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Integration of reward with cost anticipation during performance monitoring revealed by ERPs and EEG spectral perturbations

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ABSTRACT

Effort expenditure has an aversive connotation and it can lower hedonic feelings. In this study, we explored the electrophysiological correlates of the complex interplay of reward processing with cost anticipation. To this aim, healthy adult participants performed a gambling task where the outcome (monetary reward vs. no-reward) and its expectancy were manipulated on a trial by trial basis while 64-channel EEG was recorded. Crucially, on some trials, the no-reward outcome could be transformed to a rewarding one, pending effort expenditure by means of an orthogonal dot clicking task, enabling us to compare at the electrophysiological level reward processing when cost was anticipated or not. We extracted and compared different markers of reward processing at the feedback level using both classical ERPs and EEG spectral perturbations in specific bands (theta, delta and beta-gamma). At the behavioral level, participants reported enhanced pleasure and relief when the outcome was rewarding but effort expenditure could be avoided, relative to a control condition where the outcome was rewarding but no extra effort was anticipated. In this condition, EEG results showed a larger Reward Positivity ERP component and increased power in the Delta and Beta-gamma bands. By comparison, cost anticipation did not influence the processing of the no-reward outcome at the FRN and frontal midline theta levels. All together, these neurophysiological results suggest that effort avoidance is associated with increased reward processing.

Introduction

Humans tend to obey to a principle of economy ("law of less work"; Hull, 1943). This principle applies to both physical and cognitive effort (Apps et al., 2015; Kool et al., 2010), whereby rewards are devalued by the cost required to obtain them (Charnov, 1976; Salamone et al., 2007). An increasing interest on motivational and emotional processes underlying decision making, where the integration of effort with reward occupies a central place, has been witnessed recently in a wide range of disciplines, spanning from neuroeconomics (Westbrook and Braver, 2015) to psychopharmacology (Salamone et al., 2012) and neuroscience (Apps et al., 2015; Chong et al., 2017; Ma et al., 2014; Vassena et al., 2014). These valuable efforts have substantially advanced our understanding of how motivation shapes decision making, especially from a computational perspective that provides mechanistic accounts to explain brain mechanisms responsible for value processing and effort deployment (Holroyd and McClure, 2015; Kurzban et al., 2013; Vassena et al., 2017; Verguts et al., 2015). In this literature, the dorsomedial and dorsolateral prefrontal cortex are often considered as domain-general brain regions involved in reward (d)evaluation when encountering either cognitive or physical effort (Chong et al., 2017). In particular, the anterior cingulate cortex (ACC) and the striatum are thought to signal effort anticipation (Kurniawan et al., 2013, 2010), and to process the expectation of both reward and cognitive effort (Vassena et al., 2014). At the electrophysiology level, neural activity arising from the ACC has traditionally been related to specific performance monitoring (PM) or cognitive control (CC) ERP components, such as the ERN (Error related negativity) and FRN (Feedback related negativity; see Holroyd and Coles, 2002). PM is a complex ability relying on different and interconnected mental processes, including an early evaluative component, in case errors or mismatches are detected and need to be rapidly processed to foster goal-adaptive behavior. At the electrophysiological level, this early

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evaluative component has been related to specific EEG markers, elicited both in the time and time-frequency domains (Ullsperger et al., 2014b).

In the time-domain, the FRN component is usually defined as a negative ERP deflection peaking at around 250 ms at channels FZ or FCZ after evaluative feedback (FB) onset. FB is characterized as evaluative since it provides information about performance outcome in the present case. FRN's amplitude is enhanced after negative vs. positive, and unexpected vs. expected FB, thus providing an electrophysiological marker of PM sensitive to both outcome expectation and valence information (Holroyd and Coles, 2002; Ullsperger et al., 2014a; Walsh and Anderson, 2012). Traditionally, the negative deflection (i.e. N200) giving rise to the FRN has been linked to a phasic and signed reward prediction error (RPE) signal (Holroyd and Coles, 2002). More specifically, it conveys the direction of the deviation between the actual and the expected outcome. This phasic signal is thought to be generated first in deep dopamigeric structures (midbrain), before it is relayed to the medial prefrontal cortex, including the ACC which is thought to provide the main intracranial generator of the FRN. Whereas dopamine has usually been put forward as the main neurotransmitter accounting for RPE in the context of reinforcement learning and PM, more recently, other neurotransmitter systems have also been considered in this process. These include norepinephrine (Riba et al., 2005) and the involvement of the locus coeruleus in decision-making (Aston-Jones and Cohen, 2005), $GABA_a$ (reducing the amplitude of the ERN; De Bruijn et al., 2004), but also serotonin and adenosine (for a review see Jocham and Ullsperger, 2009). The cognitive processes giving rise to PM, its neural underpinning as well as its electrophysiological signature, are still debated in the current literature. For instance, with regard to the FRN, the ERP amplitude difference between negative and positive FB has been interpreted as a positivity associated with better than expected outcome (Eppinger et al., 2008; Holroyd et al., 2008; Holroyd and Umemoto, 2016; Sambrook and Goslin, 2014). Accumulating evidence indicates that such an outcome-dependent amplitude difference may be driven by sensitivity to rewarding rather than non-rewarding events (Arbel et al., 2013; Baker and Holroyd, 2011; Foti et al., 2011; Potts et al., 2006; Sambrook and Goslin, 2014; Weinberg et al., 2014), leading thereby some authors to name this ERP component Reward Positivity (RewP; for a review, see Proudfit, 2015), as opposed to FRN. Although sharing some similarities at the electrophysiological level, the FRN and RewP usually show non-overlapping scalp distributions (i.e. topography), suggesting the existence of partly dissociable neural systems giving rise to them, as we recently confirmed (Gheza et al., 2017).

Evaluative FB processing during PM also influences non-phase locked EEG activities that cannot be captured using a standard ERP analysis (Cohen, 2014). Among them, frontal midline theta (FMT, 4–8 Hz) measured at the same recording sites as the FRN and during a similar time window (~200–400 ms post-feedback onset) corresponds to a slow oscillation aggregating mostly the phase-locked activity reflected by the FRN (as well as its neighboring positivities, such as P2 and P3) as well as a non-phase locked (induced) component (Cohen and Donner, 2013; Hajihosseini and Holroyd, 2013). Unlike the FRN which has been put forward as a signed RPE signal (Holroyd and Coles, 2002; Ullsperger, 2017), FMT is thought to reflect an unsigned electrophysiological signal that captures dynamic interaction effects between medial frontal cortex (including ACC) and lateral prefrontal areas. Compatible with this view, its power is usually enhanced when cognitive control is needed (Cavanagh et al., 2010; Cavanagh and Shackman, 2015; Cohen et al., 2007; Cohen and Donner, 2013; Hajihosseini and Holroyd, 2013), or higher cognitive effort and task demands are required (Mussel et al., 2016; Wascher et al., 2014). Besides this cognitive control signal represented by FMT, evaluative FB processing usually influences the spectral content of the EEG signal in at least two other non-overlapping bands. The power in the Delta band (0–4 Hz), measured at central and posterior-parietal sites, usually increases for rewarding compared to non-rewarding conditions (Webb et al., 2017). Last, in the Beta-gamma range (from 20 to 35 Hz) at fronto-central sites, (monetary) reward is also associated with increased power (Cohen et al., 2007; Marco-Pallares et al., 2008; Mas-Herrero et al., 2015). The link between power changes in Beta-gamma activity and reward was substantiated by studies showing effects of reward probability (HajiHosseini et al., 2012) and reward magnitude (Marco--Pallares et al., 2008) in this specific frequency band.

Whereas feedback valence and expectation strongly influence the expression of these different feedback-based electrophysiological effects (Ullsperger et al., 2014a), as reviewed here above, it is nowadays much less clear to which extent the cost associated with effort anticipation also does, and if so, for which of them and in which direction. Specifically, to which extent the evaluation of a given outcome is shaped by effort anticipation has never been investigated at the electrophysiological level. This paucity is somewhat surprising given that effort is profoundly linked to reward processing. As mentioned above, recent theoretical models advocate their integration in decision making, both in animals (Salamone et al., 2012, 2007, 2003) and in humans (Apps et al., 2015; Kool et al., 2010), corroborating the assumption that PM, and more generally CC, might exploit specific incentive signals or values where both reward and effort/cost have been integrated with one another. In particular anticipated reward and effort rely on a similar cortico-limbic network (Vassena et al., 2014), and are integrated (at the ACC level) during decision making so that the value of an option decreases as a function of associated effort (Croxson et al., 2009; Prévost et al., 2010). These studies suggest that reward processing during PM may be influenced by effort or cost, and more specifically its prospect or anticipation. Moreover, according to some recent models (Pizzagalli, 2014), the most prevalent emotional illness in Western developed countries, namely Major Depressive Disorder (MDD), is thought to be associated with abnormal dopaminergic (DA) signaling in specific corticostriatal networks. Yet, these alterations do not seem to affect hedonic reactions per se (i.e. "liking"; Berridge et al., 2010; Salamone et al., 2007). Instead, they appear to alter incentive salience and reward learning (Admon and Pizzagalli, 2015; Whitton et al., 2016), in interaction with an abnormal stress reactivity (Pizzagalli, 2014). This impairment might also account for the blunted motivation to approach rewarding or pleasurable stimuli (wanting) in these patients, or alternatively engage effort to do so (Salamone and Correa, 2012; Treadway et al., 2012). Further, according to a recent neuro-computational model (Holroyd and McClure, 2015; Holroyd and Umemoto, 2016) the ACC, which provides the main generator of the FRN and FMT oscillations (Smith et al., 2015), is deemed responsible for selecting and motivating extended behavior (see also Holroyd and Yeung, 2012). The ACC would serve as the main node within a hierarchical neural system that translates reward evaluation into CC, implemented in dorsolateral prefrontal areas. Following this model's tenets, control signals in the form of FMT oscillations may be generated at the ACC level, as a function of both the learned value and the effort required by the selected, reinforced behavioral response. In this study, we sought to test these predictions, and assess the extent to which the different electrophysiological components described here above could show systematic amplitude variations depending on cost anticipation. More precisely, FMT was expected to increase during the anticipation of effort, due to its putative role in signaling the need for increased control to dorsolateral prefrontal areas, which ultimately coordinate and implement the appropriate behavior. On the other hand, the main ERP components of reward processing (FRN and/or RewP) which are generated in the ACC, might therefore also capture a rapid integration of reward with effort or cost anticipation, given that previous neuroimaging studies pinpointed the ACC as one of the brain regions where this integration took place (Chong et al., 2017; Kurniawan et al., 2013; Vassena et al., 2014).

To this aim, we capitalized on a previously validated gambling task (Hajcak et al., 2005; Paul and Pourtois, 2017) allowing to manipulate on a trial by trial basis FB outcome (either reward or no reward) and reward expectation (being high, intermediate or low) in a factorial design, and eventually measure clear-cut FMT power, FRN, RewP components as well as centroparietal Delta and Beta-gamma power changes elicited by