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Beyond the FN: A spatio-temporal analysis of the neural correlates of feedback processing in a virtual Blackjack game

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ABSTRACT

Studies using event-related brain potentials (ERPs) to examine feedback processing in gambling tasks have focused almost exclusively on components elicited between 200 and 500 ms after feedback over the frontal-central region of the scalp (i.e., P2, feedback negativity (FN), and P3a). In contrast, studies examining the functional neuroanatomy of feedback processing reveal activation in a distributed network that includes the anterior and posterior cingulate, the lateral and medial orbitofrontal cortex, the occipital cortex, and the basal ganglia. In the current study, we used ERPs in combination with spatial principal components-massive univariate analysis and distributed source analysis to examine the time course, topography, and neural generators of ERPs elicited in a virtual Blackjack game from 0 to 2000 ms after feedback was delivered. The ERP data revealed the P2–FN–P3a complex, as well as, broadly distributed transient and slow wave activity that was sensitive to the magnitude and valence of an outcome. The ERPs reflected activation in the anterior and posterior cingulate, in addition to the occipital, temporal and medial frontal cortices. These data demonstrate that ERPs can provide valuable insight into the timing of neural recruitment within a distributed cortical network during the first two seconds of feedback processing.

1. Introduction

1.1. Background for the study

A central goal of decision neuroscience is to elucidate the neural architecture underpinning feedback processing related to gains and losses. Studies using functional neuroimaging methods reveal that feedback processing involves a neural network that includes subcortical structures (e.g., striatum), cortical structures (e.g., anterior cingulate cortex (ACC), orbital frontal and occipital cortex), and the cerebellum (Cox, Aizenstein, & Fiez, 2008; Hewig et al., 2008; Liu, Hairston, Schrier, & Fan, 2011; O'Doherty et al., 2003). Complimenting this literature, studies using event-related brain potentials (ERPs) to examine the feedback negativity (FN) provide insight into the timing of neural activity within the ACC or medial frontal cortex in the first few hundred milliseconds of feedback processing (Gehring & Willoughby, 2002; Hajcak, Holroyd, Moser, & Simons, 2005; Hewig et al., 2007; Yeung & Sanfey, 2004). In contrast to the extensive literature related to the FN, very little is known about ERP components that may be related to the recruitment of orbital frontal and posterior cortical structures observed in the functional neuroimaging literature (for an exception see West, Bailey, Tiernan, Boonsuk, & Gilbert, 2012). Given this limitation of the extant literature, the current study examined the full spatio-temporal distribution of ERP activity reflecting activation in the anterior and posterior cingulate, the medial frontal cortex, and anterior temporal and occipital cortices that was elicited during feedback processing in a virtual Blackjack card game. A novel data analytic approach (Spatial Principal Components – Massive Univeriate Analysis (SPC-MUA)) in combination with distributed source analysis was used to examine the full spatio-temporal distribution of the ERPs.

1.2. The P2–FN–P3a

Studies using ERPs to examine the neural correlates of feedback processing have focused almost exclusively on two or three

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components (i.e., P2, FN, P3a[1]) that are observed over the midline frontal-central region between 200 and 500 ms after feedback is delivered. The FN (Hajcak, Moser, Holroyd, & Simons, 2007) is the most extensively studied component, and has also been labeled the medial frontal negativity (MFN; Gehring & Willoughby, 2002), feedback-related negativity (FRN) and feedback error-related negativity (fERN; Holroyd & Coles, 2002) by different investigators. The FN reflects a transient negativity over the midline frontal-central region that peaks between 250 and 350 ms after feedback and is greater in amplitude for losses than for gains (Gehring & Willoughby, 2002; Hajcak et al., 2007). The P2 or P2a peaks earlier than the FN and reflects greater positivity for gains, particularly when unexpected, than for losses or non-rewards (Potts, Martin, Burton, & Montague, 2006). The P3a follows the FN and is often greater in amplitude for gains than for losses (Hajcak et al., 2007), for larger than smaller outcomes (Bellebaum, Polezzi, & Daum, 2010), and for unexpected than expected outcomes (Hajcak et al., 2007). While expectancy, valence, and magnitude may have different effects on the amplitude of the P2, FN and P3a components, Holroyd, Pakzad-Vaezi, and Krigolson (2008) have argued that these three components in fact reflect a single poly-phasic complex. Consistent with this idea, other investigators have demonstrated that the P2–FN–P3a share a common topography (Foti, Weinberg, Dien, & Hajcak, 2011) and that the FN reflects an increase in EEG Theta activity between 200 and 500 ms following losses (Marco-Pallares et al., 2008).

The findings of some studies have led to the suggestion that the FN and P3 may be sensitive to different aspects of reward processing within the context of simple gambling tasks. For instance, Yeung and Sanfey (2004) reported that the FN was greater in amplitude for losses than for gains, and was insensitive to the magnitude of outcomes. In contrast, this and other studies reveal that the P3 may be sensitive to the magnitude, but not the valence, of an outcome (Goyer, Woldorff, & Huettel, 2008; Sato et al., 2005; Yeung & Sanfey, 2004). This basic pattern has been replicated in a number of studies for the FN (e.g., Goyer et al., 2008; Hajcak, Moser, Holroyd, & Simons, 2006; Sato et al., 2005). However, other evidence demonstrates that the amplitude of the FN may be sensitive to the magnitude of an outcome (Bellebaum et al., 2010; Wu & Zhou, 2009), and that the amplitude of the P3 can be greater for gains than losses (Bellebaum et al., 2010; Hajcak et al., 2007) or for losses than gains (West et al., 2012). Given the available evidence, it seems that the FN and P3 are both sensitive to the valence and magnitude of an outcome in simple gambling tasks.

1.3. The P3a vs. P3b

The reason for the inconsistent findings related to the sensitivity of the P3 to the magnitude and valence of an outcome is unclear based upon the available evidence. One possibility is that some studies lacked the statistical power to identify small effects of these variables on the P3. A second possibility is that the P3 has generally been treated as a unitary component in the feedback processing literature (Bellebaum et al., 2010; Yeung & Sanfey, 2004); however, extensive evidence demonstrates that the P3 in fact reflects two or more distinct components (i.e., P3a and P3b; for a review see Polich, 2007). The P3a is maximal in amplitude over the frontal or frontal-central region, while the P3b is maximal in amplitude over the central-parietal or parietal region. The latency of the P3a is typically shorter than that of the P3b; however, these two components certainly overlap in time. Within the context of the feedback processing literature, the P3a may reflect the second positive deflection of the P2–FN–P3a poly-phasic component (Foti et al., 2011; Holroyd et al., 2008) arising from interactions between a basal ganglia-ACC dopaminergic pathway that codes the valence (Holroyd & Coles, 2002) or expectedness (Alexander & Brown, 2011) of an outcome. In contrast, the P3b may arise from interactions between the locus coeruleus–posterior cingulate involving norepinephrine that codes the motivational significance (Nieuwenhuis, 2011) or magnitude of an outcome. The data analytic approach and characteristics of the current sample allowed us to address both of these issues. The SPC-MUA approach allowed us to disentangle the overlapping topographies of the P3a and P3b; and the large sample provided sufficient statistical power to test for the effects of the magnitude and valence of an outcome on these two ERP components.

1.4. Slow wave activity

The functional neuroimaging literature reveals that feedback processing is associated with the recruitment of a distributed neural network that includes the striatum, anterior and posterior cingulate, orbital frontal and occipital cortex, and cerebellum (Hewig et al., 2008; Liu et al., 2011). The variety of regions associated with feedback processing in studies using fMRI can be contrasted with the focus on the P2–FN–P3a in the ERP literature that are typically ascribed to neural generators in the ACC (Gehring & Willoughby, 2002) or basal ganglia (Foti et al., 2011). A recent study using the Blackjack game incorporated in the current research (West et al., 2012) demonstrated that there are other components of the ERPs associated with outcome processing outside of the midline frontal region. Following previous research, this study revealed that the FN and P3 distinguished losses from gains. Additionally, this study revealed slow wave activity over the left frontal-temporal and parietal regions that increased in amplitude from wins to losses – hands where the player had a lower total than the dealer – to busts – hands where the player's cards exceeded 21.

This slow wave activity differentiated the three outcomes beginning around 500 ms after the onset of feedback and differences between the outcomes persisted for nearly 1500 ms (i.e., until 2000 ms after the feedback was presented). Source analysis using dipole modeling revealed that the neural generators of the left frontal-temporal and parietal slow wave activity could be modeled with a pair of dipoles in the left anterior region and the midline posterior region, respectively. These findings converge with the functional imaging literature wherein, relative to gains, losses are associated with greater neural recruitment in lateral frontal and posterior cingulate cortex (Hewig et al., 2008; Liu et al., 2011). The findings of West et al. (2012) indicate that feedback processing is associated with neural activity within anterior and posterior cortical structures that last for several hundred milliseconds after feedback is delivered in contrast to the relatively transient activity observed in the ACC. The current study was designed to replicate the effect of the valence of an outcome on the slow wave activity in the Blackjack game, examine the effect of the magnitude of an outcome on this slow wave activity, and to determine whether or not there are other components of the ERPs associated with outcome processing that may have been overlooked in the extant literature.

1.5. The current study

The current study was designed to examine four issues that emerge from the existing literature and guide the presentation of the results and discussion. First, we sought to replicate the finding

[1] Within the extant literature the label P3 is often used to describe a component that follows the feedback negativity. The amplitude of this component has been quantified at electrodes Fz, FCz and Pz in different studies. Here we use the label P3a for the frontal-central component that follows the FN as the results of the SPC-MUA clearly demonstrate that both the P3a and P3b contribute to the ERPs elicited during feedback processing.