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Human oscillatory activity associated to reward processing in a gambling task

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Abstract

Previous event-related brain potential (ERP) studies have identified a medial frontal negativity (MFN) in response to negative feedback or monetary losses. In contrast, no EEG correlates have been identified related to the processing of monetary gains or positive feedback. This result is puzzling considering the large number of brain regions involved in the processing of rewards. In the present study we used a gambling task to investigate this issue with trial-by-trial wavelet-based time–frequency analysis of the electroencephalographic signal recorded non-invasively in healthy humans. Using this analysis a mediofrontal oscillatory component in the beta range was identified which was associated to monetary gains. In addition, standard time–domain ERP analysis showed an MFN for losses that was associated with an increase in theta power in the time–frequency analysis. We propose that the reward-related beta oscillatory activity signifies the functional coupling of distributed brain regions involved in reward processing.

Keywords: Feedback; Gambling; Medial frontal negativity; Reward; Wavelet analysis

1. Introduction

In order to successfully navigate through a busy day, we need to constantly assess the values and uncertainties attached to different options and to adapt our behavior according to the outcome of an action which might or might not match our predictions and hopes. The function of positive (rewards) and negative feedback signals (punishments) in this scenario is to guide behavior and to mediate learning (Schultz, 2006). The brain network activated in reward processing comprises the orbitofrontal cortex, amygdala, ventral striatum/nucleus accumbens, prefrontal cortex and anterior cingulate cortex (Delgado, Nystrom, Fissell, Noll, & Fiez, 2000; Gottfried, O'Doherty, & Dolan, 2003; Knutson, Fong, Bennett, Adams, & Hommer, 2003; Knutson, Westdorp, Kaiser, & Hommer, 2000; O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001). However, although the neural circuit involved in reward processing is quite well defined, the specific roles of each region and the integration of information in this circuit are not well understood.

Several authors have proposed that in order to integrate a disparate number of different rewards the brain uses a common network that converges in a final pathway that informs about the nature of the reward (comparison process) and about the possible courses of action in the future (Montague & Berns, 2002; Shizgal, 1997). Neurophysiological studies in animals revealed dopaminergic neurons in the midbrain projecting, among other regions, to the ventral striatum responding selectively to unpredicted events: (i) they are mostly responsive to appetetive events that are better than predicted, (ii) they do not respond to well-predicted rewards, and (iii) a negative signal (i.e. decreased activity) is elicited when an appetetive event is worse than predicted (Mirenowicz & Schultz, 1994; Schultz, Dayan, & Montague, 1997; Tremblay & Schultz, 2000; for similar results in humans: Berns, McClure, Pagnoni, & Montague,

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2001; O'Doherty et al., 2001). The pattern observed in these neurons contrasts to that observed in prefrontal, anterior, and posterior cingulate cortex neurons which exhibit only a unidirectional "error signal" (Ito, Stuphorn, Brown, & Schall, 2003; McCoy, Crowley, Haghighian, Dean, & Platt, 2003; Watanabe, 1989, however see Kim, Shimojo, & O'Doherty, 2006; Tom, Fox, Trepel, & Poldrack, 2007).

In non-invasive electrophysiological studies in humans using event-related brain potentials (ERPs), a similar "*error signal*" has been observed emanating from the medial prefrontal cortex (Ullsperger & von Cramon, 2001). Frontocentral negativity, called error-related negativity (ERN, Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990; Gehring, Goss, Coles, Meyer, & Donchin, 1993) has been recorded after performance errors. In addition, a similar medial frontal negativity (MFN) has also been observed after feedback informing that a response had been incorrect (Holroyd & Coles, 2002; Muller, Moller, Rodriguez-Fornells, & Munte, 2005) or after feedback informing about the amount of money lost in a gambling task (Gehring & Willoughby, 2002). Gehring and Willoughby (2004) have used a Morlet wavelet-based time–frequency analysis of the average ERN and MFN components to analyze oscillatory activity underlying these ERP responses. A theta oscillatory response (4–7 Hz) with a maximum at midline electrodes was found in relation to both ERP components. This result corroborated previous time–frequency studies of the ERN component (Luu, Tucker, & Makeig, 2004; Yordanova, Falkenstein, Hohnsbein, & Kolev, 2004). As the scalp distribution of the theta oscillatory activity was slightly lateralized to the right and more anterior than for the MFN compared to the ERN component, their neural generators may be partially distinct (Nieuwenhuis, Slagter, von Geusau, Heslenfeld, & Holroyd, 2005; Muller et al., 2005). Luu and Tucker (2001) have suggested that the midline theta oscillatory process underlying the ERN component may reflect the broad coordination of several brain regions (which include the anterior cingulate cortex and several subcortical regions) that participate in the action regulation system. This system might be involved in learning the appropriateness of a behavior in a specific context, monitoring the outcome of actions and switching to a different behavior when unexpected outcomes occur.

One important limitation of the Gehring and Willoughby (2004) study is that the time–frequency analysis was applied only to averaged ERP activity, which only accounts for the electrical activity reflected by the evoked potential. In contrast, single trial time–frequency analysis provides information that cannot be gleaned from averaged ERPs or time–frequency analysis of average data (see, for example, Makeig et al., 2002; Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1997): (i) there is no information loss due to the averaging process in the time or spectral domains; (ii) it is possible to study systematic variations between single trials, and (iii) changes of power of non-phase-locked activity in a given frequency band can be assessed (Tallon-Baudry et al., 1997), which is especially important for higher frequencies. Thus, fine-grained wavelet-based time–frequency analysis could help to solve the question as to why no specific electrophysiological effects have been recorded for affirmative feedback information, monetary gains or correct responses using standard time–domain ERP analysis or time–frequency analysis applied to averaged ERP data. In the present study we therefore employed trial-by-trial wavelet-based time–frequency analysis in addition to standard ERP analysis in a simplified version of the gambling task developed by Gehring and Willoughby (2002).

2. Materials and methods

2.1. Participants

Twenty-five right-handed healthy undergraduate psychology students of the University of Barcelona participated in the experiment (seven men, mean age 23.7 ± 5.4 (S.D.)) for monetary compensation. Written consent was obtained prior to the experiment. The experiment was approved by the local ethical committee.

2.2. Design

We used a simplified version of the gambling task (Gehring & Willoughby, 2002) in which valence (reward/monetary gain or punishment/monetary loss) and correctness (correct or incorrect choice) always coincided. The original task in addition comprised trials that could be considered a wrong choice but still afforded a monetary gain (i.e., trials in which the volunteer's choice resulted in a smaller win than the alternative choice).

Participants began with 1000 points (1 point = 1 Euro cent) and were instructed to gain as much points as possible. The task consisted in choosing one of two numbers presented in white on black background in the middle of a video-screen. Only two possible displays were presented, either [25][5] or [5][25]. Participants had to make an obligatory button press response with their left or right index-finger, indicating the selected number. For example, in the [25][5] display, a left button press would indicate the selection of the number 25, and a right button press the selection of the number 5. One second after the choice one of the numbers turned red while the other turned green. If the number selected by the participant changed to red, this signaled a loss of the corresponding amount in Euro cent; a green number indicated a gain of this amount in Euro cents. Money was given to the subjects at the end of the experiment. Two seconds after the feedback stimulus the next trial began with the presentation of a warning signal ("*"; 1000 ms duration) followed by a new pair of numbers.

The experiment comprised sixteen blocks of 48 trials each (warning signal, presentation of numbers, response and feedback). In each block, the four different feedback types were presented in random order **[25]**[5], [25]**[5]**, **[5]**[25], and [5]**[25]** (note: non bold font stands for red [loss], while bold font on black background stands for green [win]). Combined with the two response options this yielded eight different types of stimulus-response combinations. For example, if the volunteer had chosen the left number in a **[25]**[5] event, this was scored as a "maximum gain" trial. If the participant had opted for the right number, however, the trial was scored as a minimum loss. For the analysis presented here, left and right choices were combined into four different averages: maximum gain (+25), minimum gain (+5), minimum loss (−5) and maximum loss (−25). Notice that these combinations correspond to the loss-error and gain-correct conditions in Gehring and Willoughby (2002), see also Fig. 1 in (Nieuwenhuis, Yeung, Holroyd, Schurger, & Cohen, 2004). Combinations yielding a monetary gain which would still be considered a wrong choice (e.g., choosing 5 in the following outcome: **[25][5]**) or combinations yielding a monetary loss in spite of being the most advantageous choice (e.g., choosing 5 in the following outcome: [25][5]) were not possible in the present study, because the two numbers always changed to different colors. This was done to avoid possible confounds between the direction of the outcome (gain versus loss) and correctness (correct versus error) of the decision. After each block, the participant was informed about his/her current gains to stress the monetary incentive.

2.3. Electrophysiological recording

EEG was recorded using tin electrodes mounted in an elastic cap and located at 29 standard positions (Fp1/2, Fz, F7/8, F3/4, Fc1/2 Fc5/6, Cz, C3/4, T7/8,

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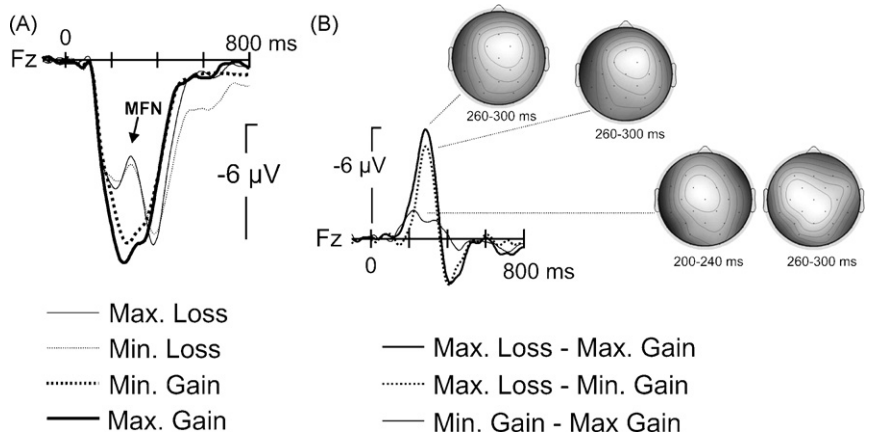

Fig. 1. Grand average waveforms and scalp topography showing the MFN effect. (A) At a frontal location, a large increase in the MFN is observed in response to monetary losses (either 5 or 25 points). No differences were observed between maximum and minimum losses. After a maximum gain (25 points) a larger positivity is observed when compared to minimum gains (5 points). (B) Scalp distribution of the MFN component derived from difference waveforms (spherical spline-interpolated isovoltage maps; 40 ms interval centered on the peak amplitude value). Notice the widespread scalp distribution of the MFN in the loss minus gain difference. In contrast, the difference waveform between gain conditions showed a more posterior central distribution (relative scale, maximum/minimum values for each map: maximum loss–maximum loss, −2/−7 μV; maximum loss–minimum loss, −2/−7 μV; minimum gain–maximum gain, −0.5/−1.4 μV).

Cp1/2, Cp5/6, Pz, P3/4, P7/P8, Po1/2, O1/2). Biosignals were rereferenced off-line to the mean of the activity at the two mastoid processes. Vertical eye movements were monitored with an electrode at the infraorbital ridge of the right eye. Electrode impedances were kept below 5 kΩ.

The electrophysiological signals were filtered with a bandpass of 0.01–50 Hz (half-amplitude cutoffs) and digitized at a rate of 250 Hz. Trials with base-to-peak electro-oculogram (EOG) amplitude of more than 50 μV, amplifier saturation, or a baseline shift exceeding 200 μV/s were automatically rejected off-line. The percentage of rejected trials was 14%.

2.4. Data analyses

ERPs time-locked to the color-change of the number-displays were averaged for epochs of 1024 ms starting 100 ms prior to the stimulus (baseline), and the possible differences were tested by using an ANOVA with the four conditions (maximum gain, minimum gain, minimum loss, maximum loss) and midline electrode locations (Fz, Cz, Pz) as within subject factors.

To study time–frequency behavior of the electrical activity elicited by the feedback, single trial data were convoluted using a complex Morlet wavelet:

$$w(t, f_0) = (2\pi\sigma_t^2)^{-1/2}\, e^{-t^2/2\sigma_t^2}\, e^{2i\pi f_0 t}$$

The relation f_0/σ_f (where $\sigma_f = 1/(2\pi\sigma_t)$) was set to 6.7 (Tallon-Baudry et al., 1997). Changes in time varying energy (square of the convolution between wavelet and signal) in the studied frequencies (from 1 to 40 Hz; linear increase) with respect to baseline were computed for each trial and averaged for each subject before performing a grand average. Mean increase/decrease in power in the different conditions (maximum gain, minimum gain, minimum loss, maximum loss) were obtained for the three midline electrode locations (Fz, Cz, Pz) and entered into an ANOVA.

For all statistical effects involving two or more degrees of freedom in the numerator, the Greenhouse-Geisser epsilon was used to correct for possible violations of the sphericity assumption. *P*-value after the correction is reported.

3. Results

The mean gain of the participants after performing the 768 trials was 7.4 ± 467.3 points. Ten participants ended the experiment gaining some points, 14 participants lost points and one participant ended the experiment with 0 points.

3.1. Event-related brain potentials

A mediofrontal negativity (MFN) with a frontocentral maximum peaking around 280 ms was observed for loss trials (Fig. 1). An analysis of variance (ANOVA) on the mean amplitude in the time-window 200–300 ms was performed with trial type (four levels) and electrode site (midline locations: Fz, Cz, Pz) as factors. A significant effect of trial type ($F(3,72) = 23.3$, $P < 0.001$) was found, but the interaction between trial type and electrode site was not significant ($F < 1$). Further pairwise comparisons showed that the MFN did not differ between both loss conditions ($F(1,24) < 1$; mean amplitude at Fz: minimum loss, 7.9 ± 5.1 μV and maximum loss, 7.9 ± 4.8 μV; maximum gain, 11.4 ± 5.5 μV; minimum gain, 10.3 ± 5.3 μV). The gain conditions, on the other hand, were different ($F(1,24) = 5.6$, $P < 0.05$). As is shown in Fig. 1B, the difference between minimum and maximum gains showed a more posterior distribution when compared to the difference between loss and gain conditions.

3.2. Time–frequency analysis

The time–frequency analysis of the four conditions indicated a clear enhancement of theta activity (4–8 Hz) between 100 and 500 ms after feedback onset which appeared to be most pronounced for maximum loss trials (Fig. 2A). In addition, an increase in the beta band (20–30 Hz) was revealed for gains between 250 and 400 ms (Fig. 2A).

An ANOVA of the mean power change for the theta frequency band (4–6 Hz, time-window 100–500 ms) was performed including trial type (maximum gain, minimum gain, minimum loss, maximum loss) and electrode (midline locations: Fz, Cz, Pz) as within-subject factors. A significant increase of the theta frequency was encountered at frontocentral electrodes (interaction between trial type × electrode $F(6,114) = 18.6$, $P < 0.001$; trial type $F(3,72) = 7.97$, $P < 0.005$;

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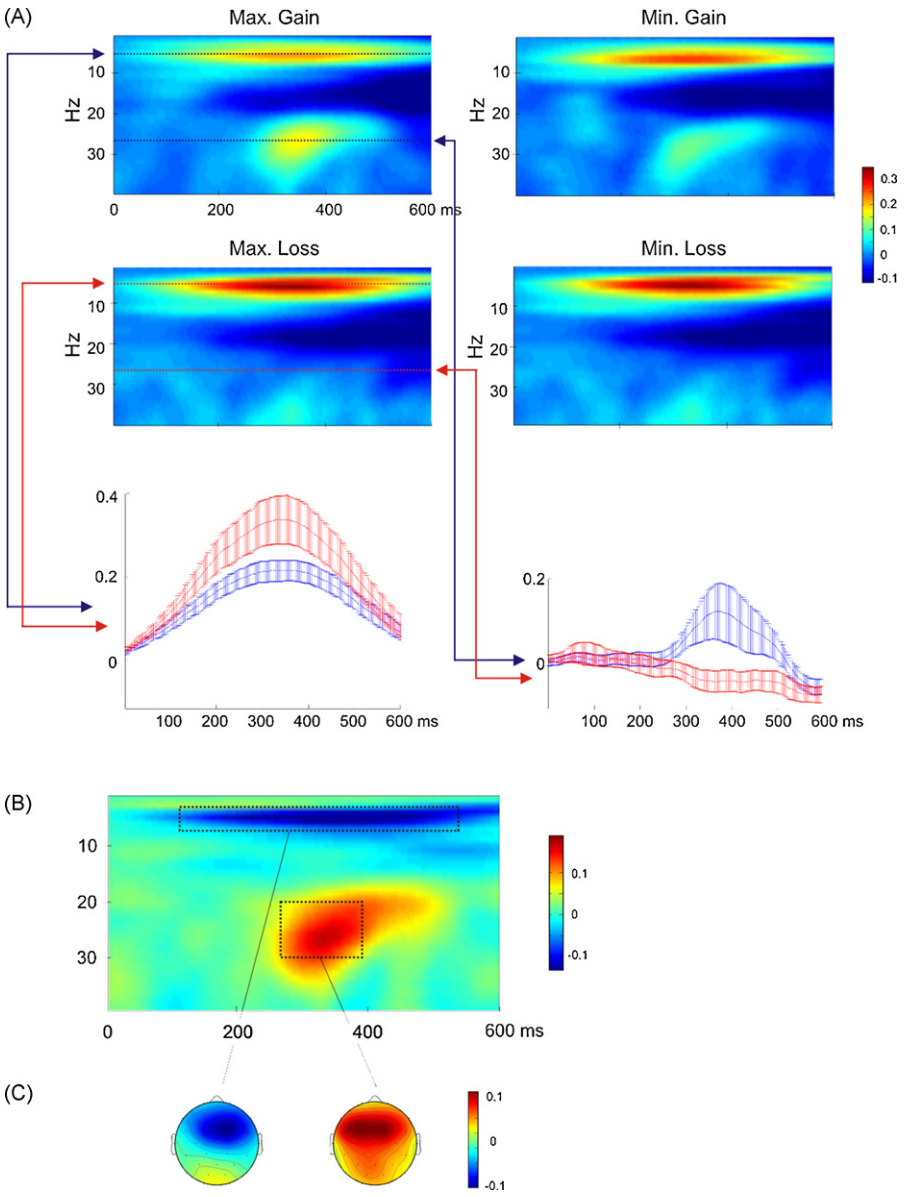

Fig. 2. (A) Changes in power with respect to baseline (100 ms period prior to feedback stimulus) of the maximum gain (left top), minimum gain (right top), maximum loss (left bottom) and minimum loss (right bottom) conditions at Fz. The time course at selected frequencies (dotted lines) is plotted for maximum gain and loss conditions with corresponding standard error of the mean. (B) Differences between maximum gain and maximum loss conditions. Dotted contours show the areas where significant differences were encountered ($P < 0.05$). (C) Difference of power (maximum gain minus maximum loss) scalp maps for theta (4–6 Hz, 100–500 ms) and beta (20–30 Hz, 250–400 ms) responses at the intervals of maximum difference. Note the different sign of the values for the theta (power of loss > power of gain) and beta (power of gain > power of loss).

electrode condition $F(2,48) = 4.68$ $P < 0.05$), with a topography resembling the MFN (see Figs. 2B and C). Pairwise comparisons revealed neither significant differences between maximum and minimum gain ($t(24) < 1.3$, $P > 0.2$) nor significant differences between maximum and minimum loss ($t(24) < 1$, $P > 0.3$).

Fig. 3 (left) illustrates the power changes in the beta band (20–30 Hz) for the four conditions in the 250–400 ms time-window during which most pronounced difference between maximum gain and maximum loss was observed (see Fig. 2C). The corresponding ANOVA performed in this time-window (250–400 ms) showed a main effect of trial type ($F(3,72) = 6.89$, $P < 0.01$), which reflects the increase of the beta power (20–30 Hz) in gain trials when compared to loss trials after the appearance of the feedback. Again, a frontocentral scalp distribution was observed (electrode condition $F(2,48) = 5.63$, $P < 0.05$; interaction between trial type x electrode, $F(6,114) = 2.38$, $P = 0.1$; see Fig. 2C). The corresponding ANOVA also showed a significant linear decrease ($F(1,24) = 8.3$, $P < 0.01$), which suggests a gradual change in beta power across conditions (see Fig. 3). Further pairwise comparisons revealed that there were significant differences between maximum and minimum gain conditions at the Fz location ($t(24) = 2.35$, $P < 0.05$) and marginal differences at Cz ($t(24) = 1.78$, $P < 0.08$) but not at Pz ($t(24) = 1.16$, $P = 0.26$).

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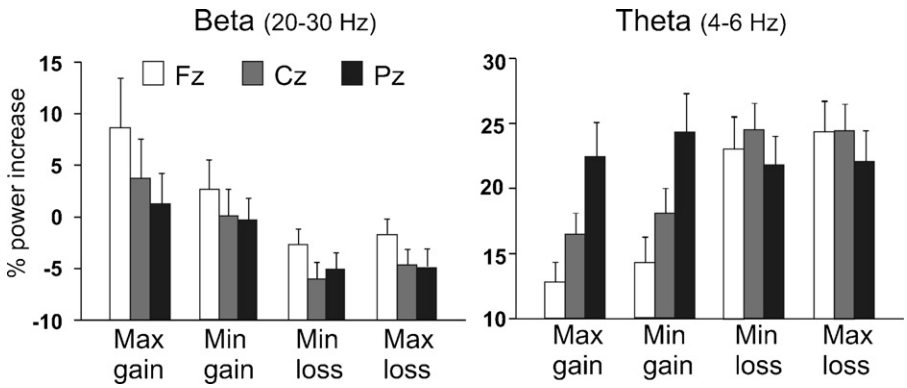

Fig. 3. Power changes (in percent) for the time and frequency windows that showed the greatest differences between maximum gain vs. maximum loss conditions. Beta—time range: 250–400 ms, frequency range: 20–30 Hz; theta—time range: 100 and 500 ms, frequency range: 4–6 Hz.

By contrast, no significant differences were encountered when maximum and minimum loss conditions were compared (all midline locations, $t(24) < 1$, $P > 0.3$).

These results indicate the existence of two functionally different oscillatory responses: frontocentral theta oscillations related to negative feedback (losses) and frontocentral beta oscillations related to positive feedback (reward). While the magnitude of the negative feedback did not affect the theta component, the beta component was sensitive to the magnitude of the positive feedback.

4. Discussion

Rewards and punishments are major forces in the modification of behavior. Using event-related brain potentials in the human, a negative component (MFN) has been observed for feedback information signaling negative outcomes (e.g. monetary loss; Gehring & Willoughby, 2002; Holroyd & Coles, 2002; Muller et al., 2005; Nieuwenhuis et al., 2005). By implementing trial-by-trial time–frequency analysis we were able to study the relationship between oscillatory activity and the processing of reward and punishment and thus to extend earlier observations in gambling paradigms (Gehring & Willoughby, 2002). As Nieuwenhuis et al. (2004) have demonstrated, the utilitarian (gain = low MFN versus loss = high MFN) and the performance (correct = low MFN versus incorrect = high MFN) aspect of the feedback both modulate the MFN amplitude with their respective contributions depending on which aspect is more salient. We therefore simplified the paradigm and investigated only the utilitarian aspect of feedback, yielding a substantial MFN-amplitude which allows to reliably observe this phenomenon at the single subject level.

With regard to the standard ERP analysis there were no amplitude differences between the maximum and minimum loss conditions. Interestingly, however, we encountered a significant difference between the maximum and minimum gain conditions which is in line with several other studies using gambling paradigms (Hajcak, Moser, Holroyd, & Simons, 2006; Holroyd, Larsen, & Cohen, 2004), although this effect has not always been significant in earlier studies. This result is also in agreement with a previous study in which the magnitude and the valence of the reward was dissociated (Yeung & Sanfey, 2004). In that study, the magnitude of the reward determined the amplitude of the late positive component while the valence (positive or negative) determined the presence or absence of the MFN component (independently of the magnitude). Indeed, the present results showed a more prominent posterior positive component for the largest reward. Its distribution (see Fig. 3 in Yeung and Sanfey (2004), for a similar topography) suggests that it represents a modulation of the late positive complex (P3b), a component related to the assignment of attention to a stimulus. In contrast, no amplitude difference was observed for the MFN comparing the loss conditions, which is consistent with the notion that the MFN in reward experiments reflects a binary process, being present for negative and absent for positive feedback (Hajcak et al., 2006; but see Muller et al. (2005), for an experiment in which feedback related activity was boosted by uncertain, "equivocal" feedback).

Maximum loss (negative) feedback when compared to maximum gain (positive) feedback showed a power increase in the theta-band most pronounced for midline electrode sites, thus replicating several studies that have shown the involvement of the theta band in the generation of the ERN and MFN (Gehring & Willoughby, 2002; Gehring & Willoughby, 2004; Luu, Tucker, Derryberry, Reed, & Poulsen, 2003; Luu et al., 2004). With regard to the ERN both Luu et al. (2004) and Trujillo and Allen (2007) suggested that it emerges from phase-locking of ongoing theta-band activity in addition to a general increase in theta power in response to errors. Although the phase-resetting mechanism underlying the generation of the ERN component has recently been questioned (Yeung, Bogacz, Holroyd, Nieuwenhuis, & Cohen, 2007), there is a general consensus about the theta nature of the ERN (Gehring & Willoughby, 2004; Luu & Tucker, 2001; Trujillo & Allen, 2007; Yeung et al., 2007) and the MFN components (Gehring & Willoughby, 2004). Because theta-oscillations in the hippocampus have been shown to reflect adaptive adjustments in the regulation of actions (see, Buzsaki, 2002 for a review), Luu et al. (2003) proposed that the theta activity underlying the ERN is not simply reflecting the activation of the anterior cingulate cortex, but tracking the action regulation functions of a broader circuit involved in the processing of error and negative feedback. With regard to

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the MFN and theta oscillations for losses, we replicated previous studies reporting a right lateralization of these responses (see Figs. 1 and 2) (Gehring & Willoughby, 2004; Muller et al., 2005; Nieuwenhuis et al., 2004).

A novel finding of the present study is the presence of a high-frequency beta oscillatory component associated with monetary gains. Previous studies have either used time–domain analysis exclusively, that due to its poor high frequency retention has prevented investigation of higher frequency parts of the signal, or have looked only at frequencies below 12 Hz. Importantly, the high-frequency oscillations were enhanced for gains relative to losses, thus, showing an inverse pattern compared to the theta band (see Figs. 2 and 3). This high frequency activity is therefore a candidate for a neural marker of reward associated with monetary gains. Using a probabilistic reinforcement learning task (Cohen, Elger, & Ranganath, 2007) also described an increase in power in gains compared to losses for frequencies between 21 and 29 Hz. In addition (Cohen et al., 2007) found that this high frequency power increased with the probability of winning. Complementary our data suggest that the beta power increases with the magnitude of the positive outcome. Hence, both studies suggest a possible role of the beta oscillatory component in two basic aspects of reward processing: probability and magnitude. In addition, our results parallel the outcome of recent fMRI studies (Nieuwenhuis et al., 2005; Marco-Pallares, Muller, & Munte, in press) showing a clear activation in the rostral anterior cingulate cortex, right superior frontal gyrus, posterior cingulate cortex and striatum for positive relative to negative performance feedback. In addition, the frontocentral topography of the beta component observed in our study would also be compatible with the ventral medial orbitofrontal activations as described in studies on reward processing and loss aversion (Kim et al., 2006; Knutson et al., 2003; Nieuwenhuis et al., 2005; Tom et al., 2007). Several recent studies have indeed related fast beta EEG oscillations with fMRI activations, suggesting a positive correlation between the BOLD signal and beta power, and a negative correlation between fMRI and lower EEG frequencies (Kilner, Mattout, Henson, & Friston, 2005; Laufs et al., 2003). Therefore, beta activity present in the positive feedback condition, appears to parallel the findings observed with fMRI (Nieuwenhuis et al., 2005). Due to the large neural network involved in processing of reward (Knutson, Fong, Adams, Varner, & Hommer, 2001; O'Doherty et al., 2001) or positive feedback (Nieuwenhuis et al., 2005) as evidenced by fMRI, a possible role for this beta activity may be to synchronize neural populations over long distances. The evaluation of positive outcomes might be carried out using this mechanism and through the orchestration of the different reward/emotion-related structures. This would be in line with earlier proposals that beta oscillations are suited for the functional coupling of distributed brain regions (Berns et al., 2001; Steriade, 2006). Moreover, Bressler, Coppola, and Nakamura (1993) recorded local field potentials in the cortex of monkeys and described an increase in the beta and gamma band coherence of distant electrodes in a Go-Nogo study. It has been proposed that frequency coherence in the beta and gamma band between distant structures can act as mechanism for large-scale integration (Varela, Lachaux, Rodriguez, & Martinerie, 2001). In addition, Courtemanche, Fujii, and Graybiel (2003) found an increase in beta activity (10–25 Hz) in the striatum of normal macaque monkeys when performing a simple motor task to earn rewards. Furthermore, an increase in the beta power of the EEG after application of a reward has been described in humans (Hallschmid, Molle, Fischer, & Born, 2002). Thus, these studies are compatible with the notion that processing of positive feedback is mediated by beta oscillations that serve to couple fronto-striatal structures involved in reward processing. The existence of two separate oscillatory mechanisms for the processing of positive and negative feedback information is also consistent with recent fMRI data suggesting that two dissociable neural networks can be delineated for the processing of gains and losses (Yacubian et al., 2006). The first system comprises the ventral striatum including nucleus accumbens and makes predictions about positive reinforcements which are compared to actual outcomes and therefore, its activation is sensitive to the magnitude of the expected reward (Knutson et al., 2003; Yacubian et al., 2006). Activation changes in the ventral striatum are thought to be driven by activity of midbrain neurons that project to this part of the striatum. The second system involved the activation of the amygdala in the generation of predictions of aversive or negative events and in the comparison of these predictions against actual outcomes (Breiter, Aharon, Kahneman, Dale, & Shizgal, 2001; LaBar, Gatenby, Gore, LeDoux, & Phelps, 1998; Yacubian et al., 2006).

In addition, other studies have shown a relationship of the theta/beta power during rest with motivation, arousal and decision making (Schutter & Van Honk, 2005; Snyder & Hall, 2006). For example, Schutter and Van Honk (2005) recently reported that disadvantageous decisions in the Iowa gambling task were associated with an increase in the theta/beta EEG ratio. This ratio was calculated from an initial EEG recording of the individuals before performing the gambling task. Following the interpretation of this study, high theta/beta ratios may be associated with a relatively poor inhibitory control over motivational drives causing increased reward dependency and reduced punishment sensitivity (Schutter & Van Honk, 2005). At present, it is unclear whether and how resting theta/beta ratio and the beta and theta responses in the present task are related. It is interesting to speculate that the resting theta/beta ratio reflects the resting state of the mesolimbic dopaminergic reward areas, while the phasic responses to negative and positive feedback in the current study reflect the dynamic response of this system. Clearly, more work is needed to substantiate such speculations.

How do the current findings fit in with the wealth of current animal literature on the neurophysiology of reward (for a recent review, see Schultz, 2006)? It is a well known phenomenon that midbrain dopamine neurons do not show a phasic response to well-predicted rewards and that their activity is depressed when a predicted reward does not substantiate (Mirenowicz & Schultz, 1994; Tremblay & Schultz, 2000). Complementary to these activations, some neurons in the medial prefrontal, anterior, and posterior cingulate cortex reflect an error signal (Ito et al., 2003; McCoy et al., 2003; Watanabe, 1989). In a recent overview

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about medial frontal negativities evoked by negative feedback, Nieuwenhuis et al. (2004) discussed this phenomenon in terms of the reinforcement learning theory of the ERN (Holroyd & Coles, 2002). This theory holds that the ERN and by extension, the feedback related MFN, reflects the impact of the negative prediction error signal, conveyed by the midbrain dopamine system, on the anterior cingulate cortex, which is generated when events are worse than expected. Thus, the MFN as well as the oscillatory theta-activity in the current study behaves similar to the neurons serving as unidirectional error detectors that have been described in animal studies (Ito et al., 2003; McCoy et al., 2003; Watanabe, 1989; however see Kim et al., 2006; Tom et al., 2007 for fMRI studies describing bidirectional error signals in orbitofrontal and ventromedial areas, that increase their activity with reward and decrease it with punishment). On the other hand, the reward-related beta oscillatory component identified in the present study might be a specific response to positive reward. If this is so, we predict that it should be boosted by unexpected large rewards.

Finally, it is worth mentioning that it is difficult to judge the importance of the present findings considering the different theoretical models which compete for explaining the ERN/MFN phenomena: the response conflict monitoring model (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Yeung, Botvinick, & Cohen, 2004) and the reinforcement-learning theory (Holroyd & Coles, 2002). For example, the response-conflict model has remained silent regarding the appearance of the MFN component in presence of feedback and monetary loses. In fact, each model still requires explaining the functional role of reported theta activity (but see Luu & Tucker, 2001; Luu et al., 2003). These models will also have to accommodate the present findings regarding the existence of a beta oscillatory component sensitive to positive feedback and its magnitude. It is also important to consider that analyses going beyond the traditional ERP time–domain approach, such as the time–frequency analysis in the present study, can add important information for a deeper understanding of neural implementation of error and feedback processing.

5. Conclusion

Time–frequency analysis of feedback related activity revealed two different oscillatory responses. First, a frontocentral theta component was seen in response to negative feedback, which underlies the previously described medial frontal ERP negativity. By contrast, a high-frequency frontocentral beta response was associated with positive feedback (monetary gains), whose function might be to functionally couple different brain areas during reward processing.

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