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Temporal dynamics of reward anticipation in the human brain

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ABSTRACT

Reward anticipation is a complex process including cue evaluation, motor preparation, and feedback anticipation. The present study investigated whether these psychological processes were dissociable on neural dynamics in terms of incentive valence and approach motivation. We recorded EEG when participants were performing a monetary incentive delay task, and found a cue-P3 during the cue-evaluation stage, a contingent negative variation (CNV) during the motor-preparation stage, and a stimulus-preceding negativity (SPN) during the feedback-anticipation stage. Critically, both the cue-P3 and SPN exhibited an enhanced sensitivity to gain versus loss anticipation, which was not observed for the CNV. Moreover, both the cue-P3 and SPN, instead of the CNV, for gain anticipation selectively predicted the participants' approach motivation as measured in a following effort expenditure for rewards task, particularly when reward uncertainty was maximal. Together, these results indicate that reward anticipation consists of several sub-stages, each with distinct functional significance, thus providing implications for neuropsychiatric diseases characterized by dysfunction in anticipatory reward processing.

1. Introduction

Reward anticipation ('wanting') is crucial for human adaptation to the environment (Bubic, von Cramon, & Schubotz, 2010). The ability to predict future motivational events permits us to organize our behavior proactively to cope with the impact of those events. For instance, gain anticipation can promote approach behavior whereas loss anticipation can promote avoidance behavior (Knutson & Greer, 2008). On the other hand, dysfunction in reward anticipation has been identified as a critical contributor to psychopathologies such as schizophrenia (Gard, Kring, Gard, Horan, & Green, 2007), depression (Treadway & Zald, 2011), and addictive behaviors (Robinson & Berridge, 2008).

A well-validated task designed to evaluate reward anticipation is the monetary incentive delay (MID) task (Knutson, Westdorp, Kaiser, & Hommer, 2000), which has been extensively used across healthy and clinical populations in conjunction with functional magnetic resonance imaging (fMRI; Lutz & Widmer, 2014). In a typical MID task trial, participants initially observe a cue signaling trial information (i.e., gain, loss, or neutral), followed by a delayed period during which the participants prepare a motor response for an imperative visual target. Following the motor response, another interval is provided during which the participants wait for the outcome of their performance on that trial. In healthy individuals, reward anticipation mainly implicates the mesocorticolimbic dopaminergic pathway, including ventral striatum, anterior insula, and anterior cingulate cortex (Knutson & Greer, 2008). However, despite its excellent spatial resolution, fMRI cannot provide the necessary temporal resolution to fully characterize the temporal dynamics of reward anticipation in the human brain. Specifically, it remains largely unexplored whether those sub-stages (e.g., cue evaluation, motor preparation, and feedback anticipation) coarsely labelled reward anticipation are dissociable on the neural level.

Electroencephalography (EEG) with its superior temporal resolution provides a narration of distinct psychological processes as they unfold during reward anticipation millisecond-by-millisecond. Three anticipatory slow waves are associated with reward anticipation. The first slow negative-going wave, labelled the contingent negative variation (CNV), is typically observed between a warning stimulus (cue) and an imperative stimulus (target) and is maximal at central sites (Walter, Cooper, Aldridge, McCallum, & Winter, 1964). The CNV is believed to reflect neural activity within the thalamo-cortico-striatal network and has been linked with anticipatory attention, motivation, as well as

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motor preparation (Brunia, van Boxtel, & Böcker, 2012; Fan et al., 2007). Analogous to the CNV, a broad slow negative-going wave during the waiting period of a motivationally relevant stimulus (e.g., the period between the target and feedback in the MID task), called the stimulus-preceding negativity (SPN), is manifest as a plateau-shaped distribution at frontal areas with a right hemisphere dominance (Brunia, Hackley, van Boxtel, Kotani, & Ohgami, 2011). The most likely neural generator of the SPN, given its frontotemporal focus, is the right anterior insula (Bocker, Brunia, & van den Berg-Lenssen, 1994; Brunia, de Jong, van den Berg-Lenssen, & Paans, 2000). In contrast to the CNV, the SPN reflects anticipatory processing more purely due to the exclusion of motor preparation in the waiting period (van Boxtel & Böcker, 2004). Finally, incentive cues during the cue-evaluation stage often elicit a P3 component (i.e., the cue-P3), a positive-going wave peaking between 300 and 600 ms at parietal sites (Broyd et al., 2012; Goldstein et al., 2006). The cue-P3 is generally associated with attentional resources for stimulus evaluation based on motivational significance (Nieuwenhuis, Aston-Jones, & Cohen, 2005).

Previous research has thus identified three ERP correlates of reward anticipation: the cue-P3 during the cue-evaluation stage, the CNV during the motor-preparation stage, and the SPN during the feedback-anticipation stage. However, it remains to be determined whether these anticipatory ERP components reflect a common neural process or a set of distinct neural processes. Supporting the former hypothesis, all these ERP components have a close association with the mesocorticolimbic dopaminergic pathway. Specifically, previous research has demonstrated that the dopaminergic system plays a critical role in the generation of the P3 (Pogarell et al., 2011; Takeshita & Ogura, 1994) and that P3 amplitude variation is correlated with brain activity in the ventral striatum (Pfabigan et al., 2014). Similarly, CNV amplitude is influenced by dopaminergic manipulation (Linssen et al., 2011) and is associated with ventral striatal activity (Plichta et al., 2013; but see Pfabigan et al., 2014). Finally, recent research has shown that the SPN is moderated by genetic variation in dopamine (Foti & Hajcak, 2012) and that SPN amplitude is reduced in individuals with Parkinson's disease, a disorder with well-known deterioration of dopamine pathway (Mattox, Valle-Inclan, & Hackley, 2006).

However, despite the fact that all these anticipatory ERP components are associated with reward anticipation (Broyd et al., 2012; Goldstein et al., 2006; Gruber & Otten, 2010; Kotani, Hiraku, Suda, & Aihara, 2001; Krebs, Boehler, Appelbaum, & Woldorff, 2013; Schevernels, Krebs, Santens, Woldorff, & Boehler, 2014; van den Berg, Krebs, Lorist, & Woldorff, 2014), recent evidence suggests that they are dissociable in terms of reward valence (i.e., gain anticipation vs. loss anticipation). On the one hand, the CNV appears to be insensitive to reward valence such that it is comparable for gain and loss anticipation (Novak & Foti, 2015; Pfabigan et al., 2014). On the other hand, both the cue-P3 and SPN seem to be modulated by reward valence. The cue-P3 is observed with larger amplitude after gain cues relative to loss cues (Pfabigan et al., 2014; Santesso et al., 2012; Zheng et al., 2017; but see Schmitt, Ferdinand, & Kray, 2015). Similarly, the SPN appears to be more sensitive in gain context as compared to loss context (Ohgami et al., 2006; Zheng, Li, Wang, Wu, & Liu, 2015).

To address this issue, we first investigated whether the anticipatory ERP components (i.e., the cue-P3, CNV, and SPN) elicited in an MID task were modulated by incentive valence (gain vs. loss anticipation) commonly or selectively. If these ERP components are driven by common neural mechanisms, then they should be modulated by incentive valence similarly. Moreover, given its close relationship with the mesocorticolimbic dopaminergic pathway, these anticipatory ERP components should also relate to other measures of the dompaminergic pathway. One such an index is approach motivation (Salamone & Correa, 2012). Here, we then examined the relationship between the ERP correlates of gain anticipation and a novel behavioral index of approach motivation as measured by the effort expenditure for rewards task (EEfRT; Treadway, Buckholtz, Schwartzman, Lambert, & Zald, 2009) to further determine whether these ERP components were driven by common or distinct neural mechanisms. If they reflect similar neural substrates, the gain-anticipation ERP components should be associated with the behavioral index of approach motivation in a similar way. Otherwise, different patterns should be observed.

As a human analog of rodent paradigms designed to evaluate the approach motivational functioning of the dopamine system (Salamone, Cousins, McCullough, Carriero, & Berkowitz, 1994), the EEfRT requires participants to make a choice between a low-effort low-reward task and a high-effort high-reward task during a series of trials. Participants' willingness to expend effort (i.e., approach motivation) increases following *d*-amphetamine administration (Wardle, Treadway, Mayo, Zald, & de Wit, 2011), is related to individual differences in dopamine receptor sensitivity (Treadway et al., 2012), and left frontal cortical activity (Hughes, Yates, Morton, & Smillie, 2015), as well as anticipatory pleasure trait (Geaney, Treadway, & Smillie, 2015). Moreover, these associations appear to be specific to trials with low probability of reward receipt, indicating that dopamine mitigates perceived effort costs when pursuing large but unlikely rewards.

In the current study, participants performed both an MID task and an EEfRT. During the MID task, the participants were presented with incentive cues indicating that they would either win or lose monetary (i.e., the cue-evaluation stage), then waited for a variable preparatory period (i.e., the motor-preparation stage) and responded to a rapidly presented target to either won or avoided losing money, then waited for another delay period (i.e., the feedback-anticipation stage) to see the outcome of their performance. During the EEfRT, the participants were presented with a series of choices in which they could expend either minimal effort to obtain a small reward or greater effort to obtain a larger reward with varying probability levels of reward receipt. In light of the findings reviewed above, we hypothesized that the cue-P3 and SPN, rather than the CNV, would be sensitive to gain anticipation. Importantly, higher gain cue-P3 and SPN amplitudes would be associated with a greater willingness to expend effort (i.e., a greater proportion of hard-task choices in the EEfRT) for rewards especially when reward probability was low. No clear predictions were made for the CNV because of its various functional significances. If the CNV reflects gain anticipation, then it would also be associated with approach motivation as the cue-P3 and SPN.

2. Materials and methods

2.1. Participants

Fifty-six right-handed undergraduates (30 females and 26 males, 17–23 years of age) participated in this study. All had normal or corrected-to-normal visual acuity and reported no history of psychiatric or neurological disorders. The participants received a base payment of ¥30 (roughly equal to $4.5) for participation, as well as a bonus money based on their performance in the two tasks (see details below). All the participants provided written, informed consent. This study was approved by the Dalian Medical University Institutional Review Board.

2.2. Procedures

The participants were seated in a dimly lit and sound-attenuating chamber and performed both the MID task and the EEfRT. The EEfRT was always performed after the MID task. EEG data were collected only during the MID task.

2.3. ERP task—the MID task

In order to elicit anticipatory brain activity, the participants performed a modified version of the MID task (Knutson et al., 2000), during which they could maximize rewards and minimize losses by responding as quickly as possible to a visual target. On each trial