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Motivated to win: Relationship between anticipatory and outcome reward-related neural activity



Narun Pornpattananangkul*, Robin Nusslock

Department of Psychology, Northwestern University, 2029 Sheridan Rd., Evanston, IL 60208, USA

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ABSTRACT

Reward-processing involves two temporal stages characterized by two distinct neural processes: rewardanticipation and reward-outcome. Intriguingly, very little research has examined the relationship between neural processes involved in reward-anticipation and reward-outcome. To investigate this, one needs to consider the heterogeneity of reward-processing within each stage. To identify different stages of reward processing, we adapted a reward time-estimation task. While EEG data were recorded, participants were instructed to button-press 3.5 s after the onset of an Anticipation-Cue and received monetary reward for good time-estimation on the Reward trials, but not on No-Reward trials. We first separated reward-anticipation into event related potentials (ERPs) occurring at three sub-stages: reward/no-reward cue-evaluation, motor-preparation and feedback-anticipation. During reward/no-reward cue-evaluation, the Reward-Anticipation Cue led to a smaller N2 and larger P3. During motorpreparation, we report, for the first time, that the Reward-Anticipation Cue enhanced the Readiness Potential (RP), starting approximately 1 s before movement. At the subsequent feedback-anticipation stage, the Reward-Anticipation Cue elevated the Stimulus-Preceding Negativity (SPN). We also separated reward-outcome ERPs into different components occurring at different time-windows: the Feedback-Related Negativity (FRN), Feedback-P3 (FB-P3) and Late-Positive Potentials (LPP). Lastly, we examined the relationship between reward-anticipation and reward-outcome ERPs. We report that individualdifferences in specific reward-anticipation ERPs uniquely predicted specific reward-outcome ERPs. In particular, the reward-anticipation Early-RP (1-.8 s before movement) predicted early reward-outcome ERPs (FRN and FB-P3), whereas, the reward-anticipation SPN most strongly predicted a later rewardoutcome ERP (LPP). Results have important implications for understanding the nature of the relationship between reward-anticipation and reward-outcome neural-processes.

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1. Introduction

Prior animal-model and human research suggests that reward-processing can be separated into two temporal stages: reward-anticipation and reward-outcome (Berridge & Robinson, 2003; Knutson, Fong, Adams, Varner, & Hommer, 2001; Liu, Hairston, Schrier, & Fan, 2011; Salamone & Correa, 2012). These stages are thought to be different from each other neuro-chemically,

neuro-anatomically, and neuro-physiologically. What remains unclear, however, is the extent to which neural-activity during reward-anticipation is related to individual-differences in neural-activity during reward-outcome. A challenge in investigating this question is that there are several distinct psychological processes embedded within both reward-anticipation and reward-outcome. To investigate the relationship between reward-anticipation and reward-outcome neural activity, it is important to determine which specific components of reward processing are related to each other. The strong temporal resolution of event-related potentials (ERP; Luck, 2005) makes it an ideal method for unpacking the distinct psychological processes within reward processing, and for examining the relationship between reward-anticipation and reward-outcome neural activity.

Several ERP studies have investigated different aspects of reward-anticipation (Brunia, Hackley, van Boxtel, Kotani, & Ohgami, 2011; Goldstein et al., 2006; McAdam & Seales, 1969).

Abbreviations: ERPs, event-related potentials; Cue-P3, cue-locked P3 ERP; FB-P3, feedback-locked P3 ERP; RP, Readiness Potential ERP; Early-RP, early part of the RP; Late-RP, late part of the RP; SPN, Stimulus-Preceding Negativity ERP; FRN, Feedback-Related Negativity ERP; LPP, Late-Positive Potential ERP.

^{*} Corresponding author at: Department of Psychology, National University of Singapore, Centre for Life Sciences, Neurobiology Programme, 28 Medical Drive #04–19, Singapore 117456, Singapore.

 $[\]label{lem:email} \textit{E-mail addresses:} \quad nonnarun@u.northwestern.edu \quad (N. Pornpattananangkul), \\ nusslock@northwestern.edu \quad (R. Nusslock).$

From this work it is clear that reward-anticipation is not a homogenous construct, but comprised of at least three sub-stages: (i) reward/no-reward cue-evaluation, (ii) motor-preparation and (iii) feedback-anticipation. Similarly, the reward-outcome stage has also been associated with different ERP components along the temporal scale, each of which is sensitive to different types of outcome evaluation (San Martín, 2012). Nonetheless, how reward-cues modulate ERPs within each of these sub-stages is not well-understood. During motor-preparation, for instance, it is unknown at which time-point reward-related stimuli start to modulate neuralactivity to prepare for action. More importantly, the majority of studies to date have focused only on one sub-stage of rewardprocessing. Few, if any, studies have directly examined the relationship between reward-anticipation and reward-outcome ERPs. Accordingly, we first aimed to isolate ERP components corresponding to different aspects of reward-anticipation and rewardoutcome within the same task. By doing so, we clarify the role that reward-related stimuli play at different time points during the anticipation and outcome of reward, as indexed by ERPs. Our second and primary aim was to assess whether (and if so how) ERPs during sub-stages of reward-anticipation relate to individualdifferences in reward-outcome ERPs. Examining the relationship between reward-anticipation and reward-outcome neural activity has important implications for understanding the temporal dynamics of reward processing in the brain as well as individual differences in reward-related neural activity.

1.1. Reward-anticipation ERPs

The reward/no-reward cue-evaluation stage occurs when individuals first evaluate whether their actions can lead to reward. Reward-anticipation cues that signal the possibility of receiving reward lead to more a positive P3 ERP component (Cue-P3; Cuelocked P3) (Broyd et al., 2012; Goldstein et al., 2006; Ramsey & Finn, 1997; Santesso et al., 2012). The P3 is a positive, centroparietal component that appears around 300-500 ms post-cue onset. An elevated Cue-P3 to reward-anticipation cues is consistent with the association between the P3 and stimulus-categorization (Johnson & Donchin, 1980). That is, a stimulus categorized as a response "target" usually elicits a more positive P3, and thus, in the case of reward processing, the rewarding features of a cue may act as a criterion for categorization. In addition to the Cue-P3, recent studies have documented the involvement of the N2, an earlier (around 200-400 ms post-cue onset), more anterior (fronto-central sites), negative-going ERP component at the cueevaluation stage (Potts, 2011; Santesso et al., 2012). Potts (2011), for instance, assigned reward and punishment conditions to stimuli of a response-selection task. He found reward stimuli elicited a less negative N2 than punishment stimuli, which signaled the possibility of losing money if performance failed to meet accuracy standards. Yet, the mechanism underlying the influence of reward-anticipation cues on the N2 is not clear, given that there are two, relatively independent, known roles of the N2: cognitive-control and template mismatch (Folstein & Van Petten, 2008). Interpreting the N2 as reflecting cognitive-control, Potts (2011) construed variation in N2 amplitude as signaling enhanced cognitive-control devoted to avoiding loss on punishmentanticipation cues. Alternatively, reward-anticipation cues may affect the N2 via a template mismatch mechanism (Folstein & Van Petten, 2008). Specifically, participants may have a positive bias to expect the reward-anticipation cue over the punishmentanticipation cue, making a reward-anticipation cue a "template." Enhanced N2 to the punishment-anticipation cue may in turn reflect a mismatch with this reward expectation template (Donkers, Nieuwenhuis, & van Boxtel, 2005; Gehring, Gratton, Coles, & Donchin, 1992). To help resolve this issue, the current study will compare the N2 to both reward-anticipation and no-reward-anticipation cues (as opposed to punishment-anticipation cues). Results in line with the cognitive-control account would likely involve a more negative N2 to reward-anticipation cues, given that reward-anticipation cues should elicit stronger cognitive-control relative to no-reward-anticipation cues. Alternatively, results in line with the mismatch account would likely involve a more negative N2 to a no-reward-anticipation cue, given that the presence of a no-reward-anticipation cue indicates a mismatch with one's reward expectation template. Importantly, if either the N2 or the Cue-P3 is modulated by the reward-anticipation cue in the present study, we next will examine the relationships between the N2 and/or Cue-P3 during the reward/no-reward cue-evaluation stage with reward-outcome ERPs.

The second sub-stage of reward-anticipation, motorpreparation, involves preparing to initiate an action required to pursue or obtain reward. Neural-activity during motorpreparation can be measured by the Readiness Potential (RP), a negative, pre-movement ERP component at central sites contralateral to the side of movement (Kornhuber & Deecke, 1965). Compared to other anticipatory ERPs, the influence of reward on the RP has not been frequently studied. A classic ERP study showed a heightened RP when monetary reward was distributed randomly following a self-paced movement (McAdam & Seales, 1969). A recent study demonstrated that a goal-directed movement (e.g., moving after 3 s as opposed to a self-paced movement) elicited a more negative RP (Baker et al., 2012). However, whether (and if so, how early before the movement) a reward-anticipation cue leads to a more negative RP preceding a goal-directed movement remains unknown. Understanding the timing of when reward starts to modulate the RP is important, given that the RP has two main temporally-distinct subcomponents: the Early-RP (i.e., earlier than 600 ms before movement) and the Late-RP (Bortoletto et al., 2011; Kutas & Donchin, 1980; Shibasaki, Barrett, Halliday, & Halliday, 1980). The Early-RP and Late-RP are thought to be different not only in neuralsubstrates, but also in their functional-processes (for review, see Shibasaki & Hallett, 2006). Neuroanatomically, the Early-RP corresponds to the supplementary motor area (SMA) and pre-SMA. whereas the Late-RP corresponds to the primary motor cortex (M1) and lateral premotor cortex (Cunnington, Windischberger, Deecke, & Moser, 2002; Shibasaki & Hallett, 2006). Functionally, the Early-RP is associated with abstract representation of motorpreparation, whereas the Late-RP is related to concrete representation of motor-preparation and execution. The current study aimed to examine whether both the Early-RP and Late-RP were modulated by reward, and if so, whether were related to reward-outcome ERPs.

The third sub-stage of reward-anticipation, feedback-anticipation, occurs after an individual has engaged in the goal-directed action and is now waiting for feedback as to whether their action was successful in obtaining the reward. This process can be quantified through the Stimulus Preceding Negativity (SPN), a negative, pre-Feedback, ERP component at fronto-central sites (Brunia, Hackley, et al., 2011). The SPN is thought to index activity in the

¹ Research has investigated the influence of monetary reward on both motor-preparation (Readiness Potential, RP) and feedback-anticipation (Stimulus-Preceding Negativity, SPN) in the same task (e.g., Kotani et al., 2003; Ohgami, Kotani, Hiraku, Aihara, & Ishii, 2004; Ohgami et al., 2006). In fact, these studies employed a time-estimation task similar to the current paper. However, these studies focused much more on the SPN than RP. Accordingly, the numbers of trials in these studies are adequate for analyses with the SPN (e.g., around 40 trials), but fewer than what are typically used in RP studies, which are around 90 or more trials (e.g., Baker, Piriyapunyaporn, & Cunnington, 2012; Bortoletto, Lemonis, & Cunnington, 2011). Perhaps due to this inadequate number of trials (thereby low signal-to-noise ratio), these studies often failed to demonstrate RP enhancement from reward cues. Given that on average 90.02 trials were analyzed for both the SPN and RP in the current study (see Section 3), we believe the influence of monetary reward cues on the RP is more appropriately investigated here.

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