Beyond the FRN: Broadening the time-course of EEG and ERP components implicated in reward processing

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ABSTRACT

Most reward-related electroencephalogram (EEG) studies focus exclusively on the feedback-related negativity (FRN, also known as feedback negativity or FN, medial-frontal negativity or MFN, feedback error-related negativity or fERN, and reward positivity or RewP). This component is usually measured approximately 200–300 ms post-feedback at a single electrode in the frontal-central area (e.g., Fz or FCz). The present review argues that this singular focus on the FRN fails to leverage EEG's greatest strength, its temporal resolution, by underutilizing the rich variety of event-related potential (ERP) and EEG time-frequency components encompassing the wider temporal heterogeneity of reward processing. The primary objective of this review is to provide a comprehensive understanding of often overlooked ERP and EEG correlates beyond the FRN in the context of reward processing with the secondary goal of guiding future research toward multistage experimental designs and multicomponent analyses that leverage the temporal power of EEG. We comprehensively review reward-related ERPs (including the FRN, readiness potential or RP, stimulus-preceding negativity or SPN, contingent-negative variation or CNV, cue-related N2 and P3, Feedback-P3, and late-positive potential or LPP/slow-wave), and reward-related EEG time-frequency components (changes in power at alpha, beta, theta, and delta bands). These electrophysiological signatures display distinct time-courses, scalp topographies, and reflect independent psychological processes during anticipatory and/or outcome stages of reward processing. Special consideration is given to the time-course of each component and factors that significantly contribute to component variation. Concluding remarks identify current limitations along with recommendations for potential important future directions.

1. Introduction

Rewards play an integral role in almost every aspect of our daily life. Although reward may at first appear to be a unitary construct reflecting the hedonic experience of pleasure, substantial evidence over the past few decades indicates that reward processing doesn't begin or end with reward attainment. Rather, reward processing is a heterogeneous construct composed of multiple distinct stages and psychological processes that dynamically play out over time. Broadly construed, reward processing can be decomposed into two temporally distinct stages: reward-anticipation and reward-outcome (Breiter et al., 2001; Knutson et al., 2001; Berridge and Robinson, 2003; Salamone and Correa, 2012; McClure et al., 2003; Rogers et al., 2004). Reward-anticipation is related to "wanting" and reflects incentive salience, a motivational process that promotes anticipatory approach toward reward-related stimuli or upcoming actions. Reward-outcome, on the

other hand, is largely associated with "liking" characterized by the hedonic impact of pleasure upon reward attainment (Berridge et al., 2009; Knutson et al., 2001). Another foundational aspect of reward processing, learning, reflects predictive associations and cognitions that are used to guide future behavior, but is more difficult to temporally isolate from reward-anticipation and reward-outcome (Berridge et al., 2009).

Prior animal and human research suggest that reward-anticipation and reward-outcome display separate neurochemical, neuroanatomical, and neurophysiological correlates, indicating distinct neural systems mediate each stage (Berridge et al., 2009; Schultz, 2007; Liu et al., 2011). At the neurochemical level, animal and human research highlight the involvement of dopamine signaling in reward-anticipation or "wanting" (see Berridge, 2007; Berridge et al., 2009 for review) and endogenous opiods and endocannabinoids in reward-outcome, consumption, or "liking" (see Nusslock and Alloy, 2018; Treadway and

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Zald, 2011 for reviews). At the neuroanatomical level, both reward-anticipation and reward-outcome have been linked to a fronto-striatal 'reward circuit' involving the basal ganglia (e.g., the ventral striatum, including the nucleus accumbens) and cortical target regions (e.g., the orbitofrontal cortex, medial prefrontal cortex, anterior cingulate cortex), among other regions (Haber and Knutson, 2010). Relatedly, functional-magnetic resonance imaging (fMRI) studies with humans link reward-anticipation with activation in the bilateral anterior insula, ventral striatum, and brainstem and reward-outcome with the medial orbitofrontal cortex (OFC) and amygdala (see Liu et al., 2011, for meta-analytic review). Furthermore, both anticipatory and outcome stages of reward processing can be further divided into several discrete psychological processes associated with their own distinct neurobiological mechanisms (Berridge and Robinson, 2003; Everitt and Robbins, 2005; Kringelbach, 2005; Berridge and Kringelbach, 2008; Leknes and Tracey, 2008; Schultz, 2006). For example, reward-anticipation can be broken up into cue-evaluation, motor preparation, and feedback anticipation while reward-outcome is comprised of early reward impact, subsequently updating working memory, and extended affective processing of feedback information. Finally, each of these substages embedded within reward-anticipation and reward-outcome is composed of numerous separate electrophysiological components that can provide their own unique insight into underlying psychological functions. However, these embedded substages often overlap very close together in time, making it difficult to experimentally isolate one from another without carefully considering the wider temporal dynamics of reward processing.

1.1. Leveraging the strong temporal resolution of EEG

While prior fMRI work has elucidated a variety of independent neuro-anatomical correlates between reward-anticipation and reward-outcome, neuroimaging techniques suffer from relatively weak temporal resolution operating on the level of a few seconds (Belliveau et al., 1991; Kwong et al., 1992; Hämäläinen et al., 1993). The poor temporal resolution of fMRI may conflate separate but temporally proximal psychological processes embedded within a particular stage of reward processing, such as motor preparation and anticipatory attention during reward-anticipation. Electroencephalogram (EEG) techniques, on the other hand, can utilize event-related potentials (ERPs) and event-related spectral perturbations (ERSPs or EEG time-frequency components) to unpack the temporal heterogeneity of reward processing on the level of milliseconds (Luck, 2005; Luck and Kappenman, 2012; Cohen, 2014). The superior temporal resolution of the EEG method is largely unrivaled by other non-invasive neuroscientific techniques and is perfectly suited to decompose the time-course of neural activity during reward processing (Nusslock et al., 2014). Furthermore, different reward-related electrophysiological components are often unrelated to each other, and each component tends to be associated with distinct scalp topographies and discrete psychological functions. However, importantly, EEG methods suffer from weak spatial resolution. Despite recent advances in source localization techniques investigating possible neuroanatomical generators of reward-related ERPs (Foti et al., 2011a), spatial inferences from EEG data remain controversial (Cohen et al., 2011b; Foti et al., 2011b). For this reason, we review relationships between ERP and EEG components and their covariation with neuroanatomical regions rather than making causal inferences.

Surprisingly, however, most electrophysiological studies investigating reward processing ignore its rich temporal heterogeneity and rather tend to focus exclusively on a single reward stage and only one or two individual ERP components. The vast majority of reward-related ERP studies, for example, contain at least 3 s of continuous EEG data per trial, but tend to focus exclusively on a single outcome-related component known as the Feedback-Related Negativity (FRN) elicited approximately 200–300 ms following feedback (see Sambrook and Goslin, 2015 for meta-analytic review). This approximately 100 ms

measurement window around the FRN amounts to analyzing only roughly 3% of the total collected EEG data per trial. Although these single-component approaches have produced important literatures on each component in isolation, they neglect the temporal precision of the ERP method. Accordingly, little is known about the dynamic progression of reward-related EEG and ERP components across reward-anticipation and reward-outcome along with their embedded psychological processes. Extending the time-course of analysis by leveraging the temporal power of ERP and EEG methods can deepen our understanding of reward processing and help unify partially disparate literatures that tend to investigate only singular components in isolation.

1.2. Why multicomponent analysis of reward-related ERPs is important

Multicomponent analysis of reward-related ERPs is important for two primary reasons. First, separating reward-anticipation from reward-outcome is important given that both animal and human research suggest these stages are neurochemically, neuroanatomically, and neurophysiologically distinct (Berridge et al., 2009; Haber and Knutson, 2010; Schultz, 2007; Liu et al., 2011). Understanding when ERP components capture independent processes within each stage, and when they do not, is critical to make sound interpretations. Second, a primary challenge of traditional ERP analysis is that directly preceding and following ERP components may "bleed" into components of interest, confounding their measurement (Luck and Kappenman, 2012). Multicomponent analyses that decompose the time-course within each stage of reward processing are helpful in isolating activity of interest from surrounding components elicited in close temporal proximity. These component overlap considerations have led to a wide variety of experimental paradigms and measurement techniques (Luck and Kappenman, 2012), especially among reward-outcome components (see Sambrook and Goslin, 2015 for review), resulting in an overly complex and frequently contradictory literature which is beyond the scope of this review. Rather, we argue here that individual reward-related ERPs cannot be studied in isolation without risking possible measurement confounds arising from component overlap. Therefore, carefully considering multiple components is essential not only for separating processes related to reward-anticipation and reward-outcome, but also for isolating activity unique to each ERP from their surrounding components within each substage.

1.3. Goals of the current review

The first goal of the present paper is to provide a comprehensive review of reward-anticipation and reward-outcome electrophysiology, with a particular focus on the temporal dynamics of ERP and EEG correlates of reward processing (see Table 1 for overview). A third aspect of reward processing - learning - will primarily be discussed in the context of reinforcement learning theories associated with reward-outcome. Our second objective is to argue that multistage and multicomponent analyses are critical to both capture the dynamic time-course of reward processing and to isolate singular components of interest within reward-anticipation and reward-outcome stages. We first review each ERP component relevant to reward processing, emphasizing their specific time-course, scalp topographies, covariation with unique neuroanatomical correlates, and distinct psychological functions. Following each section of the text, we review the known relationships between each ERP with every other component and then discuss the known relationships between reward-anticipation and reward-outcome stages. Finally, we briefly review EEG time-frequency components in the context of reward-anticipation and reward-outcome with a focus on how each EEG component may contribute to traditional ERP generation. Concluding remarks will address current limitations and promising future directions. Finally, we provide a link to our laboratory's website where we include resources for researchers interested in multicomponent analysis, including EEG time-frequency

Table 1

ERP and EEG Components Associated with Reward-Outcome and Reward-Anticipation. Each substage of reward-anticipation and reward-outcome are listed along with their underlying ERP components. For ERP components, the following information is listed from left to right: their typical time-window of measurement, their minimum recommended trial count, a minimum recommended baseline window prior to their respective event (e.g. cue-stimulus, response, or feedback stimulus), and their associated EEG time-frequency components.

Stage	Substage	ERP component	ERP time window (ms)	ERP trial count	ERP baseline (ms before event)	EEG Time-frequency component
Reward-anticipation	Cue-evaluation	Cue N2	200–350	> 20	> 100	Alpha, Beta, Delta
		Cue P3	300–600			
	Motor-preparation	Early RP/CNV	500–1500	> 90	> 1500	Beta
		Late RP/CNV	0–500			
	Feedback anticipation	SPN	0–200 +	> 20	> 1000	Alpha
Reward-outcome	Feedback evaluation	FRN/RewP	200–300	> 20	> 100	Beta, Theta, Delta
		FB P3	300–600	> 20		
		FB LPP	600 +	> 12		

tutorials and principal component analysis toolkits (see Appendix A Supplementary Material). It is our hope that future ERP and EEG reward processing studies will broaden their scope of analysis to systematically examine the temporal dynamics of reward processing, and that this review may help guide future investigations toward multistage designs and multicomponent analyses.

2. Reward-anticipation ERPs

Reward-anticipation can be deconstructed into three temporally distinct substages that unfold sequentially over time depending on their experimental context: cue-evaluation, motor-preparation, and feedback-anticipation (Brunia et al., 2011a; Goldstein et al., 2006; McAdam and Seales, 1969). These embedded psychological processes are involved in motivational approach directed toward upcoming actions or stimuli that may lead to or signal reward attainment. First, cue-evaluation signals whether a future reward is possible or not. Next, motor responses are prepared and executed. Finally, attentional resources are recruited in anticipation of impending reward attainment. Each substage is composed of its own unique set of reward-related ERP components that differ in their underlying psychological function, topographical scalp distribution, and covary in part with distinct neuroanatomical correlates. The following sections will review each of these substages and their commonly studied ERP components.

2.1. Cue evaluation

Cue-evaluation contains information that requires individuals to evaluate whether their actions can lead to reward (e.g. reward vs. no-reward cue) and occasionally to determine what type of reward is possible (e.g. large vs. small, unlikely vs. likely, etc.). This substage largely involves stimulus categorization processes to facilitate early preparation for an impending task-relevant event, such as upcoming motor preparation or anticipatory attention. Two ERP components are typically observed during this stage: the Cue-N2 and the Cue-P3.
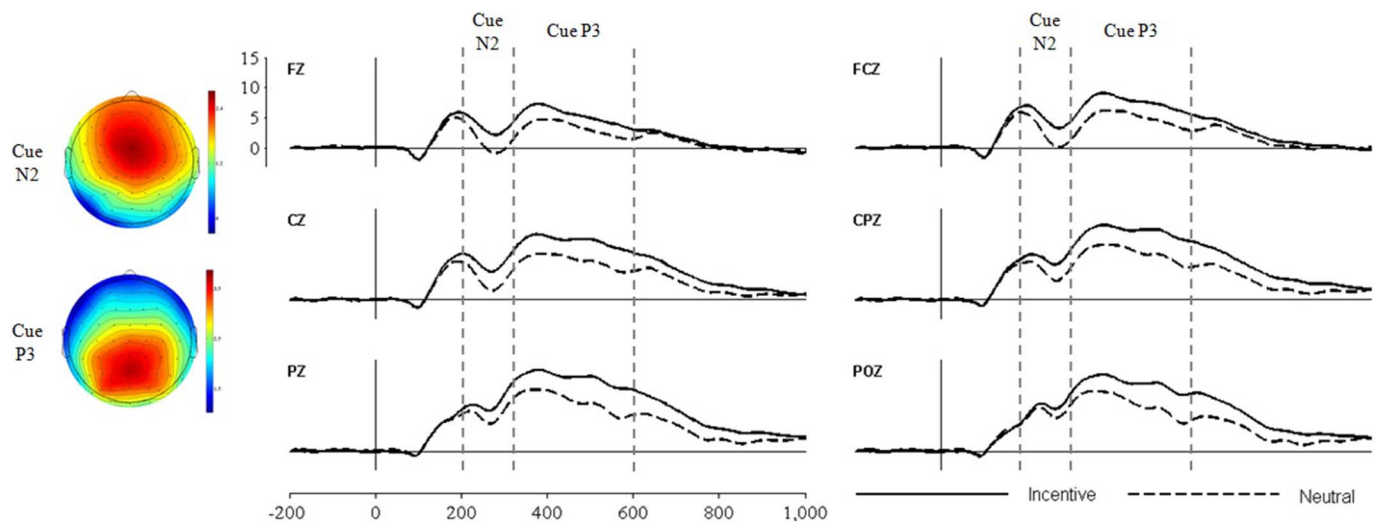
2.1.1. Cue-N2

An early ERP component modulated by reward cues is the Cue-N2 (see Fig. 1). The Cue-N2 is a negative-going fronto-central ERP elicited approximately 200–300 ms following cue onset (Potts, 2011; Santesso et al., 2012) and is importantly distinguished from other more posterior N2 negativities found in the same time-window (e.g. selection negativity or SN, and lateralized N2pc: Ritter et al., 1982; Ritter et al., 1983; Simson et al., 1977). During cue-evaluation, the Cue-N2 displays greater negativity for punishment and neutral cues over reward cues (Potts, 2011; Novak and Foti, 2015; Pornpattananangkul and Nusslock, 2015; Dunning and Hajcak, 2007; Osinsky et al., 2013). There are two major theories of Cue-N2 function to explain a reduced N2 following reward cues: cognitive-control and template mismatch (Folstein and Van Petten, 2008). Cognitive-control accounts argue the enhanced punishment Cue-N2 signals an increase in cognitive-control to avoid

potential future losses (Potts, 2011). These theories suggest the Cue-N2 is related to conflict detection and may be generated in part by the anterior cingulate cortex (ACC: Nieuwenhuis et al., 2003; Yeung et al., 2004). However, two recent reward processing studies without a punishment condition reported a less negative Cue-N2 for reward over non-incentive cues (Pornpattananangkul and Nusslock, 2015; Novak and Foti, 2015), supporting a template mismatch perspective. From this angle, participants display a positivity bias or enhanced expectation directed toward reward-cues. This positivity bias then generates an enhanced Cue-N2 following punishment cues because these punishment cues deviate from the predetermined "template" expectation (Donkers et al., 2005; Gehring et al., 1992; Folstein and Van Petten, 2008). As suggested by others, the N2 may reflect either cognitive control during response-conflict or template mismatch during stimulus-expectation depending on the experimental context (Folstein and Van Petten, 2008). Future studies should further examine the independent effects of response-conflict and stimulus-expectancy on the Cue-N2 amplitude during reward processing.

2.1.2. Cue-P3

A subsequent ERP component elicited within the cue-evaluation substage, the Cue-P3, directly follows the Cue-N2 (see Fig. 1). The Cue-P3 is a positive-going centro-parietal component peaking approximately 300–600 ms following cue onset. This component reflects stimulus categorization processes related to context updating in working memory (Donchin and Coles, 1998; Johnson and Donchin, 1980; see Polich, 2007 for review) and is reliably enhanced for salient stimuli (Polich and Kok, 1995), especially reward cues (Goldstein et al., 2006; Hughes et al., 2013). In support of reward-specific modulation, the Cue-P3 for incentive (vs. neutral) cues has been found to covary with activation in the ventral striatum (Pfabigan et al., 2014), a region highly implicated in reward processing (Delgado et al., 2000; Haber and Knutson, 2010; Schultz, 2000; Knutson et al., 2003; Breiter et al., 2001). However, the Cue-P3 likely originates from a wide range of additional neuroanatomical regions (Eichele et al., 2005; Linden, 2005; Soltani and Knight, 2000) and, as a result, displays moderate differences in scalp topography depending on the experimental context and stimulus characteristics (Berti et al., 2004; Debener et al., 2002; Gaeta et al., 2003; Polich and Comerchero, 2003). Importantly, mirroring their topographical differences, the Cue-N2 and Cue-P3 appear to track different psychological processes embedded within cue-evaluation. While the Cue-N2 is specifically modulated by template mismatches or changing cognitive control demands, rather than stimulus probability per se, the Cue-P3 is robustly associated with cue likelihood (Polich and Margala, 1997; Donchin et al., 1978; Pritchard, 1981; see Polich, 2007 for review) and uniquely sensitive to categorically salient stimulus features (such as gender: Kutas et al., 1977). Additionally, unlike the Cue-N2, the Cue-P3 is typically insensitive to cue-valence during reward processing. For example, both reward and punishment cues tend to elicit greater Cue-P3 amplitudes than neutral stimuli, and both reward and punishment Cue-P3s are highly correlated with one another

Fig. 1. Cue-N2 and Cue-P3 during reward-anticipation period. Cue-locked ERPs during reward-anticipation period of a time-estimation task at central sites across the midline (FCz/Cz/CPz/Pz/POz). Dotted grey vertical lines show the approximate time-course for each component (Cue-N2 and Cue-P3). Solid black lines show incentive cues (e.g. monetary reward) while dotted black lines show neutral cues (e.g. no monetary reward). Waveforms were generated from unpublished data on 25 participants collected using a reward electrophysiological monetary-incentive delay task (Novak and Foti, 2015).

(Broyd et al., 2012; Goldstein et al., 2006; Pfabigan et al., 2014; Pornpattananangkul and Nusslock, 2015; Novak and Foti, 2015). These results suggest an important role for motivated attention in addition to stimulus-categorization. Together, these results emphasize the opportunity afforded by temporally precise ERP methods to carefully decompose the rapid time-course of cue-evaluation into two distinct processes: an early process that may reflect template mismatch or cognitive control depending on the experimental context, and a subsequent process involving motivated attention and stimulus-categorization.

### 2.2. Motor preparation: The readiness potential (RP)

Motor-preparation is the second substage of reward-anticipation. During this stage, motor responses are prepared in service of motivated reward pursuit. One negative-going ERP component commonly investigated during motor-preparation is known as the Bereitschaftspotential (BP: Bereitschaftspotential is German and translates to "readiness potential": RP), hereafter referred to as the RP (see Fig. 2). The RP precedes the execution of voluntary movement and reflects an increase in neural efficiency to prepare and execute an upcoming motor response. Time-locked to movement onset, the RP can be decomposed into an early and later subcomponent, each of which display separate scalp topographies, covary with different neuroanatomical correlates, and appear to reflect distinct but related psychological processes occurring close together in time (see Shibasaki and Hallett, 2006 for review). While the Early-RP typically begins between 1500 and 2000 ms prior to movement, the Late-RP displays a sharper negative shift from approximately 500 ms up until movement onset (Bortoletto et al., 2011; Kutas and Donchin, 1980; Shibasaki et al., 1980). Their respective scalp topographies similarly differ: while the Early-RP is maximal at central sites, the Late-RP is maximal on the hemisphere contralateral to the movement side. In agreement with their scalp distributions, the Early- and Late-RP subcomponents likely differ in both their cortical and subcortical neural generators. Cortically, the Early-RP is likely related to activation within the pre-supplementary motor area (SMA) and SMA proper, while the subsequent Late-RP is likely more related to activation within the primary motor cortex and lateral premotor cortex (et al., Cunnington et al., 2003; Shibasaki and Hallett, 2006; for review see Jahanshahi and Hallett, 2003; Böcker et al., 1994; Knösche et al., 1996; Praamstra et al., 1996; Lang et al., 1991; Ball et al., 1999). Finally, mirroring their anatomical

and topographical divisions, both subcomponents reflect separate psychological functions as well. While the Early-RP may be related to an internal focus that facilitates early selection of an appropriate movement strategy from memory, or "abstract" motor-preparation (Kornhuber and Deecke, 1965; Lang et al., 1991), the Late-RP in contrast may reflect an external focus that precisely specifies the parameters for an impending movement execution, or "concrete" motor-preparation.

Although the RP has been previously linked to reward processing, few studies have systematically investigated reward-specific variation in the RP compared to other anticipatory ERPs. Traditionally, the RP is recorded during tasks that consist of a series of self-paced button presses without the need for stimuli. An early study initially implicated the RP in reward processing and reported an enhanced RP amplitude when monetary rewards were randomly distributed following self-paced movements (McAdam and Seales, 1969). More recently, the RP has been assessed using time-estimation tasks (Miltner et al., 1997), which find an elevated RP amplitude during goal-directed movement over self-paced movement (Baker et al., 2012). Extending these findings, a recent time-estimation study reported that reward-cues elicited a more negative RP than neutral cues as early as 1000 ms before the response (Pornpattananangkul and Nusslock, 2015). However, multiple other studies found little to no effect of reward on RP amplitude (Kotani et al., 2003; Ohgami et al., 2004; Ohgami et al., 2006; Angus et al., 2017), possibly due to task differences. For example, while Pornpattananangkul and Nusslock (2015) included an equal number of trials in reward and neutral conditions, Angus et al. (2017) included mostly incentive trials with very few neutral "no-reward" trials. Future studies should carefully dissect the time-course of earlier and later reward-related activation in the RP under a variety of reward contexts. In summary, although both Early- and Late-RP subcomponents are clearly connected by motor-preparation, they show considerable topographical, neuroanatomical, and functional differences. These results highlight the need to carefully dissect the time-course of reward-related motor-preparation and the unique insights afforded by temporally-precise ERP methods.

2.3. Motor preparation: The Contingent-Negative Variation (CNV)

Depending on the experimental context, another ERP component called the contingent-negative variation (CNV) can take the place of the RP when an external stimulus determines the precise timing of a
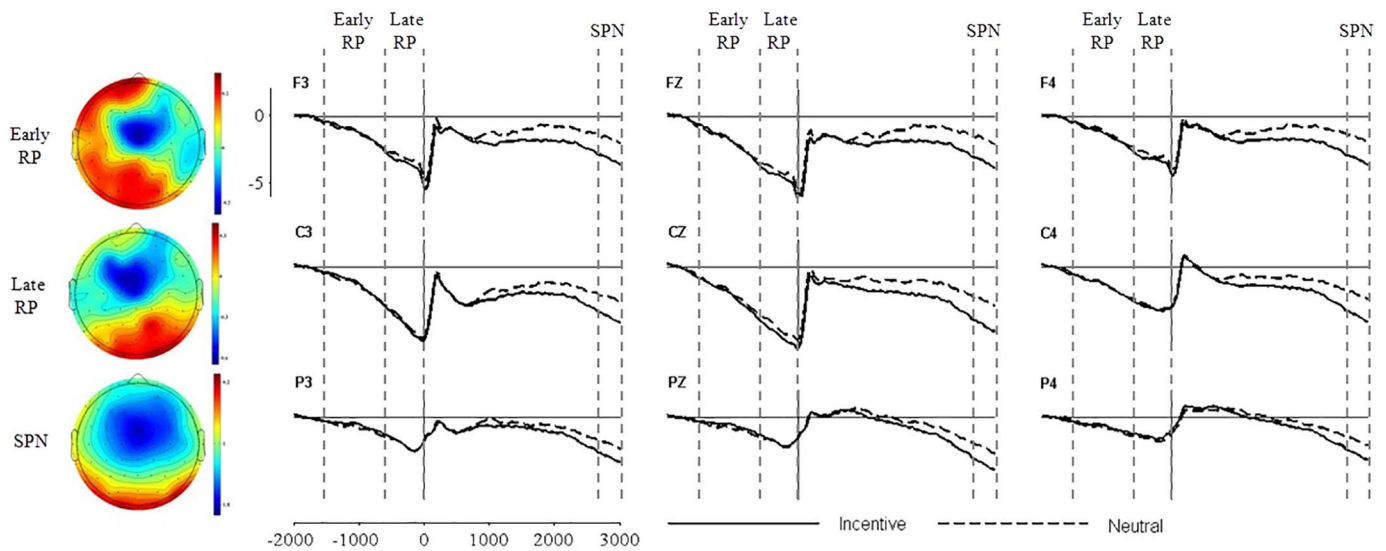
Fig. 2. Response-locked early Readiness Potential (RP), Late-RP, and Stimulus-Preceding Negativity (SPN) during Reward-anticipation Period. Response-locked ERPs at central sites across the midline (FCz/Cz/CPz), sites contralateral to movement (FC3/C3/CP3), and sites on the same hemisphere as movement (FC4/C4/CP4). Dotted grey vertical lines show the approximate time-course for each component (Early-RP, Late-RP, and SPN). Solid black lines show incentive responses (e.g. monetary reward) while dotted black lines show neutral responses (e.g. no monetary reward). Waveforms were generated from unpublished data on 47 participants collected using a reward time-estimation task (Pornpattananangkul and Nusslock, 2016).
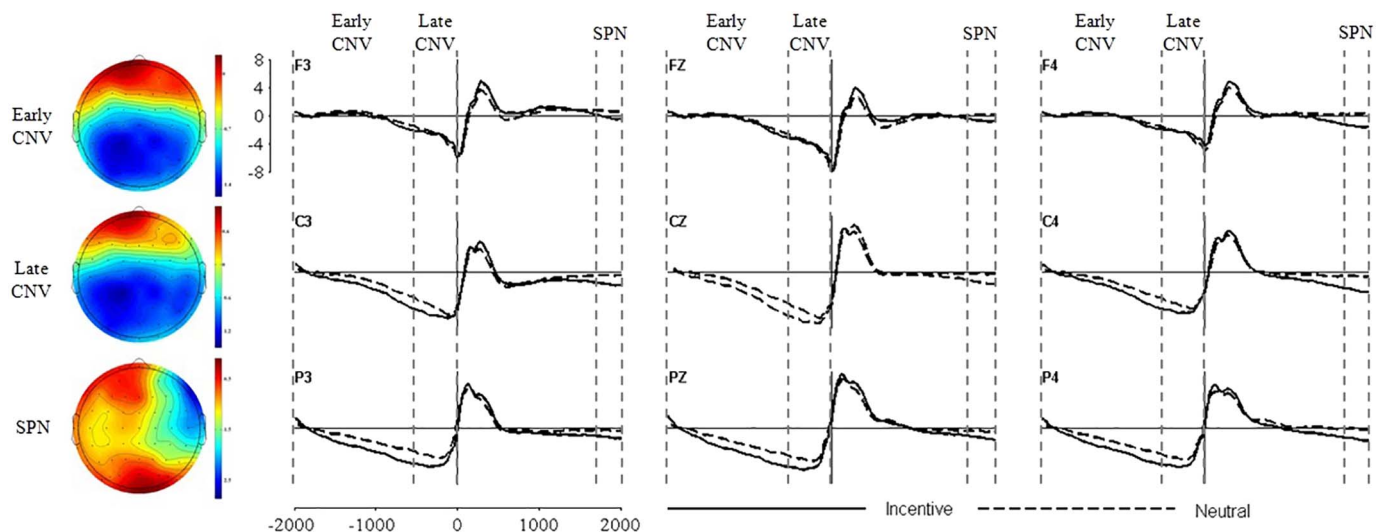
Fig. 3. Response-locked Early Contingent-Negative Variation (CNV), Late-CNV, and Stimulus-Preceding Negativity (SPN) during Reward-anticipation period. Response-locked ERPs at central sites across the midline (FCz/Cz/CPz), sites contralateral to movement (FC3/C3/CP3), and sites on the same hemisphere as movement (FC4/C4/CP4). Dotted grey vertical lines show the approximate time-course for each component (Early-CNV, Late-CNV, and SPN). The SPN here differs from the SPN in Fig. 2 only in task design (Fig. 2 was generated form a time-estimation task while the current figure was generated from a electrophysiological monetary-incentive delay task). Solid black lines show incentive responses (e.g. monetary reward) while dotted black lines show neutral responses (e.g. no monetary reward). Waveforms were generated from unpublished data on 25 participants collected using a reward electro-physiological monetary-incentive delay task (Novak and Foti, 2015).

response (see Fig. 3). Specifically, the CNV is triggered by an external cue stimulus indicating that a quick response is required, resulting in faster reaction times than without the warning (Walter et al., 1964; Rohrbaugh et al., 1976). This warning stimulus is the defining feature of the CNV that distinguishes it from the RP. For example, a runner waiting for a gunshot signaling the start of a race will leave their starting blocks quicker if the gunshot is preceded by a warning stimulus, such as the words "Ready…Set…". In this way, the CNV requires both a warning stimulus, such as a cue, and a subsequent target stimulus requiring a quick response, while the RP requires neither. Similar to the RP, the CNV is another slow wave growing in negativity prior to movement onset and is related to motor-preparation (Kotani et al., 2011). However, the CNV also contains some additional degree of anticipatory attention directed toward the upcoming imperative stimulus

(Ikeda et al., 1996; Brunia, 1988). Several studies suggest the CNV may be modulated by motivation (Cant and Bickford, 1967; Irwin et al., 1966) and effort (Falkenstein et al., 2003; Gómez et al., 2007) as well as related to increased behavioral performance in a variety of timing tasks (Birbaumer et al., 1990; Fan et al., 2007; Haagh and Brunia, 1985), although inconsistently (Van Rijn et al., 2011; Kononowicz and Van Rijn, 2014). Anatomically, largely the same neural regions are found for self-initiated movements, such as the RP, and externally triggered movements, as with the CNV, although at different levels of strength (Jahanshahi et al., 1995). Broadly, CNV amplitude during reward-anticipation has been linked to coactivation within the ventral striatum, supplementary motor area, and the thalamus (Plichta et al., 2013), and may be additionally associated with dopaminergic activity (e.g., Amabile et al., 1986; Gerschlager et al., 1999; Linssen et al., 2011).

However, the topographical distribution of the CNV is complex and reflects area-specific processing closely coupled to experimental parameters, such as stimulus modality, task-relevant goals, affective-state contributions (Birbaumer et al., 1990; Brunia, 2003).

Akin to the RP, the CNV can be decomposed into two separate subcomponents occurring close together in time. Once again, these two embedded subcomponents display different time courses of activation, discrete scalp topographies, and functionally distinct psychological processes occurring close together in time. The CNV is composed of an early frontal component and a subsequent central component showing a sharper spike in negativity directly preceding movement onset (Järvilehto and Fruhstorfer, 1970), although the precise time-course of these two components can vary by experimental design. While the Early-CNV is typically understood as a reaction to a warning stimulus (Rohrbaugh and Gaillard, 1983), the Late-CNV is involved in motor preparation (Low and McSherry, 1968; Rohrbaugh et al., 1976) and, like the Late-RP, appears to reflect concrete specifications of impending movement execution. Finally, support for reward-related modulation of the CNV by monetary incentives is mixed. While several studies have found that variation in Early- and Late-CNV amplitude is enhanced following incentive cues (Pfabigan et al., 2014; Schevernels et al., 2014; Vuillier et al., 2015; Novak and Foti, 2015; Zhang et al., 2017), others found no reward-related effects on the CNV (Goldstein et al., 2006; Sobotka et al., 1992; Broyd et al., 2012; Schevernels et al., 2015). Future research should consider the time-course of the Early- and Late-CNV during reward processing and differences in experimental designs to help resolve these inconsistencies.

2.4. Feedback-anticipation: The Stimulus-Preceding Negativity (SPN)

The final substage of reward-anticipation is feedback-anticipation. During this substage, anticipatory attentional resources are mobilized directly preceding an impending feedback stimulus. In contrast to actively pursuing rewards during motor-preparation, passive reward-anticipation does not require motivated effort or pursuit, but rather involves simply waiting for feedback. Just as the act of writing an article for publication is a very different experience than waiting for peer-review feedback, motor-preparation and feedback-anticipation are associated with distinct neural systems, different psychological processes, and may contain their own unique implications for clinical science, especially for disorders affecting motivational processes. Importantly, due to their close temporal proximity, dissociating motor-preparation from feedback-anticipation requires utilizing methodologies with strong temporal resolution, such as ERPs. Feedback-anticipation is most commonly captured by an ERP component known as the stimulus-preceding negativity (SPN), a broad index of anticipatory attention frequently measured in a 200 ms interval directly prior to feedback onset (see Figs. 2 and 3). Similar to the RP, the SPN is an asymmetrical negative slow wave that grows with anticipation. However, unlike either the RP or CNV, the SPN precedes an impending informative stimulus in the absence of movement, and is associated with increases in attentional and perceptual anticipatory systems.

Multiple studies have extended the functional significance of the SPN to include affective-motivational processes involved in anticipation (Chwilla and Brunia, 1992; Kotani et al., 2001; Kotani et al., 2003). Anatomically, multi-modal studies suggest the pre-feedback SPN covaries with activation in the insula cortex (Böcker et al., 1994; Kotani et al., 2009; Brunia et al., 2000), especially the right anterior insula, an area strongly activated during anticipation of either gains or losses (Knutson and Greer, 2008). Interestingly, the pre-feedback SPN typically displays a right-lateralized fronto-central distribution (Brunia et al., 2011a). However, similar to the CNV, this scalp distribution is modulated by the modality of the expected stimulus, suggesting several additional neural generators may contribute to SPN amplitude depending on the experimental context (Brunia and Van Boxtel, 2004; Ohgami et al., 2004).

Numerous studies have investigated the SPN preceding feedback during reward processing. These studies confirm that the pre-feedback SPN is elevated preceding reward-related feedback (Donkers et al., 2005; Foti and Hajcak, 2012; Fuentemilla et al., 2013; Kotani et al., 2003; Masaki et al., 2006; Morís et al., 2013; Ohgami et al., 2004), especially when feedback is associated with monetary reward (Chwilla and Brunia, 1991; Kotani et al., 2001, 2003; Masaki et al., 2006; Ohgami et al., 2004, 2006). Furthermore, a number of recent studies suggest the SPN is related to reinforcement expectations (Masaki et al., 2010; Masaki et al., 2006) and dopaminergic processes involved in reinforcement learning (Foti and Hajcak, 2012; Mattox et al., 2006; Morís et al., 2013). Reinforcement learning, and its associated dopaminergic processes, are discussed at length in the reward-outcome section. These results converge with numerous studies reporting that larger reward magnitude, increased effort, and prior action-outcome contingencies all tend to increase the SPN (Mühlberger et al., 2017; Morís et al., 2013; Fuentemilla et al., 2013; Mattox et al., 2006; Zheng et al., 2015; Zheng and Liu, 2015; Zheng et al., 2017; Poli et al., 2007; but see Masaki et al., 2006; Wang et al., 2017). However, associations between the SPN and reward probability have been more mixed. For example, although two studies found that unpredictable outcomes increased the SPN (Catena et al., 2012; Foti and Hajcak, 2012), another study found that the SPN showed an inverse relationship with outcome probability (Fuentemilla et al., 2013). Although quite a few studies have investigated the pre-feedback SPN, the vast majority of outcome-focused studies tend to ignore this component altogether. This is easy to remedy as most EEG/ERP reward paradigms are appropriate for measuring the SPN with minor adjustments to inter-stimulus intervals. We encourage future research investigating reward processing using EEG to take advantage of the pre-feedback SPN as an index of reward-related anticipatory attention.

2.5. Relationships between anticipatory ERP components

Surprisingly few studies have investigated the relationships between anticipatory components. Converging with prior neuroimaging evidence, these studies suggest that some ERP components within reward-anticipation substages are unrelated to other anticipatory components, highlighting the potential orthogonality among certain anticipatory components. For example, both the Cue-N2 and Cue-P3 during cue-evaluation are typically unrelated to other reward-related anticipatory and outcome ERP components (Novak and Foti, 2015; Novak et al., 2016; Pornpattananangkul and Nusslock, 2015; however, see Zheng et al., 2017 for alternative). These results suggest the Cue-P3 and Cue-N2 may capture cue-evaluatory processes that are independent of motor-preparation, feedback-anticipation, and reward-outcome.

Equally interesting, however, are the documented relationships among anticipatory components. A recent study reported that the SPN was positively associated with both the Early- and Late-RP during reward processing, suggesting at least some degree of association between motor-preparation and feedback-anticipation processes (Pornpattananangkul and Nusslock, 2015). In support of this relationship, another recent study reported a negative association between the Late-CNV and SPN during reward processing, although this study did not investigate the Early-CNV (Novak et al., 2016). The authors suggest this negative relationship may reflect a tradeoff between motivated behavior and feedback uncertainty such that reward motivation may increase the CNV while feedback certainty may increase the SPN. These successful analyses illustrate the powerful advantages of ERP methods to decompose the time-course of anticipatory substages, such as motor-preparation and anticipatory attention, that are unavailable to less temporally precise methods (such as fMRI). Future studies should leverage these temporal advantages of ERP by broadening the time-course of their analyses to assess multiple distinct anticipatory processes.

2.6. ERP component overlap within anticipatory stages

In addition to parsing activation between each substage of reward-anticipation, carefully decomposing the time-course within each substage is critical to mitigate component overlap from neighboring ERPs elicited in very close temporal proximity to one another. For example, supporting a possible template-mismatch perspective, the Cue-N2 in the cue-evaluation stage typically shows reduced negativity following incentive cues. However, it is also possible that overlapping positivity from the Cue-P3, which is typically enhanced due to the motivational salience of incentive-cues, may contribute to Cue-N2 variation. In support of this account, recent work reported that the reward-related Cue-N2 and Cue-P3 components were inversely correlated and, moreover, that a more positive Cue-N2 during incentive trials failed to remain significant after controlling for Cue-P3 (Novak and Foti, 2015; Pornpattananangkul and Nusslock, 2015).

Furthermore, many anticipatory components can be deconstructed into earlier and later subcomponents that reflect discrete psychological processes that must be carefully separated from one another to derive accurate conclusions. For example, the P3 can be separated into an early frontal component (P3a) and a later parietal component (P3b) that, although elicited very close together in time, show clear topographical and functional divisions (Courchesne et al., 1975; Debener et al., 2005; Dien et al., 2004; Donchin, 1981; Näätänen and Gaillard, 1983; Polich and Comerchero, 2003; Spencer et al., 1999, 2001; Snyder and Hillyard, 1976; see Polich, 2007 for review). While the P3a reflects modifying representations in working memory through early top-down attentional processes, the P3b subsequently reflects updating and transferring the contents of working memory to temporal and parietal structures (Soltani and Knight, 2000). In this way, two distinct but overlapping positive deflections are superimposed onto what initially appears to be a unitary parietal Cue-P3 component typically measured during cue-evaluation. However, these subtleties are lost in the vast majority of reward-related ERP studies and thus much less is known about their possible interplay during reward processing. Therefore, decomposing the rapid time-course of these cue-evaluation subcomponents by isolating the P3a and the P3b from each other, and from the earlier Cue-N2, may be a promising direction for future research into reward processing.

Components within the motor-preparation stages can be similarly decomposed into earlier and later subcomponents that each reflect distinct psychological processes that occur very close together in time. For example, because the RP is triggered internally without the presence of any enteral stimuli, it remains unclear precisely when the Early-RP ends and the Late-RP begins, making it particularly challenging to separate the two (Bortoletto et al., 2011; Kutas and Donchin, 1980; Shibasaki et al., 1980; see Shibasaki and Hallett, 2006 and Brunia et al., 2011b for reviews). Pornpattananangkul & Nusslock successfully decomposed the time course of the RP during reward processing, finding that the RP is modulated by reward as early as 1000 ms prior to response execution. Carefully decomposing the precise temporal shift from early to late RP is critical to isolate activity related to abstract versus concrete representations of motor-preparation, respectively. As another example, the CNV during motor-preparation is in a similar situation. Although the Early- and Late-CNV are somewhat functionally distinguished by early processing of the cue-stimulus and later processes involved in concrete response-preparation, each component contains some degree of both functions making it difficult to separate overlap between anticipatory attention and motor-preparation (Brunia et al., 2011a, 2011b). Finally, the SPN during feedback anticipation can be decomposed into a family of three overlapping processes representing functionally distinct psychological functions: anticipatory attention directed toward the impending stimulus, the expected information it conveys, and its emotional content (Van Boxtel and Böcker, 2004). However, very few studies have dissected the temporal progression of the SPN. Thus, decomposing the time-course of SPN may

provide interesting directions for future research to isolate activity specific to each known process.

2.7. Reward-anticipation ERPs: summary and conclusions

Reward-anticipation is a heterogeneous construct composed of at least three temporally distinct substages (i.e., cue evaluation, motor preparation, feedback anticipation), each with their own associated ERP components. Each substage contains largely independent information about reward processing, reflected in the orthogonality of cue-evaluation from components related to motor-preparation and feedback-anticipation. On the other hand, there are also important relationships among the various substages, such as a link between motor-preparation and feedback anticipation. These between-substage comparisons showcase the power of ERP to examine the temporal dynamics of reward-anticipation beyond other neuroscientific methods. However, carefully considering the time-course within each stage is necessary to mitigate temporal overlap among distinct subcomponents, such as dissecting earlier abstract from later concrete representations of motor-preparation. Isolating activity uniquely associated with individual components of interest can also help resolve important discrepancies in the literature, such as whether increased Cue-N2 positivity following reward over punishment cues is due to a primary feature of template-mismatch essential to Cue-N2 function or rather component overlap from the salience-related Cue-P3. Collectively, these results showcase the diversity of psychological processes embedded within the reward anticipatory period and the temporal power of ERP methods for examining the neurophysiological correlates of these processes. This dynamic progression of diverse ERP components implicated during reward-anticipation highlight the need to broaden the time-course of analysis and the advantages of multicomponent analysis.

3. Reward-outcome ERPs

Similar to reward-anticipation, reward-outcome can also be decomposed into multiple distinct psychological processes occurring close together in time. These processes include early reward reactivity, subsequently updating working memory, and extended affective processing of feedback information. However, while the sequential progression of reward-anticipation typically unfolds over a period of seconds, reward-outcome is more immediate with multiple psychological processes occurring within approximately a single second following reward feedback. Thus, carefully considering the time-course among outcome processes and their underlying ERP components is particularly important for mitigating temporal overlap among reward-outcome components. The typical outcome ERP components following reward feedback are the Feedback-Related Negativity (FRN/FN/fERN/RewP), the P300 (FB-P3), and the Late-Positive Potential (FB-LPP). These outcome-related ERP components, especially the FRN, are often investigated in the context of the third stage of reward processing, learning. Although learning cannot be temporally isolated like the anticipation and outcome stages of reward processing, many outcome-related ERPs have important implications for learning in a variety of contexts. As with anticipation, every outcome-related ERP component displays separate scalp topographies, covaries with distinct neuroanatomical correlates, and reflects unique psychological processes. Furthermore, each component is sensitive to a variety of common reward-outcome manipulations including performance evaluation (i.e. sensitivity to gain vs. lose feedback), reward evaluation (i.e. sensitivity to incentive vs. neutral feedback), reward probability, and reward magnitude (San Martín, 2012). The following sections will review each of these outcome-related ERP components during reward processing. Careful consideration of the time-course within reward-outcome can provide both critical insights into the nature of the relationships between outcome components and help resolve inconsistencies within the literature by isolating reward-related variation specific to each unique
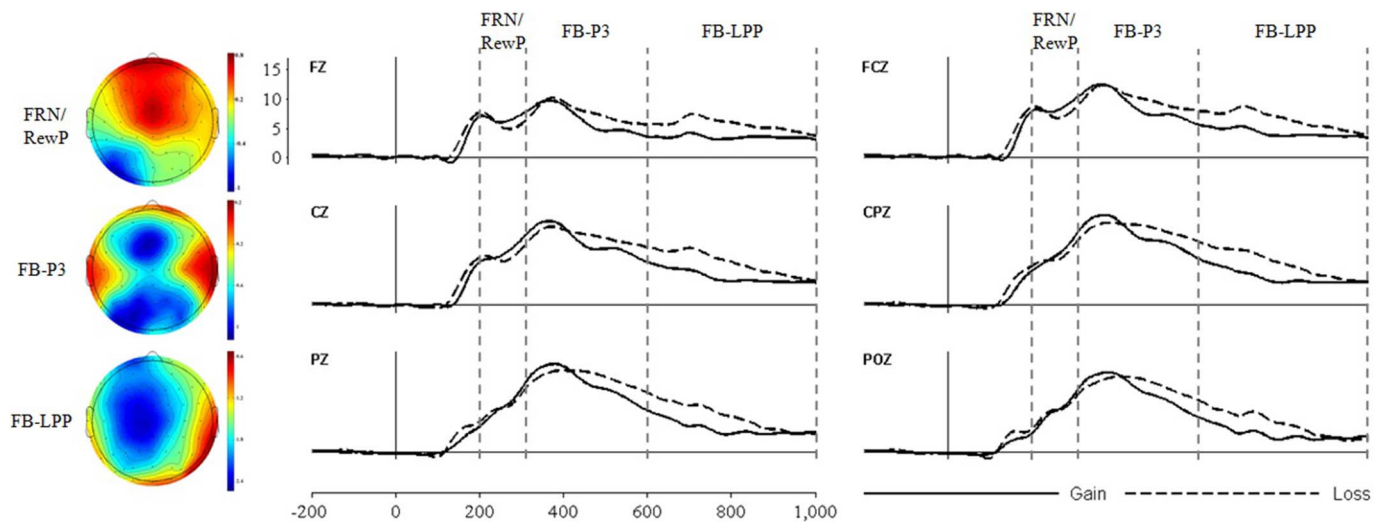
Fig. 4. Feedback-Related Negativity (FRN), Feedback-P3 (FB-P3), and Feedback-Late Positive Potential (FB-LPP) during reward-outcome period. Feedback-locked ERPs from a time-estimation task at central sites across the midline (FCz/Cz/CPz/Pz/POz). Dotted grey vertical lines show the approximate time-course for each component (FRN/FB-P3/FB-LPP). Solid black lines show gain feedback while dotted black lines show loss feedback. Waveforms were generated from unpublished data on 50 participants collected using a reward time-estimation task (Pornpattananangkul and Nusslock, 2016).

component.

3.1. Feedback-related negativity and reward-positivity (FRN & RewP)

Following feedback, the Feedback-Related Negativity (FRN also known as feedback error-related negativity or fERN, the medial-frontal negativity or MFN, and the feedback-negativity FN: Miltner et al., 1997) is the earliest ERP component differentiating gains from losses (see Fig. 4). The FRN is a fronto-central ERP component elicited between 200 and 300 ms following feedback onset that has been localized to the anterior cingulate cortex (ACC) (Gehring and Willoughby, 2002; Miltner et al., 1997; Potts et al., 2006; Ruchsow et al., 2002; Nieuwenhuis et al., 2005; Herwig et al., 2007; Zhou et al., 2010). Hundreds of studies have investigated the FRN in isolation, making it by far the most extensively investigated reward-specific ERP component (see Sambrook and Goslin, 2015 for meta-analytic review). Accordingly, a comprehensive review of this component is outside the scope of this review. Generally, however, these studies confirm the FRN is sensitive to both performance evaluation (e.g. gain vs. loss) and reward evaluation (e.g. incentive vs. neutral) during feedback processing. Traditionally, the FRN is thought to signal greater negativity when an outcome has gone worse (vs. better) than expected. However, recently several studies argue the FRN is instead driven by a positive deflection superimposed onto the ERP waveform following gains which has been termed the Reward-Positivity (RewP: Holroyd et al., 2008; Walsh and Anderson, 2012; Baker and Holroyd, 2011; Carlson et al., 2011; Foti et al., 2011a; Holroyd et al., 2011). In contrast to the loss-related FRN, the gain-related RewP reflects reward-specific activation at more central sites (Holroyd et al., 2011; Holroyd et al., 2008), possibly elicited in part by striatal reward regions in addition to the ACC and medial frontal cortex (Foti et al., 2011a; Carlson et al., 2011, 2015; Foti et al., 2014; Becker et al., 2014). A simultaneous EEG-FMRI study, for example, found that activation within the medial prefrontal cortex, cingulate, and the striatum were related to RewP amplitude specific to gains (Becker et al., 2014).

Conceptually, the RewP is frequently studied within the context of the third pillar of reward processing: learning. Although learning cannot be easily temporally separated from either reward-anticipation and reward-outcome stages, outcome-related ERP components are often studied in the context of learning. Specifically, the RewP is commonly situated within reinforcement learning theories (Holroyd and Coles, 2002). These theories posit that phasic increases or decreases in

mesencephalic dopamine signaling track violations in reward expectation (Montague et al., 2004; Schultz, 2002; Holroyd and Coles, 2002; Glimcher, 2011) immediately following outcomes that are better or worse than expected (Fiorillo et al., 2003; Caplin and Dean, 2008). These reward prediction errors are typically localized to striatal reward regions (Haber and Knutson, 2010; Knutson et al., 2003) and facilitate temporal difference learning to maximize anticipated rewards through adaptive action selection (Sutton and Barto, 1998). Modulation in RewP amplitude is consistently associated with reward prediction violations and outcome probabilities, and thus may index reward prediction errors (Walsh and Anderson, 2012; Sambrook and Goslin, 2014; Sambrook and Goslin, 2015). However, both the RewP and FRN are inconsistently related to reward magnitude (Hajcak et al., 2006, 2007; Cherniawsky and Holroyd, 2013; C Qu et al., 2013; Bernat et al., 2015; Sambrook and Goslin, 2015, 2016), leading to alternative accounts of the RewP as a possible general salience prediction error (Talmi et al., 2013; Sambrook and Goslin, 2016). Many of these inconsistencies may be partially due to the wide variety of measurement approaches used to quantify the FRN and RewP to address temporal overlap with neighboring components, such as the subsequent FB-P3 discussed in the next section (Sambrook and Goslin, 2015).

Although dopaminergic reward prediction errors likely contribute to RewP amplitude, the unifying mechanism underlying the RewP remains unclear. Alternatively, several prior studies have linked the RewP to affective processing (Gehring and Willoughby, 2002; Holroyd and Coles, 2002) and motivational states (Boksem et al., 2006; Hajcak et al., 2006) in addition to reinforcement learning signals. More recently, several studies have directly linked the RewP with approach-motivation during goal pursuit by revealing connections with the Behavioral Activation Scale (Carver and White, 1994) and enhanced performance monitoring (Threadgill and Gable, 2016; Lange et al., 2012; Angus et al., 2015). These results suggest that the RewP may reflect differences in reward sensitivity and contain important implications for psychopathological disruptions of reward-related neural circuitry, such as in depression and bipolar disorder (Proudfit, 2015; Mason et al., 2012). Clearly more work is needed to unpack the psychological meaning of the RewP. Finally, due to component overlap considerations from the subsequent FB-P3 positivity discussed below, there exists a variety of RewP measurement approaches that likely contribute to substantial inconsistencies within the literature (see below for more details).

3.2. Feedback P300 (FB-P3)

Another ERP component implicated in reward-outcome that directly follows the RewP is the post-feedback P300 or FB-P3, a centro-parietal positive-going deflection peaking from 300 to 600 ms following a feedback stimulus (see Fig. 4). Although one might assume that both the anticipation Cue-P3 and outcome FB-P3 index comparable processes to some extent, multiple recent studies suggest that these two P3 components are unrelated. This suggests that the Cue-P3 and FB-P3 reflect unique variation within anticipatory and outcome stages of reward processing (Novak et al., 2016; Pornpattananangkul and Nusslock, 2015; however, see Zheng et al., 2017 for alternative). Whereas the Cue-P3 reflects categorizing a cue to prepare for some upcoming stimulus or motor action, the FB-P3 involves attention-driven categorization of salient outcome-related information, such as context updating, and subsequently integrating the contents of working memory to maximize future rewards (Sutton et al., 1965; Donchin, 1981; see Polich, 2007 for review). Additionally, the FB-P3 may reflect affective processes by signaling the motivational salience of reward feedback (San Martín, 2012). Similar to the Cue-P3, the neuroanatomical correlates of the FB-P3 are widespread and largely uncertain. Intracranial P3-like activity has been recorded from several brain regions suggesting multiple neural generators contribute to the FB-P3 (for review see Soltani and Knight, 2000). In general, the temporo-parietal junction (TPJ) and adjacent areas appear to be the most likely sources (Kiss et al., 1989; Halgren et al., 1995), with possible contributions from the hippocampus, amygdala, and thalamus (Paller and Kutas, 1992; Halgren et al., 1980; Yingling and Hosobuchi, 1984).

Similar to the RewP, the FB-P3 is typically sensitive to reward probability and reward evaluation, showing larger amplitudes for reward-related feedback and more unexpected outcomes (San Martín, 2012; Courchesne et al., 1975; Donchin and Coles, 1988; Hajcak et al., 2007; Watts et al., 2017). However, unlike the RewP, the FB-P3 is consistently modulated by reward magnitude but is typically insensitive to performance evaluation (Yeung and Sanfey, 2004; Pfabigan et al., 2011; Foti et al., 2011a; Hajcak et al., 2005), leading some early studies to suggest that magnitude and valence are encoded separately in the brain (Yeung and Sanfey, 2004). By contrast, many other studies have found the FB-P3 is sensitive to either gains or losses in different experimental contexts (Bellebaum and Daum, 2008; Goyer et al., 2008; Wu and Zhou, 2009; Zhou et al., 2010; Hajcak et al., 2005; Hajcak et al., 2007; Holroyd et al., 2006; for review, see San Martín, 2012). These inconsistencies within the FB-P3 literature resemble inconsistencies in the RewP discussed above and likely result from strong temporal overlap with the preceding RewP and subsequent late-positive potential (LPP: discussed below), both of which appear to be sensitive to feedback valence (Bernat et al., 2011; Foti et al., 2011a; Hajcak et al., 2007; Holroyd et al., 2008; Miltner et al., 1997). Surprisingly, although there exist a wide range of RewP measurement techniques to overcome this overlap, very few similar methods exist to dissociate FB-P3 measurement from the surrounding RewP or LPP. Of note, recent success has been found using principal component analysis applied to reward-outcome ERPs (Sambrook and Goslin, 2016; Dien and Frishkoff, 2005; Dien, 2010; Foti et al., 2011a; Weinberg et al., 2014), although these analyses typically focus on isolating the FRN or RewP over the FB-P3 or LPP. Future research should consider the rapid progression of all three reward-outcome ERPs to meaningfully capture variation independent of neighboring components and to provide a clearer picture of their rapid temporal progression.

3.3. Late-positive potential (FB-LPP)

Directly following the FB-P3, the Late-Positive Potential (LPP) is the final ERP component during the outcome stage (see Fig. 4). The LPP is a positive-going centro-parietal ERP component showing sustained activation beginning from approximately 500 to 600 ms and continuing onward for up to several seconds following the onset of motivationally-salient stimuli (Schupp et al., 2004; Hajcak et al., 2009; Schupp et al., 2006). This component is typically investigated during passive emotional-picture viewing and reflects sustained attention and extended cognitive processing, even after stimulus offset (Hajcak and Olvet, 2008; Dunning and Hajcak, 2009; Hajcak et al., 2009; Cuthbert et al., 2000; Hajcak et al., 2006; Schupp et al., 2000). Despite largely unknown neural generators, some speculate the LPP may reflect perceptual processing in the visual cortex amplified by amygdala activity (Bradley et al., 2003) to facilitate the encoding of emotional stimuli in working memory (Olofsson et al., 2008). Extensive prior research confirms the LPP is largest for negative stimuli (Huang and Luo, 2006; Ito et al., 1998; Hajcak and Olvet, 2008), suggesting a "negativity bias" during extended processing of emotional information (Smith et al., 2003). In the context of reward processing, any reward task administering feedback can potentially measure a post-feedback LPP (FB-LPP). Only a small handful of studies on reward processing, however, have looked beyond 600 ms following feedback onset, and these studies frequently lump the FB-LPP into the measurement of the FB-P3. Consequently, very little is known about the FB-LPP and its functional differences from the FB-P3 during outcome processing, although it appears to display a markedly similar scalp topography and functionality as the well-studied LPP following emotional images. These similarities between the FB-P3 and FB-LPP suggest the FB-LPP likely reflects extended cognitive and attentional processing of the affective value of the feedback-outcome (Pornpattananangkul and Nusslock, 2015; Groen et al., 2008; Althaus et al., 2010; Van Meel et al., 2011; Groen et al., 2013) and may be the affective counterpart of the FB-P3 (Groen et al., 2008).

Of the few studies investigating the FB-LPP in the context of reward processing, two recent studies report the FB-LPP is sensitive to both reward expectancy and reward magnitude (Donaldson et al., 2016; Meadows et al., 2016). In addition, healthy participants tended to show an enhanced positivity following loss over gain feedback, suggesting the FB-LPP is sensitive to performance evaluation consistent with a negativity bias (Groen et al., 2008; Van Meel et al., 2005; Pornpattananangkul and Nusslock, 2015; Donaldson et al., 2016). Interestingly, two recent reinforcement learning studies have linked this negativity bias in the FB-LPP following negative feedback to subsequent behavioral adjustments (Von Borries et al., 2013; San Martín et al., 2013). Given this link with action-outcome contingencies, the FB-LPP negativity bias may reflect a motivationally-salient coupling with subsequent behavioral adjustments, rather than the performance information contained within reward feedback per se. Indeed, another recent study found no performance effects on FB-LPP amplitude when outcomes were generally known prior to feedback administration (Groen et al., 2013), suggesting that this may in fact be the case. In support of this perspective, a recent study found significant independent effects of both reward- and performance-evaluation on the FB-LPP, but only reward-evaluation on the FB-P3, although the FB-LPP was correlated with an enhanced FB-P3 (Pornpattananangkul and Nusslock, 2015). These results suggest both components reflect overlapping but partially distinct psychological processes occurring close together in time. Interestingly, these results were strongest for the later FB-LPP time windows (approximately 600–800 ms). Thus, in addition to temporally isolating FB-P3 from the FB-LPP, carefully parsing the temporal progression of the FB-LPP itself into earlier and later time-windows appears promising. Finally, a recent study reported an enhanced LPP following reward-cues during reward-anticipation in addition to a more positive LPP following loss-feedback than gains (Trimber and Luhmann, 2017). This highlights the need for future studies to investigate a possible cue-related LPP deflection in addition to the FB-LPP. Together, these results indicate that investigating the LPP during both reward-anticipation (e.g. following cues) and reward-outcome (e.g. following feedback) are promising directions for future research.

3.4. Relationships between reward-anticipation and reward-outcome ERP components

Very few studies have investigated the relationships between ERP components across the reward-anticipation and reward-outcome stages. These types of cross-stage analyses are critical to determine the degree of comparability or dissociability of anticipatory and outcome reward-related processing, especially given parallel evidence from animal and human imaging studies showing that reward-anticipation and outcome are associated with distinct and separate neural mechanisms (Berridge et al., 2009). For example, although both Cue- and FB-P3s track similar attentional processes to some extent, they appear to be uncorrelated with each other, suggesting that these two components may index separate processes within anticipatory and outcome stages of reward processing (Novak et al., 2016; Pornpattananangkul and Nusslock, 2015; however, see Zheng et al., 2017). Further support for a dissociation between anticipatory and outcome ERPs are studies reporting that none of the cue-evaluation components (e.g. the Cue-P3 and Cue-N2) or later stages of anticipatory motor preparation (e.g. Late-CNV or Late-RP) were associated with any outcome ERP components following feedback (e.g. RewP, FB-P3, and FB-LPP) (Novak et al., 2016; Pornpattananangkul and Nusslock, 2015; Zheng et al., 2017). Although these results show that many components across reward-anticipation and outcome stages are unrelated, which, for the most part, converges with animal and human neuroimaging findings (Schultz, 2007; Haber and Knutson, 2010), there are also important relationships between each stage. In contrast to later stages of motor preparation, an enhanced Early-RP during the anticipatory period has been linked to an elevated RewP following gain feedback and an enhanced FB-P3 regardless of feedback valence (Pornpattananangkul and Nusslock, 2015).

There are inconsistencies, however, in findings on relationships between anticipatory and outcome ERPs, likely due in part to the small number of studies. While some studies reported a greater anticipatory SPN was related to an enhanced FB-P3 following reward feedback, but not related to the RewP (Novak et al., 2016; Pornpattananangkul and Nusslock, 2015; Fuentemilla et al., 2013), others reported the pre-feedback SPN was instead related to the post-feedback RewP (Zheng et al., 2017; Morís et al., 2013). Whether the SPN is related to the RewP or the FB-P3, or both, will lead to very different theoretical interpretations. For example, although future work is needed to resolve these inconsistencies, it is possible that associations between the anticipatory SPN and outcome RewP may be in part due to overlap between the RewP and FB-P3 measurement windows following feedback, as discussed in detail in the next section. It is important to determine whether the RewP reflects activity unique to reward-outcome, e.g. only 'liking' rewards, or activity that is shared by both stages, including 'wanting' rewards.

A recent example highlighting the importance of cross-stage analysis comes from Novak et al. (2016). This study reported that sensation seeking was related to a reduced Cue-P3 during cue-evaluation but an enhanced RewP following reward feedback. These results suggest sensation-seeking individuals may bias 'liking' rewards by showing deficits during reward-anticipation but heightened neural activity during reward-outcome. However, this study also reported that individuals high in both impulsivity and depressive symptoms displayed the largest CNV during reward-anticipation but the smallest RewP during reward-outcome. Numerous studies have confirmed that depressive symptoms are related to a blunted RewP amplitude (see Proudfit, 2015 for review). However, a recent study suggests that depressive symptoms may lead to increases in the CNV (Novak et al., 2016) and another reported a similar increase in the SPN (Umemoto and Holroyd, 2017; however, see Pierson et al., 1987). Together, this research suggests depressed individuals who score high on impulsivity may be able to bring their reward network "online" during reward-anticipation (e.g. enhanced CNV and SPN), but are unable to sustain that activation throughout later stages such as during reward-outcome (e.g. blunted RewP).

However, these results stand in contrast to neuroimaging studies that typically find reduced activation in reward-related neural regions during reward-anticipation, but not reward-outcome (Olino et al., 2014; Chentsova-Dutton and Hanley, 2010; McFarland and Klein, 2009; Sherdell et al., 2012). Although future research is needed to resolve inconsistencies between neuroimaging and electrocortical results, these studies highlight the need for cross-stage analyses and showcase the temporal strength of EEG methods that can reveal more nuanced relationships within the reward processing literature unavailable to less temporally sensitive techniques.

3.5. ERP component overlap within reward-outcome

In addition to investigating cross-stage relationships, carefully decomposing the rapid time-course of outcome-related ERP components is critical to mitigate component overlap from neighboring components and to isolate activity specific to each. Unlike reward-anticipation, all the reward-outcome ERPs tend to be at least marginally correlated with each other (Novak et al., 2016; Pornpattananangkul and Nusslock, 2015; Zheng et al., 2017). This is likely driven, in part, by their close temporal proximity to each other, making it difficult to determine whether correlations among reward-outcome ERPs reflect meaningful relationships or merely temporal overlap.

For example, as mentioned previously, the majority of reward-related ERP experiments focus exclusively on the FRN while largely ignoring other outcome-related components. This common single-component approach is particularly problematic in the case of the FRN, which is embedded between two neighboring positive components: the immediately preceding P2 and the subsequent FB-P3 (see Fig. 4). This type of temporal overlap makes it difficult to isolate the FRN without considering its context within the broader temporal progression of the other outcome components, especially given recent research suggesting the FRN is rather a superimposed positivity called the RewP (Holroyd et al., 2008; Bernat et al., 2011; Nelson et al., 2011). For instance, while some studies report that the RewP and FB-P3 have unique relationships with performance and magnitude feedback, other studies report these two components are both modulated by performance and magnitude feedback in a similar manner. Overlap between these two components, such that activity from one components "bleeds" over into the other, may partially explain these inconsistent results and help resolve discrepancies within the literature. Within the clinical science literature, a wealth of research has confirmed depressive symptoms are related to a blunted difference between gains and losses (see Proudfit, 2015 for review). Early studies interpreted this difference as a reduced negativity following losses; however, more recent studies suggested most of the variation in the FRN time window is due to modulation of positivity indexed by the RewP following gain trials (Holroyd et al., 2011; Holroyd et al., 2008). Prior research had not considered a superimposed positivity following gains because this component overlapped with the immediately following FB-P3, which is also a positive component. Subsequent studies using principal component analysis to carefully separate the FRN and RewP time window from the following FB-P3 have confirmed that depressive symptoms are indeed related to a reduced positivity following gains, suggesting that depression leads to blunted reward sensitivity rather than a decreased sensitivity to loss per se (Whitton et al., 2016; Weinberg et al., 2015). These results highlight important misinterpretations that may result from neglecting the rapid time-course of ERPs elicited during reward-outcome.

Additionally, most previous research has typically measured the FB-P3 using a single, extended time-window overlapping with the FB-LPP, another component affected by performance following reward feedback. This approach conflates the time-course of the two components and likely contributes to the inconsistent performance findings in the FB-P3 literature (San Martín, 2012). Furthermore, similar to the Cue-P3, the FB-P3 is rarely separated into an early P3a and a later P3b component and is instead simply measured and interpreted as a single

extended parietal P3b. These component overlap considerations during the reward-outcome stage highlight the need to carefully decompose the time-course of each component in order to ensure proper measurement and interpretation. This can help resolve important discrepancies within the literature and provide a deeper richness to the study of reward processing.

3.6. Reward-outcome ERPs: summary and conclusions

In contrast to reward-anticipation, which contains temporally distinct substages that unfold on the level of seconds, reward-outcome is composed of a rapid progression of ERP components that typically resolve within a single second. As a result, decomposing the dynamic time-course within reward-outcome is especially critical to mitigate temporal overlap and isolate activity unique to each component of interest. Given the vast majority of reward processing studies tend to focus exclusively on reward-outcome, we recommend analyzing and reporting components beyond the FRN, even if results are null. For example, isolating activation specific to the "affective" FB-LPP component from the late "salience" FB-P3b may reveal important and uninvestigated associations with extended emotional processing following reward feedback. Isolating components of interest in close temporal proximity can further reveal distributed networks of function that reflect dynamic neural pathways, such as interplay between frontal and temporo-parietal regions implicated in the FB-P3a/P3b complex (Soltani and Knight, 2000; Polich, 2003; Ebmeier et al., 1995; Kirino et al., 2000). Finally, analyzing relationships between anticipatory and outcome ERP components can reveal important insights into the unique psychological processes underlying each stage and their relationships with each other. For example, the anticipation Cue-P3 and outcome FB-P3 are largely unrelated, suggesting a distinct coupling within their respective reward processing stage. However, the outcome FB-P3 is associated with the anticipatory SPN, suggesting some degree of shared reward-related processes between pre-feedback anticipatory attention and post-feedback motivational salience.

Together, these results suggest that, like reward-anticipation, reward-outcome is a heterogeneous construct in and of itself requiring careful consideration of its time-course and relationships with other stages of reward processing. Of note, recent methods such as temporo-spatial principal component analysis and classifier approaches, such as linear-discriminate analysis, have shown considerable success to partially mitigate component overlap, especially separating the P3a from the P3b and the RewP from the FB-P3 (Sambrook and Goslin, 2016; Dien, 2010; Dien and Frishkoff, 2005; Fouragnan et al., 2016). Despite these recent advances, it remains challenging for traditional ERP analysis methods to separate ERPs elicited in close succession simply due to the time-based nature of the ERP technique (Luck and Kappenman, 2012). However, broadening the scope of analysis beyond ERPs and into the EEG time-frequency domain can help overcome some of these inherent difficulties within traditional ERP measurement. As discussed in the following sections, EEG time-frequency analyses can offer complimentary information typically unavailable to traditional ERP approaches and can help mitigate challenges arising from component overlap.

4. EEG time-frequency components implicated in reward processing

Complementing traditional ERP components, EEG activity can also be quantified by the amplitude of deflections in the frequency domain, often referred to as time-frequency power. Although traditionally EEG oscillatory activity was measured over a period of seconds or minutes, recent advances in applied mathematics and computer science allow for precise fine-grained time-course analysis of these different EEG time-frequency components on a scale that is comparable with ERPs (Cohen, 2014). Time-frequency components are defined by both their frequency

band power and their time-course. They are commonly known as delta (1–3 Hz), theta (4–7 Hz), alpha (8–12 Hz), beta (13–30 Hz), and gamma (30 + Hz), which are typically reported as changes in power within their respective frequency bands.

Time-frequency analyses have some important advantages over traditional ERP. First, unlike ERPs, each frequency band can be independently measured within the same time-window and can thus complement traditional ERP analysis, especially within reward-outcome where component overlap is particularly problematic. Furthermore, methods such as principal component analysis applied to the time-frequency domain have shown considerable success beyond traditional ERP methods in separating independent processes that contribute to the RewP and successive FB-P3 during reward-outcome (Bernat et al., 2015; Bernat et al., 2011; Bernat et al., 2008). Second, techniques that average across many trials, such as ERP, are blind to EEG activity that is not phase-locked to an event and thus lose substantial variation within the data (Herrmann et al., 2005). While time-frequency transformations can be applied to an average across many trials, similar to ERPs, they can also be applied individually to single trials and subsequently averaged. Both methods can capture activity phase-locked to the stimulus, called evoked power, but single-trial transformations can also capture out-of-phase activation that is either lost or ignored in traditional ERP analysis. This out-of-phase activation, called induced power, is also well suited to study reward processing (Bernat et al., 2011; Bernat et al., 2015). Of note, higher frequency bands are typically calculated using these single-trial transformations. Finally, time-frequency components offer independent contributions to the electrophysiological literature in their own right. As with their ERP counterparts, each EEG time-frequency component elicited during reward processing tends to show different time courses, display separate scalp topographies, and reflect discrete psychological processes. However, much less is known about their temporal progression during reward processing. The following sections will briefly review each EEG time-frequency component with an emphasis on their unique contribution to reward-anticipation and reward-outcome and how each component may contribute to traditional ERP generation.

4.1. Alpha

A widely studied index of EEG oscillatory activity is suppression of alpha power (8–12 Hz) typically recorded from parieto-occipital or frontal sites, although its scalp topography can be modulated by stimulus modality (Thut et al., 2006; Bastiaansen et al., 1999; Bastiaansen and Brunia, 2001). Alpha power reflects the functional inhibition of neural activity while alpha suppression likely reflects the disinhibition of neural activity to facilitate efficient preparation in attentional systems during anticipation of an upcoming visual stimulus (Jensen and Mazaheri, 2010; Carp and Compton, 2009; Mazaheri et al., 2009; Van Driel et al., 2012; Hanslmayr et al., 2007). Numerous earlier studies investigated lateralized asymmetrical activity in the alpha frequency band over the frontal cortex (e.g., Coan and Allen, 2004; Davidson, 1998). Investigators conducting this work often use a difference score or asymmetry index [ln(right) – ln(left) alpha power] to summarize the relative activity at homologous right and left hemisphere electrodes. Given the inverse relationship between alpha power and cortical activity (Allen et al., 2004), this frontal EEG asymmetry index provides a unidimensional scale in which greater values indicate increased relative left hemispheric cortical activity. Considerable evidence indicates that increased relative left frontal activity is associated with elevated approach motivation and reward processing, and that reduced relative left frontal activity reflects decreased motivation, including anhedonia and depression (see Nusslock et al., 2015 for review). A limitation of this approach, however, is that frontal EEG asymmetry is often measured over a period of seconds or minutes, making it difficult to decompose the rapid time-course of reward processing and take advantage of the temporal resolution of EEG methods.

In contrast, other studies that utilize time-frequency approaches can decompose the time-course of alpha power on a similar resolution to traditional ERP analysis. Although alpha power is one of the most frequently studied frequency bands in general, surprisingly few studies have investigated alpha suppression during on-task reward processing. A handful of studies have linked enhanced alpha suppression at parieto-occipital sites to reward-anticipation substages, specifically during cue-evaluation and feedback-anticipation (Bastiaansen et al., 1999; Bastiaansen and Brunia, 2001; Pornpattananangkul and Nusslock, 2016). Stronger parieto-occipital alpha suppression during reward-anticipation is thought to reflect enhanced attentional preparation following reward cues and preceding monetary feedback (Hughes et al., 2013; van den Berg et al., 2014) and has also been linked to greater task-related performance (Pornpattananangkul and Nusslock, 2016). These suppression effects during anticipation are likely driven by motivationally salient aspects of the upcoming feedback rather than by stimulus-uncertainty (Pornpattananangkul and Nusslock, 2016). Interestingly, anticipatory parieto-occipital alpha power is typically measured in roughly the same time-window as the pre-feedback SPN, suggesting parieto-occipital alpha suppression during feedback-anticipation may provide complimentary information beyond the SPN alone. Given the low number of studies investigating anticipatory parieto-occipital alpha during reward processing, examining the effects of alpha suppression during both cue-anticipation and feedback anticipation, especially in conjunction with the SPN, are promising directions for future research.

4.2. Beta

Another important time-frequency component implicated during reward-anticipation is beta power (13–30 Hz) typically measured at central and frontal midline sites approximately 200–600 ms following reward feedback (for review, see Luft, 2014), although some find beta to be left-lateralized (Van de Vijver et al., 2011). Animal and human literature suggest this gain-related beta activity may be generated by reward-related regions such as the ventral striatum and orbitofrontal cortex (Berke, 2009; Courtemanche et al., 2003; Andreou et al., 2017; Mas-Herrero et al., 2015) with possible contributions from the ACC (Matsumoto et al., 2007). Some prior studies report enhanced beta power during reward-anticipation, especially during cue-evaluation (Bunzeck et al., 2011; Cohen et al., 2008), suggesting anticipatory beta power may facilitate greater incentive-motivational processes and could be related to changes in dopaminergic activity (Apitz and Bunzeck, 2014). Furthermore, recent studies suggest that beta suppression during motor-preparation may facilitate approach motivational processes to prepare and execute upcoming responses (Gable et al., 2016; Meyniel and Pessiglione, 2014). This reduced beta synchrony during motor preparation may increase flexibility allowing responses to be modified accordingly (Engel and Fries, 2010; Jenkinson and Brown, 2011).

Beta power has also been linked to reward-outcome. During feedback-processing, beta is sensitive to both performance and reward evaluation, with research reporting an increase in beta power following positive feedback and beta desynchronization following negative feedback (Cohen et al., 2007; De Pascalis et al., 2012; Hajihosseini et al., 2012; Marco-Pallarés et al., 2008; Marco-Pallarés et al., 2009; Van de Vijver et al., 2011; Hallschmid et al., 2002; Pornpattananangkul and Nusslock, 2016). Furthermore, gain-related beta is sensitive to reward expectations (Bunzeck et al., 2011; Hajihosseini et al., 2012; however, see HajiHosseini and Holroyd, 2015 for alternative) and reward magnitude (Marco-Pallarés et al., 2008). These results have led some to suggest that gain-related beta power constitutes a motivated learning signal and possibly a reward-prediction error (Marco-Pallarés et al., 2008; Van de Vijver et al., 2011; Marco-Pallarés et al., 2015; Luft et al., 2013; Luft et al., 2014), although some have questioned this account (De Pascalis et al., 2012; HajiHosseini and Holroyd, 2015) or

found opposite results (Cavanagh, 2015). Others alternatively suggest beta power is related to sustaining the status quo or active maintenance of motor commands (Engel and Fries, 2010; Cavanagh, 2015). Finally, some argue that there may be two types of post-feedback beta activity: a burst following gains and a desynchronization following losses (Luft, 2014). These authors suggest this loss-related desynchronization of beta activity may drive learning and subsequent adjustments to improve performance (Luft, 2014; Luft et al., 2013), but future research will need to dissect the independent effects of increased beta power following gains and decreased beta synchronization following losses.

4.3. Theta

Another prominent time-frequency component implicated during reward processing is power measured at frontal-midline sites in the theta (4–7 Hz) frequency range (frontal-midline theta or FMT). FMT has been consistently associated with reward processing in both human and animal literatures (Kim et al., 2012; Van Wingerden et al., 2010). Although most studies investigating FMT do so in the context of reward-outcome using common measurement windows from 200 to 500 ms (Cohen and Cavanagh, 2011a), some studies suggest theta may be involved in reward-anticipation as well, especially in relation to memory encoding (Fell et al., 2011; Axmacher et al., 2010; Gruber et al., 2013). Numerous studies suggest FMT following feedback provides a mechanism for communication between distant brain regions of the same network (Buzsáki and Draguhn, 2004; Cohen et al., 2012; Cavanagh et al., 2010; Luft et al., 2013; Van de Vijver et al., 2011). Specifically, multiple studies confirm FMT is sensitive to performance and reward evaluation showing enhanced power following negative feedback (Luu et al., 2004; Hajihosseini et al., 2012; Bernat et al., 2011; Bernat et al., 2015; Christie and Tata, 2009; Cavanagh et al., 2010; Luft et al., 2013; see Luft, 2014 for review), especially monetary losses (Cohen et al., 2007; Gehring and Willoughby, 2004; Marco-Pallarés et al., 2008). Additionally, FMT has been linked to subsequent behavioral adjustments following loss feedback (Van de Vijver et al., 2011; Cavanagh and Shackman, 2015; Cavanagh et al., 2010; Pornpattananangkul and Nusslock, 2016) and learning rate (Mas-Herrero and Marco-Pallarés, 2014), leading many to suggest FMT may be associated with loss-related learning (Cavanagh et al., 2010; Luft et al., 2013; Van de Vijver et al., 2011; De Pascalis et al., 2012; Cavanagh et al., 2009).

In addition to its own unique contribution to reward processing, many of these studies suggest FMT also plays a primary role in FRN ERP generation following loss-feedback (Marco-Pallarés et al., 2008; Gehring and Willoughby, 2004; Cohen et al., 2007; Luu et al., 2004; Cavanagh et al., 2012). In support of this perspective, converging evidence suggests that, following reward feedback, both the FRN and FMT: a) covary with activity in the medial prefrontal cortex, including the ACC (Cavanagh and Frank, 2014; Cohen and Cavanagh, 2011a; Christie and Tata, 2009; Cohen et al., 2008; Luu et al., 2004; Luu et al., 2003), b) are sensitive to reward probability (Cohen et al., 2007; Hajihosseini and Holroyd, 2013), and c) are modulated by reward- and valence-evaluation (see Luft, 2014 for review). These results have led some to suggest both the FRN and FMT may index a negative reward prediction error (Cavanagh et al., 2010; Marco-Pallarés et al., 2008; Cohen et al., 2007). However, similar to the FRN, findings are at times inconsistent. While some find FMT is modulated by reward-magnitude (Leicht et al., 2013; Hajihosseini et al., 2012), others fail to observe this relationship (Bernat et al., 2011; Bernat et al., 2015; Marco-Pallarés et al., 2008). Moreover, some studies report that FMT is insensitive to performance evaluation and instead modulated by violations in reward expectation (Cavanagh et al., 2011; Mas-Herrero and Marco-Pallarés, 2014), while others observe no such relationship between FMT and reward expectancy (Watts et al., 2017). Interestingly, recent research using interchannel phase synchrony suggests that FMT may be similar to other fronto-midline theta activations during performance monitoring and executive control tasks (Aviyente et al., 2017). Thus, as with the RewP

and FRN, future research will need to clarify the experimental factors that contribute to FMT generation.

4.4. Delta

Recently, power in the delta band has been implicated during both anticipation and outcome stages of reward processing (Cavanagh, 2015; Foti et al., 2015; Leicht et al., 2013; Pornpattananangkul and Nusslock, 2016; Bernat et al., 2011; Bernat et al., 2015). While the neural generators of delta activity during reward processing are largely unknown, some suggest potential influences from the basal ganglia (Cavanagh and Shackman, 2015; Foti et al., 2015). During reward-anticipation, delta activity has been linked to motivational processes (Knyazev, 2007; Stefanics et al., 2010) and likely plays a key role in Cue-P3 generation during the cue-evaluation phase of reward-anticipation (Ergen et al., 2008; Ishii et al., 2009; Bernat et al., 2007; Bernat et al., 2015; Demiralp et al., 2001). Specifically, two prior studies report reward cues elicited greater delta power from 100 to 500 ms at centro-parental sites (Cavanagh, 2015; Pornpattananangkul and Nusslock, 2016), suggesting a possibly similar role in reward-specific stimulus-categorization processes. Moreover, these studies reported that this enhanced Cue-delta following reward cues predicted subsequent behavioral adjustments during reinforcement learning and time-estimation tasks, suggesting Cue-delta may be further associated with motivational processes that modify behavior to maximize future rewards. These results are consistent with recent reports of a functional relationship between delta oscillations and action selection during evidence gathering (Lakatos et al., 2008; Wyart et al., 2012).

During reward-outcome, multiple studies confirm that parietal delta power from 100 to 500 ms following feedback (FB-delta) is sensitive to performance evaluation, reward evaluation, and reward magnitude, (Cavanagh, 2015; Foti et al., 2015; Pornpattananangkul and Nusslock, 2016; Leicht et al., 2013), leading some to suggest that FB-delta may be a reward-specific index of feedback processing (Bernat et al., 2011; Bernat et al., 2015). Several studies have reported that FB-delta is modulated by both primary (e.g. gain vs. loss) and secondary (such as magnitude and expectancy) characteristics of reward feedback (Bernat et al., 2015; Watts et al., 2017). Interestingly, in contrast to Cue-delta, FB-delta is only associated with subsequent behavioral adjustments during reward-evaluation, but not performance evaluation, further supporting unique reward-related variation in the delta frequency band (Pornpattananangkul and Nusslock, 2016; Cavanagh, 2015). While FMT is related to FRN generation, numerous studies suggest that FB-delta is related to FB-P3 ERP generation during reward-outcome, especially following gains (Bernat et al., 2015; Bernat et al., 2011; Delorme et al., 2007; Makeig et al., 2004). Furthermore, several recent studies show that FB-delta contributes unique variance to the FRN in addition to the FB-P3 (Nelson et al., 2011; Watts et al., 2017; Bernat et al., 2015), suggesting that parsing independent contributions from FB-theta and FB-delta on the FRN and RewP may help resolve inconsistencies within the literature.

It is important to highlight, however, that these reward-related relationships with FB-delta are at times inconsistent. For example, Cavanagh (2015) reported that enhanced FB-delta followed gains only for unexpected rewards, suggesting a possible role in generating reward prediction errors, similar to the RewP. In contrast, Leicht et al. (2013) found FB-delta was only modulated by reward magnitude, but not valence, suggesting FB-delta may reflect elevated salience and motivational impact of feedback, more similar to the FB-P3. Together, these results suggest it is likely that FB-delta contributes to both gain-related RewP and gain- or loss-related FB-P3 generation (Bernat et al., 2011; Bernat et al., 2015; Cavanagh and Frank, 2014; Leicht et al., 2013), although further research is needed to clarify these relationships.

4.5. EEG time-frequency components: summary and conclusions

Time-frequency analyses are useful for investigating the time-course of reward processing and have several strengths. Different time-frequency bands can be measured within the same time-window, an analysis unavailable to traditional ERPs. Furthermore, multiple time-frequency components have been found to differentially contribute to separate ERP latencies and amplitudes, suggesting time-frequency analysis can offer complimentary information to traditional ERP analysis. Finally, each EEG time-frequency component implicated during reward-anticipation and reward-outcome displays distinct time-courses, shows separate scalp topographies, and reflects discrete psychological processes. These insights suggest that time-frequency analyses contain a wide range of components that can both compliment traditional ERP analysis and independently contribute to the electrophysiological literature in their own right.

During reward-anticipation, cue-evaluation is accompanied by both suppression of alpha activity to facilitate attentional preparation and enhanced delta power, which reflects motivational processes and likely contributes to Cue-P3 ERP generation (Hughes et al., 2013; van den Berg et al., 2014; Knyazev, 2007; Stefanics et al., 2010; Ergen et al., 2008; Ishii et al., 2009; Bernat et al., 2007; Bernat et al., 2015; Demiralp et al., 2001). During the next stage of reward-anticipation, motor-preparation, beta synchronization may play a gating role where high beta activity serves to maintain the status quo and low beta allows for flexible modification of upcoming responses (Gable et al., 2016; Meyniel and Pessiglione, 2014; Engel and Fries, 2010; Jenkinson and Brown, 2011). During reward-outcome, enhanced theta power following losses (over gains) is related to learning from negative feedback and has been linked to FRN ERP generation (Marco-Pallarès et al., 2008; Gehring and Willoughby, 2004; Cohen et al., 2007; Luu et al., 2004; Cavanagh et al., 2012; Cavanagh et al., 2010; Luft et al., 2013; Van de Vijver et al., 2011; De Pascalis et al., 2012; Cavanagh et al., 2009). Conversely, enhanced delta and beta power following gains may reflect signals related to learning from positive feedback and likely contribute to RewP and FB-P3 ERP generation during reward-outcome (Bernat et al., 2015; Bernat et al., 2011; Delorme et al., 2007; Makeig et al., 2004; Cavanagh, 2015; Pornpattananangkul and Nusslock, 2016).

However, several similar inconsistencies associated with ERP are also present among EEG time-frequency components. For example, while some studies report loss-related theta power is associated with reward magnitude and gain-related beta is associated with reward probability, others fail to observe these relationships (Leicht et al., 2013; Hajihosseini et al., 2012; Bernat et al., 2011; Bernat et al., 2015; Marco-Pallarès et al., 2008; Bunzeck et al., 2011; Cohen et al., 2007; HajiHosseini and Holroyd, 2015; Cavanagh, 2015; De Pascalis et al., 2012). In addition, common time windows used to measure post-feedback theta activity often overlap with both the RewP and FB-P3, suggesting that decomposing the time-course of time-frequency components in a similar fashion to ERPs may help resolve inconsistencies within the literature. Together, these results suggest EEG time-frequency components contribute to the generation of traditional ERP components during both reward-anticipation and reward-outcome but also offer important complimentary information above and beyond traditional ERP analyses. Unlike their ERP counterparts, however, very little research has investigated the relationships between different time-frequency components during reward processing. Future studies are needed to investigate relationships among time-frequency components within the reward-anticipation and reward-outcome and within their respective substages.

5. Conclusions

Reward processing is a heterogeneous construct composed of two temporally and neurobiologically dissociable stages: reward-anticipation and reward-outcome. As summarized in the present review, both

stages are associated with their own distinct electrophysiological correlates. Furthermore, reward-anticipation and reward-outcome can be broken down into discrete substages that each contains their own unique set of underlying ERP and EEG time-frequency components. Each component displays distinct scalp topographies and covaries with their own unique set of neuroanatomical correlates. These different electrophysiological signatures reflect a wide range of underlying psychological processes occurring very close together in time. Traditional ERP and more recent EEG time-frequency techniques both contain strong temporal resolution that is unavailable to most neuroscientific methods and are therefore perfectly suited to decompose the dynamic time-course of reward processing.

However, the vast majority of reward-related electrophysiological studies tend to narrowly focus on singular ERP components, such as the FRN during reward-outcome, while generally ignoring the wider temporal heterogeneity of reward processing. As a result, the literature is fragmented and often contradictory. To address this gap, the current review sought to accomplish two goals. First, we comprehensively review each ERP and EEG time-frequency component implicated during reward-anticipation and reward-outcome. Together, every component reviewed here can be measured in a single experimental design, except the CNV and RP during motor preparation which are dependent on the task parameters. Second, we argue that multistage experimental designs are essential to separate independent electrophysiological correlates of reward-anticipation from reward-outcome while multicomponent analyses that carefully decompose the time-course within each stage are critical to isolate activity unique to each ERP component from those elicited nearby. Our hope is that future electrophysiological research into reward processing will utilize multistage experimental designs and implement multicomponent analyses to leverage the temporal power of EEG and broaden their time-course of analysis.

We recommend that future studies consider experimental designs that integrate information from multiple overarching stages, underlying psychological processes, and their associated ERP and EEG time-frequency components. There are numerous reasons to construct experimental designs to capture the broader temporal dynamics of reward processing even for researchers only interested in specific features of either anticipatory or outcome stages. First and foremost, it allows researchers to take advantage of the most important asset of the EEG method, namely its temporal resolution. Second, multicomponent analyses can help mitigate component overlap within each stage and substage to facilitate more robust EEG and ERP measurement windows. Robust measurement of ERP components is critical to meaningfully evaluate their associations with various behavioral measures and psychometric properties, especially relationships with clinical measures. Broadening the scope of analysis to include time-frequency components can both help mitigate component overlap and add a deeper understanding to the study of reward-processing. In addition, advanced processing methods, such as principal component analysis or linear-discriminate analysis, can also help mitigate overlap among neighboring ERP and EEG components (Sambrook and Goslin, 2016; Dien, 2010; Dien and Frishkoff, 2005; Fouragnan et al., 2016). Third, simply including brief, rudimentary analyses, such as a correlation table between multiple ERP and EEG components, could substantially contribute to the literature, especially among less-studied components. We therefore encourage reporting relationships between multiple components, including cross-stage analyses, even if briefly. Finally, research is expensive both in money and in time. Future discoveries may suggest new investigations into prior data with different temporal properties than originally analyzed. Given that most previous EEG studies likely contain a wider range of reward-related components beyond their primary investigations, we encourage hypothesis-based reanalysis of previously published (or unpublished) data when appropriate. In conclusion, we argue that the employing experimental designs and analytic strategies designed to take full advantage of the temporal resolution of EEG data will generate a deeper and more nuanced understanding of

how the brain processes reward.

Acknowledgments

Disclosure statement

Authors have nothing to disclose.

Appendix A. Supplementary data

Supplementary material that includes a list of resources for conducting multistage and multicomponent analyses can be found at the Affective and Clinical Neuroscience Laboratory website at http://acnlnorthwestern.com/resources-1.

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