



## Full Length Article

## The role of beta-gamma oscillations in unexpected rewards processing

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## ABSTRACT

Reward processing in humans is carried out by an extensive fronto-subcortical network that might be coordinated by fast oscillatory electrical activity. Previous studies have identified an increase in beta-gamma oscillatory activity after the processing of positive feedback stimuli but the functional role of this electroencephalographic (EEG) correlate remains unclear. In the present study, we used event-related brain potentials (ERPs) and trial-by-trial wavelet-based time–frequency analysis of the EEG signal to investigate the effects of expectancy and magnitude of positive and negative feedbacks associated with monetary gains and losses in a gambling task. Large increase of beta-gamma oscillatory activity only in unexpected monetary gains was observed, irrespective of its magnitude. Based on recent findings we propose that this increase in beta-gamma oscillatory activity might reflect a general cognitive mechanism in charge of monitoring unexpected positive events based on feedback processing.

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## Introduction

Reward processing in humans is carried out by an extensive fronto-subcortical network, composed by several brain structures including the striatum, amygdala, orbitofrontal and insular cortex (Camara et al., 2009; Koob and Volkow, 2010). The existence of such extensive network requires for an integration mechanism that allows the coordination of the different areas involved in it. Brain oscillations seem to be an optimal mechanism for such task (Buzsáki and Draguhn, 2004; Varela et al., 2001). Specifically high frequency oscillations (beta and gamma bands) are key candidates to synchronize these different components as they allow the integration of information across distant brain areas (Colgin et al., 2009; Steriade, 2006; Uhlhaas and Singer, 2006).

In this regard, intracranial recordings on animals have found increase in beta and gamma oscillatory activity in striatum and frontal cortex after actions that were carried out to obtain rewards (Berke, 2009; Courtemanche et al., 2003). In humans, non-invasive electroencephalographic recordings have revealed an increase in the EEG beta band power (Hallschmid et al., 2002) as well as an increase in the beta/theta ratio activity (Schutter and Van Honk, 2005; Snyder and Hall, 2006) during reward processing. In addition, beta-gamma band (20–35 Hz) power increase has been observed 200–400 ms

after positive feedback informing about monetary gains using EEG (Cohen et al., 2007; Marco-Pallarés et al., 2008, 2009; see for a recent replication using Magnetoencephalography, Doñamayor et al., 2011) which might be modulated by probability (Cohen et al., 2007) and magnitude of rewards (Marco-Pallarés et al., 2008). In addition, Marco-Pallarés et al. (2009) found a modulation of this response with the COMT Val158Met polymorphism, supporting a possible role of dopamine in this gain related response.

All these studies suggest that beta-gamma oscillatory activity might be an important brain signature of reward-related networks but little is known about the nature of this response or its functional properties. Direct recordings from the Ventral Tegmental Area of awaken monkeys have shown an increase in the dopaminergic activity after improbable rewards (Fiorillo et al., 2003; Schultz et al., 1997; Waelti et al., 2001) or after larger than expected rewards (Tobler et al., 2005). Complementarily, studies in humans have described that some brain areas such as the ventral striatum (Nucleus Accumbens), amygdala and anterior cingulate cortex are selectively activated when a mismatch is detected between the real feedback obtained from an action and the expected one (hereafter referred as *prediction error* term, PE; Hare et al., 2008; Rutledge et al., 2010; Yacubian et al., 2006). In this context, it has not been appropriately studied which aspects (i.e. probability, magnitude, expected value or prediction error) elicit and modulate beta-gamma oscillatory activity in monetary reward processing. The goal of the present study is to determine the functional significance of beta-gamma power increase after rewards using a gambling Event-Related Potential (ERP) paradigm in which probability and magnitude of rewards and punishments were carefully manipulated.

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## Materials and methods

### Subjects

Twenty-six right-handed healthy students participated in the experiment (four men, mean age  $25.6 \pm 4.8$  (S.D.)) for monetary compensation. None of the participants had any history of neurological diseases or substance abuse. Subjects were paid 30 Euros for participation plus/minus what they won/lost in the game respectively. Written consent was obtained prior to the experiment. The experiment was approved by the local ethical committee.

### Design

Experimental design is shown in Fig. 1. The experiment consisted in a choice between three cards and the subjects played for real money. There were 1400 trials that each one lasted 3–4 s depending on the speed of the response by the subject. Each trial began when a card appeared on the screen for 1 s. This card gave the subject information about the probability and magnitude of the upcoming gain or loss (blue: 10 cents, yellow: 50 cents, 1: 1/3 probability of gain, 2: 2/3 probability of gain). Subjects had to choose a card among three to win, each of them containing the amount to bet (50 cents € for the large magnitude, 10 cents € for the low magnitude). After a second, cards turned green or red. If the subject had chosen a green card, he/she won the amount of money bet; in case of being red, he/she lost this amount of money. This information lasted 1.5 s on the screen. The experiment consisted of 56 blocks, each one with 25 trials. After each block participants saw the total amount that they had gained/lost. In addition, for half of the subjects, the colors were inverted (red for gains and green for losses) in order to eliminate a possible effect of emotional correspondence of the colors. The 1400 trials in the task were presented to subjects in a pseudorandom order and were

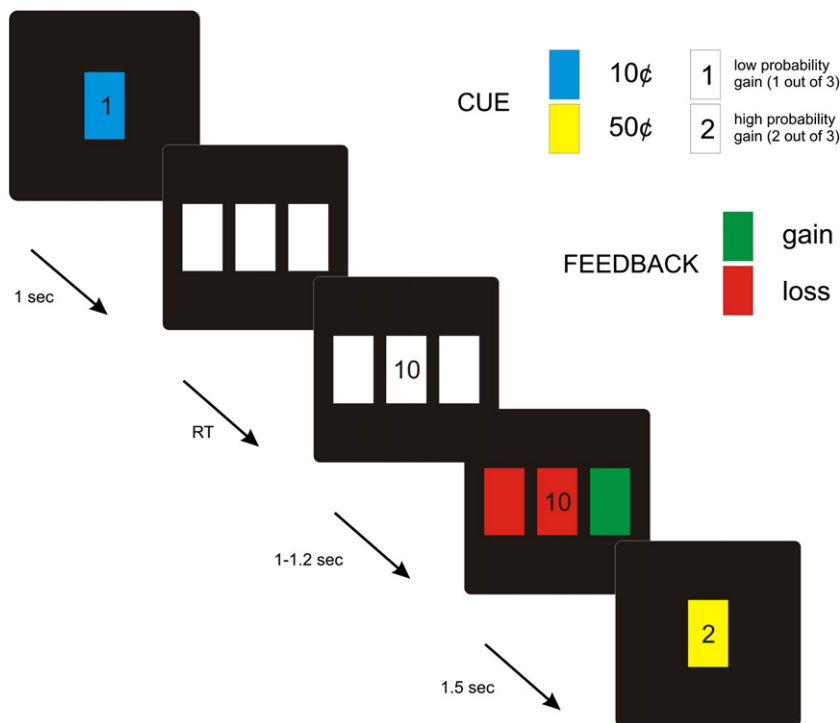
divided between the conditions to ensure the same number of gain and loss trials (700 gain and 700 loss trials). There were 300 trials starting with each of the following cues: high probability large magnitude (200 gains and 100 losses), high probability small magnitude (200 gains and 100 losses), low probability large magnitude (100 gains and 200 losses) and low probability small magnitude (100 gains and 200 losses). Finally 200 trials (100 gains and 100 losses) started with a neutral cue (a question mark) which gave no information about the probability or magnitude of the outcome.

There were three parameters that changed between conditions: valence (gain/loss), probability of gain (high/low) and Magnitude (large/small). Probability was presented as the number of the cards out of three that won: therefore the low probability was 1/3 and the high probability was 2/3. In each trial, subjects won or lost the amount that they saw on the cards.

### EEG recording and analysis

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, T4/5, Cp1/2, Cp5/6, Pz, P3/4, P7/P8, Po1/2, O1/2). Bio-signals were re-referenced offline to the mean of the activity at the two mastoids. Vertical eye movements were monitored with an electrode at the infraorbital ridge of the right eye. Electrode impedances were kept below 5 k $\Omega$ . The electrophysiological signals were filtered online with a highpass of 0.01 Hz (half-amplitude cutoffs) and digitized at a rate of 500 Hz. Epochs with the different feedback conditions were extracted from –100 ms before the feedback stimuli to 1000 ms after it. Trials with amplitudes of more than 100  $\mu$ V were automatically rejected offline. Six subjects presenting more than 20% rejection rate of trials were eliminated from the study.

To study the time-frequency behavior of the signals, the EEG data were convolved with a seven-cycle complex Morlet wavelet for all



**Fig. 1.** Experimental paradigm; the first cue represents expectation on the probability and magnitude of an upcoming reward/punishment. The number in the card indicates how many winning cards will be in the next three-card choice (if 1, P of winning = 1/3; if 2, P of winning = 2/3). If the card is blue the magnitude of the gain/loss will be 10 cents (small magnitude), while if it is yellow the gain/loss will be 50 cents (large magnitude). After 1 s, 3 white cards appear and the subject makes a choice. After 1–1.2 s (which was randomly changed in this interval to cancel the possible effect of automatic responses) cards turn red or green. If the participant has selected a green card, he/she will win the amount of money bet; if the card is red, he/she will lose this amount of money.

the desired events (from 1 to 40 Hz, linear increase). Changes in time varying energy with respect to baseline (100 ms before stimuli) were computed for each trial and averaged for each subject before performing a grand average.

### Statistical analysis

Previous studies have described a negative frontocentral event-related potential component after feedback announcing a “loss” (punishment) in gambling or decision making which appears 250–300 ms after the feedback presentation (the Feedback-Related Negativity, FRN, Gehring and Willoughby, 2002; Miltner et al., 1997). Therefore we focused our ERP analysis on this component by averaging 100 ms around its peak. Further, time-frequency data were analyzed in the theta and beta-gamma bands, which have been previously shown to be involved in reward and punishment processing (Marco-Pallarés et al., 2008, 2009). Studied time ranges were based on visual inspection of the studied conditions. Significant differences among conditions both in ERPs (amplitude) and time-frequency data (changes in power respect to baseline) were assessed by means of repeated measures ANOVA with four different factors: valence (gain/loss), probability (high/low) and magnitude (large/small) at midline electrodes (Fz, Cz, Pz). 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.

### Prediction error analysis

One of the goals of the present study was to determine whether gamma power increase after rewards was associated with the prediction error term (PE), as previously proposed for some brain electrical signatures such as FRN (Chase et al., 2011; Cohen and Ranganath, 2007; Holroyd and Coles, 2002). PE is defined as the difference between the real obtained outcome and the expected outcome. In each trial, the cue defined a probability of obtaining a reward (1/3 or 2/3) and magnitude for the subsequent reward or punishment. Therefore, for example, if the cue was blue (low magnitude of reward, 10 cents) and had the number two inside (two correct cards, 2/3 probability of winning) the expected value for this trials would be the sum of the expected value of winning and losing, that is  $10 \times 2/3 - 10 \times 1/3 = 3.33$  (see Table 1). In consequence, if a subject wins in one trial, the PE would be the difference between the outcome and the expected value ( $10 - 3.3 = 6.6$ ). In case of losing, the predicted error might yield a negative value ( $-10 - 3.3 = -13.3$ ). Values of PE for each cue-outcome combination are computed in Table 1.

In order to determine whether the FRN and beta-gamma power increase were sensible to PEs, values for the different conditions of magnitude (large/small) and probability (high/low) at the Fz electrode were sorted in decreasing order of PE. An ANOVA with the four factors (different PE) separately for gains and losses was computed to determine a possible linear trend with the PE signal.

**Table 1**

Prediction error for eight different conditions of the task depending on the cue and outcome. Large Magnitude: 50 cents, Small Magnitude: 10 cents, High probability:  $p = 2/3$  of winning; Low probability:  $p = 1/3$  of winning.

Outcome	Gain				Loss			
	Large		Small		Large		Small	
Magnitude	Low		High		Low		High	
Probability	Low	High	Low	High	Low	High	Low	High
<b>Expected Value</b>	-16.7	16.7	-3.3	3.3	-16.7	16.7	-3.3	3.3
<b>Prediction Error</b>	66.7	33.3	13.3	6.6	-33.3	-66.7	-6.6	-13.3

## Results

### Behavioral results

Participants chose the three cards from left to right in 29.6% (left), 44.3% (middle) and 26.1% (right) of trials. ANOVA showed a significant effect of card location ( $F(2,38) = 12.61, P = 0.001$ ) and post hoc *t*-tests showed that subjects chose the middle card significantly more than the left and right cards (for left and middle:  $t(19) = -2.97, p < 0.01$ , for right and middle:  $t(19) = -4.55, P < 0.001$ ) while there was no significant difference in choosing left and right cards ( $t(19) = 1.79, n.s.$ ). The average reaction times for the four different conditions were  $911.2 \text{ ms} \pm 365$  (S.D.) for high probability of gain and small magnitude,  $891.2 \text{ ms} \pm 378$  for high probability of gain and large magnitude,  $910.4 \text{ ms} \pm 347.4$  for low probability of gain and small magnitude and  $907.1 \text{ ms} \pm 364.0$  for low probability of gain and large magnitude. The ANOVA showed no significant differences among the reaction times in these four conditions. In addition, given the duration of the experiment and in order to study if reaction time (RT) changed with time, we divided the whole experiment in three blocks with equal number of trials and analyzed their RTs separately. The mean RT for the First block was  $1091 \pm 495$  ms, second block  $859 \pm 362$  ms and last block  $747 \pm 290$  ms. Repeated measures ANOVA revealed a significant decrease of RT with time ( $F(1,19) = 14.45, p < 0.001$ ).

Additionally, an ANOVA with cards (3) and conditions (4) as factors did not show any effect of condition on the choice of cards which confirms that there was no learning. The average amount of money gained at the end was  $1.35 \pm 0.91$  Euros.

### ERP results (time domain)

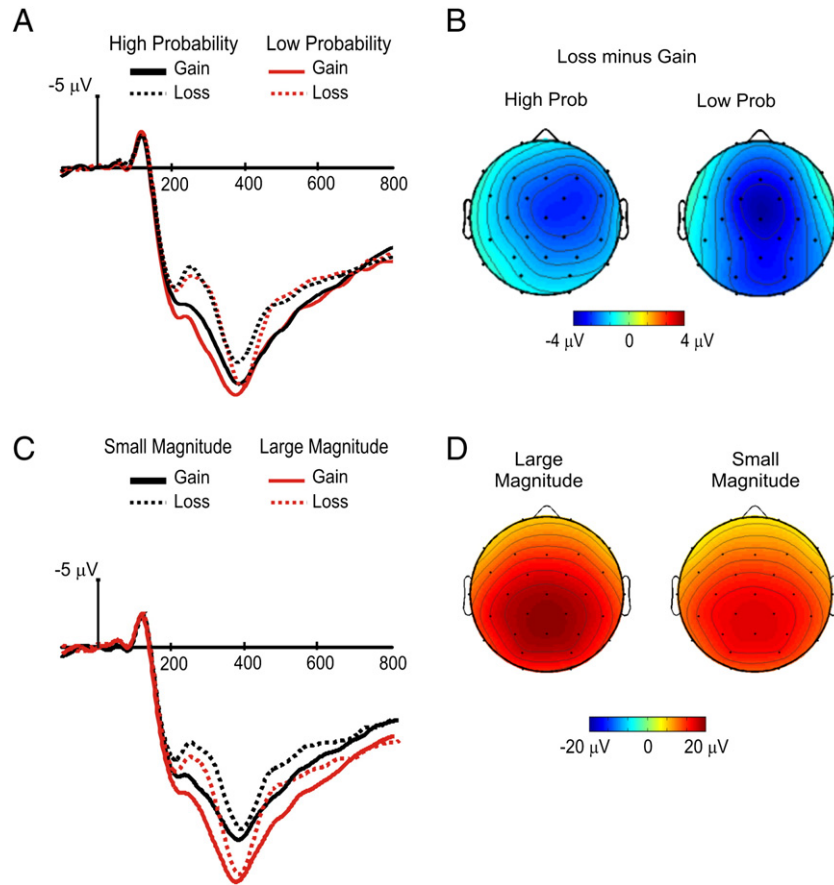
ERP waveforms presented a negative deflection approximately 260 ms after the presentation of negative feedback, compatible with the FRN (Figs. 2A,C). This increase of negativity after punishments compared to rewards was confirmed by a significant effect of Valence ( $F(1,19) = 29.2, P < 0.001$ , Fig. 2 and Table 2). The FRN component presented a frontocentral distribution (Valence  $\times$  Electrode interaction,  $F(2,38) = 8.2, P < 0.005, \epsilon = 0.88$ , Fig. 2B) as previously described in several papers (see, e.g., Gehring and Willoughby, 2002; Miltner et al., 1997).

The probability of gain also modified the responses to gains and losses after feedback (Figs. 2A,B). Low Probability of gaining trials presented greater amplitude of the FRN component compared to high probability ones (significant Probability main effect  $F(1,19) = 10.5, P < 0.005$ ). In addition, the amplitude of the difference waveform (loss minus gain) was larger for lower probability compared to higher probability trials, mainly at frontal electrodes (Fig. 2B) as indicated by significant interaction between Probability and Valence ( $F(1,19) = 5.0, P < 0.05$ , see Fig. 2B and Table 2).

As expected from previous studies (Yeung and Sanfey, 2004), Fig. 2C shows that magnitude also modified the response to feedback in the FRN interval. The response after the trials that had a large magnitude of reward showed larger amplitudes in both gains and losses with a centroparietal distribution (Magnitude  $F(1,19) = 25.2, P < 0.001$ , Magnitude  $\times$  Electrode  $F(8,152) = 7.4, P < 0.005, \epsilon = 0.80$ , see Fig. 2D), but there was no significant interaction between valence and magnitude, indicating that magnitude affected gains and losses equally (Valence  $\times$  Magnitude  $F(1,19) = 0.1, n.s.$ ).

### Time-frequency results

Time frequency analysis yielded two important modulations of the frequency components: a theta increase present in all conditions (4–8 Hz) and a high frequency beta-gamma band power increase associated with gains (25–35 Hz, Fig. 3). Theta power increase



**Fig. 2.** A. Grand-averaged ERP responses to the feedback in high (black line) and low (red line) probability conditions for gains (solid lines) and losses (dashed lines) at Fz. Note the negativity associated with losses around 250 ms after the presentation of the feedback. For illustration purposes data were lowpass filtered to 12 Hz. B. Topographical maps of the potential distribution of the difference between gain and loss trials (210–310 ms) after the presentation of feedback are presented in two probability conditions. C. Grand-averaged ERP responses to the feedback in small (black line) and large magnitude (red lines) conditions for gains (solid lines) and losses (dashed lines) at Fz. D. Topographical maps of the potential distribution in the large and small magnitude conditions (210–310 ms) after the presentation of feedback are presented.

200–500 ms after the incoming of the feedback in the 4–8 Hz band was higher for losses than for gains (Fig. 3) as revealed a marginal significant Valence effect (Valence  $F(1,19) = 3.4, P < 0.1$ ). This

**Table 2**  
ANOVA results for the studied conditions in the FRN ERP in the 210–310 ms time range after feedback incoming, and the time frequency results for the theta (4–8 Hz, 200–500 ms) and high beta bands (25–35 Hz, 200–400 ms).

Factor	d.f.	FRN	Theta	Beta-gamma
Valence	1,19	29.2***	3.5+	4.6*
Probability	1,19	10.5***	0.3	6.7*
Magnitude	1,19	25.2***	10.7**	0.0
Electrode	2,38	13.2***	7.4**	1.9
Valence × Probability	1,19	5.0*	1.7	4.4*
Valence × Magnitude	1,19	0.1	0.9	0.3
Probability × Magnitude	1,19	0.0	6.3*	2.2
Valence × Probability × Magnitude	1,19	0.1	0.5	0.0
Valence × Electrode	2,38	8.2**	12.7**	4.7*
Probability × Electrode	2,38	9.5**	0.7	0.7
Valence × Probability × Electrode	2,38	0.5	1.4	1.8
Magnitude × Electrode	2,38	7.4**	4.1*	0.7
Valence × Magnitude × Electrode	2,38	1.0	0.6	0.9
Probability × Magnitude × Electrode	2,38	0.6	0.2	2.8+
Valence × Probability × Magnitude × Electrode	2,38	0.1	0.0	1.1

\*\*\*  $P < 0.001$ .  
\*\*  $P < 0.01$ .  
\*  $P < 0.05$ .  
+  $P < 0.1$ .

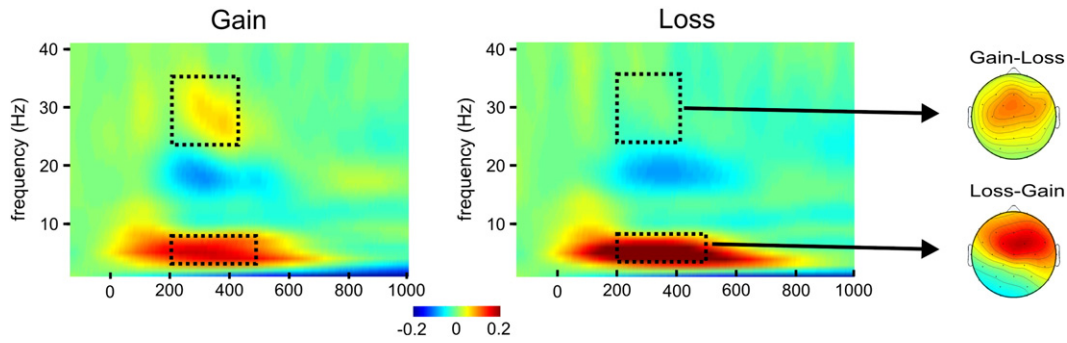
difference presented a frontocentral distribution (Valence × Electrode  $F(2,38) = 12.6, P < 0.001, \epsilon = 0.69$ , Fig. 3 and Table 2).

Beta-gamma band (25–35 Hz) between 200 and 400 ms after the incoming of the feedback showed greater activity for gains than for losses (Valence  $F(1,19) = 4.6, P < 0.05$ , Fig. 4, Table 2), which also presented a significant frontocentral distribution (Valence × Electrode  $F(2,38) = 4.7, P < 0.05, \epsilon = 0.82$ , Fig. 3 and Table 2). Fig. 4 shows time-frequency plots in 4 different conditions of valence (gain, loss) and probability (high probability of gain, low probability of gain). Increase of power in the beta-gamma band was found in gains with low probability of winning trials only (improbable gains), while no significant increase was found in the gain with high probability of winning trials, nor in the loss trials. This was confirmed by a significant effect of Valence × Probability ( $F(1,19) = 4.4, P = 0.05$ ). Therefore, gain trials presented significant increase of beta-gamma power in low probability of gaining trials compared to high probability of gaining trials ( $t(19) = 2.6, P < 0.05$ , Figs. 4 and 5B) while there were no significant differences between high and low probability loss trials ( $t(19) = -0.46, n.s.$ ).

*Prediction error signal*

Given that previous studies have related the FRN with a PE signal (Chase et al., 2011; Cohen and Ranganath, 2007), we tested to what extent our results might be explained by a modulation with a PE signal, which is defined as the difference between expected and the obtained outcome, being the Expected value (EV) the product of reward magnitude and reward probability (see Materials and





**Fig. 3.** Time–frequency plots for gain and loss conditions at Fz with the topographical maps of power difference distribution in theta band (4–8 Hz, 200–500 ms window) and beta-gamma band (25–35 Hz, 200–400 ms window).

methods). Table 1 presents the EV and PE computed for the eight different conditions depending on the cue (probability and magnitude) and the outcome. Fig. 5A shows the amplitude value of each condition sorted in the order of decreasing prediction error value at the Fz electrode. Repeated measures ANOVA was computed with the four studied conditions [combination of probability (high/low probability of gain) and magnitude (large/small)] sorted in decreasing PE order at the Fz electrode. Gain trials showed a significant linear decrease of amplitude with PE ( $F(3, 57) = 7.2, P < 0.001$ , linear effect  $F(1, 19) = 13.2; P < 0.005$ , Fig. 5A). In these trials large magnitude conditions presented larger amplitudes than small magnitude trials ( $t(19) = 3.3, P < 0.005$ ) and low probability of gaining trials showed greater amplitude than high probability trials ( $t(19) = 2.6, P < 0.05$ , Fig. 5A). In addition, a significant positive linear increase was found for negative outcomes, while this effect was not evident in Fig. 5A (main effect  $F(3, 57) = 5.3, P < 0.01$ , linear trend  $F(1, 19) = 10.1; P < 0.01$ ). In these trials, a significant effect of magnitude was encountered ( $t(19) = -3.7, P < 0.005$ , Fig. 5A), but not for probability ( $t(19) = 1.0, n.s.$ ).

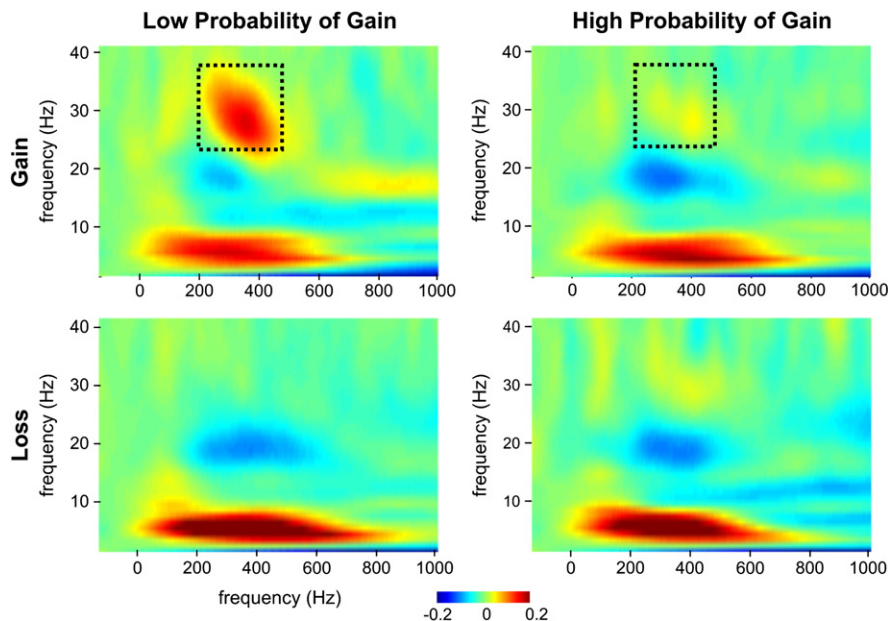
Regarding the analysis of the beta-gamma band with PE, Fig. 5B depicts the beta-gamma pattern which clearly differs from the evoked potentials pattern (Fig. 5A), especially in the gain condition. While ERPs present a linear decrease with PE in gains, beta-gamma power shows an increase in the activity for gain in low probability

trials compared to high probability trials (main effect  $F(3, 57) = 5.5, P < 0.01$ ) but not a significant linear trend with prediction (Fig. 5B,  $F(1, 19) = 2.2; n.s.$ ), indicating that the observed effect is not related to PE (effect of Probability  $F(1, 19) = 6.2, P < 0.05$ ). In addition no significant differences were found in loss conditions ( $F(3, 57) = 0.4; n.s.$ ).

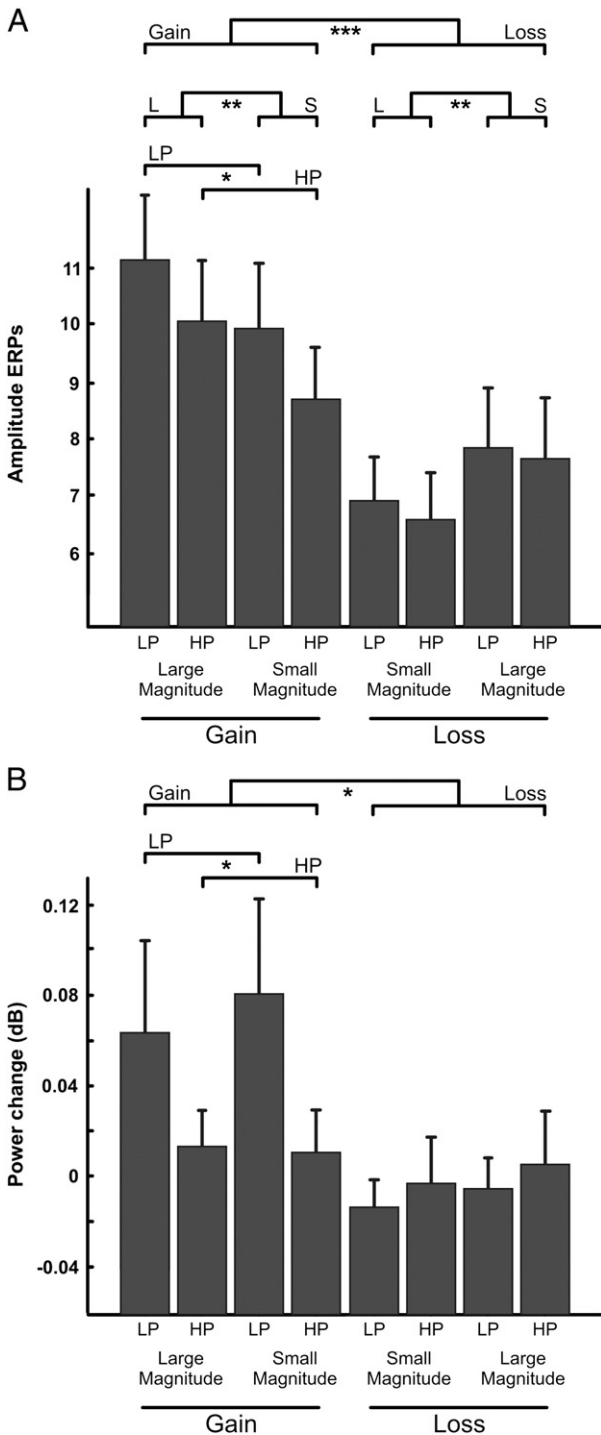
#### Relationship between oscillatory components and switch-stay behavior

Given that some studies have described a relationship between theta activity and task-switching (Cunillera et al., 2012; Sauseng et al., 2006) we studied to what extent the theta and beta-gamma oscillatory components found to be involved in positive and negative feedback processing might be related to the tendency to repeat the same decision after winning or to switch after a monetary loss. In general, subjects tended to switch their responses in the next trial more often than repeated the same response (switch:  $60.1 \pm 10.6\%$ , stay:  $39.1 \pm 10.5\%$ ,  $t(19) = 4.7, P < 0.001$ ). Notice that this pattern could be explained by the fact that there were 3 response buttons and there were no learning effects during the task. Interestingly, participants switched more after a monetary loss than after winning ( $t(19) = 2.1, P < 0.05$ ; percentage of switching after a win-trial  $56.7 \pm 18.4\%$ , win-stay:  $43.3 \pm 14.1\%$ ; loss-switch:  $65.1 \pm 5.8\%$ , loss-stay:  $34.9 \pm 5.8\%$ ).

In the time-frequency analysis, repeated measures ANOVA with four factors (valence, probability, magnitude and switch/stay) was



**Fig. 4.** Time–frequency plots for all combinations of valence and probability conditions at Fz. Note the increase in the gamma band power only for gain low probability trials.



**Fig. 5.** A. ERP amplitude and B. beta-gamma power change in the FRN window at Fz in all eight conditions in the prediction error decreasing order (see Table 1). Significant effects are marked. \*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$ .

performed to analyze changes in power at Fz for theta and beta bands. One subject was removed from this analysis as presented very few (<10) trials in some conditions. Neither theta activity ( $F(1,18) = 1.0$ , *n.s.*) nor beta activity ( $F(1,18) = 2.3$ , *n.s.*) showed significant changes in the switch/stay conditions, nor any significant interaction with the other factors (theta activity:  $F(1,18) < 0.2$ , *n.s.* for valence  $\times$  switch, magnitude  $\times$  switch and valence  $\times$  magnitude  $\times$  switch;  $F(1,18) < 2.3$ , *n.s.* for the other interactions; beta-gamma activity: probability  $\times$  switch  $F(1,18) < 2.3$ , *n.s.*;  $F(1,18) < 1$ , *n.s.* for the other interactions).

**Discussion**

In the present study we analyzed the involvement of high-frequency brain oscillatory activity in monetary reward processing in humans. In concrete, we tested whether beta-gamma power increase after a positive feedback was modulated by the probability, magnitude or expected value of the monetary outcome. We found a beta-gamma<sup>1</sup> increase only after unexpected gains, being this effect not related to the expected value or prediction error. Some fMRI studies (Haber and Knutson, 2010; Yacubian et al., 2006) and ERP (San Martín et al., 2010) have addressed the combined impact of probability and magnitude (expected value) of reward in the outcome evaluation, but to our knowledge this is the first study to address how these properties affect high-frequency EEG oscillatory activity associated with positive and negative outcomes in humans. The involvement of beta-gamma band oscillatory activity in reward processing has been observed in several animal studies (Courtemanche et al., 2003; Kalenscher et al., 2010; van der Meer and Redish, 2009). Non-invasive EEG recordings have also reported increase of beta-gamma power after improbable (Cohen et al., 2007) and large rewards (Marco-Pallarés et al., 2008). Results of present study seem to suggest that beta-gamma modulations of reward are selectively signaling salient and novel positive events in the environment, and therefore, they could be related to a general mechanism in charge of monitoring unexpected and possible encoding of positive events based on feedback processing.

The idea that beta-gamma modulations of reward are selectively signaling salient and novel positive events would also be consistent with several motivational accounts which propose different emotional and attentional processes involved when expecting improbable but positive signals. For example, some models have emphasized the important role of surprise and unexpectedness at reward occurrence and how this affects posterior motivational processing (Mellers and McGraw, 2001; Mellers et al., 1998). Interestingly, in our particular experimental setup the magnitude of the reward seems less relevant, as the processing of low and high magnitude improbable rewards elicited the same power at the beta-gamma band at the time of feedback. This increase is selective for positive events as the effect was not observed for improbable negative feedbacks. In this regard, we cannot attribute this effect to a general attentional increase in beta-gamma band to improbable feedbacks because it depends on the emotional content of the stimuli. This last observation argues in favor of the important interaction between emotion and attention. It has been well documented that emotional stimuli attract attention (e.g., Anderson, 2005; Pessoa et al., 2002), thereby increasing the likelihood that the emotional information will be perceived and stored and therefore used in the future for goal-directed behaviors (Ohman et al., 2001). Increase of power in fast oscillations has been associated with an increase in attentional processing and the enhancement of neuronal representations of attended sensory inputs, as well as for the regulation of the communication among neural groups in spatially distant areas (Buschman and Miller, 2009; Gregoriou et al., 2009; Womelsdorf and Fries, 2007). Thus, the beta-gamma increase observed in the present study could represent a brain signature that might respond to unexpected positive outcomes and in charge of transmitting a fast motivational value signal to downstream brain structures.

Several regions involved in the reward-related dopaminergic circuit, such as striatum (Yacubian et al., 2006), anterior cingulate cortex (Rutledge et al., 2010), amygdala (Yacubian et al., 2006) and insula (Pessiglione et al., 2006) have been found to encode prediction error signals. Further, seminal studies by Schultz et al. (1997) showed

<sup>1</sup> It is important to appreciate that positive monetary feedback affects partially high-beta and low-gamma bands, being normally beta attributed to 13–30 Hz and gamma band > 30).

that Ventral Tegmental Area also coded prediction error by increasing the phasic dopaminergic activity after *better than expected* outcomes and decreasing it after *worse than expected* events. In contrast, our results show increase of beta-gamma activity after unexpected gains only. Importantly, in a recent review, Bromberg-Martin et al. (2010) suggested a segregation of DA neuron populations in two groups: some encoding motivational value, as the ones described by Schultz et al. (1997) encoding prediction error; and others signaling motivational salience, that is, aversive or alerting events. This would be in line with our proposal that the beta-gamma increase found after unexpected gains might reflect a dopaminergic activation after a salient event. In addition, a close link between beta-gamma oscillations and dopamine could be inferred from recent studies showing that changes in dopamine levels are associated with the reestablishment of gamma band oscillations and a change from low to high-oscillatory activity (Brown et al., 2001; Lalo et al., 2008). Further, in a recent study we found that beta-gamma activity after positive feedbacks was modulated by differences in dopaminergic polymorphisms (Marco-Pallarés et al., 2009).

However, it is worth noticing that EEG mostly captures brain electrical activity from the cortex. The frontal topography of the beta-gamma effect encountered (Fig. 4) would argue in favor of a medial-prefrontal generator. The ventral tegmental area (VTA) and the ventral striatum (Nucleus Accumbens) project to the anterior cingulate (Haber and Knutson, 2010; Wise, 2002) showing a segregation between cells, with some neurons codifying positive and some others codifying negative prediction errors (Matsumoto et al., 2007; Rushworth and Behrens, 2008). As high frequency activity has been suggested to mediate coupling between distant structures, we proposed (Marco-Pallarés et al., 2008) that beta-gamma activity after rewards could mediate the frontostriatal coupling observed in some animal studies (Berns et al., 2001; Bressler et al., 1993; Steriade, 2006). Present data further supports this idea introducing the possibility that this activity is responsive to improbable novel positive events. While speculative, this activity might be part of a wider network which could involve the activation of the learning-memory circuit (Camara et al., 2009; Marco-Pallarés et al., 2007). In fact our results show a clear dissociation between the FRN and the beta-gamma increase of power which might be relevant in the study of neural dynamics underlying feedback learning. One of the most influential theories about FRN generation holds that this component emerges as a consequence of phasic decreases in the activity of mid-brain dopaminergic neurons reflecting negative prediction errors (worse than expected events, Holroyd and Coles, 2002), being this changes projected to the dorsal part of Anterior Cingulate Cortex (ACC). This reinforcement learning theory proposes that the amplitude of FRN reflects the size of the prediction error (PE) (Holroyd and Coles, 2002; Holroyd et al., 2003, 2008), which is computed considering the probability and magnitude of rewards and punishments. Our results, showing an association of the FRN in win trials (but not in loss trials) with PE are similar to those found recently (San Martín et al., 2010), but opposite to other studies that have described modulations of FRN with PE (Chase et al., 2010). In addition, theta band power has also been associated with negative and positive PE in probabilistic learning tasks (Cavanagh et al., 2010). Discrepancies in the literature about the relationship between FRN, theta activity and PE might be explained by a differential use of feedback in the adjustment of future actions (Cohen et al., 2011). In our study feedback information is not relevant for the next trials while in other tasks (such as probabilistic learning tasks, Cohen et al., 2007; Cavanagh et al., 2010, Chase et al., 2010, or Wisconsin card sorting task, Cunillera et al., 2012), information provided by feedback is crucial in order to adjust behavior to find an optimal strategy. However in our task, although feedback was not relevant for future behavior, beta-gamma activity presents a clear enhancement with unpredicted gain trials. Therefore, in learning paradigms beta-gamma activity should present

an increase in activation in those positive trials conveying either unexpected gains or more relevant information associated with positive feedbacks (see for a recent example, Cunillera et al., 2012). Interestingly, a recent paper by Cohen et al., 2011 have proposed a new framework to understand feedback learning mechanisms in which changes in synaptic plasticity due to learning are associated with changes in oscillatory synchronization between stimulus-processing and motor areas involved in the stimulus–response mapping. In addition, they propose the involvement of different frequency bands depending on feedback valence used during the learning process: changes in frontal theta oscillatory activity and synchronization would be associated with negative feedback learning while frontal beta activity would be linked to positive feedback. Our results on the beta-gamma increase after unexpected rewards would support this hypothesis, as these would be the win trials that potentially could provide more information in learning paradigms. However, it is interesting to note that in our results theta activity was present in both expected and unexpected loss trials (Fig. 4), indicating a possible dissociation between reward and punishment mechanisms in feedback learning. Further studies using learning paradigm and the analysis of both power changes and synchronization measures might help to validate the hypothetical dissociation of theta and beta bands in learning from negative and positive feedback respectively (see discussion in Cunillera et al., 2012).

## Conclusion

The present paper shows that beta-gamma activity might be a brain signature of unexpected gain that might reflect frontostriatal interactions in the reward network. Further studies are needed to delineate the neural network involved in the generation of this response.

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