

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

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## Abstract

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.

Keywords: performance monitoring, reward processing, FRN, reward positivity, ACC, PCC

## 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

26 (Gehring and Willoughby, 2002; Miltner et al., 1997; Yeung et al., 2004; Yu et al., 2011). According to  
27 the RL theory, the FRN reflects the processing of the outcome along a good-bad (valence/outcome)  
28 dimension, in relation to its actual expectancy. In other words, the FRN is thought to provide an  
29 integrated neural signal during PM where both the salience (absolute prediction error) and the valence  
30 (signed prediction error) of the outcome are integrated (Holroyd and Coles, 2002; Ullsperger et al.,  
31 2014). Consistent with this view, many ERP studies previously reported reliable changes of the FRN  
32 amplitude as a function of not only the valence of the feedback, but also its expectancy, usually  
33 manipulated by means of changes in reward probability across trials (for reviews, see San Martín, 2012;  
34 Walsh and Anderson, 2012).

35 More recently, researchers have begun to explore reward processing per se, as opposed to  
36 RPE. As a matter of fact, when the emphasis is put on reward processing at the feedback level  
37 (especially when monetary reward is used as main incentive), the amplitude difference seen at the  
38 FRN level (i.e. when reward is delivered vs. omitted) can be best explained by the generation of a  
39 positive activity associated with better than expected outcomes, rather than a negativity associated  
40 with worse than expected ones. In the existing ERP literature, this positivity has been named the  
41 “feedback correct-related positivity” (fCRP; Holroyd et al., 2008) or the “reward positivity” (RewP;  
42 Proudfit, 2015). It is elicited in the time range of the N200, and is thought to signal the achievement of  
43 the task goal (i.e. obtaining a reward) (Foti et al., 2011; Holroyd et al., 2008; Proudfit, 2015). In keeping  
44 with the RL-FRN theory, Holroyd et al. (2008) reinterpreted the N200 (Towey et al., 1980) giving rise  
45 to the FRN<sup>1</sup> as the neural signal indicating that the task goal has not been achieved. The N200 is usually  
46 elicited by task-relevant events in general (i.e. unexpected outcome regardless of its outcome, see also  
47 Ferdinand et al., 2012) and might thus be overshadowed by the concurrent positive deflection that is  
48 elicited by positive FB. Accordingly, given that the positive (RewP) and negative (FRN) deflections

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<sup>1</sup> 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.

49 overlap in time, it remains nowadays partly unclear which of them best captures systematic changes  
50 in reward processing at the feedback level as a function of reward expectancy (San Martín, 2012).  
51 Comparing ERP amplitudes at certain or pre-defined sites elicited by positive (reward) or negative (no-  
52 reward) FB implicitly assumes a similar source of the EEG signal accounting for them. As a matter of  
53 fact, the question remains whether the N200 component giving rise to the FRN is actually reduced for  
54 positive FB due to direct inhibition of the RCZ for example (Hajihosseini and Holroyd, 2013; Holroyd et  
55 al., 2011, 2008), or alternatively, from the superposition of another (non-overlapping) component,  
56 being reward-related primarily and best expressed by the RewP. In agreement with this latter  
57 interpretation, Foti et al. (2011) provided evidence that such a positive component could result from  
58 the activation of the putamen within the basal ganglia (but see the methodological objections raised  
59 by Cohen et al., 2011; and the following reformulation in Proudfit, 2015). Further, the same authors  
60 (Foti et al., 2015) recently argued that the FRN may be a blend of loss- and gain-related neural  
61 activities, possibly reflecting the contribution of partly distinct networks. At variance with this  
62 interpretation, other authors contend that the dACC provides the main (and most plausible) source of  
63 both ERP components, and is actually the only cortical brain region whose activation pattern is  
64 consistent with the observed modulation of their amplitude at the scalp level by valence and  
65 expectancy concurrently (Martin et al., 2009). Thus, a consensus about the neural generators of this  
66 FB-based ERP signal is currently lacking, and other potential sources have been put forward as well  
67 (among others, the ventral rostral anterior and posterior cingulate cortex; Luu et al., 2003;  
68 Nieuwenhuis et al., 2005).

69         Whereas the standard approach in ERP research consists of measuring the amplitude (and/or  
70 latency) of either the FRN or RewP at a few electrode positions, it usually falls short of confirming or  
71 disconfirming one of these competing assumptions, nonetheless. Using a standard ERP approach, it  
72 remains indeed impossible to confirm directly whether systematic changes in the amplitude of the FRN  
73 component occurs following local changes within the dACC with outcome valence and reward  
74 expectancy, or alternatively, another reward-related and non-overlapping component blurs this effect.

75 To address this question, the standard ERP analysis can be supplemented by an advanced topographic  
76 ERP mapping analysis informing about the actual expression of the scalp configuration in the time  
77 range of the FRN and RewP (Murray et al., 2008; Pourtois et al., 2008). Furthermore, possible neural  
78 generators giving rise to them can be estimated with appropriate source localization methods.  
79 However, caution is needed when interpreting EEG source estimations. Converging evidence obtained  
80 when crossing different imaging techniques (such as EEG and fMRI for example) could eventually help  
81 validate and confirm localization results based on EEG only, as performed here.

82         Following standard practice (Keil et al., 2014), an ERP component is usually defined not only by  
83 its polarity, amplitude and latency, but also by its actual topography and neural generators.  
84 Topography refers here to the actual spatial configuration of the electric field at the time where the  
85 ERP component of interest, here FRN and RewP, is best expressed at the scalp level, including all  
86 channels available concurrently. Noteworthy, changes in the topography necessarily denote changes  
87 in the underlying configuration of brain generators (Lehmann and Skrandies, 1980; Vaughan, 1982).  
88 Accordingly, characterizing ERP components accurately using complementing topographical evidence  
89 provides an important source of information regarding the actual (dis)similarity between conditions in  
90 terms of underlying brain networks; a level of analysis that cannot be reached directly when  
91 considering only the amplitude changes occurring at a limited number of electrode positions (usually  
92 Fz or FCz only in the case of the FRN). Further, some of these local amplitude changes can in principle  
93 be confounded or inflated by more global changes in the topography (and/or global strength) of the  
94 electric field across conditions, challenging the validity of some of the interpretations made when using  
95 a standard ERP analysis only. Moreover, local amplitude measurements at a few electrode positions  
96 strongly depend on the specific reference montage used. By comparison, the actual topography of an  
97 ERP component is reference-free (Murray et al., 2008). Additionally, a clear asset of recent  
98 topographical ERP mapping analyses (Michel and Murray, 2012) is that user/experimenter-related  
99 biases and priors can be strongly limited, including the selection of specific time-frames for further  
100 statistical analyses. In this framework, the main topographical components are revealed using a

101 stringent clustering method that allows to identify the specific time periods in the ERP signal where  
102 they are best expressed. As a result, there is no need to select a priori specific electrode locations or  
103 time-frames for statistical analyses, decreasing ultimately the likelihood of type I error (Luck and  
104 Gaspelin, 2017).

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

117 To address them and inform about reward processing during externally-driven PM, we  
118 recorded high-density (64 channels) EEG in 44 adult healthy participants while they performed a  
119 previously validated gambling task (Hajcak et al., 2005) where FB outcome (reward vs. no-reward) and  
120 expectancy (low, intermediate of high reward probability) were manipulated on a trial by trial basis  
121 using a factorial design. First, we carried out a standard ERP analysis and extracted the mean amplitude  
122 of the FRN and RewP, using and contrasting different scoring methods available in the literature: peak  
123 to peak vs. mean amplitude measurement. Second and crucially, we ran an advanced topographic ERP  
124 mapping analysis on the exact same average ERP data time-locked to FB onset, and isolated the  
125 dominant topographical components accounting for them, in an unbiased way. For the standard ERP

126 analysis, we surmised a larger FRN for no-reward compared to reward FB, with the opposite effect  
127 found for the RewP, as well as a possible modulation of each of these two ERP components by  
128 expectancy (i.e., larger amplitude for unexpected than expected outcome each time; Walsh and  
129 Anderson, 2012). At the topographical level, we tested the prediction that the FRN and RewP could  
130 lead to partly dissociable spatial configurations of the global electric field (i.e., topography), and hence  
131 non-overlapping intracranial generators, as has been suggested before. More specifically, given that  
132 the FRN is usually maximal at fronto-central scalp locations (for negative/no-reward FB) and was  
133 previously related to the dACC (among others, Gehring and Willoughby, 2002; Miltner et al., 1997;  
134 Yeung et al., 2004; Yu et al., 2011), we conjectured that topographical ERP variance associated with  
135 no-reward could be associated with this specific brain region in our study. In comparison, since  
136 positive/reward-related ERP activity during FB processing was previously linked to activation in more  
137 posterior parts of the cingulate cortex (Cohen et al., 2011; Fouragnan et al., 2015; Nieuwenhuis et al.,  
138 2005), and/or specific regions of the basal ganglia (Foti et al., 2015, 2011), we hypothesized that these  
139 regions (especially the posterior cingulate cortex) could account for the reward-related activity during  
140 feedback processing in our study. Furthermore, we sought to explore whether these two spatial  
141 configurations of the electric field depending on FB outcome, if clearly dissociable from one another,  
142 could show a similar or instead different sensitivity to FB expectancy.



143

## Methods

### 144 **Participants**

145 Existing EEG data from two previous (and separate) studies by Paul and Pourtois (2017 -  
146 Experiment 1) and Gheza et al. (submitted – Experiment 2), where the same gambling task was used,  
147 were pooled together. A total of forty-five undergraduate students from Ghent University (right-  
148 handed, with normal or corrected-to-normal vision, and no history of neurological or psychiatric  
149 disorders) were included in the present study. They all gave written informed consent prior to the start  
150 of the experiment and were compensated about 30€ for their participation. The study by Paul and  
151 Pourtois (2017) had a between-groups design and involved a mood-induction paradigm. Only the  
152 control group (with a neutral-mood state, 25 participants) from this study and the whole sample (20  
153 participants) from Gheza et al. (submitted, where no specific mood induction was used) were merged  
154 together. One participant had to be excluded due to noisy EEG recording. Hence, the total sample  
155 included 44 participants (34 females, age:  $M = 22.0$  years,  $SD = 2.6$ ). Both studies were approved by  
156 the local ethics committee at Ghent University. A post hoc power analysis was conducted using GPower  
157 (Faul et al., 2007). The sample size of 44 was used for the statistical power analyses and the power to  
158 detect a small ( $\eta^2=0.01$ ), medium ( $\eta^2=0.06$ ) or large ( $\eta^2=0.14$ ) effect for the interaction between  
159 valence and expectancy was estimated. The alpha level used for this analysis was set to .05. The post  
160 hoc analyses revealed the statistical power for this study was .22 for detecting a small effect, .91 for  
161 detecting a medium effect size, and exceeded .99 for a large effect. Thus, this sample size was more  
162 than adequate to detect a moderate/large effect, but not a small one.

### 163 **Stimuli and task**

164 A previously validated gambling task (Hajcak et al., 2007) was adapted and administered in  
165 both studies. On each and every trial, participants had to choose one out of four doors by pressing  
166 with their right index finger the corresponding key on the response box. After a fixation dot (700 ms)  
167 this choice was followed by either positive FB (green “+”), indicating a win, or no-reward FB (red “o”)

168 (1000 ms). The two studies differed slightly in the amount of monetary reward, being either 8 cents  
169 (Paul and Pourtois, 2017) or 5 cents (Gheza et al., submitted). At the beginning of each trial,  
170 participants were informed about reward probability with a visual cue (600 ms), followed by a fixation  
171 dot (1500 ms). This cue was presented in the form of a small pie chart shown at fixation. Either one,  
172 two or three quarters were filled (black/white) corresponding to a reward probability of 25, 50 or 75  
173 %. A reward probability of 25% indicated that only one door contained the reward, two doors in the  
174 case of 50% reward probability and three doors for 75% reward probability. Unbeknown to  
175 participants, the outcome was actually only related to these objective probabilities (but not the actual  
176 choices made by them), ending up with a preset winning of €14.72 (Paul and Pourtois, 2017) or €12.40  
177 (Gheza et al., submitted). Inter trial interval was fixed and set to 1000 ms. Hence, by crossing the three  
178 possible reward probabilities with the two opposite outcomes, six trial types were included in a  
179 factorial design<sup>2</sup>. To ensure participants paid attention to the cue and outcome, catch trials were  
180 randomly interspersed in the trial series. In 24 trials, at the cue offset they were asked to report their  
181 winning chance (“how many doors contain a prize?”, allowing responses from 1 to 3). In 24 different  
182 trials, they were asked about the expectedness of the outcome at FB offset, and answers were  
183 collected by means of a visual analog scale (VAS) anchored with “very unexpected” and “very  
184 expected”.

185 All stimuli were shown against a grey homogenous background on a 21-in CRT screen and  
186 controlled using E-Prime (V 2.0, Psychology Software Tools Inc., Sharpsburg, PA).

## 187 **Procedure**

188 In both studies, after reading the instructions, participants were first familiarized with the  
189 gambling task using 12 practice trials. The presentation of the 6 trial types (3 reward probabilities x 2  
190 outcomes) was randomized, and the same trial type could be presented consecutively. The main

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<sup>2</sup> Beside the conditions described above (“regular” trials), the task for Gheza et al. (in preparation) also included “special” trials, that were discarded from the analyses conducted in the present study.

191 experiment consisted of four blocks each comprising 92 (Exp. 1 – Paul and Pourtois, 2017) or 124 trials  
192 (Exp. 2 – Gheza et al., submitted). After each block, a short break was included and participants were  
193 informed about their current (cumulative) payoff.

194 In Paul and Pourtois (2017), a total of 368 trials was presented (80 with 50%, 144 with 25% and  
195 144 with 75% reward probability). A neutral-mood induction procedure was applied before the task  
196 and repeated after each block to maintain the specific mood state (here neutral) throughout. In Gheza  
197 et al. (submitted), a total of 392 trials was used (104 with 50%, 144 with 25% and 144 with 75% reward  
198 probability).

### 199 **Recording and Preprocessing of Electrophysiological Data**

200 EEG was recorded using a 64-channel Biosemi Active Two system (<http://www.biosemi.com>)  
201 with four additional electrodes measuring horizontal and vertical eye movements. EEG was sampled  
202 at 512 Hz and referenced to the Common Mode Sense (CMS) active electrode and Driven Right Leg  
203 (DRL) passive electrode. The EEG was preprocessed offline with EEGLAB 13.5.4b (Delorme and Makeig,  
204 2004), implemented in Matlab R2012b. A 0.05/35 Hz high/low pass filter was applied after re-  
205 referencing the EEG signal to the averaged mastoids. An independent component analysis was run on  
206 the continuous data to correct manually for eye artifacts and spatial or temporal discontinuities.  
207 Individual epochs were extracted from -250 to 750 ms around the FB onset and a pre-feedback baseline  
208 was subtracted (-250 to 0). A semi-automatic artefact correction procedure was applied to eliminate  
209 trials with voltage values exceeding  $\pm 90 \mu\text{V}$  or slow voltage drifts with a stronger slope than  $\pm 90 \mu\text{V}$ ,  
210 as well as based on visual inspection. For each subject separately, artefact-free epochs were grouped  
211 according to the six main experimental conditions: expected, no-expectations<sup>3</sup> and unexpected FB  
212 associated with reward (deriving from 75%, 50%, 25% reward probability trials respectively), or  
213 expected, no-expectations and unexpected FB associated with no-reward (deriving from 25%, 50%,

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<sup>3</sup> The no-expectation term refers here to the objective reward probability and not the subjective expectation or uncertainty. The condition provides equal (objective) probability of reward or no-reward FB and therefore goes along with the highest uncertainty regarding feedback outcome during the experiment.

214 75% reward probability trials respectively). To avoid different signal to noise ratios between  
215 conditions, the same number of trials (randomly sampled) was used for all of them, being defined  
216 subject-wise based on the condition with the lowest trial count.

### 217 **Standard peak analysis**

218 **FRN: peak to peak.** The FRN and RewP were determined peak-to-peak at FCz (FRN-pp) as the  
219 difference between the most negative peak (N200: within 200 - 350 ms) and the preceding positive  
220 peak (P200: within 150 - 250 ms) assumed as the onset of the (relative) negativity (Holroyd et al., 2008,  
221 2003).

222 **FRN: mean amplitude.** We also used an alternative scoring method for the FRN and RewP (FRN-  
223 m), defined at FCz as the mean amplitude within the 213-263 ms interval post-feedback onset (i.e. the  
224 50 ms window surrounding the peak of the N200 for no-reward; Novak and Foti, 2015; see also  
225 Weinberg and Shankman, 2017 for the use of a mean-amplitude approach in a different time window).  
226 This time window and location were based on the FRN-pp maximal amplitude from the grand average  
227 of no-reward FB trials (merging all three expectancy levels; "collapsed localizer" approach, see Luck &  
228 Gaspelin, 2016).

229 **P2 and N2.** Supplementary peak analyses on P200 and N200 components (when considered  
230 separately) were carried out in order to verify their relative sensitivity to FB expectancy and its  
231 interaction with FB valence. In accordance with the FRN-pp scoring method, P200 was defined as the  
232 maximum positivity occurring within the 150-250 ms interval post FB onset, while the N200 as the  
233 maximum negativity within the 200-350 ms interval post FB onset.

### 234 **Topographical ERP mapping analysis (TA)**

235 The dominant topographies accounting for the ERP data set under scrutiny were extracted  
236 using CARTOOL software (Version 3.60; developed by D. Brunet, Functional Brain Mapping Laboratory,  
237 Geneva, Switzerland). The basic principles of this method have been described extensively elsewhere  
238 (Brunet et al., 2011; Michel et al., 1999; Murray et al., 2008; Pourtois et al., 2008). In short, it is based

239 on two successive data analysis steps. First, the dominant topographical maps are isolated from the  
240 grand average ERP data by means of a clustering algorithm that takes into account the global  
241 dissimilarity, i.e. the difference in terms of spatial configuration between two normalized maps  
242 independent of the global strength of the ERP signal (Lehmann and Skrandies, 1980). Next, these main  
243 and dissociable topographical configurations are fitted back to the individual subject ERP data and a  
244 quantification of their representation across subjects and conditions is then provided, including the  
245 global explained variance (or goodness of fit), the correlation and the time point of the best fit.  
246 Parametric tests are eventually performed on these variables in order to compare different  
247 experimental conditions at the statistical level.

248 **TA: Segmentation.** First, using a competitive T-AAHC cluster analysis (Topographic - Atomize  
249 and Agglomerate Hierarchical Clustering) (Brunet et al., 2011; Tibshirani and Walther, 2005) of the  
250 entire epoch (i.e. from -250 prior to and up to 750 ms following feedback onset, corresponding to 512  
251 time frames-TFs at a 512-Hz sampling rate), the dominant topographical maps were identified. The  
252 specific (and default) settings for the clustering method followed the recommendations implemented  
253 in CARTOOL and were the following. 1) Minimum and maximum number of clusters were predefined  
254 to one and nine, 2) a smoothing kernel (Besag factor 10), of three TFs was applied, and 3) segments  
255 shorter than three TFs were rejected. The choice of the best segmentation result was based on an  
256 objective meta criterion of 7 criteria proposed previously (see Charrad et al., 2014) and visual  
257 inspection of the results.

258 **TA: Fitting.** The dominant topographies identified in the preceding step were then fitted back  
259 to the individual averages (n=6 per subject) to determine their expressions across participants and  
260 conditions. As the focus of the analysis was on reward processing (and expectancy), we mostly  
261 examined possible changes in the topography of the ERP signal as a function of reward and/or  
262 expectancy occurring 200-500 ms post-feedback onset, in keeping with many previous ERP studies  
263 (Foti et al., 2015; Hajcak et al., 2007; Sambrook and Goslin, 2015; Ullsperger et al., 2014b). Fitting

264 parameters also followed the recommendations implemented in CARTOOL and included 1) a  
265 smoothing kernel (Besag factor 10) of three TFs and 2) rejection of segments shorter than three  
266 consecutive TFs. The fitting procedure was done as a non-competitive process to validate that one of  
267 the topographic configurations fitted better than the other one depending on the condition (based on  
268 global explained variance - GEV - and the mean correlation of the map with the signal). Furthermore,  
269 the time course of these topographic maps could be evaluated, i.e. the TF of the best correlation could  
270 be compared between the maps and across conditions. If the last approach revealed a significant  
271 temporal difference between the dominant maps, the fitting procedure was repeated separately for  
272 the different time windows.

### 273 **Source Localization**

274 To estimate the configuration of the neural generators underlying the previously identified  
275 reward related topographical maps, a distributed linear inverse solution was used—namely,  
276 standardized low-resolution brain electromagnetic tomography (sLORETA; Pascual-Marqui, 2002).  
277 sLORETA solutions are computed within a three-shell spherical head model coregistered to the MNI152  
278 template (Mazziotta et al., 2001). LORETA estimates the 3-D intracerebral current density distribution  
279 within a 5-mm resolution. The 3-D solution space is restricted to the cortical gray matter and  
280 hippocampus. The head model uses the electric potential field computed with a boundary element  
281 method applied to the MNI152 template (Fuchs et al., 2002). Scalp electrode coordinates on the MNI  
282 brain are derived from the international 5% system (Jurcak et al., 2007). The calculation was based on  
283 the conditions specific average per subject in the time window of interest identified in the previous  
284 analysis.

### 285 **Statistical Analysis**

286 At the behavioral level, the subjective ratings related to catch trials after the FB (probing FB  
287 expectation) were first transformed to percentages, arbitrarily setting one anchor ('very unexpected')  
288 to 0 and the other one ('very expected') to 100. These evaluations were considered to be correct if

289 they fell within a  $\pm 25\%$  range around the correct response (see Paul and Pourtois, 2017 for a similar  
290 procedure). The amount of correct responses to these catch trials as well as catch trials corresponding  
291 to the cue (probing reward probability) were eventually reported as percentage of correct responses.

292 At the ERP level, repeated measures ANOVAs with FB expectancy (expected, no-expectations,  
293 unexpected) and outcome (reward vs. no-reward) as within-subject factors were performed (individual  
294 trial count, balanced across the six conditions:  $M = 27.4$ ,  $SD = 4.3$ ) separately for FRN-pp and FRN-m.

295 At the topographical level, each of the three dependent variables gained by the fitting  
296 procedure (i.e., GEV, mean correlation, TF of best correlation) was entered in a  $2 \times 3 \times 2$  repeated  
297 measurement ANOVA with the within-subject factors map configuration (FRN vs. RewP-map),  
298 expectancy (unexpected, no-expectations, expected) and FB valence (reward vs. no-reward). If the  
299 previous analysis based on TF of best correlation hinted at a potentially interesting difference in the  
300 time-course of the main maps, another ANOVA was run with the same within-subject factors, but  
301 adding a factor “time-window” (early vs. late).

302 The inverse-solution results were compared between the two reward outcomes (reward vs.  
303 no-reward) using paired-sample t-tests performed on the log-transformed data. To reveal potential  
304 differences in the inverse-solution space through direct statistical comparison, a stringent  
305 nonparametric randomization test was used (relying on 5,000 iterations, see Nichols and Holmes,  
306 2001).

307 For all analyses, significance alpha cutoff was 0.05.

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## Results

### 310 Behavioral Results

311 The accuracy for the cue ( $M_{\text{correct}} = 88.1\%$ ,  $SD = 8.0$ ) and for the outcome evaluation ( $M_{\text{correct}} =$   
312  $60.7\%$ ,  $SD = 25.3$ ), as inferred from the catch trials, were high and well above chance level, suggesting

313 that participants correctly monitored reward probability (based on the visual cue) and outcome (based  
314 on the feedback).

### 315 ERP Results

316 **FRN: peak to peak.** The analysis performed on the FRN-pp amplitudes showed a significant  
317 main effect of FB valence ( $F(1, 43) = 16.78, p < .001, \eta^2 = .281$ ) and an interaction between FB valence  
318 and FB expectancy ( $F(2, 86) = 12.49, p < .001, \eta^2 = .225$ ). The FRN component was larger (more  
319 negative) for no-reward compared to reward FB ( $M_{\text{reward}} = -5.08, SE = 0.30, M_{\text{no-reward}} = -6.55, SE = 0.36$ ).  
320 The multivariate simple effect of FB expectancy was significant for no-reward ( $F(2, 42) = 7.06, p = .002,$   
321  $\eta^2 = .252$ ), but not for reward FB ( $F(2, 42) = 1.65, p = .203, \eta^2 = .073$ ), confirming its sensitivity to RPE,  
322 when scored peak to peak<sup>4</sup> (see Fig. 1).

323 **FRN: mean amplitude.** The analysis performed on the FRN-m amplitudes showed a significant  
324 main effect of FB valence only ( $F(1, 43) = 62.39, p < .001, \eta^2 = .592$ ), without a significant interaction  
325 between FB valence and FB expectancy, however ( $F(2, 86) = 2.19, p = .118, \eta^2 = .048$ ). The FRN-m was  
326 larger (more negative) for no-reward compared to reward FB ( $M_{\text{reward}} = 2.42, SE = 0.51, M_{\text{no-reward}} = -$   
327  $0.41, SE = 0.44$ ). These results indicated that, on this critical time window and fronto-central channel,  
328 the FRN, when scored using a stringent mean amplitude measurement, was sensitive to FB valence  
329 only (reward being present or absent), without any significant modulation due to FB expectancy (see

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<sup>4</sup> In order to rule out that these neurophysiological effects were different between the two samples, we used a Bayesian factor analysis which is suited for estimating the amount of evidence in favor or against the null hypothesis (Rouder et al., 2017). More specifically, the data from the FRN-pp method was examined in a Bayesian repeated measure ANOVA in which the factors were FB outcome (reward or no-reward), FB expectancy (expected, no-expectations, or unexpected) and Group (Exp 1 or Exp 2). We used the JASP software package (JASP Team, 2017 - version 0.8.1.2) with default prior settings. First, the likelihood for each alternative models (derived from the combination of the 3 factors) was tested against a Null model. The models that best explained the variance were the main effect of Outcome, followed by the one including the two main effect of Expectancy and Outcome and their interaction (BF10 for Outcome = 40266, BF10 for Expectancy + Outcome + Expectancy \* Outcome = 9031). In order to rule out the Group factor effects, we then included the model terms Expectancy, Outcome and Expectancy \* Outcome (i.e. flagged as Nuisance) in every model (including the Null model) and we looked at the BF01 (likelihood of the Null model over the others). The Null model (assumed probability of 1) was 6.8 times more likely to be true compared to the model including the main effect of Group (BF10 = 0.145), and much more likely compared to any other model that included an interaction with Group (BF10 < 0.068). These results provide moderate to very strong evidence for the absence of a Group effect on these FRN-pp results.



330 Figure 1). Hence, these results suggest a qualitatively different outcome at the FRN level depending on  
331 the specific scoring method used.

332 **P2 and N2.** Repeated measure ANOVAs were run on the two components separately, with FB  
333 valence and FB expectancy used as within subject factors. The analysis for the P200 revealed significant  
334 main effects of Valence ( $F(1, 43) = 9.23, p = .004, \eta^2 = .177$ ) and Expectancy ( $F(2, 86) = 4.49, p = .014,$   
335  $\eta^2 = .095$ ). The analysis on the N200 revealed a significant main effect of Valence ( $F(1, 43) = 47.64, p <$   
336  $.001, \eta^2 = .526$ ) and crucially, a significant interaction between Valence and Expectancy ( $F(2, 86) = 6.45,$   
337  $p = .002, \eta^2 = .130$ ). Thus, although the FRN-pp scoring method could potentially inflate the effect of  
338 Expectancy driven by the P200 (as opposed to N200) component, it is clear from the N200 only analysis  
339 that this deflection alone was significantly modulated by both factors concurrently in our study.

#### 340 **Topographic Analysis**

341 **Segmentation.** Following the meta-criterion, a solution with sixteen different dominant maps  
342 was found to explain the ERP data set the best. The solution explained 93.71 % of the variance, see  
343 Figure 2. During the time window corresponding to the FRN and RewP, two different dominant maps  
344 were clearly evidenced. One map, sharing similarities with the FRN ERP component, showed a fronto-  
345 central negativity and started at a similar time point (i.e. 217 ms) regardless of feedback expectancy's  
346 level, but only for negative FB. Moreover this distinctive map was immediately followed by a different  
347 map showing a broader central positivity. This RewP-map was present and lasted until the same time  
348 point for all six FB types (i.e. 386 ms). The spatial correlation between these two maps was 0.84.

349 **Fitting.** The extracted the GEV and the mean correlation, provided by the fitting of the two  
350 dominant maps in the time window of interest (217 – 386 ms) revealed a significant main effect of map  
351 ( $F(1, 43) \geq 9.04, p \leq .005, \eta^2 = .17$ ). Both variables showed a significant interaction between FB valence  
352 and map ( $F(1, 43) \geq 34.47, p < .001, \eta^2 \geq .45$ ) and FB expectancy and map ( $F(2, 86) \geq 7.86, p \leq .001, \eta^2 \geq$   
353  $.16$ ), see Figure 3. While the RewP-map explained more variance and showed a higher mean  
354 correlation for reward than no-reward FB ( $M_{\text{reward-meanCorr}} = .70, SE = .02, M_{\text{no-reward-meanCorr}} = .63, SE = .02,$

355  $p \leq .002$ ), the FRN map showed only a non-significant trend to fit better with the no-reward compared  
356 to the reward FB ( $M_{\text{reward-meanCorr}} = .57$ ,  $SE = .03$ ,  $M_{\text{no-reward-meanCorr}} = .60$ ,  $SE = .03$ ,  $p \geq 0.25$ ). Regarding the  
357 GEV, both maps seemed to be sensitive to the expectancy manipulation as well. More variance was  
358 explained for the unexpected than the expected condition (FRN-map:  $M_{\text{unexpected}} = .08$ ,  $SE = .006$ ,  
359  $M_{\text{expected}} = .06$ ,  $SE = .005$ ,  $p \leq 0.05$ ). Especially the positivity map showed a steeper increase with  
360 unexpectedness (positivity map:  $M_{\text{unexpected}} = .10$ ,  $SE = .006$ ,  $M_{\text{expected}} = .07$ ,  $SE = .004$ ,  $p < .001$ ). For the  
361 mean correlation, the RewP-map showed a similar pattern ( $M_{\text{unexpected}} = .68$ ,  $SE = .02$ ,  $M_{\text{expected}} = .65$ ,  $SE$   
362  $= .02$ ,  $p < .015$ ), while the FRN-map did not differentiate between levels of expectancy ( $M_{\text{unexpected}} = .58$ ,  
363  $SE = .03$ ,  $M_{\text{expected}} = .58$ ,  $SE = .03$ ,  $p \geq 0.34$ ).

364 Importantly the TF of the best correlation for each map within this time large segment showed  
365 again a significant interaction between map and FB valence ( $F(1, 43) = 8.31$ ,  $p = .006$ ,  $\eta^2 = .16$ ), indicating  
366 that for reward FB, both maps fitted equally well at 306 ms ( $M_{\text{FRN-map}} = 305$  ms,  $SE = 7.69$ ,  $M_{\text{RewP-map}} =$   
367  $307$  ms,  $SE = 6.04$ ,  $p = .81$ ), while for no-reward FB, the FRN-map fitted the best much earlier than the  
368 RewP-map ( $M_{\text{FRN-map}} = 277$  ms,  $SE = 6.97$ ,  $M_{\text{RewP-map}} = 318$  ms,  $SE = 5.79$ ,  $p < .001$ ). This result clearly  
369 indicated that the initial time window of interest (217 – 386 ms) was probably too broad and likely  
370 encompassed two dissociable processes in terms of spatial-temporal dynamic. To corroborate this  
371 assumption at the statistical level, we repeated the fitting within two short non-overlapping time  
372 windows lasting for 40 ms centered around 277 and 318 ms, respectively. The repeated measures  
373 ANOVA on the GEV values revealed, besides several significant main effects, two significant three way  
374 interactions between time-window, map and FB valence ( $F(1, 43) = 66.37$ ,  $p < .001$ ,  $\eta^2 = .61$ ) and time-  
375 window, map and FB expectancy ( $F(2, 86) = 5.01$ ,  $p = .009$ ,  $\eta^2 = .10$ ), see Figure 4. Whereas the FRN-  
376 map fitted the best in the early time window for no-reward FB ( $M_{\text{no-reward-early}} = .07$ ,  $SE = .007$ ,  $M_{\text{no-reward-}}$   
377  $\text{late}} = .06$ ,  $SE = .006$ ,  $p \geq .139$ ), the RewP-map fitted the best for reward FB in the later time window  
378 ( $M_{\text{reward-early}} = .07$ ,  $SE = .006$ ,  $M_{\text{reward-late}} = .10$ ,  $SE = .006$ ,  $p \leq .059$ ). Furthermore, while the FRN-map did  
379 not vary with expectancy for none of the two time windows ( $M_{\text{unexpected}} = .07$ ,  $SE = .006$ ,  $M_{\text{expected}} = .06$ ,  
380  $SE = .006$ ,  $p \geq .139$ ), the positivity map showed this effect, especially in the later time window

381 ( $M_{\text{unexpected-late}} = .11$ ,  $SE = .006$ ,  $M_{\text{expected-late}} = .08$ ,  $SE = .005$ ,  $p \leq .003$ ). Using the mean correlation as fitting  
382 parameter, as opposed to the GEV, led to a similar statistical outcome.

### 383 **Source Localization**

384 The statistical comparison in the inverse-solution space between reward and no-reward within  
385 the time window of the FRN- and RewP-map (217-386 ms) revealed two non-overlapping  
386 suprathreshold ( $t$  value  $> 4.13$ , corrected for multiple comparisons) clusters showing opposing reward-  
387 related effects, see Figure 5. One cluster, being more active for no-reward than reward FB, was located  
388 within the dACC, including Brodmann area (BA) 32; (maximum at 15x, 25y, 40z,  $t(43) = -5.31$ ,  $p < .001$ )  
389 and spreading to adjacent frontal areas, including BAs 6, 8 and 9. The other non-overlapping cluster  
390 showed the opposite pattern (more active for reward than no-reward FB) and was located in the  
391 posterior cingulate cortex (PCC; BA 23; maximum at -5x, -60y, 15z,  $t(43) = 5.85$ ,  $p < .001$ ), extending to  
392 adjacent (medial) parietal regions (such as the Precuneus or retrosplenial cortex; BA 31), as well as  
393 more ventrally to the posterior part of the Parahippocampal gyrus (BA 27). It also spread to the  
394 posterior part of the left insula (BA 13; max. at -30x, -40y, 20z,  $t(43) = 4.89$ ,  $p < .001$ ).

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### **Discussion**

398 RPE signals recorded at the electrophysiological level during PM are thought to provide an integration  
399 of expectancy and valence of the outcome, such that a differential response to rewarding vs non-  
400 rewarding outcome increases as a function of its unpredictability (Holroyd and Coles, 2002; Schultz et  
401 al., 1997). If the evidence for a mismatch between expectation and outcome is motor based (e.g., clear  
402 response error), then such an effect can be tracked at the level of response-locked ERPs, such as the  
403 ERN. However, if the evidence cannot be computed at the response level (e.g., during gambling or  
404 probabilistic learning), then FB provides the main source of information to estimate RPE, with  
405 neurophysiological effects visible at the level of the FRN/RewP. The present study focussed on this

406 latter effect. More specifically, we aimed to characterize the topographical properties of the FRN  
407 component, when compared to the RewP, in order to assess whether they share common or instead  
408 dissociable topographic variance and neural generators. Importantly, we could compare the outcome  
409 of this data-driven method (taking into account all electrodes and time-frames) to two standard ERP  
410 scoring methods available in the literature, focussing on a circumscribed time-window and FCz  
411 electrode only.

412 To this aim, 44 participants carried out a previously used gambling task (Hajcak et al., 2007; Paul and  
413 Pourtois, 2017), where FB valence and expectancy were manipulated on a trial-by-trial basis, while 64-  
414 channels EEG was recorded concurrently. This enabled us to estimate the contribution of these two  
415 independent variables to systematic changes in the ERP signal following FB onset, when it  
416 corresponded either to amplitude modulations recorded at FCz only, or alternatively, when  
417 considering the spatial configuration of the entire electric field (i.e., topography). A number of new  
418 results emerge from the current study. (i) When comparing two different, albeit standard, scoring  
419 methods for the FRN in the existing ERP literature, our results show that this component was reliably  
420 modulated by FB valence and expectancy when using a peak to peak measurement only (FRN-pp, i.e.,  
421 measuring peak amplitude of the N200 relative to the preceding P200 at FCz component). Importantly,  
422 a similar outcome was reported when measuring the N200 alone. By comparison, when we used a  
423 more stringent mean amplitude measurement at the same lead (FCz) (FRN-m, i.e., measuring FRN as  
424 a mean ERP activity spanning from 213 to 263 ms interval centered around the N200 peak), it was  
425 modulated by valence without significant change by expectancy, suggesting in turn a dissociation  
426 between them. (ii) These somewhat inconsistent results were supplemented with a topographical  
427 pattern analysis that strongly reduced the number of priors in terms of location and latency for  
428 identifying reward-related effects following FB onset, and possible interactions with expectancy. This  
429 analysis unambiguously showed the existence of two dissociable topographies during the time-interval  
430 corresponding to the FRN and RewP. A main topography characterized by a short-lasting prefrontal  
431 negative component was generated relatively early after negative FB onset and was somehow

432 independent from its expectancy. Another one showed a broad positivity at more central and parietal  
433 sites during the same early time interval, and was generated in response to reward. Crucially, this latter  
434 reward-related topography lasted longer and best represented the variance of the ERP signal in a later  
435 time window, where it also varied systematically as a function of reward expectancy, accounting for  
436 more variance for unexpected than expected positive FB, in agreement with the tenets of the  
437 dominant RPE framework (Schultz, 2013). Given these specific electrophysiological properties and  
438 opposing sensitivity to FB valence, we tentatively linked the first one to the FRN and the second one  
439 to the RewP, when corresponding to local amplitude variations of specific deflections measured at a  
440 single scalp channel. Because different topographies necessarily denote non-overlapping intracranial  
441 generators (Lehmann and Skrandies, 1980; Michel and Murray, 2012; Vaughan, 1982), we estimated  
442 their sources using a linear inverse solution algorithm (sLORETA, see Pascual-Marqui, 2002). While the  
443 FRN-compatible topographical activity had a main cluster within the dACC, the RewP-one was source  
444 localized to a distributed and extended network, comprising primarily the PCC. Here below, we discuss  
445 the implications of these new results, and eventually formulate some recommendations for the  
446 definition and use of feedback-based reward-related ERP activities in future studies.

447         At FCz scalp location, independently of the scoring method adopted and actual definition used  
448 for the ERP component of interest (either local amplitude changes or topography), we consistently  
449 found across these different methods used that the FRN amplitude varied reliably with valence, i.e. it  
450 was consistently larger for no-reward than reward FB, while conversely, the RewP amplitude was  
451 systematically larger for reward than no-reward FB. Noteworthy, the FRN component was sensitive to  
452 FB expectancy only when using a peak to peak analysis (FRN-pp). Thus the peak to peak scoring method  
453 was the only one with which the FRN was found to be coherent with the generation of a dopamine-  
454 dependent RPE signal (Holroyd et al., 2003; Holroyd and Coles, 2002; Schultz et al., 1997; Ullsperger et  
455 al., 2014b). No such modulation was found for the RewP, no matter which ERP scoring method was  
456 actually adopted. In light of the existing debate in the ERP literature about the sensitivity of the FRN,  
457 or instead RewP to FB expectancy (bearing in mind that these two hypotheses are not necessarily

458 mutually exclusive and are both consistent with the original FRN-RL theory; see Holroyd et al., 2008;  
459 San Martín, 2012), our results lend support to the classical FRN hypothesis (Holroyd and Coles, 2002;  
460 Ullsperger et al., 2014b; Walsh and Anderson, 2012).

461         When the FRN was scored as mean amplitude around the peak of the N200 (FRN-m), no reliable  
462 modulation by FB expectancy was found. This inconsistency across the two scoring methods might be  
463 explained by several factors. On one hand, the peak to peak measurement may have artificially inflated  
464 the component's amplitude due to noise in the data (Luck and Gaspelin, 2017). On the other, scoring  
465 the FRN using the mean amplitude computed for a relatively long and pre-defined time window, albeit  
466 being a more conservative approach that is less sensitive to noise in the measurement, might have  
467 overshadowed an effect of expectancy due to inter-individual variability in the latency (and  
468 morphology) of the P200-N200-P300 complex, and/or to the possible temporal overlap of the N200  
469 with the preceding P200 and/or the following P300. The N200 is usually flanked by these two positive  
470 components, which usually do show amplitude modulations with stimulus frequency, and thus  
471 expectancy (Donchin and Coles, 1988; Polich et al., 1996), although with an affect going in the opposite  
472 direction compared to the N200. Neglecting these features of the ERP signal can in turn potentially  
473 smear amplitude effects which are small in size, such as the expectancy effect on the FRN. Indeed, the  
474 peak to peak approach (FRN-pp, where preceding P200 is used as baseline peak for N200 peak  
475 measurement) was put forward as an alternative scoring method to control for this confounding effect  
476 (Holroyd et al., 2003; Sallet et al., 2013). Notably, by further exploring amplitude modulations brought  
477 about by FB expectancy (and valence) for each deflection separately (i.e., P200 and N200), we could  
478 confirm that the significant interaction effect between FB valence and FB expectancy at the N200 level  
479 (hence FRN) was not merely resulting from the preceding P200 (see Results). As a rule of thumb,  
480 depending on the experimenter's goal and research interest, one of the two scoring methods could be  
481 preferred above the other one. For instance, if the focus is on reward itself, the use of the FRN-m  
482 appears warranted. By comparison, if more subtle influences of expectancy are explored at the FB (and  
483 FRN) level, then a FRN-pp scoring method appears more appropriate than the FRN-m. However, in light

484 of these slight discrepancies between the different scoring methods used, and for comparison  
485 purposes with previous work in the literature, it appears important to report and compare the  
486 outcome of these different scoring methods when it comes to assessing the sensitivity of an ERP  
487 component, like the FRN or RewP, to FB valence and expectancy.

488         Although these classical peak analyses informed about the complex interplay between reward  
489 and expectancy during feedback-based PM, yet they are necessarily based on local amplitude  
490 variations only (here measured at FCz), and as such, they could therefore potentially overlook more  
491 global changes in the ERP signal occurring with these two factors, including topographical alterations.  
492 To explore this possibility, we supplemented these analyses with a topographical ERP mapping analysis  
493 that considered the FB-locked ERP signal when measured at all (64) electrodes concurrently, and  
494 during a large time interval following FB onset (hence, not restricted to local peaks or maxima only),  
495 reducing in turn strongly the number of priors. This analysis confirmed the presence of a clear  
496 topographical change depending on actual FB outcome during the time interval usually associated with  
497 the FRN or RewP. Whereas a main topography shared many similarities with the FRN component (no-  
498 reward dominance), the other competing spatial configuration of the electric field closely resembled  
499 what is usually referred to as RewP in the existing ERP literature and showed enhanced activity for  
500 reward. Moreover, source estimation using sLoreta confirmed the presence of two non-overlapping  
501 networks accounting for these two dissociable maps. As predicted by many models and earlier ERP  
502 studies (Bush et al., 2000; Fouragnan et al., 2015; Gehring and Willoughby, 2002; Miltner et al., 1997;  
503 Shackman et al., 2011; Ullsperger et al., 2014b), we found that the dACC provided the main intracranial  
504 generator of this FRN-compatible map. In comparison, the RewP activity was source localized to more  
505 posterior regions, including the PPC, an area known to be involved in reward processing (Knutson et  
506 al., 2001; Liu et al., 2011; Luu et al., 2003; Nieuwenhuis et al., 2005). Even though some caution is  
507 needed in the interpretation of these source localization results (as they correspond to imperfect  
508 mathematical reconstructions of the intracranial sources), this dissociation along the cingulum  
509 depending on FB valence is not odd, but very much in line with the taxonomy of functionally-distinct

510 sub-regions composing it, as previously put forward by Vogt (2005). In this framework, the anterior  
511 midcingulate cortex (aMCC) is linked with the processing of negative emotions (and the need for  
512 cognitive control, see Shackman et al., 2011), especially fear, anxiety, and even pain. Conversely, the  
513 PCC is assumed to play a predominant role in attention control, especially in orienting to targets that  
514 are potentially of high motivational value for the individual, in integrating the history of rewards  
515 previously experienced, as well as in the assessment of personal relevance of incoming (emotional)  
516 information, and controlling the balance between internal and external attention (Leech and Sharp,  
517 2014). Using this neuro-anatomical framework, we could thus conjecture that the stronger aMCC  
518 response to no-reward FB in our study might reflect an (whole or none) alarm or alert signal in case  
519 the outcome turns out to be relatively “negative” (no-reward) (Shackman et al., 2011). In comparison,  
520 the stronger PCC activation to reward FB seems consistent with an attentional orienting effect towards  
521 an approach-related or motivationally significant event for the participant, namely getting a small  
522 financial reward after gambling in the present case. Similar interpretations of related findings have  
523 been drawn in the context of error monitoring (Paul et al., 2017) and reinforcement learning  
524 (Fouragnan et al., 2015).

525 Turning to the possible changes of these global ERP activities with FB expectancy, our  
526 topographical analysis additionally showed a striking modulation that none of the two classical ERP  
527 analyses (using FCz only) could actually reveal. Not only was FB valence clearly modulating the  
528 expression of the global electric field, but FB expectancy influenced its expression as well and in a  
529 condition-specific manner. As our analysis revealed (see Figure 2), the RewP-related map appeared to  
530 be the default ERP activity somehow in this long interval (from 210 to 380 ms following FB onset),  
531 progressively building up across this specific interval and reaching its maximum at ~320 ms following  
532 FB onset. No-reward outcome turned out to “break up” this default processing at an early latency  
533 (~280 ms following FB onset), with the generation of a unique and distinctive topography (being also  
534 short-lived), namely the FRN map. This result supports the idea that in case of a “negative” event (here  
535 corresponding to the lack of reward), a phasic negative ERP activity similar to the N200-component



536 (Heydari and Holroyd, 2016; Shahnazian and Holroyd, 2017) is elicited, which temporarily overrides  
537 the standard (reward-driven) ERP response. Although remaining largely speculative, this break-up  
538 effect might be caused by a phasic dip or transient pausing in dopaminergic firing, as the RL-theory  
539 would suggest (Fiorillo et al., 2003; Schultz, 2013; Warren and Holroyd, 2012). At variance with this  
540 interpretation, a positivity associated with better than expected positive outcome (Proudfit, 2015)  
541 could have been overridden by a more generic brain response to salient events in general (Holroyd et  
542 al., 2008; Talmi et al., 2013). Importantly, in line with the FRN-m analysis, this FRN-compatible  
543 topographical map did not show however a systematic modulation (in explained variance) with  
544 expectancy. We may speculate that both the FRN-m and the topographic mapping for the FRN map  
545 overlook a phasic, short-lived, local modulation of expectancy that only the FRN-pp and the N200 peak  
546 analyses were able to capture. Such a modulation was well evidenced in our topographic ERP mapping  
547 analysis, but for the RewP-related topography and at a later time point, however. Accordingly, these  
548 topographical results inform about the actual spatio-temporal dynamic of reward processing,  
549 suggesting that early on following FB onset, FB valence mostly influenced the expression of the ERP  
550 signal (irrespective of expectancy). In the present case, this FB valence effect was characterized by the  
551 transient blocking of the (normal) reward-related activity and replacement for a short period of time  
552 by another, negative or loss-related, ERP activity sharing many similarities with the FRN. Because our  
553 ERP results suggest the existence of two separate and dissociable networks depending on actual FB  
554 valence (yet having both an early time-course following FB onset), they clearly speak against the use  
555 of difference waves, where a new and undefined ERP activity would likely be created as a result of this  
556 transformation, in case no-reward would be subtracted from reward FB for example. Such an  
557 approach, although possibly reducing the number of factors/variables included in the statistical  
558 analysis (Luck and Gaspelin, 2017), would nonetheless overlook and mitigate the existence of  
559 independent sources and effects that each contributes to both (local) amplitude as well as (global)  
560 topographical changes in the ERP signal following FB onset. Hence, a clear methodological implication

561 of our new ERP results is that the use of difference waves should not be recommended as it could blur  
562 or smear important differences between the processing of reward vs. no-reward outcome during PM.

563 As mentioned here above, we succeeded to evidence systematic modulations of the feedback-  
564 locked ERP signal with expectancy with the elected topographic ERP mapping analysis. They were  
565 found for the RewP-related map exclusively, and became stable at the statistical level when  
566 considering a later time interval following FB onset (compared to the FRN map). Interestingly, the PCC  
567 and adjacent areas which are thought to give rise to this ERP activity, has previously been shown to be  
568 involved in detecting novel, or unpredicted events (Gabriel et al., 2002; McCoy et al., 2003). Moreover,  
569 earlier ERP studies already clearly showed that during a comparable time window following FB onset,  
570 the amplitude of the RewP was modulated by expectancy and hence RPE (Sambrook and Goslin, 2015;  
571 Talmi et al., 2012). Accordingly, given this clear modulation of the ERP signal with expectancy for the  
572 RewP-related map, our novel results lend indirect support to earlier studies and models available in  
573 the ERP literature that posited that effects of expectancy on the FRN component might very well be  
574 driven in part by responses to unexpected reward as well (Holroyd et al., 2008; Walsh and Anderson,  
575 2012). Yet, this effect was found when considering the topography only, and a relatively late time  
576 interval (i.e., 298-338 ms following FB onset). Although we failed to find evidence of a systematic  
577 change in the explained variance of the FRN-compatible topography with FB expectancy, some  
578 cautious is needed in the interpretation of this “null” result. For example, it remains to be tested  
579 whether using monetary loss or punishment for the no-reward outcome might not yield stronger  
580 modulations of the FRN-compatible topography with expectancy, as this manipulation would  
581 necessarily increase the salience of the no-reward outcome (Esber and Haselgrove, 2011). Accordingly,  
582 whether or not the FRN-compatible topography varies (in explained variance) with expectancy awaits  
583 additional empirical work where other contrasts at the outcome level should be used and compared  
584 systematically using similar ERP methods (including loss-related ones and hence the activation of a  
585 defensive motivational system; Hajcak and Foti, 2008). Notwithstanding this caveat, our new  
586 topographical ERP results are important because they clearly suggest that the processing of FB valence

587 during gambling may obey a two-stage process: first FB valence is evaluated (with no-reward  
588 interfering with the default reward-related ERP activity apparently), before a strong expectancy effect  
589 comes into play during a later stage and dynamically shapes reward processing, selectively.  
590 Presumably, this modulation might reflect the assignment of a different motivational value to the  
591 reward-related FB depending on its expectancy. This interpretation aligns well with recent  
592 neurophysiological evidence that reveals a specific temporal sequence during evaluative FB processing  
593 (Fouragnan et al., 2015; Philiastides et al., 2010): the early (around 220ms post FB onset) categorical  
594 evaluation of the outcome (i.e. valence) is later followed (around 300ms) by the processing of its actual  
595 deviation relative to the expectation (i.e. salience). More generally, such rapid and fine-grained  
596 changes in the actual spatio-temporal dynamic of reward processing during PM could hardly be  
597 captured by means of a standard ERP data analysis. Hence, we contend that future ERP studies focused  
598 on reward processing and PM should better incorporate this important feature of any ERP component  
599 (FRN, RewP, P200, P300 or N200), namely the topography, as it carries relevant information about the  
600 complex interplay between FB valence and expectancy. This approach might also help to revise or  
601 amend some of the current models available in the field that directly use these specific ERP  
602 components to generate testable predictions about the neurophysiology of reward processing and PM  
603 (Ullsperger et al., 2014b).

604         Despite its apparent strengths and added value, some limitations related to this topographic  
605 ERP mapping analysis warrant comment. Because this approach is based on an estimation (and  
606 clustering) of the dissimilarity in terms of spatial configuration of the electric field across successive  
607 TFs, it is not suited to reveal the contribution of putative independent components/sources that would  
608 be active and compete with one another at the exact same time, for which an ICA or PCA (Foti et al.,  
609 2015, 2011; Proudfit, 2015) should preferably be used for example (Eichele et al., 2010). Previously  
610 published findings (Holroyd et al., 2008; Proudfit, 2015) suggested that the ERP responses to reward  
611 and loss mostly differ by means of a positivity that is unique to reward trials, as opposed to a negativity  
612 to no-reward ones. By comparison, the outcome of our ERP topographic mapping analysis suggests the

613 presence of a phasic FRN-map (characterized by a fronto-central negativity) generated in an early time  
614 window following no-reward (around 277ms), which seems to overlap and interfere with a longer-  
615 lasting reward-related activity (characterized by a positivity showing a centro-parietal scalp  
616 distribution). Tentatively, this discrepancy between our current and these previous ERP studies could  
617 be related to the abovementioned methodological factors, as well as the actual incentive used to guide  
618 performance monitoring (being sometimes either primarily reward-related or instead loss-related).  
619 Presumably, for these reasons our topographic ERP mapping analysis failed to reveal a specific (short-  
620 lived) topography associated with reward outcome that would mainly be characterised by a central  
621 positivity culminating when the N200 (no-reward) reached its maximum amplitude, as previously  
622 suggested for the RewP ERP component (Novak and Foti, 2015; Proudfit, 2015). The RewP  
623 topographical map revealed in our study showed instead a broader (central and posterior parietal) and  
624 longer-lasting positivity that presumably partly overlapped with the P300 component. Therefore, it  
625 remains to determine to which extent the RewP map found in our study corresponds to the RewP ERP  
626 component exclusively, or also encompasses the P300 component. Last, it would also be beneficial in  
627 future studies to assess whether these two different topographies identified here may also be related  
628 somehow to different variations in the spectral content of the EEG/ERP, as recently reward processing  
629 has been associated with systematic changes in the power of either theta or delta oscillations (Bernat  
630 and Nelson, 2008; Cohen et al., 2007; Marco-Pallares et al., 2008). Considering the ERP results obtained  
631 with the different scoring methods used in our study (FRN-m, FRN-pp, or N2 peak) and some  
632 dissociations found between them, it appears challenging to relate complex cognitive processes, such  
633 as expectancy or reward, to single and temporal-specific ERP deflection, such as the P2 or N2. In this  
634 context, a better understanding of the actual neurophysiology of these complex cognitive processes  
635 could probably be achieved by supplementing classical ERP analyses with time/frequency methods  
636 that can inform about the actual spectral content of the P2-N2-P3 complex, its modulation by reward  
637 and expectancy (Cavanagh et al., 2012, 2010; Cohen et al., 2007; Cohen and Donner, 2013; Mas-  
638 herrero and Marco-pallarés, 2014; Paul and Pourtois, 2017), and the relative role of phase locked

639 (captured by ERPs) and non-phase locked oscillatory activity in explaining these effects (see also Cohen  
640 and Donner, 2013; Hajihosseini and Holroyd, 2013).

641 To sum up, the present ERP results advance our understanding of reward processing during  
642 gambling (in healthy adult participants) and more specifically how reward is actually shaped by  
643 expectancy when the topography, as opposed to amplitude measurements performed at a single scalp  
644 location, is carefully considered and properly analysed. Our new results lend support to the existence  
645 of two – spatially and temporally – dissociable networks during FB processing. One is driven by no-  
646 reward and comprises the dACC, meeting many of the electrophysiological criteria used previously to  
647 define the FRN component in the extant ERP literature. The other one competes with the first one,  
648 and is primarily reward-related (as well as sensitive to expectancy), sharing in turn many similarities  
649 with the RewP. Since abnormal reward processing (and anhedonia) is a cardinal diagnostic feature of  
650 several affective disorders, such as major depression, addiction, schizophrenia or pathological  
651 gambling, the topographic ERP mapping analysis performed in this study, and meant to explore  
652 thoroughly the spatio-temporal dynamic of reward processing during PM, could be used more  
653 systematically in the future in clinical settings to elucidate which component of reward processing (in  
654 relation to expectancy) could be impaired in these patients, and whether depending on the actual  
655 affective disorder being diagnosed, some specific (and stable) topographical ERP anomalies could  
656 eventually be evidenced.

**Author Note**

This work is supported by a Concerted Research Action Grant from Ghent University and by a research grant from the Research Foundation Flanders (FWO). GP is the recipient of an (2015) independent investigator grant awarded by the NARSAD foundation. KP is supported by the FWO (PhD student mandate).

**Conflict of interest:** none declared.

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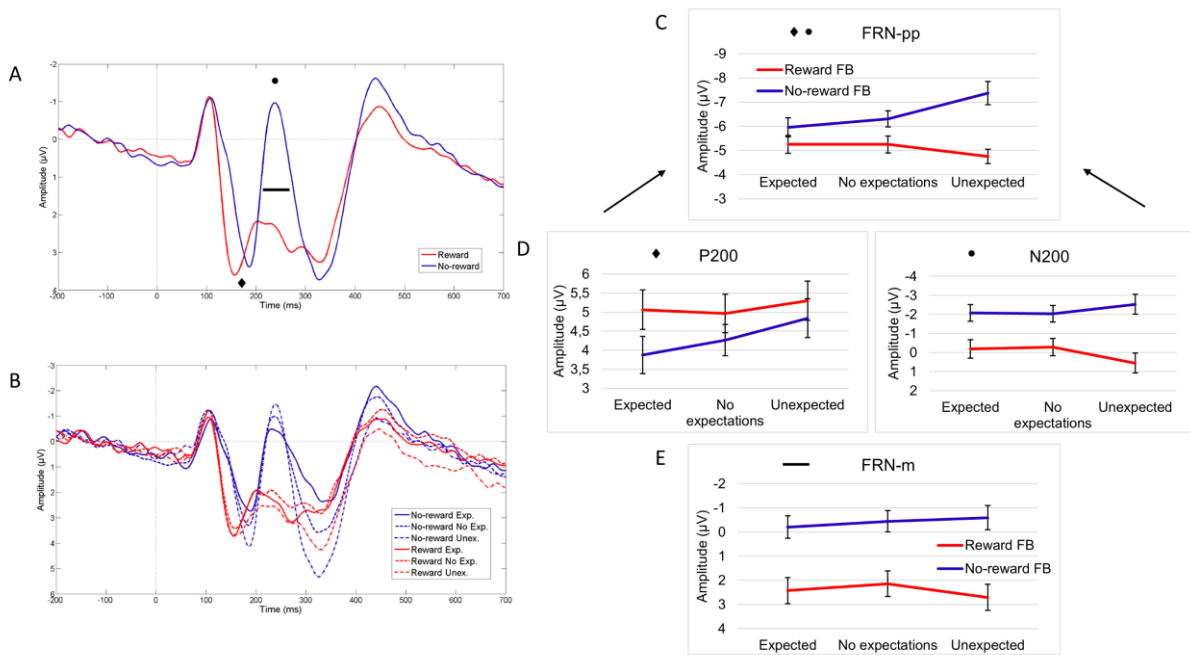
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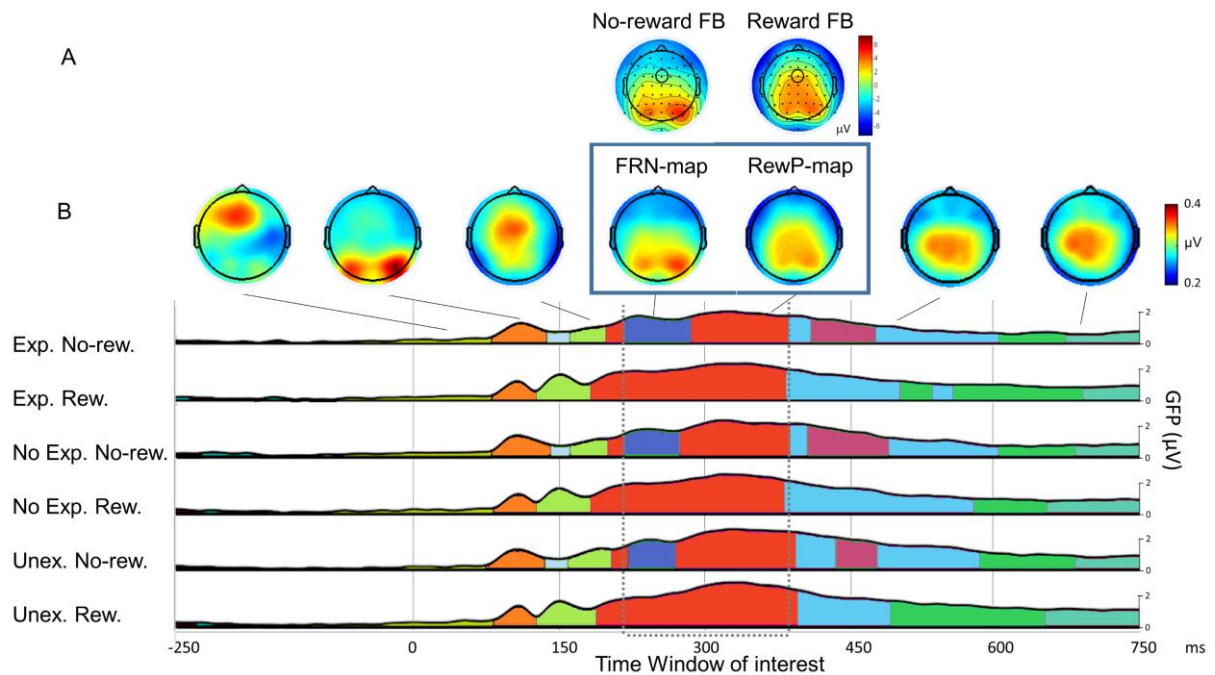
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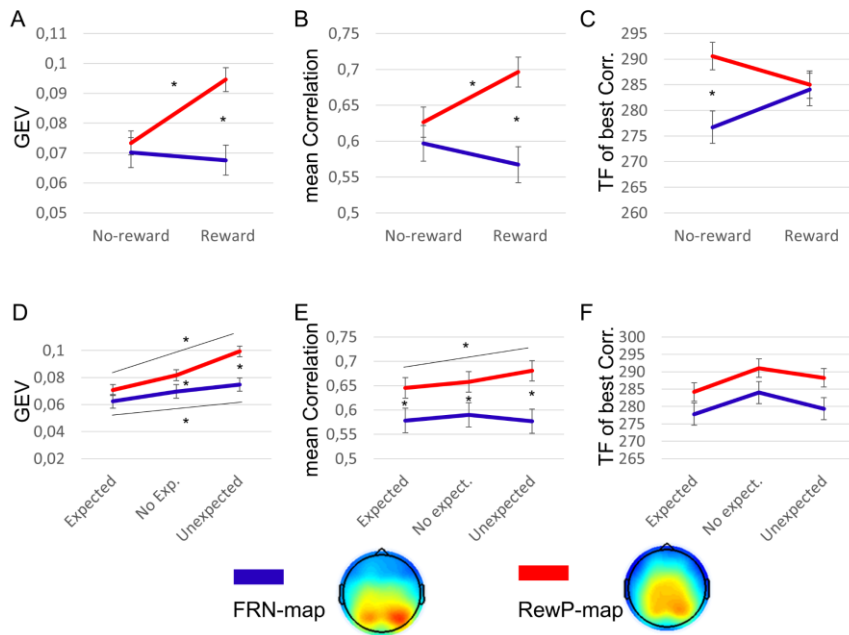
## Figures



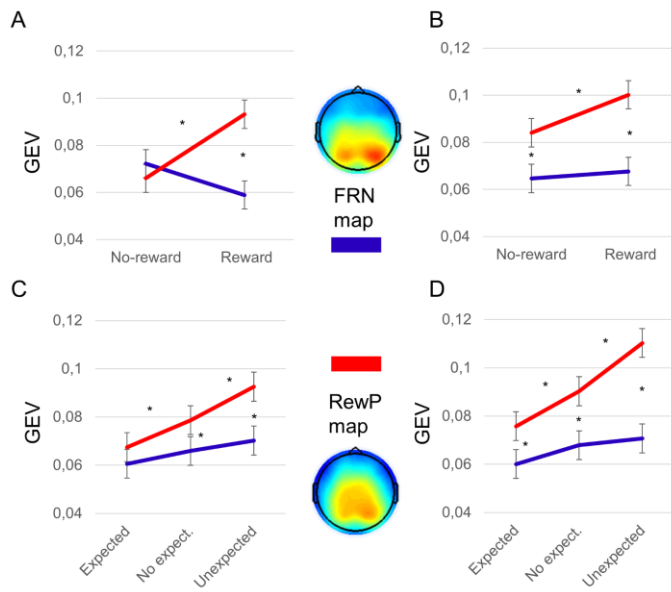
**Figure 1.** (A) Grand average ERP waveforms computed at FCz for reward and no-reward separately, collapsing across the three levels of FB expectation each time. A conspicuous N200 (giving rise to the FRN component) was elicited for no-reward FB, compared to reward FB. The diamond symbol refers to the preceding P200 (see Figure 1D – left panel for analysis of this component only). The dot symbol refers to the N200 proper (see Figure 1D – right panel for analysis of this component only). The small horizontal black line depicts the fixed interval used when the FRN is measured as mean amplitude (see Figure 1E). The FRN was analyzed using either peak to peak (FRN-pp, using the preceding P200 as initial peak – baseline, see Figure 1C) or as a mean ERP activity (FRN-m, see Figure 1E). (B) Grand average ERP waveforms computed at FCz for all six main conditions. At the N200 level, FB valence interacted with FB expectancy, whereby the N200 was the largest for unexpected negative FB. (C) Mean amplitudes of the FRN when computed peak to peak, showing a significant interaction between FB valence and FB expectancy. (D) Mean amplitudes for P200 (left panel) and N200 (right panel) alone. (E) Mean amplitudes of the FRN when computed using a mean amplitude measurement, showing a main effect of FB valence only. The error bar corresponds to 1 standard error of the mean.



**Figure 2.** (A) Topographies (voltage maps) of the main ERP activities of interest (irrespective of expectancy), showing the RewP topography (left inset) and the FRN topography (right inset). The circle superimposed of the topographies corresponds to FCz electrode location. Each map is computed as the mean ERP activity during a 50 ms time interval around the N200 peak elicited by no-reward (see Figure 1A). (B) Outcome of the spatio-temporal segmentation of the grand average ERP data (with the six main experimental conditions considered, and showing the entire epoch starting 250 ms prior to and ending 750 ms after feedback onset). A solution with 16 different topographical maps (where only 7 are actually depicted here) was found to explain 93.71 % of the total variance. During the time interval corresponding to the FRN/RewP components, two dissociable activities were evidenced based on FB valence. These two maps had different properties, including a longer duration for the reward-related one, and showed different sensitivity to FB expectancy (see Results section and Figure 3 for results after back fitting to individual subject ERP data).

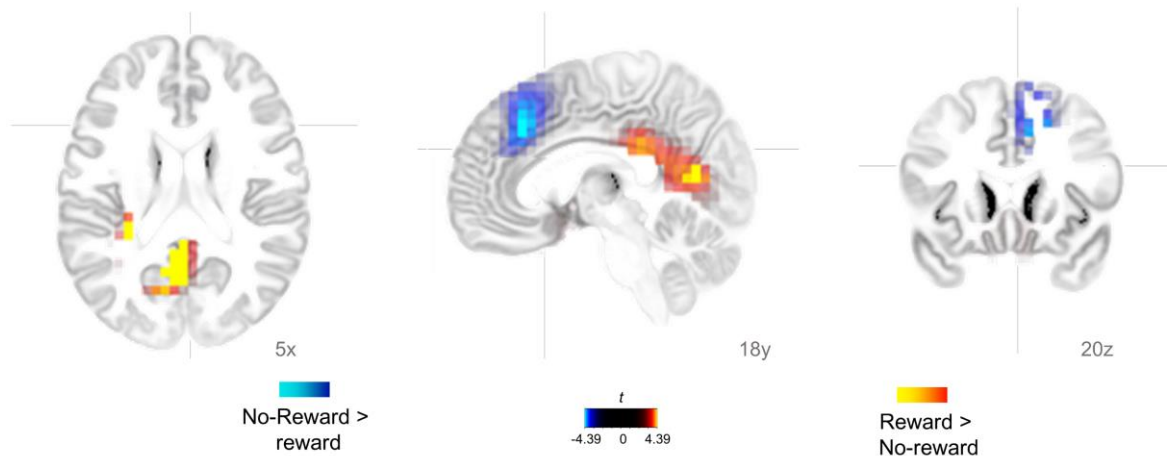


**Figure 3.** (A-F) Results obtained after fitting back the two dominant maps (FRN and RewP, regardless of expectancy) identified during the clustering step (see Figure 2B) during the 217-386 ms time interval following FB onset to individual subject ERP data, separately for the three main dependent variables used in this analysis: global explained variance (GEV), mean correlation and time-frame (TF) of best correlation. The error bar corresponds to 1 standard error of the mean. For each of them, a significant interaction effect between valence and map was found (A,B), explained by the generation of a reward-specific map for positive feedback, except for the TF of best correlation where a significant earlier time-course was found for the FRN-related map for negative feedback compared to the RewP map (C). (D-E-F) Results obtained after fitting showing differential effect of expectancy on the behavior of the two main maps. While the FRN-related map was weakly modulated by levels of expectancy, such an effect was clearly evidenced for the RewP map that showed a monotonic increase (in GEV or mean correlation) with increasing unexpectedness.



**Figure 4.** Fitting results (GEV only) shown separately for the early (left column) and late time-window (right column) identified by the main analysis (see Results section for details). Whereas the FRN-map discriminated better no-reward from reward FB during the early time interval (A), the RewP-map discriminated better reward from no-reward FB during the later time interval (B). (C) The FRN-map did not vary with expectancy (in none of the two time intervals). (D) By comparison, the RewP-map varied with expectancy, especially during the later time interval. The error bar corresponds to 1 standard error of the mean.





**Figure 5.** Source localization results. Hot colors provide activations (corrected for multiple comparisons, see Results section for details) for the contrast between reward and no-reward FB, while cold colors provide suprathreshold activations for the reverse contrast. These statistical maps were generated for the mean ERP activity generated within the 217-386 ms time interval following FB onset. No-reward compared to reward yielded activation in the dACC (BA 32; see right inset), spreading to nearby frontal areas (BAs 6, 8, and 9). Conversely, reward compared to no-reward led to activations in the PPC (BA 23; see left inset), spreading to parietal and more ventral regions, including the Precuneus and Parahippocampal gyrus (BAs 23, 27, 29, 30, 13, and 18). It also extended to the left posterior insula (BA 13).