Biological Psychology 129 (2017) 242–252

Contents lists available at ScienceDirect

Biological Psychology

journal homepage: www.elsevier.com/locate/biopsycho

Research paper

Expectancy effects in feedback processing are explained primarily by time-frequency delta not theta☆

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ARTICLE INFO

Keywords:
Expectancy
Time-frequency
Feedback processing
Delta
Theta
FN
P300
Gambling
Event-related potential
ERP

ABSTRACT

The roles of outcome valence and expectancy in feedback processing have been investigated as important factors modulating event-related potential (ERP) measures including the feedback negativity (FN) and P300, but results have been inconsistent. Recent work from our group has shown that processes underlying the FN and P300 are better represented as separable processes in the theta (3–7 Hz) and delta (0–3 Hz) ranges using time-frequency analysis. The current study evaluated the modulation of time-domain FN and P300 and time-frequency theta and delta to outcome valence and expectancy in a gambling feedback task paradigm. Results revealed that the FN was sensitive to valence but not expectancy, and that valence effects were driven by loss-sensitive theta and gain-sensitive delta. Alternatively, the P300 was sensitive to the expectedness of outcomes but only for gain trials, and these expectancy differences were explained by time-frequency delta not theta. These results add to a growing body of research showing that time-frequency measures reflect separable processes underlying time-domain components, where theta is more sensitive to primary task features and less sensitive to secondary features while delta is sensitive to primary and more complex, secondary task features.

1. Introduction

The current study evaluated valence- and expectancy-related processing in a gambling feedback task. Many characteristics of gambling feedback processing, including outcome valence (Bernat, Nelson, & Baskin-Sommers, 2015; Gehring & Willoughby, 2002; Miltner, Braun, & Coles, 1997; Proudfit, 2015 (review); San Martín, 2012 (review); Wu & Zhou, 2009; Yeung & Sanfey,2004), outcome magnitude (Bernat et al., 2015; San Martín, 2012 (review); Wu & Zhou, 2009; Yeung & Sanfey,2004), relative outcome (Bernat et al., 2015), outcome context (Holroyd, Larsen, & Cohen, 2004; Kujawa, Smith, Luhmann, & Hajcak, 2013), and outcome expectancy (Cohen, Elger, & Ranganath, 2007; Hajcak, Holroyd, Moser, & Simons, 2005; Holroyd & Coles, 2002; Holroyd, Krigolson, & Lee, 2011; Holroyd, Pakzad-Vaezi, & Krigolson, 2008; Oliveira, McDonald, & Goodman, 2007; San Martín, 2012; Wu & Zhou,2009), have been investigated as important factors modulating event-related potential (ERP) measures. Gambling outcome valence (i.e., monetary gains and losses) has been widely examined as a key factor modulating time-domain ERP components, including the feedback negativity (FN) and P300. Outcome expectancy, or the degree to which one event is anticipated over others, has also been evaluated as an important feature of feedback processing. Previous work has demonstrated increases in P300 amplitude when an event is unexpected, but FN findings have been more inconsistent (Hajcak et al., 2005; Holroyd & Coles, 2002; Holroyd et al., 2008; Oliveira et al., 2007; Proudfit, 2015; Wu & Zhou, 2009; Yeung & Sanfey, 2004). Substantial work has revealed that ERPs generally contain delta (0–3 Hz) and theta (3–7 Hz) activity which overlap partially in time (Başar, Başar-Eroglu, Karakaş, & Schürmann, 2001; Bernat, Malone, Williams, Patrick, & Iacono, 2007; Cavanagh, Zambrano-Vazquez, & Allen, 2012; Cohen et al., 2007; Demiralp, Ademoglu, Istefanopulosdemoglu et al., 2001). Recent research from our group has demonstrated that delta and theta underlying ERP components, such as the N2 or FN and the P300, index separable processes, which can be obscured in conventional time-domain measures (Bernat et al., 2015; Bernat, Nelson, Steele, Gehring, & Patrick, 2011; Harper, Malone, Bachman, & Bernat, 2016; Harper, Malone, & Bernat, 2014). With regard to gambling feedback more specifically, when outcome stimuli provide multiple pieces of information, we have recently demonstrated that theta activity is modulated by the most salient, or primary stimulus features (such as outcome valence), while delta is sensitive to both primary characteristics as well as a range of higher-level secondary

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☆ This research was supported by K08MH080239 (Bernat).

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http://dx.doi.org/10.1016/j.biopsycho.2017.08.054
Received 10 June 2016; Received in revised form 2 July 2017; Accepted 21 August 2017

stimulus attributes (such as comparisons with alternative outcomes not chosen and the magnitude of the outcome; Bernat et al., 2015). The current study assessed modulation of time-domain ERPs, and associated time-frequency delta and theta measures, to outcome valence and expectancy. We hypothesize that time-frequency theta and delta will be differentially sensitive to valence- and expectancy-related processes: theta will be most sensitive to outcome valence, the most salient stimulus characteristic, and less sensitive to expectancy, while delta will be similarly sensitive to valence as well as expectancy. Given inconsistent findings regarding modulation of the FN and P300 to outcome valence and expectancy as described in the sections below, we predict that these distinct feedback processes in delta and theta will account for modulation in the time-domain measures.

1.1. *Outcome valence*

The FN has been extensively studied as a marker of outcome valence, differentiating negative from positive feedback (Gehring & Willoughby, 2002; Miltner et al., 1997). Miltner et al. (1997) provided the first evidence of the FN component, a negative-going deflection at medial-frontal recording sites that peaks approximately 250 ms after negative feedback. Converging evidence from source localization techniques, fMRI, and single-unit recordings have identified medial frontal regions, and likely the anterior cingulate cortex (ACC), as the neural generator of the FN (Foti, Weinberg, Bernat, & Proudfit, 2014; Gehring & Willoughby, 2002; Hauser et al., 2014; Holroyd & Coles, 2002; Miltner et al., 1997; Potts, Martin, Burton, & Montague, 2006).

Conventional FN measures have traditionally been associated with negative feedback because the component is diminished or absent following positive feedback; however, more recent work has suggested modulation of the FN by positive feedback. Bernat, Nelson, Holroyd, Gehring, and Patrick (2008) and Holroyd et al. (2008) provided early evidence of a reward positivity (RewP) component, which is increased for positive relative to negative feedback. This work, along with other recent findings, has shown that smaller FN amplitude on positive feedback trials is partially explained by the superposition of an increase in positive-going amplitude, the RewP (Bernat et al., 2008; Foti, Weinberg, Dien, & Hajcak, 2011a; Holroyd et al., 2008; Kujawa et al., 2013; Proudfit, 2015). Recent efforts based on temporal-spatial principal components analysis (PCA) of the FN have indexed positive amplitude activity, which is heightened for gains relative to losses (Carlson, Foti, Mujica-Parodi, Harmon-Jones, & Hajcak, 2011; Foti et al., 2014, 2011a; Weinberg, Riesel, & Proudfit, 2014). Based on time-frequency decomposition, work from our group now indicates that the RewP is indexed in delta activity, not in theta (Bernat et al., 2015, 2011). Approaches based on multiple techniques suggest that the RewP has primary sources in the striatum of the basal ganglia, including EEG/ERP source localization (Foti et al., 2014, 2011a), and combined EEG/fMRI (Becker, Nitsch, Miltner, & Straube, 2014; Carlson et al., 2011). Using simultaneous fMRI-EEG recordings, Becker et al. (2014) found increased activation in the ventral striatum, midcingulate, and mid-frontal cortices to positive feedback during the FN time window, and suggested that the activation of these brain regions during reward is driving the ERP differences during the time range of the FN. Conventional fMRI analysis corroborates these findings and also implicates the ACC, amygdala, and the orbital frontal cortex in reward processing (Carlson et al., 2011; Foti et al., 2014).

To bring clarity to opposing views of the FN, the FN as an error signal or a reward signal, time-frequency analytic approaches have been used to separate electrophysiological signals that are distinct in frequency band. Regression analyses using time-frequency components as predictors have shown that theta and delta frequency bands contribute unique sources of variance to the FN, with increases in theta activity reflecting loss outcomes and increases in delta activity reflecting gain outcomes (Bernat et al., 2008; Nelson, Patrick, Collins, Lang, & Bernat, 2011), leading to the conclusion that separable neural activity indexing losses and gains contributes to the FN. Foti et al. (2014) extended this work by applying source localization to time-frequency measures of the FN, where two distinct neural generators were identified. Loss-related theta activity was localized in the ACC, while gain-related delta activity was focused in the striatum (Foti et al., 2014). These results indicate that discrepancies regarding the FN and outcome valence can be clarified by time-frequency analytic approaches.

Results implicating the P300 and outcome valence are more consistent. The majority of studies have shown no relationship between P300 amplitude and outcome valence (Foti, Weinberg, Dien, & Hajcak, 2011b; Hajcak et al., 2005; Pfabigan, Alexopoulos, Bauer, & Sailer, 2011; Yeung & Sanfey, 2004), but there is some evidence showing increases to positive feedback (Bellebaum & Daum, 2008; Hajcak, Moser, Holroyd, & Simons, 2007; Zhou, Yu, & Zhou, 2010). Work from our group has supported the idea that significant, but opposite, effects in theta and delta are often responsible for suppressing effects in time-domain P300 measures (Bernat et al., 2015, 2008, 2011).

1.2. *Outcome expectancy*

Outcome expectancy has been investigated as an important secondary stimulus characteristic of feedback processing, but findings implicating the FN as a marker of expectancy are inconsistent. Holroyd and Coles (2002) presented a reinforcement learning theory (RL-theory) of the FN, stating that FN amplitude is monotonically related to the size of the reward prediction error (RPE), which depends on the difference between expected and actual feedback. Specifically, heightened FN amplitude reflects phasic decreases in mesencephalic dopamine signals to the ACC for a negative RPE (i.e., when outcomes are worse than expected; Holroyd & Coles, 2002). According to the RL-theory, several regions of the brain are involved in reinforcement learning: (1) the basal ganglia is the adaptive critic, which hones ongoing predictions, (2) the motor controllers (e.g., amygdala, dorsolateral prefrontal cortex, and orbitofrontal cortex) are used to update state-action mappings, and (3) the ACC is the control filter, which selects a plan according to state-action associations and communicates with the motor cortex for execution (Holroyd & Coles, 2002).

Later work by the Holroyd group and others has indicated that a reward positivity (RewP) component during the FN time window is sensitive to unexpected outcomes, and in particular, unexpected positive outcomes (Holroyd et al., 2011, 2008). As outlined in the previous section, evidence suggests the superposition of the RewP, composed primarily of delta activity during the FN time window, partially accounts for FN amplitude differences between positive and negative feedback (Bernat et al., 2008; Foti et al., 2011a; Holroyd et al., 2008; Kujawa et al., 2013; Proudfit, 2015). Results have shown that the RewP is sensitive to outcome expectancy, such that unexpected feedback produces a larger RewP compared to expected feedback, and positive relative to negative unexpected feedback produces the largest RewP (Holroyd et al., 2011, 2008).

Several studies now indicate that there is an interaction between outcome valence and expectancy on FN and RewP amplitude, where the FN is largest for unexpected negative feedback and the RewP is largest for unexpected positive feedback (Bellebaum & Daum, 2008; Bismark, Hajcak, Whitworth, & Allen, 2013; Cohen et al., 2007; Hajcak et al., 2007; Holroyd & Coles, 2002; Holroyd, Krigolson, Baker, Lee, & Gibson, 2009; Holroyd et al., 2011, 2011, 2008; Pfabigan et al., 2011; Potts et al., 2006; Walsh & Anderson, 2012). Conversely, some evidence has revealed that the FN is sensitive to unexpected outcomes regardless of valence (Alexander & Brown, 2011; Oliveira et al., 2007; Wu & Zhou, 2009). The predicted response-outcome (PRO) model proposed by Alexander and Brown (2011) presents a unifying computational model of the FN relative to ACC function. They suggest that the ACC encodes multiple independent action-outcome predictions in parallel, and ACC