reward probability cue. Table 1 shows the probabilistic outcomes of each of the four probability conditions. The color correspondence of the discs to the different probability conditions was counterbalanced across participants.

After the disc was displayed for 300 ms, a blank screen, devoid of any fixation cross, was presented for 500 ms. An “x” was displayed following this. Participants were instructed to respond as fast as they could by clicking the response button on a computer mouse with their right hand upon seeing the x. The time frame in which the target “x” was displayed was varied as a function of a participant’s ongoing performance, titrated in real time using the so-called “up-down transformed-rule” (UDTR) method (Wetherill GB. and Levitt, 1965). The UDTR is akin to other simple staircase methods, and it involves adjusting the difficulty of the task to ensure a specific fixed level of performance across all participants in a given study. In the current experiment, appearance of the small target “x” marked the onset of a response time window within which the participant was required to make as fast a response as possible before the response window closed. We used a simple “one-up-two-down” UDTR rule here. That is, if the participant successfully responded within the time-window twice in a row, then the window was narrowed by 20ms to make the next iteration of the task more difficult (this is what is referred to as “two-down”). On the other hand, if the participant missed the window on the next iteration (or following just one instance of a successful response), then the window was readjusted outward by a similar increment of 20ms to make the task simpler (i.e. “one-up”). This simple rule essentially pins performance to a specific point on the psychometric curve, in this case leading to 70.7% success. Other

combinations (e.g. 3-up-2-down) can be used to fix performance levels at different points on the psychometric.

After participants responded, a tone was presented that let the participant know whether they had successfully responded within the time frame that the x was displayed. This tone was the first instance of feedback. A 100 ms high pitch (1500 Hz) tone informed of success, while a 100 ms low pitch (500 Hz) tone indicated failure. Another 500 ms blank screen followed the tone. After this blank screen, the third visual stimulus displayed a feedback symbol. This was the second stage of feedback that informed of actual reward. There were five potential feedback outcomes. Rewards, which could only occur following a response that was completed successfully within the allotted time frame during which the target x was presented, were indicated by a picture of a bag of money or a picture of two bags of money, denoting a small and large reward respectively. Losses, which could only occur following a failure to respond successfully within the allotted time frame, were indicated by a picture of a red X or a picture of two red X's, denoting a small and large loss respectively. The larger magnitude wins or losses occurred 50% of the time when a win or a loss would have occurred, and thus large and small rewards and losses were equiprobable. The other potential outcome was a black bag, which signified that nothing had been gained or lost. This outcome could occur regardless of performance. Feedback stimulus meanings were not counterbalanced, as previous research has demonstrated the feedback processing system to be insensitive to the physical features of the stimuli (Miltner et al., 1997, Holroyd and Coles, 2002). The probability of receiving neutral feedback as opposed to an actual reward or loss depended on the color of the disc at the beginning of each trial, in accordance with the probabilities described above.

The experimental probabilities were designed such that there was an equal chance of receiving a loss or a win vs. a neutral outcome if hit and miss rates were equal over a period of 1000 trials. Because the hit rate was titrated to 70% and the chance of each probability condition occurring was equal, overall chances of receiving rewarding feedback were 35%, while overall chances of receiving punishing feedback were 15%, with a 50% chance of receiving a neutral outcome.

Actual participant instructions were as follows. Participants were instructed that they must respond as quickly as they could by pressing the left mouse button when the target x appeared on the computer screen. They were informed before the experiment began that their chance of being rewarded (or penalized if they did not respond in time) depended on the color of the disc at the beginning of every trial. To minimize confusion and to ensure each participant received the same instruction, participants were told the color meanings in terms of "very high," "high," "low," and "very low" chances to win. They were also informed about the meanings of each feedback symbol in terms of points. They were told that a small reward was worth 1 point, a large reward was worth 2 points, and that the neutral outcome was worth no points. Similarly, a small loss would take away 1 point, and a large loss would take away 2 points. The design resulted in points being accumulated as the experiment went on at a rate of approximately 20–50 points per 100 trials.

Participants were informed of their cumulative point value in between each block during the short breaks. To increase motivation to perform the task and assign more salience to the feedback, participants were told that every time they achieved 200 points, it would result in reward of an extra \$12 gift card to local department stores in addition to what the participants received hourly. Since our goal was to run 2000 trials over 20 blocks, total points accumulated were in the range of 600–700, resulting in an overall gain of 3 gift cards per participant. In total, after hourly participation and the “winnings” from the experiment were combined, participants earned approximately \$100.

Electrophysiological Data Collection and Analysis

Event-related potentials (ERPs) were acquired from a 168-channel montage at a digitization rate of 512Hz with a pass-band of 0.05–100Hz using the BioSemi Amplifier System. BioSemi uses two electrodes—the Common Mode Sense (CMS), which is actively recorded, and the Driven Right Leg (DRL), a passive electrode—that together form a feedback loop that represent the reference. The acquisition of data occurs referenced to the CMS-DRL ground which drives the average potential of the participant (i.e. the common mode voltage) as close as possible to the AC reference voltage of the Analog-to-Digital box (for description of the BioSemi active electrode system referencing and grounding conventions, visit <http://www.biosemi.com/faq/cms&drl.htm>). Data were later referenced off-line to the average reference. Channels that were consistently bad were removed from analysis on a participant by participant basis to avoid biasing data. Epochs of 900ms, including a 100ms pre-stimulus baseline, were analyzed for both feedback conditions (i.e. the tone indicating task success or failure and the pictorial representation of the task reward/loss), and epochs of 1100 ms, including a 100 ms pre-stimulus baseline, were analyzed for the cue condition (i.e. the colored disc stimuli). Trials with eye movements and blinks were rejected offline based on vertical and horizontal EOG recordings. An automatic artifact rejection criterion of $\pm 70\mu\text{V}$ was used at all other scalp sites. All analyses were conducted on individual subject averages that were not digitally filtered but group data were subsequently low-pass filtered at 45Hz with a 48 db/octave slope, purely for purposes of illustration.

Experimental Conditions, ERP Component Designation and Statistical Analyses

In order to obtain a comprehensive understanding of reward processing and task monitoring, we employed three analyses. The goal of the first analysis was to investigate the effect of reward probability on mechanisms related to reward anticipation and the preparation for the task, and thus we focused this analysis upon the responses associated with the presentation of the colored discs that cued different reward probabilities. The purpose of the second analysis was to investigate mechanisms related to task performance feedback and how they interacted with reward prediction, and we focused this analysis on the responses associated with the presentation of the feedback tone. The purpose of the final analysis was to examine the response of the reward system after receipt of rewarding feedback, and thus we focused this analysis on the responses associated with the feedback stimuli that informed participants of their actual gains or losses. We focused our primary analysis on components of interest based upon information from previous research that has examined reward and task monitoring mechanisms, in addition to conducting follow-up exploratory analyses to more fully interrogate the richness of these high-density recordings. The epochs and electrode

sites for all statistical analyses were chosen on the basis of the wealth of previous literature that investigated cue- and reward- related ERP components, which have been primarily identified over fronto-central scalp regions (Hajcak et al., 2006, Foti et al., 2011, Yu, 2011, Walsh and Anderson, 2012). As such, our main dependent measure was obtained from a region-of-interest over frontal central scalp by averaging the responses from a trio of electrodes within the high-density 168-channel array, where these three sites spanned the location typically occupied by FCz in the modified international 10–20 electrode array system (American Electroencephalographic Society, 1994, Klem et al., 1999). All statistical analyses were performed on the mean amplitudes of the components within the specified time frames.

Cue-Related Effects (Reward Anticipation and Task Preparation)—Our first analysis focused upon the response of the system to the presentation of the colored discs that cued the four different probabilities of potential reward (63%, 42%, 28% and 7% absolute probability based on 70% performance). Cue-related effects were examined on all trials, regardless of success. Visual inspection of the responses and prior work pointed to two main components of interest.

The first was a negativity that arose over fronto-central scalp locations between 200 and 250 ms, which corresponded well to previous descriptions of the “Cue Related Negativity” (CRN) (Yu, 2011). A repeated measures analysis of variance (RM-ANOVA) between 200 and 250 ms was employed to test for the factor of reward probability on this component.

A second, sustained negative potential arose at approximately 500 ms over left fronto-central scalp locations and was determined to be the contingent negative variation (CNV) (Walter et al., 1964). As with the CRN, RM-ANOVA between 600 and 800 ms was employed to test the factor of reward probability on this component.

Task Feedback Related Effects (Task Monitoring)—Our second analysis focused upon the neural response to the presentation of the feedback tone that informed participants of whether or not they had successfully responded within the allotted time limit. Visual inspection of the response showed two components of interest.

While a feedback related negativity (FRN) was initially expected based upon the literature in task monitoring and reward feedback processes (Hajcak et al., 2006), the observed component did not match previous descriptions in the literature of the FRN. The component identified between 200 and 250 ms was in fact a strongly positive-going deflection over fronto-central scalp locations rather than a negativity. In fact, this component much more closely resembled a classic auditory P2 (Crowley and Colrain, 2004). A 2 X 4 ANOVA between 200 and 250 ms with factors of valence (success versus failure) and reward probability was employed to test for differences in the amplitude of this component.

The second component of interest was a centro-parietal positivity arising between 300 and 500 ms, which matched previous descriptions of the well-characterized P300 component that has also been observed in previous reward paradigms (Wu and Zhou, 2009). As with the

P2, A 2 X 4 ANOVA between 300 and 500 ms with factors of valence and reward probability was employed to test for differences in the amplitude of this component.

Reward Feedback Related Effects (Reward Receipt)—Our third analysis focused upon the response of the system to the presentation of the feedback stimuli that informed participants of the actual magnitude of their gains or losses. Visual inspection of the response showed two components of interest.

The first component of interest was a classical FRN arising between 200–250 ms over central scalp. A 2 X 4 X 3 RM-ANOVA between 200 and 250 ms with factors of valence, probability and reward magnitude was employed to test for differences in this component.

A later positive potential followed the FRN at approximately 300 ms, and was again referred to as the P300. A 2 X 4 X 3 RM-ANOVA between 300 and 500 ms with factors of valence, probability and magnitude was employed to test for differences in this component.

Source Localization Procedures

We performed inverse source modeling using the Brain Electric Source Analysis software suite (BESA 5.1. software; Scherg, 1985, Simpson et al., 1995). BESA employs a least squares fitting algorithm, defining location and orientation of dipoles for which the maximal amount of variance is explained (Scherg and Picton, 1991). For the purpose of modeling, an idealized four-shell ellipsoidal head model with a radius of 90mm and scalp and skull thickness of 6 and 7 mm respectively was assumed. We used a data-driven stepwise approach, with each segment of the epoch that encompassed an ERP deflection successively fitted with a pair of symmetric sources. Note that in dipole source analysis, the modeled dipoles represent an oversimplification of the activity in the areas indicated by the dipoles and should be considered as representative of “centers of gravity” of the observed activity rather precise localizations of generators.

For source modeling of the cue condition, we used a time window of 200–250 ms for the CRN and a time window of 600–800ms for the CNV. For modeling of both the condition in which the feedback tone was presented and for the condition in which the rewarding feedback was presented, we used a time window of 200–250ms for the P2 (for task monitoring) and the FRN (for reward receipt) and a 300–500 ms time window for the P300 in both conditions. For the cue condition, a difference wave was calculated between the Very High and Very Low probability conditions. For the condition in which participants heard the feedback tone, a difference wave was calculated between the Very High and Very Low probability conditions for the successful outcome, and a separate difference wave was calculated between the Very High and Very Low probability conditions for the failure outcome. For the reward condition, a difference wave was calculated between the Large Reward and No Reward conditions for the successful outcome, and a separate difference wave was calculated between the Large Loss and No penalty conditions for the loss outcome. Source analysis was exclusively performed on these difference waves.

Exploratory Analysis Approach: Statistical Cluster Plots (SCPs)

An exploratory analysis was performed to more fully probe the richness of these high-density data. The SCP approach is a simple method for testing the entire data matrix for putative effects and involves the derivation of cluster plots by calculating pointwise, paired, two-tailed t -tests between the ERP responses to a given pair of experimental conditions. The results of the pointwise t -tests from 168 electrodes are displayed as an intensity plot to efficiently summarize and facilitate identification of differences within and between groups in the onset and general topographic distribution of differential activation associated with the ERP. The abscissa and ordinate axes represent time and electrode location respectively, while the color represents the t -value for each data point. We are aware that conclusions based on statistical cluster plots are undermined because of the large number of t -tests calculated across the electrode montage and recording epoch. In the present data treatment, periods of significant difference were only plotted if an alpha criterion of 0.05 or less was obtained and then only if this criterion was obtained for at least 11 consecutive data points. The rationale for this method of multiple comparison correction is that the likelihood of multiple false positive results occurring by chance at n consecutive time points is ∞ , assuming statistical independence between the time points. However, since actual EEG signals cannot change arbitrarily fast, one needs to account for the small amount of dependence between adjacent time points, which can be easily achieved by considering the autocorrelation of the signal. Even for high autocorrelations and long sequence lengths, a criterion of 11 consecutive time points has been shown to be quite conservative in avoiding type I errors (Guthrie and Buchwald, 1991, Foxe and Simpson, 2002). These SCP analyses are considered *post-hoc* and simply serve as a means to more fully describe effects uncovered in the primary analyses and as hypothesis generation tools for future work.

RESULTS

Behavioral Data

Because performance on this task was continuously titrated online to a 70% success rate, there was no possibility for differences in accuracy between probability conditions. An analysis of accuracy across the different probability conditions confirmed that this indeed was the case (Means: Very High condition: 71.04, St.Dev: 7.2; High condition: 70.5, St.Dev: 7.8; Low condition: 70.25, St.Dev: 8.3; Very Low condition: 71.54, St.Dev: 5.1; ($F_{22} = .5$, $p > .7$). However, it is possible that motivational changes based upon the different cued reward probabilities might have resulted in differences in reaction time, i.e. low reward probability could possibly have led to more lackadaisical responding. This was not the case though since analyses revealed no differences in reaction times between any of the probability conditions. (Means: Very High condition: 350.9, St.Dev: 782.8; High condition: 351.9, St.Dev: 85.1; Low condition: 348.3, St.Dev: 84.4; Very Low condition: 350.1, St.Dev: 84.9) ($F_{22} = .7$, $p > .6$).

Electrophysiological Comparisons

Reward Anticipation and Task Preparation—The goal of this analysis was to investigate reward anticipation and processes related to task preparation. Figure 2A displays the electrophysiological responses after the presentation of the cue for each probability

condition. Figure 2B displays this information in a topographical map of the voltage distribution across the entire scalp. The information in figure 2B is displayed at two time points that reflect the peak latency of our components of interest (i.e. the CRN and the CNV). Source modeling was also performed to estimate the neural generators of this activity, and these models are displayed in Figure 2C.

A repeated measures ANOVA was performed on the amplitude of the response associated with the reward-predictive cue, which peaked at 230 ms over central scalp. This component was consistent with prior reports of the cue-related negativity (CRN). RM-ANOVA revealed a significant effect of cue probability on the amplitude of this potential ($F_{3,20} = 4.8$, $p = .01$). The Very High and High probability conditions were associated with more negative amplitudes. Protected pairwise comparisons to follow up this significant main effect revealed significant differences between the Very High and Very Low condition ($t_{22} = 2.29$, $p = .04$) and between the Very High and Low condition ($t_{22} = 2.1$, $p = .05$). A source analysis of the difference wave (Very High “minus” Very Low) fit to the time period encompassing the peak of this component (200–250 ms) using symmetric dipoles estimated generators in the putamen, which explained all but 10% of the residual variance.

A second RM-ANOVA was performed on the subsequent response, a sustained negative potential that was entirely consistent with prior descriptions of the CNV (Rohrbaugh et al., 1986, Foxe et al., 2005). Once again, the analysis revealed a significant effect of cue probability on the amplitude of this potential ($F_{3,20} = 4.5$, $p = .03$), with cues associated with a higher chance of reward (the Very High and High conditions) associated with more sustained negative amplitudes. Pairwise follow-up comparisons revealed significant differences between the Very High and Very Low condition ($t_{22} = 2.31$, $p = .04$) and between the High and Very Low condition ($t_{22} = 2.25$, $p = .04$). As can be observed both in the waveforms and in the topographies in Figure 2, the CNV had a somewhat left-lateralized topography, very likely owing to the fact that our participants performed the task with their right hand and that the CNV is also associated with motor preparation (Leuthold et al., 2004)¹. A source analysis of the difference wave (Very High-Very Low) fit across a 50 ms time-window centred around the peak of this component (700–750 ms) using symmetric dipoles revealed generators in the cingulate in the region of the supplementary motor area, but only 70% of the variance was explained by this solution. Adding a third dipole did not improve the solution however.

Motor Performance Feedback: Task Monitoring—The purpose of this analysis was to investigate the response of the task monitoring system to task performance feedback. Figure 3A displays the electrophysiological activity in response to the tone that informed participants whether they had performed the task successfully or not. The figure displays the activity in the case of the success (hit) or failure (miss) separately, and displays all four probability conditions for these two outcomes. Figure 3B plots hit and miss information on the same axis, collapsing across probability conditions. Figure 4a displays topographic maps

¹A reviewer of an earlier version of this paper raised the possibility that CNV topographies might be different in the two left-handed participants that served here. Their topographies were therefore examined separately, but were found to be essentially indistinguishable from those of the main right-handed group.

of the activity associated with task success and task failure in order to demonstrate the clear difference between the response profiles to these outcomes, and this information is displayed at two time points that reflect the peak latency of our components of interest. Figure 4b displays the source modeling solutions. Two separate analyses were performed on the separate components that arose as a result of this feedback.

A 2 x 4 RM-ANOVA revealed a significant main effect of valence (hit or miss) on the amplitude of the P2 waveform that peaked between 200 and 250 ms over fronto-central locations on the scalp ($F_{3,20} = 13.1, p = .002$). The 2 x 4 ANOVA on the observed P2 component did not reveal a significant main effect of probability ($F_{3,20} = 1.2, p > .2$) or any interaction ($F_{3,20} = .6, p > .7$). Source analyses were performed on the difference waves which were computed by subtracting the Very High and Very Low probability outcomes. This difference wave approach was used for all source localization analyses in order to isolate the source of the task monitoring response from any other ongoing processes. Analyses were fit across a 50 ms time-window spanning the peak of the P2 component (200–250 ms), and were performed separately for the Hit and Miss conditions. Source analysis pointed to generators in the putamen for a task success, explaining fully 92% of the variance for this component, and a solution in the caudate explained 98% of the variance during a failure.

We then analyzed the later P300 component, a positive-going potential that arose at approximately 400 ms over centro-parietal locations and was sustained for 300 ms. It was also noted that topographies in this processing timeframe were clearly different between the hit and miss conditions, with the topography for a successful response noticeably more frontal than for a miss (see Fig 4). A 2 X 4 RM-ANOVA of this component revealed a main effect of valence ($F_{3,20} = 3.2, p = .03$) and a main effect of probability ($F_{3,20} = 4.3, p = .01$), with an interaction of valence and probability ($F_{3,20} = 3.78, p = .03$). Follow up paired t-tests revealed that probability conditions affected the valenced outcomes differently, underlying the observed interaction. In the win outcome, significant differences were present in the High vs Low conditions ($t_{22} = -2.1, p = .05$) and in the High vs Very Low conditions ($t_{22} = -2.3, p = .04$), where both the Very High and High conditions resulted in smaller amplitudes relative to the Low and Very Low conditions. In the loss outcome, significant differences were present in the Very High vs Very Low conditions ($t_{22} = 3.4, p = .01$) as well as the High vs. Very Low conditions ($t_{22} = 2.3, p = .04$), where the High and Very High conditions resulted in larger amplitudes relative to the Very Low condition.

As before, source analyses were performed on the P300 waveforms. Dipole sources were estimated over a time-window of 50 ms spanning the sustained portion of this component (600– 650 ms). This timeframe was chosen as the differences between probability conditions were maximal in this time-window. This fitting was performed separately for the Hit and Miss outcomes, and performed on the difference wave between the Very High and Very Low probability conditions for each outcome. A source in the insula explained 90% of the variance in the event of a hit, while a solution in the anterior cingulate explained 96% of the variance when the participant was too slow to respond.

Reward Receipt—The purpose of this analysis was to examine the response of the reward system after receipt of rewarding feedback. Figure 5 demonstrates the electrophysiological responses when the participant received feedback telling them what they actually received. The topographic maps in Figure 6a illustrates the activity across the scalp associated with rewarding or punishing outcomes. As before, the information in figure 6a is displayed at two time points that reflect the peak latency of our components of interest. Source modeling is displayed in figure 6b.

The component in response to actual reward and loss appeared to be a conventional FRN, which peaked at 250ms fronto-centrally. A 4 (Probability) x 3 (Magnitude-small, large or no reward/no penalty) x 2 (valence) ANOVA revealed a significant main effect of valence (a win or a loss) on the amplitude of the FRN associated with rewarding feedback ($F_{22} = 8.1$, $p = .005$) along with a significant main effect of magnitude ($F_{22} = 10.2$, $p = .001$). There was no main effect of probability on the amplitude of the waveform. There were no interactions observed between magnitude and valence ($F_{22} = 1.2$, $p > .3$), between valence and probability ($F_{22} = 1.0$, $p > .3$), between magnitude and probability ($F_{22} = .41$, $p > .8$), or between all three factors ($F_{22} = .6$, $p > .6$). Pairwise comparisons to follow up the significant main effect of magnitude revealed significant differences between the small win and loss outcomes ($t_{22} = 3.1$, $p = .01$), the large win and loss outcomes ($t_{22} = 3.4$, $p = .01$), between the neutral outcome and large win outcome ($t_{22} = 2.1$, $p = .02$), the neutral outcome and the large loss outcome ($t_{22} = 3.2$, $p = .01$), between the neutral outcome and the small win outcome ($t_{22} = 2.1$, $p = .02$), and between the neutral outcome and the small loss outcome ($t_{22} = 3.0$, $p = .01$). Source analyses using symmetric dipoles were performed separately for losses and for wins, were collapsed across magnitude and across probability, and were fit to the peak of the FRN (200–250 ms). Source analysis of both the reward and loss outcomes suggested generators in the midbrain. This solution explained 74% of the variance for a reward and 91% of the variance for a loss.

A second 4 x 3 x 2 ANOVA with the same factors was performed on the later positive potential that peaked centro-parietally at 500 ms and was sustained for 200 ms. The analysis revealed a finding similar to what was found for the FRN. There was a significant main effect of valence on the amplitude of this waveform ($F_{22} = 5.9$, $p = .03$) along with a significant main effect of magnitude ($F_{22} = 3.7$, $p = .04$). Once again, there was no main effect of probability ($F_{22} = 1.0$, $p = .3$), nor were there any observed interactions between magnitude and valence ($F_{22} = 1.7$, $p > .19$), between valence and probability ($F_{22} = 1.1$, $p > .3$), between magnitude and probability ($F_{22} = 1.1$, $p > .3$), or between all three factors ($F_{22} = .7$, $p > .5$). Pairwise comparisons of the magnitude factor to follow up the significant finding revealed significant differences between the neutral outcome and the large win outcome ($t_{22} = 3.2$, $p = .02$), and the neutral outcome and the small loss outcome ($t_{22} = 2.7$, $p = .02$), but no significant difference was found between the small and large win outcome ($t_{22} = .72$, $p > .3$), or the small and large loss outcome ($t_{22} = .8$, $p > .3$). As before, source analyses using symmetric dipoles were performed separately for losses and for wins. For each, the source analysis was performed on the difference wave between magnitude conditions, and was fit to the sustained portion of the component where magnitude differences were maximal (600–650 ms). Generators in the cingulate were identified for

rewards, which explained 90% of the variance, and generators in the posterior cingulate were identified for losses which explained 82% of the variance.

Post Hoc Analyses—Exploratory cluster plot analyses revealed another significant finding. An early positivity, arising approximately 170 ms fronto-centrally, can be observed in figure 7. This positivity was also sensitive to reward valence ($F_{22} = 8.9$, $p = .01$) and magnitude ($F_{22} = 4.3$, $p = .05$) but not to probability ($F_{22} = 1.7$, $p > .2$). There were no observed interactions between magnitude and valence ($F_{22} = .68$, $p > .5$), between valence and probability ($F_{22} = 1.01$, $p > .2$), between magnitude and probability ($F_{22} = .61$, $p > .5$), or between all three factors ($F_{22} = .7$, $p > .6$). Follow up statistics on the significant magnitude finding revealed significant differences between the small and large win outcome ($t_{22} = 5.2$, $p = .02$), the small and large loss outcome ($t_{22} = 6.7$, $p = .01$), the neutral outcome and the large win outcome ($t_{22} = 5.9$, $p = .02$), the neutral outcome and the large loss outcome ($t_{22} = 5.4$, $p = .02$), the neutral outcome and the small win outcome ($t_{22} = 5.0$, $p = .02$), and the neutral outcome and the small loss outcome ($t_{22} = 4.3$, $p = .03$). This was identical to the pattern for the early FRN. Source analysis on this component using symmetric dipoles, collapsed across probabilities and magnitude, revealed a midbrain source for loss feedback with 93% of the variance explained and a thalamic source for reward feedback with 97% variance explained.

DISCUSSION

We set out to investigate the interaction of reward processing and task monitoring in healthy individuals. To do this we designed a task that would begin to pull apart reward processing and task monitoring, allowing us to examine how these processes interact with more precision. While there was a behavioural element to this task, participant's accuracy was titrated to 70% which eliminated any potential behavioural differences in response to the different cued probability conditions. Analyses were focused on the electrophysiological data gleaned from instances of response to the cue and the first and second stages of feedback, which we turn to now.

Reward Anticipation and Task Preparation

It has been observed in the literature that information about reward-predictive cues is processed quickly by the nervous system (Holroyd et al., 2011). Previous work examining the effects of cued reward and cued task difficulty found evidence that processing of the two concepts is temporally dissociable (Schevernels et al., 2013). While our task did not explicitly modulate difficulty, we anticipated a dissociation between cued reward response and task preparation based upon the cued probability as participants prepared more vigorously to win reward when it was more likely. Indeed, two temporally dissociable components were identified. The first peaked at 250 ms fronto-centrally in response to the cue, and was sensitive to reward probability. Generators of this early activity were localized to the region of the cingulate cortex, which has been shown repeatedly to be associated with action monitoring (Bush et al., 2002, Shidara and Richmond, 2002, Hadland et al., 2003), and this finding corroborates previous source localization of the cue related negativity (Yu, 2011).

Turning to later task preparation, of special interest in this study was the observation of more negative deflections in the CNV when the cue predicted a higher likelihood of receiving reward. Findings regarding the sensitivity of preparatory mechanisms to reward have been inconsistent so far in the literature, with evidence suggesting that they are relatively insensitive to reward magnitude (Goldstein et al., 2006) whereas other evidence has suggested these mechanisms may be sensitive to both salient and nonsalient promises of reward (Capa et al., 2013). The data presented here provide clear supportive evidence that the preparatory processes marked by the CNV are indeed sensitive to reward probability. Attempts to localize the generators of this activity revealed sources in the cingulate cortex, although this solution explained only 70% of the variance. The CNV most likely has many sources, which will have contributed to the relatively less robust localization. The finding that reward probability affected preparatory responses in the task used here implies that reward prediction affects task preparation and perhaps response speed when actually receiving that reward is contingent on task outcome. However, there were no differences in response speed between conditions, probably owing to the design of the task which titrated behavior throughout at 70% accuracy by modulating the window of reaction time within which participants could successfully respond. This probably led participants to respond as fast as possible regardless of probability condition in order to avoid losses, even in the probability conditions in which losing points after a miss was unlikely. Regardless of the lack of behavioral differences between probability conditions, it is logical that increased likelihood of reward would increase motivation to perform the task correctly, and that this would be reflected in more vigorous preparatory processes as reflected by amplitude differences in the CNV.

Task Monitoring and Reward Interactions

The evoked response to the tone indicating task success or failure was the first instance in which neural markers of task monitoring mechanisms were expected. Because of the divide between feedback informing of task outcome and feedback informing of actual reward, a unique pattern of activity was expected. The tone indeed elicited a component between 200 and 250 ms that was sensitive to task outcome, but this component much more closely resembled the P2, not the FRN. The FRN is well-characterized as a negative-going component whereas the component observed in this case was noticeably positive for both the hit and the miss outcomes.

The mechanisms which the P2 component reflects are somewhat unclear in the literature. Some work has suggested that the P2 is involved in enhancing perception of a stimulus, (Tremblay and Kraus, 2002) while other work has suggested a role of the P2 in classification of stimuli (Crowley and Colrain, 2004). It has also been implicated in cue evaluation in children and adults (Jonkman, 2006) and in work in children with ADHD (Banaschewski et al., 2003). The amplitude differences observed in the P2 here may reflect a classification of the tone as indicative of a hit or a miss in order for the participant to re-evaluate their chances of reward. Indeed, the P2 has been implicated in monitoring of performance in a study examining the effects of task difficulty during a Go/NoGo task (Benikos et al., 2013).

The P2 was not influenced by reward probability, regardless of whether it was elicited by a success or a failure. This was in contrast to findings by Yu (Yu et al, 2011), and also contrasted with other research that explicitly investigated response to feedback and found an effect of probability during positive feedback (Cohen, 2007, San Martin et al., 2010, Kreussel et al., 2012). Further, localization of the P2 elicited during the task implicated structures of the striatum, notably the putamen in the case of task success and the caudate in the case of failure. This is also in contrast with the ACC generators found in Yu et al, but coincides with other findings of striatal activity during a gambling task (Foti et al., 2011). The root of the differences noted here, and the identification of the P2 as our component of interest rather than the FRN, may lie in the division of information about task success from information about actual reward, as other studies presented reward and task outcome simultaneously whereas task success and reward outcome were presented separately in the study described here. The finding that the immediate response to task success or failure was independent of reward probability also suggests that this early process functions independently of reward, perhaps instead serving as a marker of the salience of an unexpected response. This is especially relevant to this task, where performance was titrated to 70% and miss outcomes were more uncommon than successful hit outcomes. This interpretation of feedback reflecting the salience of a response has also been put forth in some FRN research, as a result of a study where an FRN was elicited by physical pain rather than monetary reward (Talmi et al., 2013) and by a study of a time estimation task where infrequent positive and negative feedback resulted in similar FRN amplitudes compared to an intermediate feedback condition (Ferdinand et al., 2012). Like the task presented here, the task in the Ferdinand paper also titrated performance based upon reaction time, and the reported FRN in the Ferdinand paper also showed a robust positive-going trend, very much like the P2 observed in the work presented here. In other words, their feedback related "negativity" was in fact a positivity.

However, if the salience of a less common outcome was the only variable being processed by the monitoring system, we would not then expect task outcome to have an effect on subsequent reward prediction. While immediate task success evaluation did not seem to take reward into account, later processing should if the system re-evaluates the probability of receiving reward or punishment while taking into account the new information gleaned about task success or failure. While many investigators have found evidence that later processing only takes into account details about reward, like magnitude and probability, and discards information about valenced task outcome (Yeung and Sanfey, 2004, Sato et al., 2005), there is some evidence that later processing of reward feedback does take the task outcome into account (Hajcak et al., 2005, Wu and Zhou, 2009). The paradigm presented here is uniquely suited to examine this in more detail. An interaction of the reward processing and task monitoring systems, that accurately took into account information about task success in order to reevaluate predictions about upcoming reward or loss, was expected. This is precisely what was found, indicated by the P300. The pattern of P300 amplitudes observed differed depending on task outcome, where smaller amplitudes were observed in response to a higher likelihood of reward and for a higher likelihood of avoiding a loss, and larger amplitudes were observed in response to lower likelihood of reward or to a higher likelihood of a loss. This resulted in an interaction of probability and valence that

demonstrated the ability of the system to continuously and accurately update reward and loss prediction by taking into account information about task feedback.

Further, source localization of this activity revealed differing sources. The insula were implicated as the source of activity associated with expectation of possible reward, while the ACC appeared to give rise to activity associated with expectation of potential losses. The insula activity may reflect conscious awareness of upcoming reward (Elliott et al., 2000), while the ACC activity may reflect, not only loss prediction, but also processes related to correcting behavior for the next trial to try to ensure that the next response will be executed within the allotted timeframe (Holroyd and Coles, 2002).

Reward Receipt

In the condition after which participants received information about actual rewards and losses, a classical FRN was observed that peaked at approximately 250 ms with a distribution over centro-parietal areas. The FRN noted in this condition was sensitive to reward valence and to reward magnitude, but not at all to reward probability. This was a somewhat surprising finding in that we had anticipated that conditions that were unlikely to result in reward (the low and very low conditions) would be more surprising and salient when they did in fact lead to reward, but this was not what was found. It appears that by the second stage of feedback, the system only processed whether the outcome was a reward or a loss, and how large that reward or loss was. This accords well with the interpretation in the work of Pedroni and colleagues, where early processes appeared to only take basic information about reward into account (Pedroni et al., 2011). The lack of any effect of probability on the ultimate feedback response seems even more unusual considering previous data showing the effect of probability on the FRN (Holroyd et al., 2004, Hajcak et al., 2007, Holroyd et al., 2008). It is likely that the design of the task used here explains these findings, and that cued probability, used in monitoring, ceased to be relevant to reward processing mechanisms once reward was received. Other work by Holroyd and colleagues (Holroyd et al., 2009) suggested that reward probability is not reflected in the feedback response when there is no new information to be gained. Since participants were informed of the cue meanings beforehand, this may explain why they did not use probability information in their response to the final instance of feedback. Another potential consideration that may explain why probability information ceased to stay relevant to reward outcome feedback is the temporal delay between the original cue containing probability information and the receipt of feedback. Previous work has demonstrated that such a delay will lessen the effect of probability on the feedback response (Osinsky et al., 2012, Weinberg et al., 2012), although it seems unlikely that such a delay would entirely erase the effect.

The neutral outcomes resulting in no change were similar for both cases where loss was expected and where reward was expected; there was no interaction of magnitude and valence, which implies that even the information about task success or failure had been discarded at this point. This, coupled with the lack of any effect of probability, suggests to us that upon receipt of reward, the system processed only the reward feedback itself. A point of interest is our identification of the midbrain as a source of the activity related to both losses and rewards. It is possible that this solution points to a role of dopamine releasing

neurons in the substantia nigra that may have encoded this reward information (Zaghloul et al., 2009).

The feedback response was influenced by reward magnitude in both the positively and negatively valenced outcomes. This differs from previous work demonstrating a reduced effect of reward magnitude on the response to negative feedback (Yeung and Sanfey, 2004, Hajcak et al., 2006). Rather, the findings here appear to corroborate data that did demonstrate an effect of magnitude on both negative and positive feedback outcomes (Wu and Zhou, 2009, Bellebaum et al., 2010). As the task used here dissociated the response to the tone informing of task success or failure from the response related to the actual reward receipt, it is possible that the effect of magnitude was not overshadowed by the novelty response to a less likely, negatively valenced outcome. This may explain the successful observance of the effect of reward magnitude on the response to negative feedback.

The P300 in response to reward showed a similar pattern to the FRN, where only valence and probability affected the amplitude of the waveform. However, there was no difference between the small and large outcomes. This activity was more fronto-central and generators included the cingulate for rewards and posterior cingulate for losses. This activity most likely reflects the later processing of the significance of these reward and losses, perhaps in the scheme of how much the participant has gained over time (Delgado et al., 2000, Elliott et al., 2000).

Post Hoc Analyses

After the second stage of feedback, where participants received information about the exact nature of their reward or loss, statistical cluster plot analyses revealed an early positivity that arose even before the FRN, at approximately 170 ms. This very early positivity may have been influenced by reward anticipation from the previous stage of feedback, although this does not explain the quick processing of reward magnitude information, about which the previous condition gave no information. The effect of magnitude was marginal, however, and there was no effect at all of probability. Source localizations across the peak of the component (150–190 ms) on the difference wave between the large magnitude and no reward outcomes, pointed to sources in the region of the thalamus and midbrain for reward and loss respectively. This suggests quick processing by the reward system of reward stimuli. This early incidence of reward processing has been examined before in a magneto-encephalographic study that noted responses to reward in visual regions as early as 150 ms after a rewarding cue on a slot machine (Thomas et al., 2013).

Study Limitations

While the goal of this work was to differentiate task monitoring from reward processing in order to get a clearer picture of these processes and their interaction, the first feedback signal does give some information about reward, as a successful task completion will never result in a loss and a task failure will never result in a gain. As such, while these steps were pulled apart to some degree, monitoring and reward feedback were not 100% dissociated. However, if task success and failure had no effect on reward outcome, we feared that participants would stop attending as closely to the task feedback signal as it would not be

relevant, and thus we might have lost the ability to explicitly investigate the interaction of these two processes. Having the first stage of feedback provide certainty about reward probability allowed us to investigate how relevant task success or failure influenced further processing about reward.

A weakness in our design was that the feedback tones (high pitch (1500 Hz) = win vs. low pitch (500 Hz) = loss) were not counterbalanced across participants. Thus, it could be argued that pitch differences might account for some of the P2 effects that we report. We feel confident, however, that the reported effects are not compromised for a number of reasons. First, prior research suggests that the feedback processing system is a generic one that is not particularly affected by the physical features of the feedback stimuli (Miltner et al., 1997, Holroyd and Coles, 2002). Second, prior work reported no effect of pitch on P2 amplitude, although there was an effect of tone duration (Alain et al., 1997), a parameter that was not changed here. An increase in P2 amplitude to lower pitches has been reported in one study (Sugg and Polich, 1995), but the observed effects were considerably smaller in magnitude than those reported here. As such, we think it unlikely that the P2 effects seen here could be attributed to pitch differences.

Conclusions

Despite these limitations, it is apparent from the current results that a more careful delineation of task feedback and reward feedback can reveal both details of reward processing, such as reward prediction and reward feedback, and details of task monitoring when activities toward reward are taken into account and the ramifications of task success or failure are used to update reward predictions. These processes are at least partially dissociable, as evidenced by previous work (Baker and Holroyd, 2011), but clearly interact depending on context to continuously update and keep track of evolving reward contingencies as information about upcoming reward is revealed. Dissociating these two systems will lead to more careful and indepth examinations of reward and monitoring mechanisms, and tasks that provide for this dissociation may ultimately have significant utility in clinical populations, such as in those with a substance abuse disorder.

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Highlights

Reward anticipation, feedback, and task monitoring were examined under different reward probabilities

The interaction of these processes was examined using a speeded simple reaction time task

High-density brain electrical activity was recorded

Reward anticipation and task preparation are influenced by reward probability, but reward feedback is not

Reward processing mechanisms interact rapidly with monitoring mechanisms to update predictions

A. Sequence of Stimuli

B. Possible outcomes in one condition

Figure 1.

a) Figure 1a demonstrates the timing of the presentation of our stimuli as each trial goes on. A cue is presented, followed by a blank screen. During the short duration that the small x is presented, the participant must make a button press. After the response, a tone is played letting them know if they responded in time. After the tone, the actual outcome is displayed.

b) Figure 1b demonstrates what a succession of trials looks like for each condition. The disc cue informs participants of the probability of being rewarded or penalized depending upon performance. Upon a successful response that falls into the time window within which the small x is presented, they will hear a high pitched tone informing them and see one of three outcomes: a small win, a large win, or a neutral outcome. Upon a response that does not fall into the time window within which the small x is presented, they will hear a low pitched tone informing them and then see one of three outcomes: a small loss, a large loss, or a neutral outcome.

Figure 2.

a) 2a displays the electrophysiological responses to the cue for each probability condition. ANOVAS for the cue condition revealed significant probability effects between 200–250ms and between 600–800 ms. b) 2b displays the activity over the scalp for each probability condition at specific time points, illustrating the cue related negativity and the CNV. c) Source analysis in 2c displays the generators of the activity. For all source analyses, a one dipole model was used if it explained more than 90% of the variance. A 2 dipole model was used if not.

Figure 3.

a) 3a displays the electrophysiological responses for the condition in which the participant heard the tone letting them know they responded in time or not, and displays the activity for each probability. ANOVAS for this condition revealed significant effects of valence between 200–250ms and a significant valence x probability interaction between 300–500 ms. b) 3b displays this same information collapsed across probability and plotted on the same axis in order to display the difference between a hit and a miss.

Tone related activity: Task Success or Failure

Figure 4.

a) 4a displays the electrophysiological activity over the scalp for each probability condition and each valence condition at specific time points after the instance in which the participant heard the tone letting them know they responded in time or not. b) Source analysis in 4b displays the generators of this activity.

Feedback related activity: Reward Receipt or Loss

Figure 5.

This illustration displays the electrophysiological responses for the condition in which the participants received feedback telling them of actual rewards or losses. Magnitude information in the loss and win outcomes are plotted separately, and the information is collapsed across probability. ANOVAS for this condition revealed significant magnitude effects between 200–250ms and between 300–500 ms

Figure 6.

a) 6a displays the electrophysiological activity over the scalp at specific time points for the condition in which the participants received feedback telling them of actual rewards or losses. Magnitude information in the loss and win outcomes are shown separately, and the information is collapsed across probability. b) Source analysis in 6b displays the generators of this activity.

Feedback related activity: Reward Receipt or Loss

A. Statistical Cluster Plot: Reward vs Loss

B. Topographies

C. Source Analysis

Figure 7.

a) The statistical cluster plots displayed in figure 7a illustrate tests for differences between the reward and loss condition across the entire electrode array and all timepoints in the epoch of interest. Color values indicate the result of point-wise t-tests evaluating reward vs. loss across a 900-ms epoch (x-axis) and electrode positions (y-axis: arranged from frontal to occipital sites in descending order) for the entire 168-electrode montage (see 'Materials and methods' section for details of electrode locations). For clarity, only tests where $p < .05$ are color-coded and only then when a minimum of 11 consecutive data points exceeded this criterion. As can be seen by the shaded rectangle, there is a significant difference noted

between the reward and loss condition at approximately 170 ms. b) 7b displays electrophysiological activity over the scalp for both reward and losses within this time frame. c) Source analysis displays the approximate generators of this activity.

Table 1

displays the probability conditions

Condition	Hit%	Miss%	Reward%	Loss%	Neutral%
Color 1 (Very High)	70	30	63	27	10
Color 2 (High)	70	30	42	18	40
Color 3 (Low)	70	30	28	12	60
Color 4 (Very Low)	70	30	7	3	90

Table 2

displays the conditions in this experiment, the components of interest associated with each one, and the analyses employed for each component.

Condition	Component of Interest		Analysis method (factors)	
	<i>Early</i>	<i>Late</i>	<i>Early</i>	<i>Late</i>
Cue presentation	Cue Related Negativity	Contingent Negative Variation	Repeated Measures ANOVA (Probability)	Repeated Measures ANOVA (Probability)
Task feedback	P2	P300	2 x 4 Repeated Measures ANOVA (Valence x Probability)	2 x 4 Repeated Measures ANOVA (Valence x Probability)
Reward feedback	Feedback Related Negativity	P300	2 x 4 x 3 Repeated Measures ANOVA (Valence x Probability x Magnitude)	2 x 4 x 3 Repeated Measures ANOVA (Valence x Probability x Magnitude)