Implicit predictions of future rewards and their electrophysiological correlates

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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 neutral 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 ARewP [14]. The RewP is thought to reflect a reinforcement learning signal in the ventral striatum caused by reward prediction originating in the mesocortico-limbic 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

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http://dx.doi.org/10.1016/j.bbr.2017.07.005
Received 9 March 2017; Received in revised form 17 June 2017; Accepted 6 July 2017
Available online 08 July 2017
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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, the 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 elicited 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.
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