

## Magneto- and electroencephalographic manifestations of reward anticipation and delivery

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### ABSTRACT

The monetary incentive delay task was used to characterize reward anticipation and delivery with concurrently acquired evoked magnetic fields, EEG potentials and EEG/MEG oscillatory responses, obtaining a precise portrayal of their spatiotemporal evolution. In the anticipation phase, differential activity was most prominent over midline electrodes and parieto-occipital sensors. Differences between non-reward- and reward-predicting cues were localized in the cuneus and later in the dorsal PCC, suggesting a modulation by potential reward information during early visual processing, followed by a coarse emotional evaluation of the cues. Oscillatory analysis revealed increased theta power after non-reward cues over fronto-central sites. In the beta range, power decreased with the magnitude of the potential reward and increased with reaction time, probably reflecting the influence of the striatal response to potential reward on the sensorimotor cortex. At reward delivery, negative prediction errors led to a larger mediofrontal negativity. The spatiotemporal evolution of reward processing was modulated by prediction error: whereas differences were located in PCC and putamen in the prediction error comparison, in the case of expected outcomes they were located in PCC, ACC and parahippocampal gyrus. In the oscillatory realm, theta power was largest following rewards and, in the case of non-rewards, was largest when these were unexpected. Higher beta activity following rewards was also observed in both modalities, but MEG additionally showed a significant power decrease for this condition over parieto-occipital sensors. Our results show how visual, limbic and striatal structures are involved in the different stages of reward anticipation and delivery, and how theta and beta oscillations have a prominent role in the processing of these stimuli.

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### Introduction

Since Pavlov's (1903) experiments, we have known that behavioral responses to reinforcers can be anticipated and linked to events predicting their appearance: the conditioned stimulus or cue. Operant conditioning further taught us that behavior could be modified by external feedback. A significant amount of research has since addressed how we process reward anticipation, as well as how we handle the reward feedback itself, and what occurs when predicted and actual outcome differ.

Seminal research on animal models revealed that midbrain dopaminergic neurons experience an increase in firing following a reward (see e.g. Schultz et al., 1992, 1993), which is displaced to follow the cue after conditioning, and a depression in firing if an expected reward is not delivered (Schultz et al., 1997). Inspired by these results, functional magnetic resonance imaging (fMRI) studies have uncovered the extensive neural network underlying reward expectation

in humans, which includes orbitofrontal cortex, anterior cingulate cortex (ACC), supplementary motor area (SMA), insula, postcentral gyrus, medial temporal gyrus, precuneus, inferior parietal lobule, superior parietal lobule, thalamus, putamen, caudate, globus pallidus and nucleus accumbens (Cooper and Knutson, 2008; Dillon et al., 2008; Ernst et al., 2004; Galvan et al., 2005; Izuma et al., 2008; Knutson et al., 2000, 2001a, 2005; O'Doherty et al., 2002; Preusschoff et al., 2006; Rademacher et al., 2010; Spreckelmeyer et al., 2009; Yacubian et al., 2006; Ye et al., 2011).

In spite of a considerable amount of research on the neural correlates of reward expectation, both with animal and neuroimaging models, there is a surprising scarceness of studies focusing on the neurophysiological signature of this process. Using electroencephalography (EEG), Yu and Zhou (2006) found a positive (170 ms) and a negative (270 ms) component on midline electrodes following loss compared to win cues. They suggested that the negativity could be a manifestation of the feedback-related negativity (FRN) and that it probably originated in the ACC, which would act as an early warning system to prepare for future events. Using magnetoencephalography (MEG), Bunzeck et al. (2011) recently showed that event-related fields (ERF) were modulated by the reward probability indexed by

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the cue, and that theta power decreased with reward probability, whereas beta power showed the opposite pattern.

But what happens when we do not get what we expected? The difference between expected and actual reward is called reward prediction error and it can be positive, when the outcome is better than predicted, or negative, when it is worse than anticipated (Schultz et al., 1997).

Neuroimaging research has shown that brain structures involved in reward processing include similar areas to those in charge of processing reward anticipation: prefrontal cortex (PFC), ACC, inferior frontal gyrus, insula, posterior cingulate cortex (PCC), fusiform gyrus, amygdala, thalamus, globus pallidus and striatum (Carter et al., 1998; Delgado et al., 2000; Dillon et al., 2008; Fujiwara et al., 2009; Holroyd et al., 2004; Liu et al., 2007; Marco-Pallarés et al., 2007; Menon et al., 2001; Nieuwenhuis et al., 2005; Preusschoff et al., 2006). Furthermore, blood-oxygenation-level dependent responses of anterior PFC, ACC, medial frontal gyrus, temporal pole, superior temporal sulcus, striatum, and putamen are modulated by prediction errors (Ablener et al., 2006; Davidson et al., 2004; Dillon et al., 2008; Ramnani et al., 2004; Yacubian et al., 2006).

In event-related potential (ERP) studies, it is well known that negative and neutral feedback elicit an FRN, which peaks fronto-centrally around 300 ms (Gehring and Willoughby, 2002; Hajcak et al., 2006; Holroyd et al., 2006; Miltner et al., 1997; Nieuwenhuis et al., 2004). The FRN has been localized, using dipole analysis, in ACC, SMA, right superior frontal gyrus and PCC (Gehring and Willoughby, 2002; Miltner et al., 1997; Müller et al., 2005; Nieuwenhuis et al., 2005), and the distinct temporal evolution of these sources was revealed with MEG (Doñamayor et al., 2011). The amplitude of the FRN is larger following punishment prediction errors (Holroyd and Krigolson, 2007; Holroyd et al., 2009), but research on negative reward prediction errors is contradictory. While some researchers have found a larger FRN following unexpected than expected non-rewarding feedback (Holroyd et al., 2009, 2011; Potts et al., 2011), others have rather observed this difference on the ensuing P300 (Hajcak et al., 2005). In the frequency domain, increases in beta power (20–30 Hz) have been associated to monetary gains and in theta power (4–8 Hz) to losses (Cohen et al., 2007; Marco-Pallarés et al., 2008), although with MEG both theta and beta bursts have been related to monetary gains (Doñamayor et al., 2011). Beta power has also been observed to be modulated by positive, but not negative, reward prediction error (Cohen et al., 2007).

We therefore investigated reward anticipation and the influence of expectancy on reward processing using simultaneous MEG and EEG in a monetary incentive delay task (MID) (Knutson et al., 2000, 2005). Although the numbers are slowly increasing, not a great amount of studies use both neuromagnetic and neuroelectric data. Yet research can substantially profit from combining these methods. It is well known that EEG is almost equally sensitive to tangentially and radially oriented sources, whereas MEG is most sensitive to tangential sources (Fuchs et al., 1998; Singh, 2006). However, whereas the neuroelectric signal is composed by both primary and secondary currents, the neuromagnetic signal is generated almost only by primary currents, which are the desired target of neurophysiological measures (Rippon, 2006; Singh, 2006). For these reasons, MEG and EEG provide complementary information about neural current sources, which can be used to achieve a better understanding of neurophysiological processes. In the case of this study, in the anticipation phase, we expected to find an FRN-like component in the evoked responses, in accordance with the study by Yu and Zhou (2006). Based on prior research (Bunzeck et al., 2011; Yu and Zhou, 2006), the evoked components were most likely to be located over midline electrodes and bilateral posterior sensors.

One of our main aims was to obtain a precise description of the spatiotemporal evolution of the evoked responses, which we anticipated to originate from frontal and limbic structures, as these areas have received substantial attention by previous fMRI research on

reward expectation. However, in contrast to MEG and EEG, fMRI indirectly measures neuronal activity through hemodynamic activity and has a rather low temporal resolution (for a review of the properties of fMRI see Bandettini, 2006). Yet, given the inherent difficulty of solving the inverse problem (see Singh, 2006), most neurophysiological studies, especially if performed with EEG, focus on the high temporal resolution of these methods and avoid dealing with source reconstruction. We have shown before (see Doñamayor et al., 2011) that it can be profited from the relatively high spatial resolution of MEG (Näätänen et al., 1994; Roberts et al., 1998; Singh, 2006) to characterize the spatiotemporal dynamics of reward processing. Combining neuromagnetic and neuroelectric data to solve the inverse problem has been proven to be more advantageous, resulting in superior spatial resolution, due not only to the increased number of sensors, but also to the different sensitivity patterns of both modalities and to a reduction of the problem of non-uniqueness (Babiloni et al., 2004; Fuchs et al., 1998; Sharon et al., 2007; Singh, 2006).

Another relevant aspect of the current experiment was to characterize the oscillatory components associated to reward anticipation. Though the relationship between ERFs/ERPs and event-related oscillations is still not fully understood (for a review see Bastiaansen et al., 2012), there is a wide consensus that time–frequency representations provide significant complementary information to the time- and phase-locked events depicted by ERFs/ERPs. Given the purported similarity between the neural responses to reward anticipation and delivery, we expected to find oscillatory activity in the theta and beta bands modulated by the valence of the cues. Previous research has reported an inverse relationship between theta power and reward probability, and a linear increase of beta power with reward probability (Bunzeck et al., 2011). We expected to elucidate, whether a similar pattern could be observed with respect to reward valence.

In the delivery phase of our study, we hypothesized a modulation of the FRN and mFRN by reward prediction error, since larger FRNs have been reported following unexpected non-rewarding feedback (Holroyd et al., 2009, 2011; Potts et al., 2011). As in the anticipation phase, we also sought to characterize the spatiotemporal dynamics of reward delivery and we hypothesized that sources might be localized within the cingulate gyrus and insula, as we had observed in our previous study (Doñamayor et al., 2011). However, it remained to be seen whether these areas would also be modulated by prediction errors or whether the multimodal approach of the current study would reveal new spatiotemporal patterns of activations.

Finally, in the oscillatory patterns associated to reward delivery, we anticipated theta and beta power to be modulated by both valence of the feedback and prediction error. As stated above, previous EEG studies associated theta power to monetary losses (Cohen et al., 2007; Marco-Pallarés et al., 2008), whereas with MEG it was associated to monetary gains (Doñamayor et al., 2011). Using both techniques simultaneously, we aimed to elucidate whether this pattern would be replicated or whether modulations would have the same direction. In the case of beta power, since previous results with both techniques were in agreement (Cohen et al., 2007; Doñamayor et al., 2011; Marco-Pallarés et al., 2008), we expected to find increased power for rewards compared to non-rewards. Prior research, however, has only reported modulation of the beta band by positive reward prediction error with reward probability manipulations (Cohen et al., 2007). Therefore, we aimed to explore whether negative reward prediction errors modulated either the theta or the beta band in the case of reward magnitude, but not probability, manipulations.

## Materials and methods

### Participants

Twenty healthy adults from the participant database at the Otto-von-Guericke-Universität in Magdeburg (the affiliation of all authors

at the time of the measurements) took part in the study. Data sets from 19 participants (14 women, aged 20 to 33 years,  $M=26.04$ ,  $SD=3.15$ ) were analyzed, since data from one subject could not be used due to artifacts. Participants were right-handed, had normal or corrected-to-normal (with contact lenses) vision and no history of neurological or psychiatric disorder (assessed by questionnaire). They were asked to change into a hospital gown and remove make-up and hair products. None wore any metallic implants or accessories. The study was approved by the ethics committee of the Otto-von-Guericke-Universität and all subjects gave written informed consent for their participation.

#### Stimuli and procedure

An MID task (Knutson et al., 2000, 2005) was used as illustrated in Supplementary Fig. 1. The stimuli were presented using Presentation software (Neurobehavioral Systems Inc., Albany, CA) and visualized on a rear projection screen in the MEG chamber.

Participants were asked to press a button as fast as possible with their right index finger when they saw a white square appear on the screen. The duration of this target was adjusted to the individual reaction times, such that each participant would achieve an approximate hit rate of 65%. The white square was always preceded by one of four possible cue stimuli (250 ms), indicating a potential reward if the button was pressed before the square disappeared. A randomized delay (750–1250 ms), during which a fixation cross was shown, was presented between cue and target. On trials cued by a triangle (175 trials), participants could not win any money, irrespective of their performance. On trials cued by a circle (525 trials equally divided between the three conditions), based on their performance, participants could win an amount of money indicated by the number of horizontal lines crossing the circle: 10 (one line), 50 (two lines) and 100 (three lines) points (100 points = 0.10€).

The target square was followed by a randomized delay (800–1200 ms) to avoid confounding the motor component associated to the button press with the electromagnetic response to the reward. After this delay, if the participant had been fast enough, feedback (1000 ms) was presented by displaying pictures of coins, modified so that only the value (10, 50 or 100) was shown and their nationality could not be identified. In trials cued by a triangle or if participants exceeded the response deadline, the absence of reward was indicated by a coin-sized light grey circle. The duration of the inter-trial interval was randomized between 1000 and 2500 ms.

Prior to electromagnetic data acquisition, participants took part in a brief training session inside the MEG chamber consisting of 20 trials. This was used to adjust target duration as well as to introduce subjects to the task. After the training session, all participants reported that they understood the meaning of the different cues.

#### MEG data acquisition

MEG data were acquired using a 248-channel 4D Neuroimaging Magnes 3600 WH MEG system (Biomagnetic Technologies Inc., San Diego, CA) at a sampling rate of 678.17 Hz and band-pass filtered between 0.1 and 200 Hz. Anatomical landmarks (left and right preauricular points, nasion, Cz, inion) were digitized by means of a Polhemus 3Space Fastrak system (Polhemus Inc., Colchester, VT) and brought into reference with magnetic marker fields generated by 5 electrode coils mounted on the EEG cap.

#### EEG data acquisition

EEG data were recorded using a MEG compatible EEG cap (Easy-cap GmbH, Herrsching, Germany), which harbored 29 scalp Ag/AgCl electrodes distributed according to the 10–20 system. The signal was referenced online to the activity of the right mastoid and the

left mastoid was acquired for subsequent offline re-referencing. Eye movements were monitored by electrodes below the right eye and on the outer canthi of both eyes. Data were acquired with a Synamps amplifier (NeuroScan, Inc., Herndon, VA) and sampled at 678.17 Hz, with a bandpass filter of 0.1–200 Hz and a resolution of 0.1  $\mu\text{V}$ . All impedances were kept below 5 k $\Omega$ .

#### MEG-EEG data analysis

MEG and EEG signals were analyzed with the Fieldtrip package (<http://fieldtrip.fcdonders.nl/>) using Matlab 7.2 (Mathworks Inc., Natick, MA). Both modalities were analyzed independently for the most part, but the procedures followed were analogous, unless indicated otherwise.

Firstly, EEG data were re-referenced to the average signal of both mastoid electrodes. Then, both MEG and EEG data were segmented around the onset of the cue and feedback stimuli (–1000 to 1500 ms) and independent component analysis (ICA) based on the infomax principle (Bell and Sejnowski, 1995) was performed to correct for ocular, cardiac and mechanical artifacts. Subsequently, each trial was visually inspected to eliminate residual artifacts. After artifact rejection, data were downsampled to 250 Hz. A set of averaged ERFs and ERPs time-locked to the onset of the cue and feedback stimuli and baselined between –150 and 0 ms from cue and feedback presentation, respectively, were calculated for each of the relevant conditions: non-reward (triangle) and reward (circle) cues, and unexpected non-reward (grey circle after a circle cue), expected non-reward (grey circle after a triangle cue) and reward (coin) feedback (see Supplementary Table 1 for the average number of trials used for each condition).

Nonparametric permutation testing (Maris and Oostenveld, 2007) was used to compare the ERFs /ERPs of the following pairs of conditions between 0 and 700 ms: non-reward vs. reward cues (effect of potential reward valence on reward anticipation), unexpected non-reward vs. reward feedback (effect of feedback valence with prediction error on reward processing), and expected non-reward vs. reward feedback (effect of feedback valence without prediction error on reward processing). Significant clusters were only considered for further analysis if they were formed by at least 13 contiguous time points (i.e. 52 ms) and, in the case of the ERFs, five neighboring sensors.

For the localization of the electromagnetic sources, differences between the abovementioned pairs of conditions were calculated and bandpass-filtered between 1 and 40 Hz; a notch filter was used at 50 Hz. Source analysis was performed on the significant time windows using LORETA (Pascual-Marqui et al., 1994) with an interpolated boundary element method (BEM) model, as implemented in the multimodal neuroimaging software Curry 6.0.20 (Compumedics Neuroscan Inc., Charlotte, NC), and projected on a standard brain model. The extent of the activations was defined so that solutions that explained less than 85% of the largest current were suppressed. Curry software was chosen over the Fieldtrip package, as it can simultaneously use the information from both MEG and EEG to perform source reconstruction (see Fuchs et al., 1998 for a detailed account on the computation of multimodal source reconstruction).

Using the Fieldtrip package, single-trial data were convolved with a complex Morlet wavelet:

$$w(t, f_0) = \left(2\pi\sigma_f^2\right)^{-1/2} e^{\frac{-t^2}{2\sigma_f^2}} e^{2\pi i f_0 t}$$

to study time–frequency behavior of the electromagnetic activity elicited by cues and feedback. The relation  $f_0/\sigma_f$  (where  $\sigma_f = 1/(2\pi\sigma_t)$ ) was set to 6.7 (Doñamayor et al., 2011; Marco-Pallarés et al., 2008; Tallon-Baudry et al., 1997). Oscillatory power in the studied

frequencies (1–40 Hz, linear increase) was computed for each trial and averaged for each subject before calculating a grand average.

Subsequently statistical comparisons analogous to those performed on the ERFs/ERPs were carried out separately for MEG and EEG data, within the theta (4–8 Hz) and beta (13–30 Hz) frequency bands in the 0–700 ms time segment. Nonparametric permutation testing (Maris and Oostenveld, 2007) was used, clustering sensor–time–frequency points, which were required to be formed by at least 13 contiguous time points (i.e. 52 ms) and, in the case of the MEG data, five neighboring sensors to be considered for further analysis.

## Results

### Behavioral results

On average, the target duration was set to 262 ms (SD = 47, range 205–370 ms). Reaction times were significantly faster when the target was preceded by a reward cue ( $M = 214$  ms,  $SD = 17$ ) than by a non-reward cue ( $M = 226$  ms,  $SD = 20$ ),  $t(18) = -4.77$ ,  $r = .75$ ,  $p < .001$ .

Reward feedback was presented an average of 346 times (SD = 48), whereas participants obtained non-reward feedback 179 times (SD = 48) unexpectedly and 175 times (SD = 0) expectedly. Participants ended the experiment with an average of 18.56€ (SD = 2.47).

### Analysis of the cue events

#### Event-related activity and source localization

The nonparametric permutation testing performed on both ERFs and ERPs revealed significant and marginally significant differences in several time windows for the comparison between non-reward and reward cues. As can be seen in Table 1, these were mostly localized over parieto-occipital sensors and electrodes, barring an early fronto-central EEG cluster (176–244 ms) and late MEG clusters (516 ms post-cue onwards). ERFs and ERPs at representative sensors can be seen in Fig. 1.

Early differences (120 ms) were localized in the cuneus. All subsequent differences were consistently localized in the dorsal PCC. Slices showing the significant activations with the highest current density and the corresponding MEG and EEG topographies can be seen in Fig. 2 (all sources can be found in Supplementary Fig. 2); Table 2 shows the exact location of the sources.

#### Time–frequency analysis

Two statistically significant clusters were found in the theta frequency band for the EEG data (see Table 3). As can be seen in Fig. 3A, these fronto-centrally distributed clusters corresponded to a difference in the latency of the theta bursts following the reward and non-reward cues. When the cue conditions were considered separately, an increase in potential reward corresponded to an increase in theta power for the first 230 ms post-cue could be observed.

This latency distinction in the theta band was present to a lesser extent over bilateral frontal MEG sensors (Fig. 3B), forming an equivalent cluster to the second EEG cluster. However, in the case of MEG, theta power following non-reward cues was at all times higher than after reward cues. In addition, in both modalities the power change was greater for the non-reward cue than the reward conditions.

In the beta band, a centrally distributed cluster was observed in the MEG data between 176 and 700 ms (Fig. 3C), with no equivalent in the EEG. This cluster corresponded to a significant decrease in beta power following reward cues compared to non-reward cues. Beta power decreased as the magnitude of the potential reward increased.

To explore the relationship between the beta decrease and motor preparation, response times to the target following each of the cue conditions were calculated (Supplementary Fig. 3A) and then correlated with the beta power change. This revealed a non-significant weak correlation,  $r = .15$ ,  $F(1,74) = 1.66$ ,  $p > .1$  (Supplementary Fig. 3B). As there was high between-subject variability with respect to response times (see Supplementary Fig. 3C), k-means clustering was used to divide the participants in fast and slow responders. This uncovered two highly significant correlations (Bonferroni-corrected, Supplementary Fig. 3D). With a smaller increase in response time (range 184–224 ms), fast responders experienced a more pronounced increase in beta power (range  $-.39$  to  $.21$ ),  $r = .50$ ,  $F(1,38) = 12.62$ ,  $p < .0005$ , whereas slow responders exhibited greater response time variability (range 205–263 ms) paired with a smaller beta power increases (range  $-.39$  to  $-.02$ ),  $r = .65$ ,  $F(1,34) = 24.58$ ,  $p < .005$ .

### Analysis of the feedback events with reward prediction error

#### Event-related activity and source localization

A number of significant and marginally significant time–sensor clusters were found for MEG and EEG (see Table 4). Neuromagnetic data revealed significant differences in centro-parietal sensors spanning between 140 and 424 ms, which shifted towards parieto-occipital sensors in the last 272 ms of the analyzed time window. On the other hand, differences in the EEG data had a minimal onset latency of 80 ms post-feedback and were located over parieto-occipital sensors. See Figs. 4 and 5 for the ERFs/ERPs and topographies, respectively.

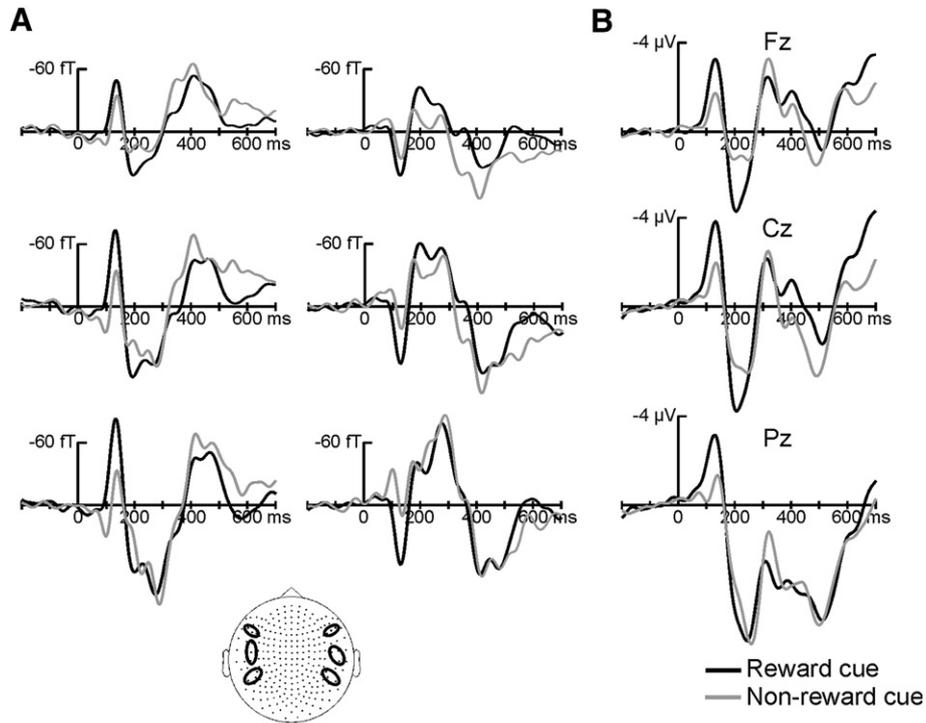
The analysis of the differences between unexpected non-reward and reward feedback yielded a source in the PCC at 224 ms and a similar posterior cingulate source almost 80 ms later, at 300 ms post-feedback (see Fig. 5 and Table 5 for the exact locations). In a later time window, differences between unexpected non-reward and reward originated from the putamen, peaking 480 ms after the presentation of the feedback stimuli.

#### Time–frequency analysis

Significant clusters in the theta band were found immediately after the presentation of the feedback (see Table 6). There was an increase in theta power following reward feedback compared to unexpected non-reward feedback, although differences in the MEG data lasted for the whole analyzed time window, whereas EEG differences

**Table 1**  
Results of the nonparametric permutation testing performed on the ERFs and ERPs for the non-reward vs reward cues comparison. Positive and negative signs represent the surfaces of the magnetic field contours of the difference, in the case of the ERFs, and the direction of the difference, in the case of the ERPs.

| Event-related fields        |             |          | Event-related potentials        |             |          |
|-----------------------------|-------------|----------|---------------------------------|-------------|----------|
| Cluster                     | Time window | <i>p</i> | Cluster                         | Time window | <i>p</i> |
| left parieto-occipital (+)  | 84–160 ms   | .008     | parieto-occipital (+)           | 84–168 ms   | .000     |
| right parieto-occipital (–) | 84–164 ms   | .000     | fronto-central (–)              | 176–244 ms  | .008     |
| right parieto-occipital (–) | 200–404 ms  | .000     | bilateral parieto-occipital (–) | 304–364 ms  | .018     |
| left parieto-occipital (+)  | 312–440 ms  | .016     | occipital (–)                   | 404–464 ms  | .076     |
| left frontal (–)            | 516–692 ms  | .008     | parieto-occipital (+)           | 620–700 ms  | .004     |
| right central (+)           | 528–672 ms  | .014     |                                 |             |          |



**Fig. 1.** From top to bottom, stimulus-locked (A) ERFs at frontal, central and parietal sensors (left and right), and (B) ERPs at Fz, Cz and Pz to reward (black line) and non-reward (grey line) cues. Note that all negative values are up, in accord with ERP convention and to maintain consistency between both modalities. A 20 Hz low-pass filter was used for a better visualization.

were significant merely until 396 ms post-feedback (Fig. 6A and Supplementary Fig. 4A). Both MEG and EEG showed similar time courses of power changes in the case of rewards, but the relative difference between reward and unexpected non-reward was considerably smaller in the case of EEG than in the case of MEG.

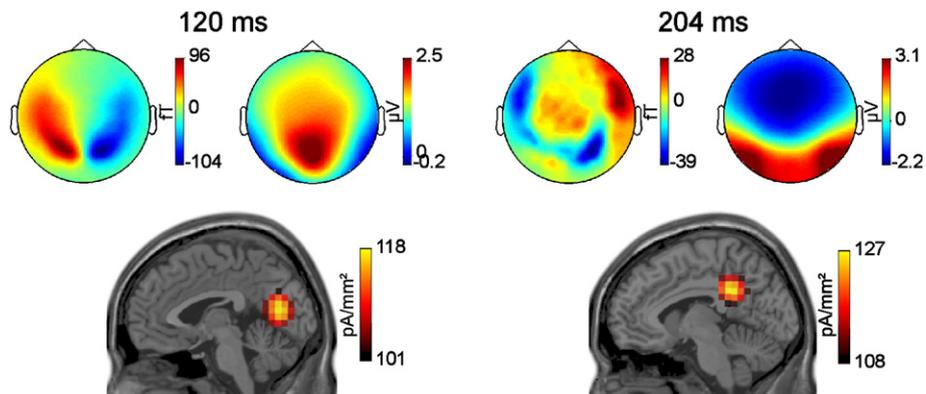
Beta clusters were also found in both modalities. Fronto-central clusters in both modalities (Fig. 6B and Supplementary Fig. 4B) showed lower beta values in the unexpected non-reward than in the reward condition. Interestingly, whereas neuromagnetic data showed increases in power with respect to baseline for both conditions, the EEG time course revealed a decrease compared to baseline, although beta power after rewards was still higher than after unexpected non-rewards. MEG beta power over parieto-occipital sites was significantly higher for unexpected non-reward than for reward feedback (Fig. 6B), with no analog in the EEG data. This showed a more prominent power decrease following rewards, with beta

power associated to unexpected non-rewards increasing over baseline 600 ms after feedback presentation.

*Analysis of the feedback events without reward prediction error*

*Event-related activity and source localization*

Four significant and marginally significant time–sensor clusters were found for MEG and EEG (see Table 4). Both MEG clusters, representing both poles of the magnetic dipole, were located bilaterally over central sensors and spanned for over 450 ms. In the case of the ERPs, there was a marginally significant cluster, which peaked over centro-parietal electrodes and was more positive for expected non-reward than for reward. An EEG negative significant cluster was largest over right parieto-occipital sensors and lasted for almost the entire analyzed time window (564 ms). See Figs. 4 and 5 for the ERFs/ERPs and topographies.



**Fig. 2.** Topographies of the differences between non-reward and reward cues for both neuromagnetic (left) and neuroelectric activity (right), and brain slices showing the neural activation resulting from the source analysis.

**Table 2**

Localization of the sources for the non-reward vs reward cues comparison. BA, Brodmann's area.

| Maximum peak | Area       | BA | Talairach coordinates |
|--------------|------------|----|-----------------------|
| 120 ms       | Cuneus     | 30 | −3, −68, 8            |
| 204 ms       | Dorsal PCC | 31 | −7, −42, 28           |
| 404 ms       | Dorsal PCC | 31 | −2, −49, 29           |
| 552 ms       | Dorsal PCC | 31 | −2, −53, 26           |

The source of the early differences between expected non-reward and reward feedback was first located in the PCC, peaking at 220 ms (see Fig. 5 and Table 5 for the exact locations). At 320 ms post-feedback, the difference could be localized in the caudal portion of the ACC. Within the significant time windows, a final peak in current density was localized bilaterally in the parahippocampal gyrus (432 ms).

#### Time–frequency analysis

Immediately after the presentation of the feedback, there was an increase in theta power following rewards compared to expected non-rewards, which lasted until the end of the analyzed time window in both modalities (see Table 6, Fig. 6A and Supplementary Fig. 4A). In contrast to what could be observed following reward prediction errors, MEG and EEG showed similar time courses of power changes in the case of expected non-rewards.

Beta clusters were also found in both modalities. MEG (Fig. 6B) and EEG (Supplementary Fig. 4B) fronto-central and right frontal clusters, respectively, exhibited lower beta values following expected non-reward feedback than after rewards. Though beta power decreased below baseline levels in both modalities in the expected non-reward condition, neuromagnetic data showed an increase in power with respect to baseline for reward feedback. As with unexpected non-rewards, a negative beta cluster was found in MEG over parieto-occipital sites (Fig. 6B). This showed a more prominent power decrease after rewards than after expected non-rewards.

## Discussion

### Reward Anticipation

The first goal of this study was to investigate reward anticipation by characterizing the evoked components and the spatiotemporal evolution of their neural sources. Consistent with prior literature, we have found significant differences between the event-related responses to reward and non-reward cues. Similar to Yu and Zhou (2006) albeit somewhat earlier, our EEG data show a positivity and negativity, which occur around 120 ms and 200 ms post-cue and are most prominent over midline electrodes. In the case of the neuromagnetic data, significant differences are mostly located over parieto-occipital sensors, as we anticipated based on a study by Bunzeck et al. (2011). As mentioned before, the simultaneous MEG and EEG in this study can improve the understanding of the neural mechanisms by conjugating complementary information (Rippon, 2006; Singh, 2006), but also because the combination of neuromagnetic and neuroelectric data to solve the inverse problem results in superior spatial

resolution (Babiloni et al., 2004; Fuchs et al., 1998; Sharon et al., 2007; Singh, 2006).

Combining EEG and MEG, the differences found in the ERFs/ERPs can be localized in the cuneus (approximately at 120 ms) and later in the dorsal PCC (about 204 ms). Differential activity in the visual cortex is usually ascribed to differences in the perceptual characteristics of the used stimuli and, hence, is often neglected when an experiment is focused on higher forms of processing. However, a number of studies have recently challenged the notion of the sensory cortical areas as mere processors of lower level features. For example, animal models have shown that neurons in the rat primary visual cortex predict the timing of the cued reward (Shuler and Bear, 2006), or that neurons in the primate auditory cortex increase firing during reward expectation depending on the outcome of the previous trial (Brosch et al., 2011). Human studies have further confirmed that activity in the visual cortex is modulated by the expectation of rewards of different magnitudes (Engelmann et al., 2009; Weil et al., 2010) and it has been suggested that the reward history of a stimulus might influence its sensory processing in the visual cortex (Serences, 2008). Visual cortex also receives feedback signals from higher cortical areas, influencing its role on spatial attention (Noesselt et al., 2002). Our data suggest, therefore, that this early difference between reward and non-reward cues in the cuneus reflects a modulation related to the valence of the potential reward. It seems obvious that discriminating as fast as possible between predictive signals to reinforcers with different values would be highly adaptive. A question that arises is, hence, how many trials it takes for this change to take place in the visual cortex, which could be addressed by not informing participants about the reward values indexed by the cues and controlling when the contingencies are learned.

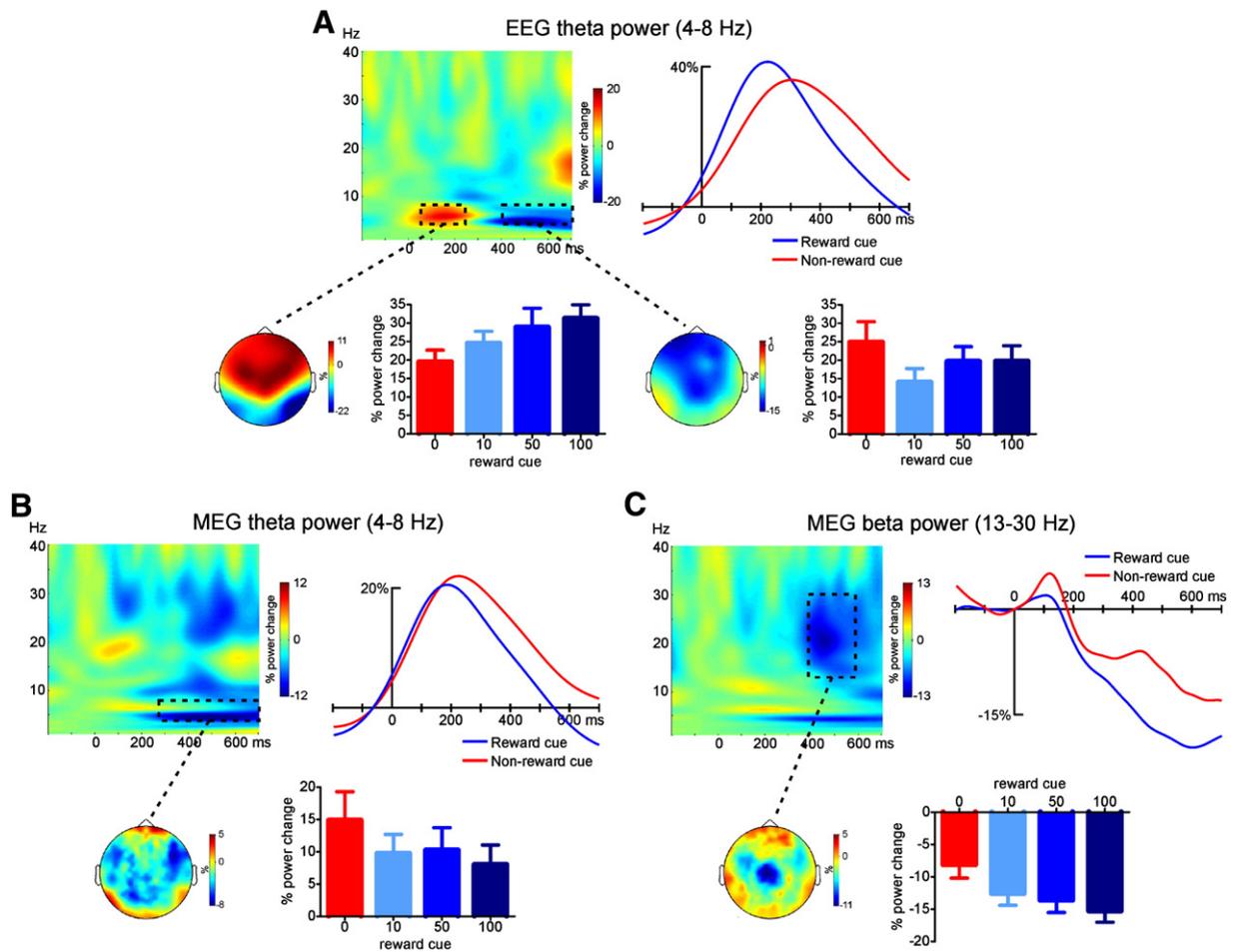
Yu and Zhou (2006) viewed their negative component as an instance of the FRN and expected it to originate from the ACC. Our analysis, however, shows that the source of this difference is localized in the dorsal PCC. In fact, most studies have localized the FRN in ACC, PCC or both (Gehring and Willoughby, 2002; Miltner et al., 1997; Müller et al., 2005; Nieuwenhuis et al., 2005). In a previous MEG study (Doñamayor et al., 2011), we posited that, in the case of the responses to feedback outcomes, the dorsal PCC might support an initial emotional evaluation, and the ACC would subsequently assess possible changes in response strategy. The present results with respect to feedback anticipation appear to be in line with the former hypothesis regarding feedback delivery: cues are emotionally salient and informative stimuli (corresponding to the PCC source), but there is no need for any further evaluation of response strategies, since the participants' task is a simple response time task to a unique target stimulus (hence, no ACC activity).

Another relevant aspect of the current study is to identify the oscillatory components associated to reward anticipation. In contrast to ERFs/ERPs, changes in oscillatory activity are time- but not phase-locked to the eliciting events (Bastiaansen et al., 2012) and are thought to reflect communication within functional networks of information processing (Singer, 1993; Varela et al., 2001). However, the way in which evoked and oscillatory components are related is not evident and remains controversial (see Bastiaansen et al., 2012 for a review), with some researchers suggesting that ERFs/ERPs and oscillations can be considered (partially) independent processes

**Table 3**

Results of the nonparametric permutation testing performed on the time–frequency data for the reward vs non-reward cues comparison. Positive and negative signs indicate the direction of the difference.

| MEG                          |                  |             |          | EEG                 |                  |             |          |
|------------------------------|------------------|-------------|----------|---------------------|------------------|-------------|----------|
| Cluster                      | Frequency window | Time window | <i>p</i> | Cluster             | Frequency window | Time window | <i>p</i> |
| bilateral fronto-central (−) | 4–8 Hz           | 256–700 ms  | .018     | central (+)         | 4–8 Hz           | 0–228 ms    | .014     |
| central (−)                  | 13–30 Hz         | 176–700 ms  | .002     | centro-parietal (−) | 4–8 Hz           | 236–700 ms  | .014     |



**Fig. 3.** Percentage changes in power with respect to baseline of reward compared to non-reward cues in significant sensors, and topographies of the time–frequency clusters signaled by the dotted lines. Bar graphs (M, SEM) show the percentage power change for the individual cue conditions within these clusters. The time courses of the theta and beta bands are plotted for the conditions of interest in the same sensors shown in the spectra.

(see e.g. Shah et al., 2004) and others postulating that they are derived from the same neuronal event (see e.g. Makeig et al., 2002).

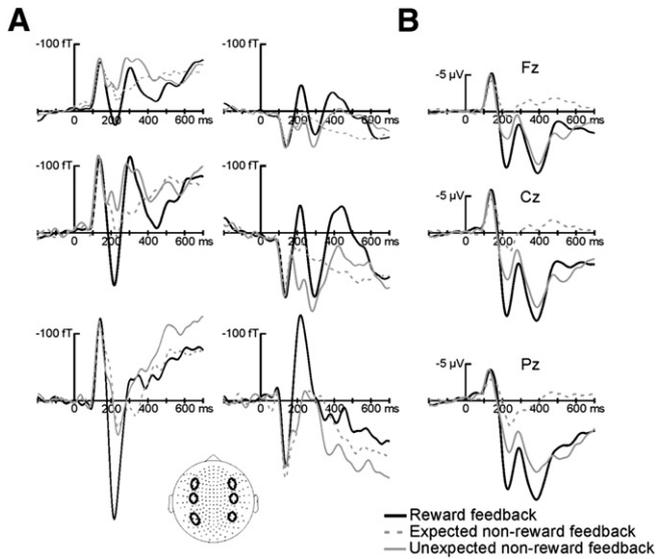
With regard to oscillatory responses associated to reward anticipation, Bunzeck et al. (2011) recently observed that theta power for right centro-parietal and temporal sensors was highest when the cue signaled non-reward and decreased with reward probability. Our MEG data show a similar pattern with the highest theta power after non-reward. In addition, a small cluster in the first 230 ms was found with higher theta power following reward cues. The time courses reveal that this can mainly be attributed to a difference in latency of the theta power peak in both modalities, which peaks around 50–80 ms later for non-reward cues. In contrast to the posterior distribution of the evoked responses, differences in the theta band

exhibit topographies indicative of anterior sources. Activations in anterior brain areas are a common finding in fMRI studies on reward anticipation (Dillon et al., 2008; Ernst et al., 2004; Izuma et al., 2008; Knutson et al., 2000, 2005; Rademacher et al., 2010; Ye et al., 2011), and the link between brain oscillations and hemodynamic activity has been demonstrated in numerous occasions (see e.g. Kayser et al., 2004; Logothetis et al., 2001; Niessing et al., 2005; Scheeringa et al., 2009). Moreover, it is known from animal research that reward cues provoke a phasic increase in neuronal firing in the midbrain (Schultz et al., 1997; Waelti et al., 2001), but it has also been observed that different ventral striatal neurons respond with increases in firing to either rewarding and non-rewarding cues (Roitman et al., 2005). Therefore, it is possible that our theta band observations are to a

**Table 4**

Results of the nonparametric permutation testing performed on the ERFs and ERPs for the feedback comparisons. Positive and negative signs represent the surfaces of the magnetic field contours of the difference, in the case of the ERFs, and the direction of the difference, in the case of the ERPs.

| Event-related fields            |             |          | Event-related potentials        |             |          |
|---------------------------------|-------------|----------|---------------------------------|-------------|----------|
| Cluster                         | Time window | <i>p</i> | Cluster                         | Time window | <i>p</i> |
| Unexpected non-reward vs reward |             |          | Unexpected non-reward vs reward |             |          |
| right centro-parietal (+)       | 140–272 ms  | .002     | parieto-occipital (+)           | 80–180 ms   | .098     |
| left centro-parietal (–)        | 176–276 ms  | .000     | right parieto-occipital (–)     | 80–468 ms   | .000     |
| centro-parietal (–)             | 288–424 ms  | .028     |                                 |             |          |
| right parieto-occipital (+)     | 428–700 ms  | .004     |                                 |             |          |
| left parieto-occipital (–)      | 436–700 ms  | .01      |                                 |             |          |
| Expected non-reward vs reward   |             |          | Expected non-reward vs reward   |             |          |
| right central (+)               | 124–580 ms  | .000     | centro-parietal (+)             | 120–456 ms  | .07      |
| left central (–)                | 156–456 ms  | .000     | right parieto-occipital (–)     | 136–700 ms  | .000     |



**Fig. 4.** From top to bottom, stimulus-locked (A) ERFs at frontal, central and parietal sensors (left and right), and (B) ERPs at Fz, Cz and Pz to reward (solid black line), unexpected non-reward (solid grey line) and expected non-reward (dashed grey line) feedback. Note that all negative values are up and that a 20 Hz low-pass filter was used.

certain extent reflection of the frontal and subcortical processes previously depicted by these techniques.

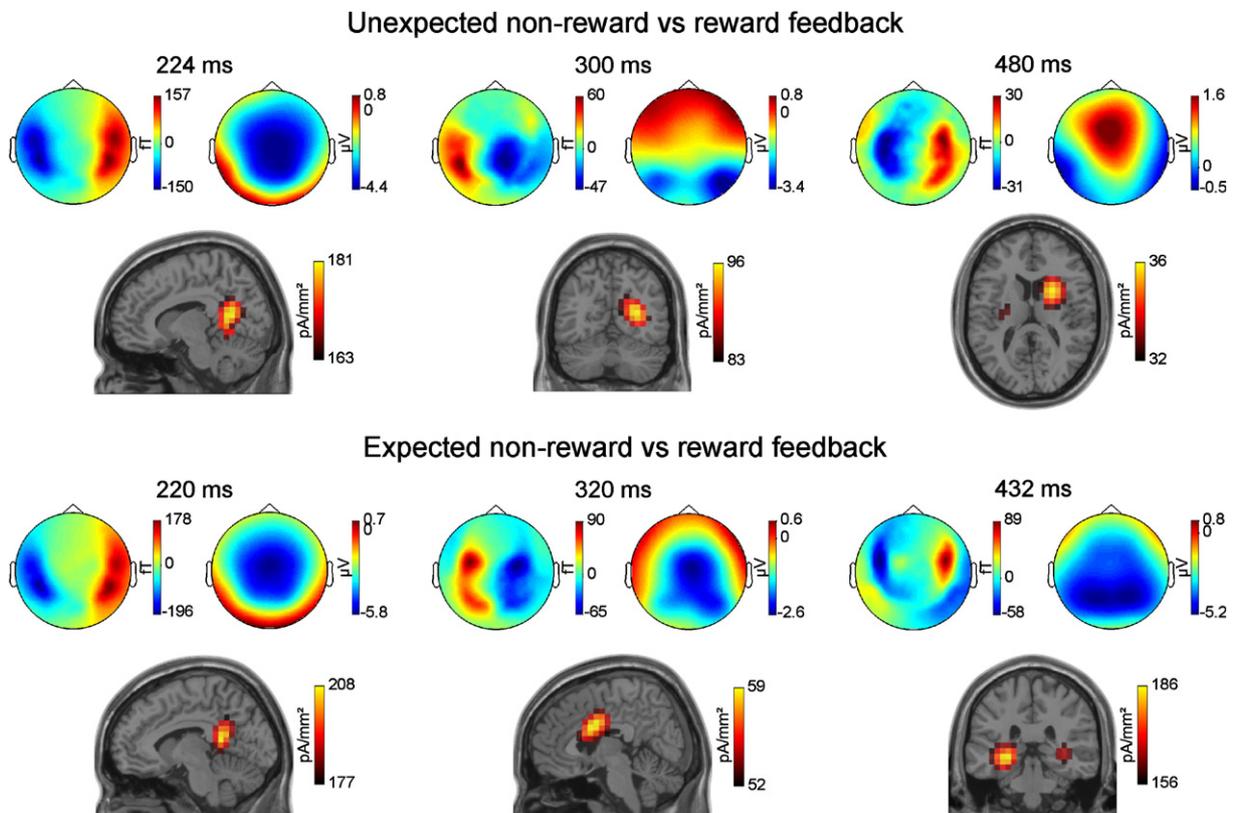
The cue-related decrease in MEG beta power was more pronounced as the magnitude of the potential reward decreased. Given the scalp topography of this beta response, it might be related to the preparation of the motor reaction required shortly after cue presentation. In humans and monkeys the decrease of beta power below baseline at or near sensorimotor areas is known to be related

**Table 5**

Localization of the sources for the feedback comparisons. BA, Brodmann's area.

| Maximum peak                           | Area                  | BA | Talairach coordinates       |
|--|-----------------------|----|-----------------------------|
| <i>Unexpected non-reward vs reward</i> |                       |    |                             |
| 224 ms                                 | PCC                   | 30 | 9, -57, 10                  |
| 300 ms                                 | PCC                   | 30 | 24, -63, 9                  |
| 480 ms                                 | Putamen               | *  | 22, 2, 18<br>-29, -15, 6    |
| <i>Expected non-reward vs reward</i>   |                       |    |                             |
| 220 ms                                 | PCC                   | 30 | -7, -29, 9                  |
| 320 ms                                 | Caudal ACC            | 32 | 5, -5, 34                   |
| 432 ms                                 | Parahippocampal gyrus | 27 | 32, -38, -4<br>-24, -31, -3 |

to movement preparation and execution (Bai et al., 2005; Neuper and Pfurtscheller, 2001; Pfurtscheller and Lopes da Silva, 1999; Pfurtscheller et al., 1994; Szurhaj et al., 2003; Zhang et al., 2008). Additionally, just as we observed in our data, prior studies in animals and humans have reported that response times decrease as the potential reward magnitude increases (Cromwell and Schultz, 2003; Galvan et al., 2005). Indeed, beta power in the different conditions was highly correlated to reaction times in both fast and slow responders. Previous neuroimaging research has mostly found changes in the striatum proportional to the cued reward magnitude (Galvan et al., 2005; Knutson et al., 2001a, 2003, 2005) or probability (Ablner et al., 2006; Preusschoff et al., 2006). Cromwell and Schultz (2003) posited that the striatum might use the information coming from other brain areas to link the knowledge acquired about the potential reward with the motor outputs necessary to create the behavioral reaction. Because of its topography and its relation to the individual reaction times, we hypothesize that the decrease in beta power following reward cues is related to motor preparation. Based on the proposal of Cromwell and Schultz (2003), we further suggest that beta



**Fig. 5.** Topographies of the differences between the feedback conditions for both neuromagnetic (left) and neuroelectric activity (right), and brain slices showing the results from the source analysis.

**Table 6**

Results of the nonparametric permutation testing performed on the time–frequency data for the feedback comparisons. Positive and negative signs indicate the direction of the difference.

| MEG                                      |                  |             |          | EEG                                      |                  |             |          |
|--|------------------|-------------|----------|--|------------------|-------------|----------|
| Cluster                                  | Frequency window | Time window | <i>p</i> | Cluster                                  | Frequency window | Time window | <i>p</i> |
| Reward vs unexpected non-reward feedback |                  |             |          | Reward vs unexpected non-reward feedback |                  |             |          |
| bilateral central (+)                    | 4–8 Hz           | 0–700 ms    | .000     | right fronto-central (+)                 | 5–8 Hz           | 0–396 ms    | .006     |
| fronto-central (+)                       | 13–29 Hz         | 216–700 ms  | .02      | fronto-central (+)                       | 14–30 Hz         | 88–636 ms   | .000     |
| parieto-occipital (–)                    | 13–30 Hz         | 76–700 ms   | .002     |  |                  |             |          |
| Reward vs expected non-reward feedback   |                  |             |          | Reward vs expected non-reward feedback   |                  |             |          |
| bilateral central (+)                    | 4–8 Hz           | 0–700 ms    | .000     | right central (+)                        | 4–8 Hz           | 0–700 ms    | .000     |
| parieto-occipital (–)                    | 13–30 Hz         | 0–576 ms    | .022     | right frontal (+)                        | 13–30 Hz         | 156–700 ms  | .002     |
| fronto-central (+)                       | 13–30 Hz         | 192–700 ms  | .000     |  |                  |             |          |

power decrease proportional to response time is a reflection of the influence of the striatal response to reward magnitude on the sensorimotor cortex.

#### Reward delivery

In the delivery phase of the study, as hypothesized, ERPs to expected non-rewards show notable differences to ERPs following rewards as well as unexpected non-rewards. Evoked responses to expected non-rewards show a striking absence of peaks following the first negativity. Likewise, with regard to MEG responses, peaks are mostly absent from the ERF following expected non-rewards, i.e. in the absence of prediction error. These results are in accord with previous reports, which had observed that the amplitude of either the FRN (Holroyd et al., 2009, 2011; Potts et al., 2011) or the ensuing P300 (Hajcak et al., 2005) is considerably reduced following expected compared to unexpected non-rewarding outcomes. Moreover, it has been suggested that the expectancy modulation depends on whether the participant infers a causal relationship between behavior and feedback (Holroyd et al., 2009).

The distinctions between the three analyzed conditions translate to a series of time–sensor clusters in which there are significant differences and which are not identical for both modalities. It needs to be taken into account that radial and tangential sources, and primary and unwanted secondary currents contribute to the EEG signal; whereas the MEG signal is mostly generated by primary currents from tangential sources (Fuchs et al., 1998; Rippon, 2006; Singh, 2006). Therefore, even when measuring the same neural processes, neuromagnetic and neuroelectric signals may differ to some extent.

As in the case of reward anticipation, one of the goals of this study is to delineate the temporal evolution of the sources in the case of reward delivery, which we had hypothesized to involve the cingulate gyrus and insula. Indeed, the initial differential activity between non-rewarding outcomes, with or without prediction error, and rewards could be located to the PCC. This area has been linked to feedback processing in humans (Dillon et al., 2008; Fujiwara et al., 2009; Knutson et al., 2001b; Marco-Pallarés et al., 2007; Müller et al., 2005; Nieuwenhuis et al., 2005) and monkeys (McCoy et al., 2003) and plays a crucial role in the evaluation of emotionally salient stimuli (Maddock, 1999; Maddock et al., 2003; Vogt et al., 1992). In the current experiment, unexpected non-reward stimuli appear to be emotionally most salient and the comparison between these stimuli and expected reward stimuli indeed revealed a PCC source. Therefore, these differences might be a reflection of a coarse initial evaluation of the value of the outcome (Doñamayor et al., 2011). Interestingly, the latency of this difference very much resembles that of the posterior cingulate activity following cues, which might indicate that the role of the PCC in the processing of cues is actually closely related to its role in the processing of the outcomes.

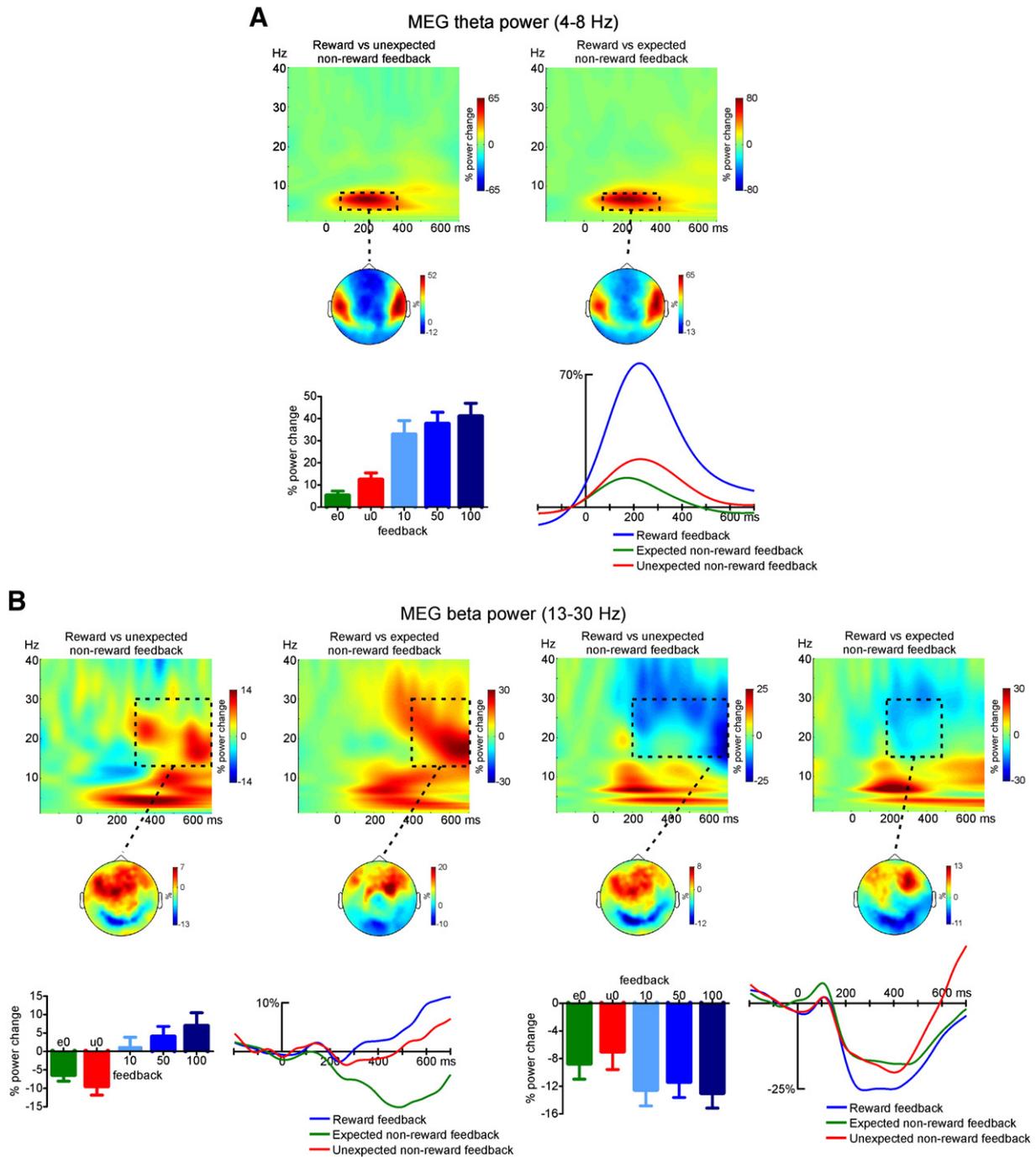
The dynamics of the subsequent sources, however, differ from what we originally hypothesized. Differential PCC activity is found at 300 ms in the negative prediction error comparison. In a later

time window, peaking at 480 ms, differences are located in the putamen. The long-sustained assumption that EEG and MEG are insensitive to deep sources is based on the consideration that these host large numbers of stellate cells and are hence closed-fields, in contrast to the cortex, which is largely composed by open-field pyramidal cells (Lorente de Nó, 1947). However, recent findings have challenged this concept, demonstrating that spiny stellate cells yield current densities comparable to those of pyramidal cells (Murakami and Okada, 2006). This led other researchers to demonstrate that activity in deep structures, such as hippocampus and basal ganglia can be detected in both MEG and EEG (Attal et al., 2009). In fact, the elevated number of trials generally used in cognitive tasks provides a signal-to-noise ratio high enough for the detection of deep sources in the EEG. In MEG detectability is even better as long as the sources are tangential (Sander et al., 2010). Moreover, we jointly employed MEG and EEG for source estimation in the current study and localization results from multimodal MEG-EEG data have been shown to be superior to unimodal (EEG or MEG) results, an effect that is not due to the increased number of sensors but rather to the different sensitivity patterns of both modalities (Babiloni et al., 2004; Fuchs et al., 1998; Sharon et al., 2007).

Our finding is to some extent in line with a recent study by Foti et al. (2011), who localized the differences between monetary gains and losses in a gambling task with equal chance of win-loss in the putamen. The role of the striatum in reward-related paradigms is well known from neuroimaging studies and invasive animal studies, but it has been mostly overlooked in EEG/MEG studies for the abovementioned reasons. Primate research has shown that dopamine neurons projecting to the striatum decrease firing following negative prediction errors (Schultz et al., 1997, 1998), whereas greater striatal responses have been found with larger negative prediction errors in fMRI experiments (Ablner et al., 2006; Dillon et al., 2008).

Subsequent differences between reward and non-reward with no prediction error were localized in ACC and bilateral parahippocampal gyrus. Whereas the involvement of the ACC in outcome processing is a common finding (Carter et al., 1998; Gehring and Willoughby, 2002; Holroyd et al., 2004; Marco-Pallarés et al., 2007; Miltner et al., 1997; Nieuwenhuis et al., 2005; Niki and Watanabe, 1979; Nishijo et al., 1997; Quilodran et al., 2008; Yacubian et al., 2006), parahippocampal activity has been a frequent and consistent finding that has received only peripheral consideration, however. For instance, activation in the parahippocampal gyrus has been related to prediction errors (Dickerson et al., 2011; Ramnani et al., 2004), increases in reward magnitude (Alexander and Brown, 2010; Marsh et al., 2007), and contingency awareness, such as when a negative reinforcer is expected (Carter et al., 2006). Parahippocampal activation has also been related to the processing of negative emotions (Blood et al., 1999; Carter et al., 2006; Colibazzi et al., 2010; Lane et al., 1997).

As we hypothesized, our data reveal differences in the oscillatory responses in both the theta and beta bands. There is an increase in theta power following reward compared to non-reward in both EEG and MEG, irrespective of prediction error. Again, although the link between evoked and oscillatory responses is not clear (see Bastiaansen



**Fig. 6.** Results of the time–frequency analysis showing oscillatory activity in the theta (A) and beta (B) bands for MEG data. Spectra show percentage changes in power with respect to baseline of the feedback comparisons in significant sensors, and topographies of the time–frequency clusters signaled by the dotted lines. Bar graphs (M, SEM) show the percentage power change for the individual feedback conditions within these clusters. The time courses of the theta and beta bands are plotted for the conditions of interest in the same sensors shown in the spectra.

et al., 2012), it is likely that the theta burst is related to the FRN, as has been suggested before (Cohen et al., 2007; Luu et al., 2003). Similar to the ERFs/ERPs, the oscillatory responses to expected non-rewards also remain closer to baseline levels during the whole epoch. This finding relates to a recent observation by Cavanagh et al. (2010), who showed that theta oscillations originating in the medial PFC covary with the magnitude of the negative prediction error, hence providing a possible explanation as to why the theta power found in our data is greater for unexpected non-reward (negative prediction error) than for expected non-reward (no prediction error). Although the observation of greater theta power following rewards differs from previous EEG experiments that found a theta increase following

negative feedback (Gehring and Willoughby, 2004; Marco-Pallarés et al., 2008), it is in accord with a previous MEG study carried out in our group (Doñamayor et al., 2011), as well as with EEG studies performed by Papo et al. (2007). The ACC has been posited as a likely source of the theta oscillations following feedback delivery (Christie and Tata, 2009; Doñamayor et al., 2011; Papo et al., 2007), although theta power has also been recorded from frontal sites in both humans (Cavanagh et al., 2010) and animals (van Wingerden et al., 2010).

In both modalities, greater fronto-central beta power is found for reward than both non-reward conditions. Fronto-central beta power increase associated to positive compared to negative feedback is a common observation in gambling and feedback-learning studies

(Cohen et al., 2007; Doñamayor et al., 2011; Marco-Pallarés et al., 2008; Papo et al., 2007; van de Vijver et al., 2011) and it has been suggested to be a sign of the long-distance communication between reward-related structures (Marco-Pallarés et al., 2008). We have also found greater beta power over parieto-occipital MEG sensors for both types of non-reward compared to reward. At present, we can only speculate about the physiological role of this previously undescribed posterior beta activity. Activation of the inferior parietal lobule (IPL) has been a common finding in action monitoring studies in the fMRI domain, however (e.g., Marco-Pallarés et al., 2008). The rostral IPL seems to be involved in motor planning and action-related functions in general and has also been implicated in the human mirror neuron system (Caspers et al., 2010; Iacoboni, 2005; Keysers and Gazzola, 2009; Rizzolatti, 2005). The caudal IPL, in particular on the right, has been found to be involved in spatial and nonspatial attention as well as motor preparation (Corbetta et al., 2008; Fink et al., 2001). In light of these results, one role of the posterior beta increase for non-rewards represents activity related to the evaluation of the negative outcome and, possibly, the implementation of remedial actions.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.neuroimage.2012.04.038.

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