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Dissociable effects of reward and expectancy during evaluative feedback processing revealed by topographic ERP mapping analysis

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Evaluative feedback provided during performance monitoring (PM) elicits either a positive or negative deflection ~250–300 ms after its onset in the event-related potential (ERP) depending on whether the outcome is reward-related or not, as well as expected or not. However, it remains currently unclear whether these two deflections reflect a unitary process, or rather dissociable effects arising from non-overlapping brain networks. To address this question, we recorded 64-channel EEG in healthy adult participants performing a standard gambling task where valence and expectancy were manipulated in a factorial design. We analyzed the feedback-locked ERP data using a conventional ERP analysis, as well as an advanced topographic ERP mapping analysis supplemented with distributed source localization. Results reveal two main topographies showing opposing valence effects, and being differently modulated by expectancy. The first one was short-lived and sensitive to no-reward irrespective of expectancy. Source-estimation associated with this topographic map comprised mainly regions of the dorsal anterior cingulate cortex. The second one was primarily driven by reward, had a prolonged time-course and was monotonically influenced by expectancy. Moreover, this reward-related topographical map was best accounted for by intracranial generators estimated in the posterior cingulate cortex. These new findings suggest the existence of dissociable brain systems depending on feedback valence and expectancy. More generally, they inform about the added value of using topographic ERP mapping methods, besides conventional ERP measurements, to characterize qualitative changes occurring in the spatio-temporal dynamic of reward processing during PM.

1. Introduction

Performance monitoring (PM) is crucial to foster goal adaptive behavior. According to most recent models (Ullsperger et al., 2014a) it is best conceived as a feedback loop whereby action values are learned and updated, especially when mismatches between goals and actions occur unexpectedly. Although these mismatches can sometimes be processed based on internal or motor cues (e.g., response errors), in many situations, external evaluative feedback provides the primary source of information to guide the course of PM. At the psychophysiological level, there has been a rich tradition of event-related brain potentials (ERP) research aimed at exploring the putative brain mechanisms underlying this loop during feedback-based PM.

Traditionally, the feedback-related negativity (FRN, sometimes termed FN, fERN, or MFN) was put forward as the main electrophysiological correlate of evaluative feedback processing during PM (Holroyd and Coles, 2002; Miltner et al., 1997; Ullsperger et al., 2014b; Walsh and Anderson, 2012). The FRN corresponds to a phasic negative fronto-central ERP component (N200) peaking around 250 ms after evaluative feedback (FB) onset, being typically larger for negative compared to positive outcome, as well as unexpected relative to expected one. This negative deflection is usually preceded by a positive ERP component (P200; Sallet et al., 2013), as well as followed by the P300, corresponding to a large positive deflection being maximal around 300–400 ms at central and posterior parietal scalp electrodes.

Initially, amplitude changes of the FRN (very much like the ERN, error-related negativity, which is time-locked to response onset) have been interpreted against a dominant reinforcement learning theory (RL-ERN theory; Holroyd and Coles, 2002; Sambrook and Goslin, 2015; Walsh and Anderson, 2012). In this framework, changes in the amplitude of the FRN capture indirectly dopaminergic-dependent reward prediction error signals (RPE; i.e. outcome either better or worse than expected). Moreover, the (dorsal) anterior cingulate cortex (dACC, sometimes termed rostral cingulate zone - RCZ; Ullsperger et al., 2014a) is thought to be the main intracranial generator of this phasic ERP component (Gehring and Willoughby, 2002; Miltner et al., 1997; Yeung

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et al., 2004; Yu et al., 2011). According to the RL theory, the FRN reflects the processing of the outcome along a good-bad (valence/outcome) dimension, in relation to its actual expectancy. In other words, the FRN is thought to provide an integrated neural signal during PM where both the salience (absolute prediction error) and the valence (signed prediction error) of the outcome are integrated (Holroyd and Coles, 2002; Ullsperger et al., 2014a, 2014b). Consistent with this view, many ERP studies previously reported reliable changes of the FRN amplitude as a function of not only the valence of the feedback, but also its expectancy, usually manipulated by means of changes in reward probability across trials (for reviews, see San Martín, 2012; Walsh and Anderson, 2012).

More recently, researchers have begun to explore reward processing per se, as opposed to RPE. As a matter of fact, when the emphasis is put on reward processing at the feedback level (especially when monetary reward is used as main incentive), the amplitude difference seen at the FRN level (i.e. when reward is delivered vs. omitted) can be best explained by the generation of a positive activity associated with better than expected outcomes, rather than a negativity associated with worse than expected ones. In the existing ERP literature, this positivity has been named the "feedback correct-related positivity" (fCRP; Holroyd et al., 2008) or the "reward positivity" (RewP; Proudfit, 2015). It is elicited in the time range of the N200, and is thought to signal the achievement of the task goal (i.e. obtaining a reward) (Foti et al., 2011; Holroyd et al., 2008; Proudfit, 2015). In keeping with the RL-FRN theory, Holroyd et al. (2008) reinterpreted the N200 (Towey et al., 1980) giving rise to the FRN[2] as the neural signal indicating that the task goal has not been achieved. The N200 is usually elicited by task-relevant events in general (i.e. unexpected outcome regardless of its outcome, see also Ferdinand et al., 2012) and might thus be overshadowed by the concurrent positive deflection that is elicited by positive FB. Accordingly, given that the positive (RewP) and negative (FRN) deflections overlap in time, it remains nowadays partly unclear which of them best captures systematic changes in reward processing at the feedback level as a function of reward expectancy (San Martín, 2012). Comparing ERP amplitudes at certain or pre-defined sites elicited by positive (reward) or negative (no-reward) FB implicitly assumes a similar source of the EEG signal accounting for them. As a matter of fact, the question remains whether the N200 component giving rise to the FRN is actually reduced for positive FB due to direct inhibition of the RCZ for example (Hajihosseini and Holroyd, 2013; Holroyd et al., 2011, 2008), or alternatively, from the superposition of another (non-overlapping) component, being reward-related primarily and best expressed by the RewP. In agreement with this latter interpretation, Foti et al. (2011) provided evidence that such a positive component could result from the activation of the putamen within the basal ganglia (but see the methodological objections raised by Cohen et al., 2011; and the following reformulation in Proudfit, 2015). Further, the same authors (Foti et al., 2015) recently argued that the FRN may be a blend of loss- and gain-related neural activities, possibly reflecting the contribution of partly distinct networks. At variance with this interpretation, other authors contend that the dACC provides the main (and most plausible) source of both ERP components, and is actually the only cortical brain region whose activation pattern is consistent with the observed modulation of their amplitude at the scalp level by valence and expectancy concurrently (Martin et al., 2009). Thus, a consensus about the neural generators of this FB-based ERP signal is currently lacking, and other potential sources have been put forward as well (among others, the ventral rostral anterior and posterior cingulate cortex; Luu et al., 2003; Nieuwenhuis et al., 2005).

Whereas the standard approach in ERP research consists of measuring the amplitude (and/or latency) of either the FRN or RewP at a few electrode positions, it usually falls short of confirming or disconfirming one of these competing assumptions, nonetheless. Using a standard ERP approach, it remains indeed impossible to confirm directly whether systematic changes in the amplitude of the FRN component occurs following local changes within the dACC with outcome valence and reward expectancy, or alternatively, another reward-related and non-overlapping component blurs this effect. To address this question, the standard ERP analysis can be supplemented by an advanced topographic ERP mapping analysis informing about the actual expression of the scalp configuration in the time range of the FRN and RewP (Murray et al., 2008; Pourtois et al., 2008). Furthermore, possible neural generators giving rise to them can be estimated with appropriate source localization methods. However, caution is needed when interpreting EEG source estimations. Converging evidence obtained when crossing different imaging techniques (such as EEG and fMRI for example) could eventually help validate and confirm localization results based on EEG only, as performed here.

Following standard practice (Keil et al., 2014), an ERP component is usually defined not only by its polarity, amplitude and latency, but also by its actual topography and neural generators. Topography refers here to the actual spatial configuration of the electric field at the time where the ERP component of interest, here FRN and RewP, is best expressed at the scalp level, including all channels available concurrently. Noteworthy, changes in the topography necessarily denote changes in the underlying configuration of brain generators (Lehmann and Skrandies, 1980; Vaughan, 1982). Accordingly, characterizing ERP components accurately using complementing topographical evidence provides an important source of information regarding the actual (dis)similarity between conditions in terms of underlying brain networks; a level of analysis that cannot be reached directly when considering only the amplitude changes occurring at a limited number of electrode positions (usually Fz or FCz only in the case of the FRN). Further, some of these local amplitude changes can in principle be confounded or inflated by more global changes in the topography (and/or global strength) of the electric field across conditions, challenging the validity of some of the interpretations made when using a standard ERP analysis only. Moreover, local amplitude measurements at a few electrode positions strongly depend on the specific reference montage used. By comparison, the actual topography of an ERP component is reference-free (Murray et al., 2008). Additionally, a clear asset of recent topographical ERP mapping analyses (Michel and Murray, 2012) is that user/experimenter-related biases and priors can be strongly limited, including the selection of specific time-frames for further statistical analyses. In this framework, the main topographical components are revealed using a stringent clustering method that allows to identify the specific time periods in the ERP signal where they are best expressed. As a result, there is no need to select a priori specific electrode locations or time-frames for statistical analyses, decreasing ultimately the likelihood of type I error (Luck and Gaspelin, 2017).

Surprisingly, to the best of our knowledge, the topography of the FRN and RewP components have not been scrutinized yet in the existing ERP literature. For example, it remains currently unclear whether the FRN and RewP share common topographical variance, or instead, can clearly be dissociated from one another when considering this global level of analysis, especially when a high density montage (64 channels or more) is used. Further, possible modulatory effects of reward expectancy on the topography of the FRN and RewP remain also poorly understood. However, such an analysis has the potential to address one of the main theoretical questions raised in the current ERP literature about these two ERP components and as reviewed here above: is the negative component (N200) giving rise to the FRN clearly different (at the topographical level) relative to the RewP? Moreover, considering the topography as level of analysis can also shed new light on the actual interplay of feedback outcome with feedback expectancy.

[2] Here we refer to "FRN" as the negative deflection elicited by no-reward FB, and to "RewP" as the positive deflection (or lack of negative one) elicited by reward FB. For ease of reading, in Methods and Results sections we will refer solely to the scoring method adopted for quantifying both deflections.