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Research report

Implicit predictions of future rewards and their electrophysiological correlates

Elizabeth M. Trimber*, Christian C. Luhmann

Stony Brook University, United States

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ABSTRACT

Information that is motivationally relevant to an organism's survival demands preferential attention. Affective mechanisms facilitate attentional shifts and potentiate action to allow organisms to respond appropriately to motivationally relevant information. Previous work has demonstrated that the late-positive potential (LPP) is an event-related potential elicited by inherently emotional stimuli. For example, the LPP typically is evoked by images of weapons or erotica. The present study investigates stimuli that are not inherently emotional, but that implicitly (without participants' awareness) predict future monetary gains and losses. Results indicate that, relative to non-predictive cues, these predictive cues elicited frontally distributed positive potential. These results suggest that prediction of future rewards evokes neural responses that are similar to those evoked by inherently emotional stimuli. Results also indicate that monetary gains and losses elicit a frontally distributed LPP.

1. Introduction

The capacity to attend to and respond to novel, threatening, and rewarding stimuli allows organisms to survive in dynamic and dangerous environments. Signs that an organism's survival is threatened demand immediate and preferential attention. It is for these reasons that organisms have developed emotional mechanisms which facilitate appropriate responses to motivationally relevant information. Researchers interested in the neural bases of these processes have used event-related potentials (ERP) to study emotions such as fear and related cognitive processes such as attention to affective information [1–5]. It remains unclear, however, whether the same affective processing occurs for monetary rewards or neutral stimuli with affective relevance.

1.1. Stimuli with direct motivational relevance

Prior work on this topic has frequently explored the neural consequences of motivationally relevant stimuli. For example, many past studies have used images of objects and scenes with direct motivational relevance, and have found evidence that positive (e.g., wedding scenes, happy couples) and negative (e.g., plane crashes, funeral scenes) images evoke enhanced cognitive processing [6,7]. As one concrete example, electrophysiological work has found that, relative to affectively neural images, motivationally relevant images elicit what has been referred to a late positive potential (LPP). The LPP is a positive-going, P300-like ERP typically beginning 300 ms after stimulus presentation [8,9]. The LPP is thought to be generated from a variety of brain regions, including the visual cortex, temporal cortex, amygdala, orbitofrontal cortex, and insula, with differences among categories of affective stimuli [10]. The LPP, much like the highly related P300, has been hypothesized to reflect the additional, sustained processing that occurs when motivationally relevant information is encountered [3,11]. In support of this explanation, researchers have found that transient changes in the motivational importance of a stimulus appear to modulate the LPP [12].

With regards to the processing of rewards, past electrophysiological work has largely focused on an ERP component called the reward positivity (RewP, previously referred to as the FN). The RewP is typically observed at fronto-central sites approximately 250–300 ms after reward feedback is presented [13]. The RewP is measured as the difference between the physiological responses to positive monetary outcomes (e.g., gains) and negative monetary outcomes (e.g., losses), which has led some researchers to also refer to it as ΔRewP [14]. The RewP is thought to reflect a reinforcement learning signal in the ventral striatum caused by reward prediction originating in the mesocorticolimbic dopamine system [15]. Specifically, it is thought to be a positive-going effect elicited by positive outcomes [16]. Prior work [17] has found that these dopaminergic reward prediction signals only occur when reward outcomes are unexpected; when reward-related

* Corresponding author at: Department of Psychology, Stony Brook University, Stony Brook, NY 11794-25001, United States.
E-mail address: elizabeth.trimber@stonybrook.edu (E.M. Trimber).

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expectations are violated. In line with these findings, several studies have reported that the RewP is sensitive to expectations and increases in magnitude as rewards become less predictable [18,13]. However, other studies have found that RewP to be insensitive to expectations [19,20]. Reinforcement learning theory also dictates that reward prediction should occur at the earliest possible prediction about the outcome [21]. In classic reinforcement learning models, as cues and the outcomes they predict are repeatedly encountered, reward prediction signals gradually "migrate" backwards in time [22]. Initially, prediction signals are only generated when feedback information is received. After sufficient learning, however, reward prediction signals can be generated earlier in the trial, when predictive cues are presented. Thus, per reinforcement learning theory, we would anticipate the RewP to occur at the earliest possible learned predictive cue.

1.2. Stimuli with indirect motivational relevance

Though much of the existing work on affective processing, and reward processing in particular, has focused on the neural and cognitive consequences triggered by directly motivating stimuli, considerably less work has addressed stimuli with only indirect relevance. For example, work employing fMRI [23,24] has found that superficially neutral cues that predict negative, emotional images engage regions such as the anterior cingulate cortex, ventrolateral prefrontal cortex, and amygdala. Similar studies have been conducted using electrophysiological measures, but these studies have largely used predictive cues that are themselves affective [25,26]. Emotional content such as facial expressions and emotional words are known to cause affect-related neural responses [27,28] which renders these past studies somewhat ambiguous. The neural responses elicited by predictive cues could reflect the anticipation of future affective stimuli or the inherent affective value of the cues themselves (or some combination thereof). A handful of studies has presented evidence that neutral cues (e.g. Gabor patches or colored shapes) that predict affective outcomes (e.g. affective images, sweet liquids) can elicit P300/LPP effects [29,30]. For example, recent research has found that neutral geometric cues paired with images of cigarettes elicit an LPP relative to cues that predict neutral images [31]. Additionally, several researchers have found that neutral cues that predict an impending shock also elicit an LPP [32].

One of the most prevalent examples of a cue with indirect affective association is money. Despite being an evolutionarily recent invention, money has considerable motivational relevance because it allows one to obtain survival-related goods such as food. Like primary reinforcers such as food and pain, monetary rewards are highly motivating and can be used to create and reinforce affective associations to otherwise neutral cues [33]. Likely due to its motivational relevance, an P300/LPP complex has been observed in response to monetary wins and losses relative to neutral controls in a handful of studies. Van Meel et al. [34] found that small monetary losses elicited an LPP relative to gains, but do not provide a neutral control. Though they do not discuss it, Yeung and Sanfey [35] do appear to observe an ERP component resembling an LPP for both large gains and losses relative to small wins and losses. Consistent with current explanations of the LPP, large monetary wins and losses are certainly more motivationally relevant than small wins and losses. One example of an LPP to monetary gains is reported by Broyd et al. [36] who found an LPP was elicited by loss and gain feedback relative to a neutral non-monetary feedback condition [36].

Other research has examined the neural responses to cues that predict monetary rewards. Löw et al. [37] used images of guns or dollar bills that reliably predicted imminent monetary losses or gains. Results indicated that the predictive images (i.e., the images of the dollar bill and the gun) elicited an LPP relative to affectively neutral, non-predictive images of clocks. These results are provocative, however, interpretation is clouded for the same reasons as the conditioning studies reviewed above. That is, participants likely had prior affective associations involving the predictive gun (negative) and dollar bill (positive) images. Thus, the effects in the LPP/P300 complex observed by Löw et al. [37] may have been elicited by pre-existing affective associations involving the cues (e.g., the image of the gun per se) or by the expectations regarding subsequent monetary outcomes (or both). In the Broyd et al. [36] study mentioned above, monetary gain, loss, and neutral trials were cued beforehand, and, unlike Löw et al. [37], the cues used by Broyd et al. were affectively neutral. Broyd et al. found that cues predicting gain trials elicited enhanced P300 relative to cues predicting control trials, though cues predicting loss trials did not differ from control cues. This finding suggests that non-affective cues predicting monetary losses can elicit P300 effects, however, the absence of loss-related effects is somewhat curious. In addition, the fact that all monetary outcomes were based on participant performance may have influenced the results in unknown ways. Finally, participants were explicitly aware of what all cues predicted.

1.3. Implicit processing of stimuli

The critical role of emotional processing necessitates rapid and automatic processing. A substantial amount of research has been dedicated to demonstrating that emotional processing can occur without explicit awareness of the affective information itself [38–41]. Further, researchers have argued that implicit associations can be formed when subliminal cues reliably predict positive and negative outcomes [42]. For example, studies may create implicit associations by showing participants neutral, masked cues before presenting either a monetary win or a loss. In one such study, participants chose a risky response (i.e. "go" or "no-go") after viewing a predictive, but masked cue. People consistently chose to take the risk when the masked cue predicted a monetary win despite having no explicit knowledge of having seen the cues [43]. Thus, learned associations involving monetary rewards can influence behavior without explicit knowledge of the acquired associations.

Within the electrophysiological literature, particularly that dealing with the LPP specifically, discussion of "implicit" emotional processing frequently refers to paradigms in which participants are attending to non-affective dimensions of affective images [44,9,45]. A typical task used in such studies (e.g., [46] asks participants to either assess whether images are positive or negative (an evaluative judgment) or to assess how many people are present in the image (a non-evaluative judgment). Typically, these studies find an LPP for affective images (relative to neutral images) and find similar, though weaker LPP effects when participants are explicitly attending to the non-evaluative dimension. The attenuated LPP effect is then said to reflect implicit affective processing [44]. However, the affective images are still explicitly accessible and participants are presumably aware of the emotional content of each image. For these reasons, it seems more accurate to characterize these studies as reflecting the neural consequences of top-down processing on affective processing. Thus, despite a variety of ERP studies claiming to investigate implicit affective processing, it remains unclear whether the reported effects reflect processes that require explicit awareness or not.

The current experiment seeks to investigate the electrophysiological correlates of monetary rewards and the otherwise neutral stimuli that predict such rewards. Specifically, we employed a novel task involving affectively neutral cues that reliably predict monetary wins and losses. Furthermore, the task is designed such that the predictive associations of interest were highly non-obvious which allowed us to investigate physiological effects that are likely occurring in the absence of explicit knowledge. We hypothesize that neutral cues that predict monetary gains and losses will elicit an LPP relative to affectively neutral cues.

2. Method

2.1. Participants

All participants were informed about the experimental procedures and provided written consent in accordance with State University of New York at Stony Brook policies for testing human subjects. The experiments had approval by the Institutional Review Board (Stony Brook University's Committee on Research Involving Human Subjects, CORIHS). Twenty-five undergraduates from Stony Brook University participated for partial course credit. Participants were told that they would earn an additional monetary bonus based on points earned during the experimental task; all participants received $5.00 at the end of the session regardless of their performance on the task.

2.2. Choice task

Participants were told that their task was to earn points by making simple decisions based on shapes presented on the computer screen. Participants chose either a left or right button press when viewing each shape [46]. There were six trial types, each of which began with the presentation of a cue represented by a visual, geometric shape (see Fig. 1). At the beginning of each trial, one of the six cues was displayed on a gray background with a small fixation point placed at the center of the screen. Each shape was displayed for one second during which time participants could not make responses. The fixation point then disappeared, cuing participants to respond. Participants had 4000 ms to make a choice of either a right or left button press. If no response was made within this window, participants lost 60 points on that trial. For each trial type, the two responses reliably yielded different outcomes (see Table 1). Upon making a response, the outcome was presented (1000 ms) followed by an inter-trial interval of 1000–1500 ms. Information about whether a participant had lost or won was presented in either red or green font, respectively. When a response was not made, the 60-point penalty was presented in black font to make it readily identifiable. Of the six trial types included in the design, five were of theoretical interest and one simply acted as a filler. Loss trials only had possible outcomes of −50 and −60 points and, after practice, reliably yielded a large negative outcome (i.e., −50). Win trials reliably yielded a large positive outcome (i.e., 60 points) and were designed so their absolute value would be larger than that of losses [47]. Relative to the Control outcomes, the Loss and Win outcomes were designed to be highly detrimental and beneficial, respectively, to point totals and thus motivationally relevant. The remaining three trials of interest (Pre-Win, Pre-Loss, and Control) each yielded an identical, moderate outcome (i.e., 10 points) and moderate loss (i.e., −20). That is, the Pre-Loss, Pre-Win, and Control cues were identical with respect to their outcomes.

Table 1
Each of the six trial types was associated with a pair of possible outcomes, one for each of the two possible responses (i.e., left and right button press). Before the experiment, participants were given a practice session which allowed them to learn the responses needed to maximize their rewards.

	Left Button Press	Right Button Press
Loss	−50	−60
Win	60	50
Pre-Loss	−20	10
Pre-Win	−20	10
Control	−20	10
Filler	25	−10

The trial sequence was pseudo-random, but included two reliable inter-trial pairings. Pre-Loss trials always preceded Loss trials and Pre-Win trials always preceded Win trials. Likewise, Loss and Win trials always followed Pre-Loss and Pre-Win trials, respectively. Participants were not explicitly instructed about the existence or nature of these pairings. As a consequence of these inter-trial associations, the Pre-Win and Pre-Loss cues allowed for the accurate prediction of the outcomes to be received on the following trial. That is, the Pre-Win cue reliably predicted the outcome expected on that given trial (10 points) and additionally predicted the Win trial that followed (worth 60 points). Thus, even though the Pre-Win, Control, and Pre-Loss cues each had functionally identical *intra*-trial associations, they had different *inter*-trial associations. Thus, we could compare trials that reliably predicted upcoming motivationally relevant trials (Pre-Win and Pre-Loss) with functionally identical trials that did not reliably predict subsequent trials (Control). Control trials and Filler trials were not predictive of other trials and could precede Control, Filler, Pre-Win, or Pre-Loss trials. No trial type was presented more than three times in a row.

2.3. Procedure

The experiment began with participants reading brief instructions. Next, electrodes were attached and participants completed a practice session. The practice session consisted of three practice blocks, each including 60 trials (180 trials total) that were identical to the actual experimental task. This practice was designed to give participants an opportunity to learn both the intra-trial cue-outcome associations, and thus maximize their earnings, as well as the inter-trial associations (e.g., that Pre-Win trials were always followed by Win trials). By the end of the practice session, participants responded such that they earned the

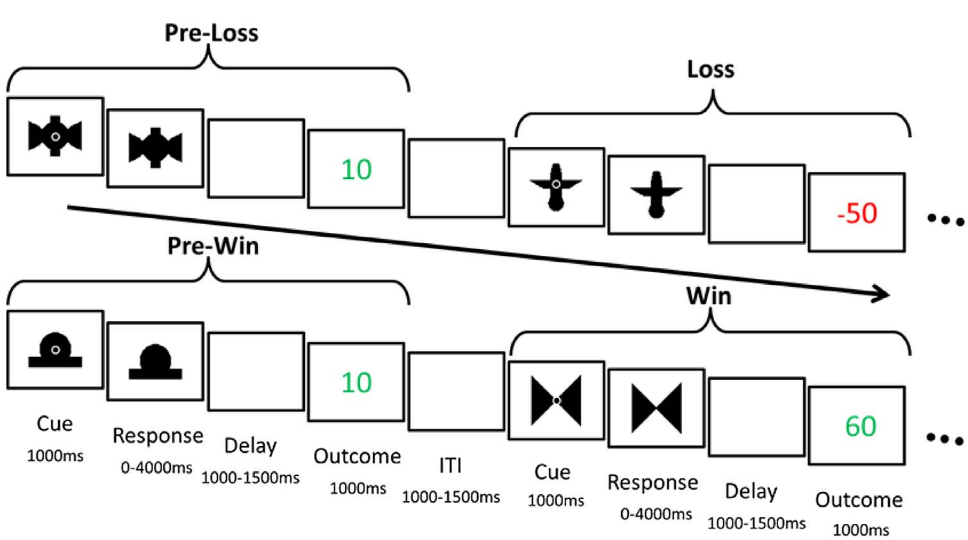

Fig. 1. Illustration of the choice task. Cues were presented for a fixed, 1000 ms interval before participants could respond. Outcomes were presented 1000–1500 ms after a response. Within the otherwise randomly ordered trial sequence, Pre-Loss trials were always followed by Loss trials (above) and Pre-Win were always followed by Win trials (below). Inter-trial intervals lasted 1000–1500 ms.

Table 2
Participants responded at chance levels to a surprise post-test of their explicit knowledge of inter-trial cue pairings. Enhanced positivity was observed for Pre-Win and Pre-Loss cues relative to Control cues at the anterior electrode cluster during the early time window. Loss cues also elicited an LPP relative to Control at the anterior and posterior clusters during the early time window.

LPP Mean Amplitude and Post-Test Performance

	Post-test % Correct		Anterior cluster 300–650 ms		Anterior cluster 650–1000 ms		Posterior cluster 300–650 ms		Posterior cluster 650–1000 ms	
Condition	M	SE	M	SD	M	SD	M	SD	M	SD
Pre-Win	50	14	2.00	2.36	0.48	2.56	4.17	2.61	0.04	2.52
Pre-Loss	57	14	2.27	1.98	0.68	2.59	3.98	1.87	0.10	2.19
Win	29	12	1.92	2.74	−0.36	2.59	4.41	2.83	−0.20	1.85
Loss	43	14	2.88	2.36	0.10	2.27	5.51	2.82	0.23	2.17
Control	50	13	1.14	2.18	0.06	2.13	3.90	2.09	−0.23	2.47
Filler	35	13	2.24	2.73	0.35	2.87	5.15	3.18	0.48	2.66

larger of the two available rewards for each trial type, indicating that they had learned the intra-trial cue-outcome associations. EEG data for the actual experiment was recorded for seven blocks of 60 trials each (a total of 420 trials). After each block, participants received feedback about how many points they had earned during that block. Participants were given an opportunity to rest between block. After completion of the task, participants completed a surprise post-test.

2.4. Post-Test

To test explicit awareness of the inter-trial pairings, a surprise post-test was administered to participants immediately following the experiment. Of the twenty-five participants, fourteen participated in the post-test. Participants were presented with one of the six cues and asked to indicate, “Which shape was most likely to immediately follow this?” Below this query were two additional cues presented on the left and right sides of the screen. Participants responded using the left and right buttons on the button box. The post-test included six items, one for each cue type. The Pre-Loss and Pre-Win post-test trials queried the inter-trial pairings and included a correct answer (the Loss or Win cues respectively) and one incorrect foil. For example, the Pre-Loss post-test trial asked what cue followed the Pre-Loss cue. The correct answer would be the Loss cue and the incorrect foil was the Pre-Win cue. As an additional example, the Control post-test trial asked which cue followed the Control cue. The correct answer was always one of the cues that could that could conceivably follow the Control cue, such as the Pre-Win cue. The incorrect answer was selected from options that could not follow the Control cue, such as the Loss cue (which could only follow Pre-Loss cues). Anecdotally, participants interviewed after the post-test reported that they were not aware of any inter-trial pairings. Most were surprised to learn that there were reliable inter-trial pairings and stated that they were focused on the intra-trial, cue-outcome associations.

2.5. Data acquisition, reduction, and analysis

Sixty-four Ag/Ag-Cl Electrodes were attached with a Compumedics Neuroscan Quick-Cap arranged with a standard 10–20 layout. Recordings were referenced to the left and right mastoids. Electrodes placed on the outer canthi of left and right eyes and above and below the right eye recorded vertical and horizontal electrooculogram. Impedances were kept below 10 Ω at all electrode sites. Electroencephalogram (EEG) data was recorded with SynAmp amplifiers (Neuroscan Inc.) at a sample rate of 500 Hz and digitized using SCAN 4.3 software (Neuroscan Inc.). Behavioral data acquisition and stimuli presentation were controlled by custom software written in Python using the PsychoPy package [48]. Offline, data was processed using EEGLAB [49] and ERPLAB [50]. Data was resampled at 250 Hz and 1500 ms epochs were extracted (100 ms baseline). Data was bandpass filtered between 0.1 and 30 Hz. EEG epochs with non-stereotypical artifacts were excluded from analysis by a semi-automated artifact detection routine and remaining ocular artifacts were corrected using the algorithm developed by Miller et al. [51]. The ERP waveform was quantified at an anterior channel cluster Fz, F1, F2, and FCz and a posterior channel cluster Pz, P1, P2, and CPz. To avoid creating potentially artificial distinctions between different components (e.g., the LPP and the P300) we scored the P300/LPP complex in an early window (300–650 ms post-stimulus) and a late window (650–1000 ms post-stimulus).

Additional, exploratory analyses assessed the reward positivity (RewP), a component often associated with reward outcome information, for predictive cues and outcomes. The RewP was scored as the mean amplitude between 250 and 350 ms at an electrode cluster including Fz and FCz [52].

3. Results

To assess participants' awareness of the inter-trial associations we first investigated participants' performance on the surprise post-test. Proportions of correct answers were transformed using an arcsine transformation and compared to chance performance using one-sample t-tests. On Pre-Loss trials, participants answered 57% (SD = 14%) of questions correctly ($t(13) = 0.13$, $p = 0.90$) and on Pre-Win trials, participants answered 50% (SD = 14%) of questions correctly ($t(13) = 0.65$, $p = 0.56$). On Control trials, participants answered 50% (SD = 13%) of questions correctly ($t(13) = 0.65$, $p = 0.56$). On Loss trials, participants answered 43% (SD = 14%) of questions correctly ($t(13) = 1.18$, $p = 0.32$) and on Win cue trials participants answered 29% (SD = 12%) of questions correctly ($t(13) = 2.43$, $p = 0.09$). Participants answered 35% (SD = 13%) of questions correctly ($t(13) = 1.18$, $p = 0.17$) on non-critical Filler cue trials (see Table 2). Given the chance-level performance of our participants on the post-test, we have little evidence for explicit awareness of these associations.

In order to assess the impact of the inter-trial pairings, we first examined the electrophysiological effects associated with the Pre-Loss and Pre-Win cues. Average LPP amplitudes were computed separately for the Pre-Loss, Pre-Win, and Control cues (see Fig. 2). We first performed a 3 (Cue: Control, Pre-Win, Pre-Loss) by 2 (Time window: Early vs. Late) by 2 (Cluster: Anterior vs. Posterior) repeated measures ANOVA on LPP amplitude. Degrees of freedom were adjusted using the Greenhouse-Geisser correction where appropriate. Benjamini-Hochberg adjusted significance levels were calculated for the unplanned comparisons associated with each ANOVA [53]. We observed a main effect of time window ($F(1, 24) = 51.49$, $p < 0.001$, $\varepsilon = 1$), a main effect of cluster ($F(1, 24) = 11.98$, $p = 0.002$, $\varepsilon = 1$), and an effect of cue ($F(2, 48) = 3.71$, $p = 0.03$, $\varepsilon = 0.87$). The main effect of time window was driven by more positive stimulus-evoked effects in the early time window ($M = 2.97$, $SD = 1.51$) than in the late time window ($M = 0.14$, $SD = 1.69$, $t(24) = 7.18$, $p < 0.001$). The main effect of cluster was largely due to the posterior cluster ($M = 1.95$, $SD = 1.23$) exhibiting more positive stimulus-evoked effects than the anterior

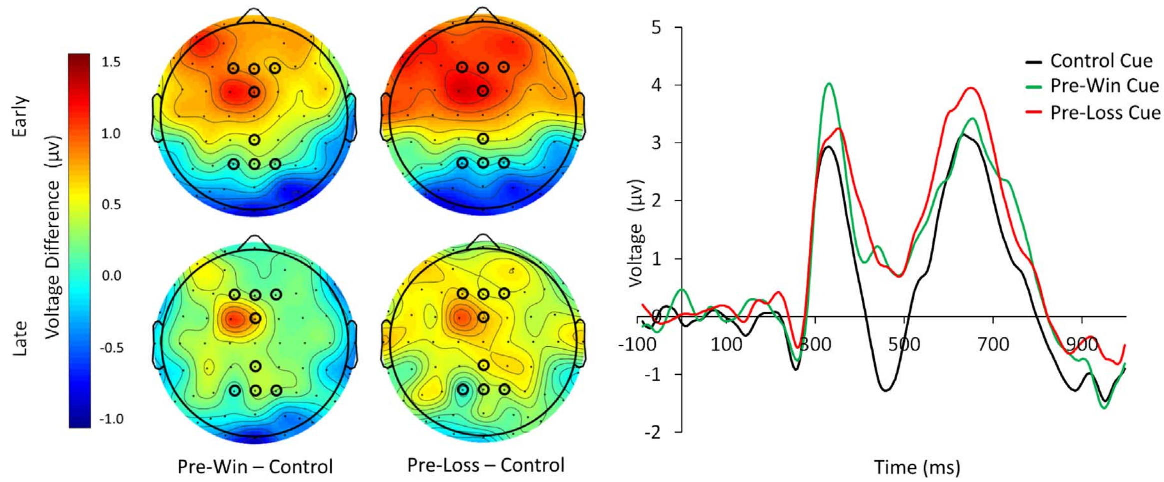

Fig. 2. Average voltage differences between Pre-Win and Pre-Loss cue amplitudes and the Control cue amplitudes at 300–650 ms and 650–1000 ms at clusters of electrodes Fz, F1, F2, and FCz and a cluster of Pz, P1, P2, and CPz. Pre-Loss and Pre-Win cues differed from Control cues during the early time window at the anterior location. Pre-Win cues did not differ from Pre-Loss cues. Cue-related effects for Pre-Win and Pre-Loss cues relative to the Control are shown at the anterior cluster of electrodes.

cluster ($M = 1.16$, $SD = 1.52$, $t(24) = 3.46$, $p < 0.005$). We also observed a significant interaction between time window and cluster ($F(1, 24) = 83.62$, $p < 0.001$, $\varepsilon = 1$). During the early time window, Pre-Win cues ($M = 3.16$, $SD = 1.83$) and Pre-Loss cues ($M = 3.19$, $SD = 1.48$) elicited significantly more positive potentials than early Control cues ($M = 2.58$, $SD = 1.57$, $t(24) = 2.45$, $p < 0.05$; $t(24) = 3.64$, $p < 0.001$). In contrast, differences among conditions were not observed during the Late time window. Of more theoretical interest, an interaction was observed between cluster and cue ($F(2, 48) = 4.59$, $p = 0.02$, $\varepsilon = 97$) and a significant interaction between time window, cluster, and cue ($F(1.5, 36.4) = 8.56$, $p < 0.005$, $\varepsilon = 0.68$). These findings were driven by the fact that Pre-Win and Pre-Loss cues elicited significantly more positive potentials than Control cues, but this difference was confined to the anterior cluster and the early time window (see Fig. 2). In this combination of cluster and this time window, we observed that the Pre-Loss cue ($M = 2.42$, $SD = 1.59$) elicited more positive potentials than elicited by the Control cue ($M = 1.28$, $SD = 1.69$, $t(24) = 5.78$, $p < 0.001$). The Pre-Win cue ($M = 2.19$, $SD = 1.90$) also elicited more positive potentials than the Control cue ($t(24) = 3.59$, $p < 0.005$). Pre-Win cues were statistically indistinguishable from Pre-Loss cues ($p = 0.37$). The same pattern was present in the posterior cluster and during the later time window but did not reach statistical significance (See Table 2).

The Win and Loss cues, relative to Control cues, appeared to elicit patterns similar to those described above for Pre-Win and Pre-Loss (see Fig. 3). We assessed these effects using a 3 (Cue: Control, Win, Loss) by 2 (Time window: Early vs. Late) by 2 (Cluster: Anterior vs. Posterior) repeated measures ANOVA. We observed a significant main effect of cue ($F(1.36, 34.29) = 3.88$, $p = 0.03$, $\varepsilon = 0.68$), cluster ($F(1, 24) = 23.60$, $p < 0.001$, $\varepsilon = 1$), and time window ($F(1, 24) = 67.54$, $p < 0.001$, $\varepsilon = 1$). Significant interactions between time window and cluster location ($F(1, 24) = 116.67$, $p < 0.001$, $\varepsilon = 1$) and between cue and time window ($F(1.93, 46.36) = 18.89$, $p < 0.005$, $\varepsilon = 0.99$), and between time window, cluster, and cue ($F(1.96, 47.0) = 3.95$, $p < 0.005$, $\varepsilon = 0.98$) were also observed. The effect of time window was driven by more positive stimulus-evoked effects in the early time window ($M = 3.40$, $SD = 1.67$) compared to the late time window ($M = -0.13$, $SD = 1.33$, $t(24) = 8.22$, $p < 0.001$). The effect of cluster was driven by the fact that the posterior cluster ($M = 2.23$, $SD = 1.31$) elicited greater positivity than the anterior cluster ($M = 1.04$, $SD = 1.14$, $t(24) = 4.86$, $p < 0.001$). The theoretically relevant main effect of cue was driven by the Loss cue ($M = 2.17$, $SD = 1.46$) which elicited greater positivity than the Control cue ($M = 1.22$, $SD = 1.33$, $t(24) = 4.56$, $p < 0.001$). The interaction effect of time window, cluster, and cue was driven by Loss cues differing from Control cues at the anterior and posterior clusters only during the

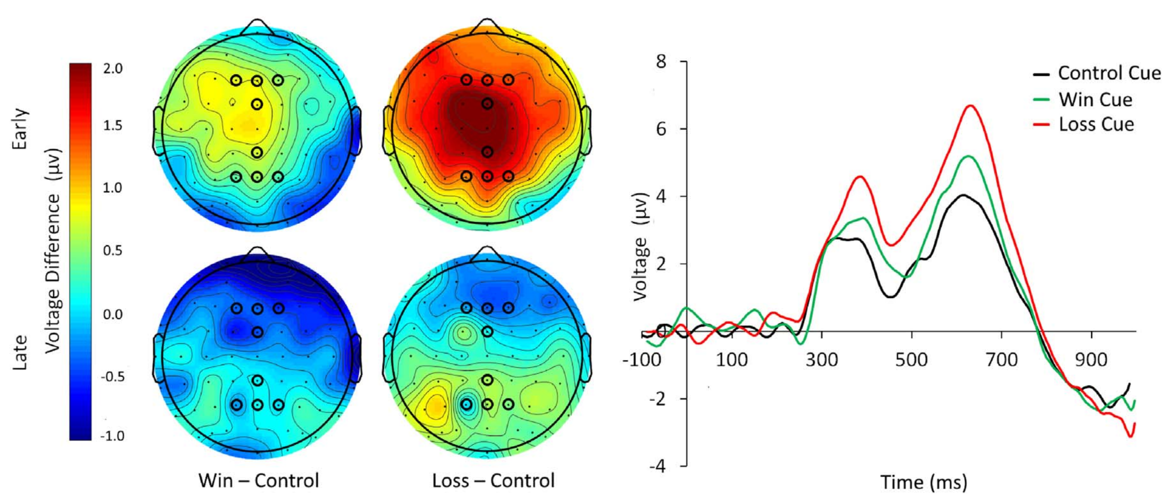

Fig. 3. Average voltage differences between Win and Loss cue amplitudes and the Control cue amplitudes at 300–650 ms and 650–1000 ms a cluster of electrodes Fz, F1, F2, and FCz and a cluster of Pz, P1, P2, and CPz. Cue-related effects for Win and Loss cues relative to the Control cue reflect an average of activity at both clusters. The Loss cue elicited a relatively sustained positivity relative to the Control cue.

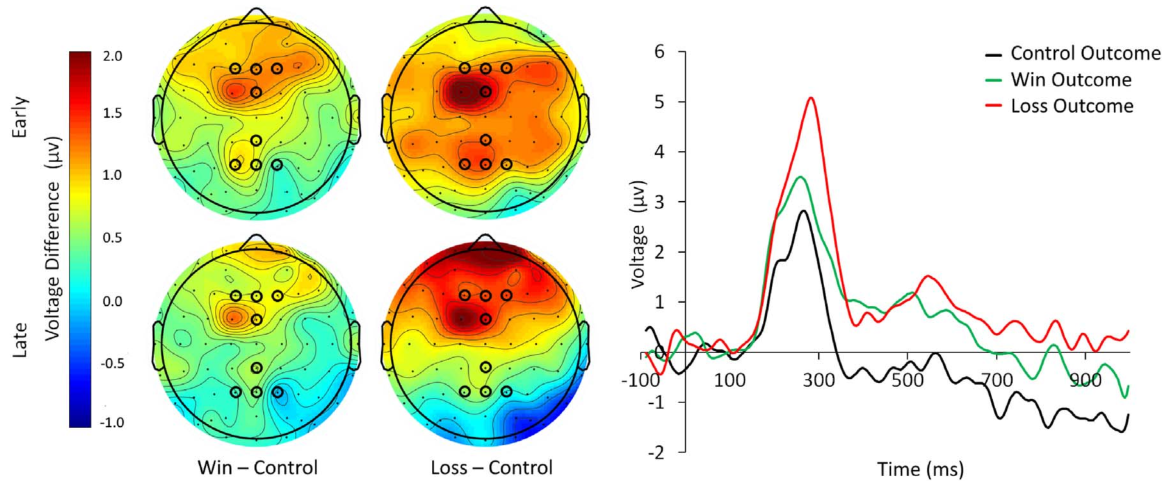

Fig. 4. Average voltage differences between Win and Loss outcome amplitudes and the Control amplitudes at 300–650 ms and 650–1000 ms at clusters of electrodes Fz, F1, F2, and FCz and a cluster of Pz, P1, P2, and CPz. Outcome-related effects for Win and Loss outcomes relative to Control outcomes at the anterior cluster. Loss and Win outcomes differed from Control outcomes. Win outcomes did not differ from Loss outcomes.

early time window (all $t(24)$'s > 5.82, p's < 0.01). Loss cues ($M = 5.51$, $SD = 2.46$) also differed from Win cues ($M = 4.40$, $SD = 2.42$) only at the posterior cluster during the early time window ($t(24) = 3.50$, $p < 0.005$). Win cues did not differ from Control cues (See Table 2).

We also examined the LPP effects associated with the Loss and Win outcomes (see Fig. 4). We assessed these effects using a 3 (Outcome: Control, Win, Loss) by 2 (Time window: Early vs. Late) by 2 (Cluster: Anterior vs. Posterior) repeated measures ANOVA. We observed a main effect of time window ($F(1, 24) = 8.16$, $p < 0.001$, $\varepsilon = 1$), a main effect of cluster ($F(1, 24) = 16.01$, $p = 0.001$, $\varepsilon = 1$), and an effect of outcome ($F(1.86, 44.8) = 4.96$, $p < 0.05$, $\varepsilon = 0.93$). The main effect of time window was driven by more positive stimulus-evoked effects in the early time window ($M = 2.36$, $SD = 2.67$) than in the late time window ($M = 0.27$, $SD = 1.49$, $t(24) = 2,86$, $p < 0.01$). The main effect of cluster was due to the anterior cluster ($M = 2.37$, $SD = 0.47$) exhibiting more positive stimulus-evoked effects than the posterior cluster ($M = 1.50$, $SD = 1.83$, $t(24) = 4.00$, $p = 0.001$). The main effect of outcome was driven by the Loss outcome ($M = 1.36$, $SD = 2.47$) exhibiting more positive stimulus-evoked effects than the Control outcome ($M = 0.15$, $SD = 1.83$, $t(24) = 3.52$, $p < 0.005$) and a marginal effect elicited by the Win outcome ($M = 0.94$, $SD = 2.39$) relative to the Control outcome ($t(24) = 1.82$, $p = 0.08$). We also observed a significant interaction between time window, cluster, and outcome ($F(1.40, 33.47) = 3.73$, $p < 0.05$, $\varepsilon = 0.70$). This was driven by Loss outcomes differing from Control outcomes at the anterior cluster during the early and late time windows and at the posterior cluster only during the early time window (all $t(24)$'s > 2.89, p's < 0.01). Win outcomes ($M = 0.97$, $SD = 4.23$) differed from Control outcomes ($M = -0.25$, $SD = 3.77$) at anterior cluster at the early time window ($t(24) = 3.52$, $p < 0.05$). Differences were not observed between Win and Loss outcomes.

Finally, we assessed whether reward positivity was present for cue-related effects and outcome-related effects (see Fig. 4). We did not find evidence of an RewP when comparing Pre-Win cues ($M = 2.05$, $SD = 2.26$) and Pre-Loss cues ($M = 1.89$, $SD = 1.79$, $t(24) = 0.47$, $p = 0.64$), nor when comparing Win cues ($M = 3.95$, $SD = 2.59$) and Loss cues ($M = 2.49$, $SD = 2.66$, $t(24) = 1.68$, $p = 0.11$). Loss outcomes ($M = 3.95$, $SD = 2.59$) were enhanced relative to Win outcomes ($M = 2.49$, $SD = 2.66$, $t(24) = 0.3.05$, $p = 0.005$) which is not the order of effects that would be expected if an RewP were present.

4. Discussion

In the current study, we have investigated the neural correlates of monetary rewards and the otherwise neutral stimuli that predict such rewards. We did so by employing a novel behavioral task in which participants were provided with cues (geometric shapes) that were deterministically followed by monetary gains or losses. One of the novel aspects of this task was the presence of several inter-trial regularities. Specifically, the experiment included trial types that each yielded an identical, moderate monetary gain. The only thing that distinguished these trial types was the fact that one (Pre-Win) was reliably followed by a high-gain trial (a Win trial), one (Pre-Loss) was reliably followed by a high-loss trial (a Loss trial), and one (Control) had no reliable inter-trial pairing.

Our results bolster the evidence that neutral, but predictive cues are capable of eliciting an LPP (or effects within the P300/LPP complex). Specifically, the Pre-Loss and Pre-Win cues elicited a late positivity relative to the Control cues. Given that the Pre-Win, Pre-Loss, and Control trials were superficially identical in terms of their proximal outcomes, the only thing that could have driven these results was the monetary value of the subsequent trial. Any hedonic value the cues might have had must have been acquired by virtue of their predictive nature. Our findings, as well as others [30,29,31,32] extend previous studies by demonstrating that the LPP can be elicited by neutral cues that have only acquired emotional relevance via a learning phase.

The present study bolsters the small number of studies that have found an LPP to monetary rewards [36,34,35]. This study also broadens the range of motivationally relevant stimuli found to elicit the LPP to include stimuli associated with monetary reward. Our findings are consistent with existing research that shows enhanced P300/LPP responses to neutral cues that predict monetary gains [36]. We extend and replicate this work by providing a control condition without positive and negative affective associations and by adding evidence that these responses also occur for neutral cues that predict monetary losses. Our results also further reinforce the hypothesis that money has considerable survival and motivational value [54].

Furthermore, the LPP effects elicited by the predictive cues in the current study were observed despite the fact that our participants did not exhibit explicit knowledge of the inter-trial associations. This effect is particularly interesting because previous research has focused on affective information that is readily accessible to participants [11,30,29]. For example, Deweese et al. [31] report an LPP to neutral cues that predict affective images of cigarettes, but the predictive cues are also shown together with the affective images during the task [31].

There have been studies that have investigated whether the LPP is observed when affective processing is implicit [44,55,46]. However, in these studies, participants are simply asked to attend to non-affective dimensions of an image. Thus, participants were highly aware of the affective dimensions of the stimuli. One exception to this trend is a study [56] which presented masked, affective cues (e.g. emotional faces). Interestingly, this study failed to find P300/LPP effects under such conditions. In the present study, participants were aware of the stimuli they were observing but based on post-test results, we do not have evidence that participants were aware of the inter-trial associations between otherwise neutral cues and large monetary wins and losses. Thus, the present study provides stronger evidence that participants need not have explicit knowledge of the affective information in order to exhibit LPP effects. Indeed, the results suggest that the LPP can be elicited by implicit, affective processes.

One aspect of our results that is potentially related to the predictive features of our task is the observed scalp distribution of our cue-related effects. Effects regarding the P300/LPP complex are typically maximal at parietal sites, (though see [57,58] for exceptions). In contrast, our effects had a predominantly anterior distribution. This difference may be due to increased cognitive processing evoked by the indirectly affective cues in our study, rather than the increased perceptual processing evoked by stimuli that are inherently affective. This is consistent with a recent study that reports an LPP with an early, anterior distribution [31]. Much like our study, Deweese et al. used abstract geometric cues to predict affective stimuli. Given that most prior studies of affective processing have used inherently motivational stimuli rather than indirectly motivating cues, this possibility will require further exploration. It also remains unclear whether the early, anterior LPP elicited by motivationally relevant predictive cues should be classified as a distinct component from the LPP that is observed to directly affective stimuli.

The robust LPP effect elicited by Loss cues may also be partially attributable to the fact that Loss cues were the only cue in the experiment that directly signaled a loss. This may have yielded qualitatively different processing of Loss cues relative to Win and Control cues.

The present study did not observe an RewP to monetary outcomes, which is consistent with the reinforcement learning explanation of the RewP [59], because these outcomes were predictable. Per reinforcement learning theory, we also expected an RewP to occur at the earliest point at which those outcomes could be predicted. In the present experiment, Pre-Win and Pre-Loss cues reliably preceded wins and losses on subsequent trials, and were the earliest point at which those outcomes could be predicted. Neither these nor the predictive Win cues or Loss cues elicited an RewP. There are at least three possible explanations for the absence of an RewP in response to the Pre-Win and Pre-Loss cues. First, the Pre-Win and Pre-Loss cue predicted both proximal and distal reward outcomes. For example, the Pre-Loss cue predicted a relatively neutral, 10-point reward on the Pre-Loss trial and it additionally predicted a 50-point loss on the following trial. The fact that these cues were involved in multiple, incompatible predictive relationships makes it unclear exactly how the RewP should behave. Second, the implicit/explicit nature of our predictive cues may have interacted with the predictive nature to eliminate the RewP. Participants were likely aware of the proximally predicted outcomes (i.e., those occurring on the same trial) but were unaware of the distally predicted outcomes (i.e., those occurring on the next trial). The RewP may be modulated by explicit expectations [13], but it remains to be established whether an implicitly learned predictive cues can also elicit an RewP at the point that future rewards can be predicted. Third, the enhanced LPP/P300 elicited by Pre-Loss and Loss cues may have made it difficult to detect. For these reasons, it is unclear whether an RewP should be observed in the current design, when the RewP should be observed (e.g., in response to the Win/Loss cues or to the Pre-Win/Pre-Loss cues), and how the RewP should reflect the multiple predictive relationships contained within our task.

One limitation of this study is that the post-test designed to test whether participants were explicitly aware of the inter-trial pairings only asked about specific configurations of cues. Participants may have had explicit knowledge that a cue (e.g. Pre-Win, Pre-Loss) predicted an upcoming win or loss without explicit knowledge of which specific cue (e.g. Win, Loss) followed. Further research on implicit affective processing should include additional surveys that specifically query predicted rewards to insure explicit knowledge is not present.

Motivationally relevant information is thought to require sustained emotional processing due to its survival value and such processing is thought to be reflected in the LPP [3]. Results of the current study indicate that monetary rewards produce a frontally distributed LPP. Additionally, cues predicting motivationally relevant events also elicit increased processing, even when the cues are not inherently affective. Further, our results suggest that this sustained processing can occur without explicit knowledge of the prediction.

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