

**Time course of the neural activity related to behavioral decision-making
as revealed by event-related potentials**

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Abstract

Objective: To study the time course of the electrocortical activity evoked by wins and losses in the Iowa Gambling Task (IGT), their source localizations, and their relationship with the task performance in order to achieve a better knowledge of the processes that lead to more wins than losses while the task is performed.

Method: Event related potentials (ERPs) were obtained from the EEG (64-channel) of 25 participants while they performed the IGT. Source localization analyses of the ERPs were also performed.

Results: ERP amplitudes were sensitive to wins and losses and also to the amount of money earned or lost. An early fronto-central negativity was elicited following feedback for both wins and losses, and its amplitude correlated with the number of wins at FCz and with both the number of wins and losses at Cz. The P200 had larger amplitude to losses and correlated positively with the number of losses. Feedback related negativity (FRN) was higher to loss trials in occipital and both left and right temporal electrodes. Frontal FRNs were more negative to loss feedback signals. Loss trials elicited larger P300 magnitudes than wins for all electrode localizations. **Conclusions:** All the wave components studied, but P300, were related to participants' performance in the IGT. P200 and P300 may reflect a similar process related to the conscious recognition of the error. Long-latency potentials in the time window of 500-600 ms are not related to P200 and P300. Performance data and source analysis underline the importance of the medial prefrontal cortex in loss feedback processing and in the performance of the IGT.

Keywords: Decision making, Evoked potentials, Feedback learning, P200 evoked potentials, P300 component.

1. Introduction

A current approach to studying reward processing in decision-making involves the use of gambling paradigms in which decisions result in some form of monetary gain and loss. These paradigms have been used in both behavioral and neuroimaging studies of normal healthy participants and neurological and psychiatric patients. However, studying the processing of choice outcomes by using event related potentials (ERPs) may provide insight into the time course of neural responses to reward and punishment and their relationship with subsequent decisions. This is especially important in those tasks used in clinical settings, as it is the case of the Iowa Gambling Task (IGT; Bechara, Damasio, Damasio, and Anderson, 1994).

The IGT is a useful tool to study risky decision-making in a variety of clinical populations, where it is employed together with other diagnostic measures (Bechara et al., 1994; 2001; Buelow & Suhr, 2009; Bolla et al., 2003; Tchanturia et al., 2007; Walteros et al., 2011). This task simulates real-life decision-making under uncertainty and has proved to be useful in the detection of decision-making impairments in several neurological and psychiatric conditions. The IGT is a 100-trial task in which **participants** must choose between four decks of cards in each trial. The four decks have **monetary** wins and losses varying in amount and probability, in such a way that two of them offer high immediate gains, but larger losses in the long run (disadvantageous decks), while the two decks remaining offer lower immediate gains but also lower long term losses (advantageous decks). Participants must adjust their choices (to choose from the advantageous decks and

to avoid the disadvantageous ones) by learning along the task what are the advantageous and disadvantageous decks from the feedback they receive immediately after each choice. Hence, this is a complex decision-making task where decisions are supposed to be made under high ambiguity and unpredictability, particularly (but not exclusively) in the first 40 trials due to the lack of knowledge about the probabilities of winning and losing associated to each option (deck).

A number of lesion and brain imaging studies indicate that IGT performance is related to the integrity and activity of different brain areas, mainly located in the frontal lobes: orbitofrontal and ventromedial prefrontal cortices, dorsolateral prefrontal cortex, and anterior cingulate cortex (see Martinez-Selva et al., 2006 for a review). However less is known about the differential brain processing of wins and losses that eventually leads to choose advantageous instead of disadvantageous decks and to succeed in the task. In many gambling tasks, including the IGT, participants do not usually know whether their choice will lead to losses or gains until a feedback is provided. These feedback signals provoke brain reactions that can be detected through the study of the electrical brain activity, such as ERPs. The brain reaction to feedback signals is supposed to lead to a better adjustment of the subsequent behavior, that is, to better choices (Holroyd and Coles, 2002). Given the importance of the contingencies associated to each decision for the subsequent choices, it would be worth to know the temporal dynamics of cortical activity related to the outcomes or feedback of the choices and this constitutes the main goal of this research. Win and loss feedback signals may promote a differential processing at a brain level, which is reflected in the ERPs they provoke, and may reveal how the brain reacts to the consequences of the

choices and how these guide the participants to mainly select the advantageous decks. The idea of separate brain processing of wins and losses is heavily supported by experimental data (event-related functional magnetic resonance, fMRI) in gambling tasks and also in the IGT (e.g., Lawrence, Jollant, O'Daly, Zelaya, and Phillips, 2009).

Previous research on ERPs in the IGT is scarce and has been mainly focused on brain potentials preceding choices (Bianchin and Angrilli, 2011; Cui, Chen, Wang, Shum, and Chan, 2013). Research on outcome feedback signals has been so far focused on the feedback-related negativity (FRN) –a negative wave with a peak latency of about 250-350 ms after feedback onset, found at frontal and central locations- and the P300 component –a positive wave peaking between 200-500 ms after feedback onset, found at parietal and frontal sites- since they are the most sensitive to outcome (gain/loss) and to the amount of money earned or lost. It has been found that, as in other decision-making tasks, the amplitudes of FRN to losses are larger than to gains (Bianchin and Angrilli, 2011; Cui et al., 2013). The amplitude of P300 has also been found to increase depending on outcome with greatest change with losses and outcome magnitude (Cui et al., 2013). Some wave components have also been found to be more sensitive to negative or positive outcomes in gambling tasks and, therefore, they might be related to a better performance in the IGT. In this regard, it has been proposed that the processing of feedback signals as indicated by the FRN and P300 components is related to the performance in the IGT. In particular the difference in FRN amplitude between advantageous and disadvantageous decks would indicate a better discrimination and eventually lead to an increased selection of the advantageous decks (Cui et al., 2013)

It is not clear, however, the function of some ERP components in decision-making in general, and in the IGT in particular, especially the short-latency components. Previous research has identified a first ERP component, mainly found in speeded tasks, the error related negativity (ERN). This is a negative wave appearing at medial fronto-central regions after an error or an unexpected negative outcome, with peak latencies ranging between 80 and 100 ms (Arbel and Donchin, 2011). The ERN seems to manifest the activity of an error-detection system (Pailing and Segalowitz, 2004; Sailer, Fischmeister, and Bauer, 2010; Scheffers and Coles, 2000).

Some authors consider that ERN and FRN depend on the same underlying cognitive and neural processes providing an early processing of response outcomes and perhaps reflecting the same neural reaction to negative outcomes (Nieuwenhuis, Yeung, Holroyd, Shurger, and Cohen, 2004b; Polesi, Lotto, Daum, Sartori, and Rumiati, 2008; Schuermann, Endrass, and Kathman, 2012). Apparently, FRN is the feedback variant of the response-locked ERN (Nieuwenhuis et al., 2004b; Sailer et al., 2010; Schuermann, et al., (2012).

Initially, since ERN is considered as the electrocortical, response-locked, reaction to incorrect responses in speeded tasks, it should not be expected to appear in the IGT in which there is a certain delay between the response of the subject and the feedback signal. However, an early negativity component in the response to feedback signals in the time range of ERN, and of the visual N1 wave (Luck, 2005), appears also in gambling and reinforcement learning tasks (e.g., Eppinger, Kray, Mock, and Mecklinger, 2008; Frank, Woroach, and Curran, 2005; Nieuwenhuis et al., 2004b; Schuermann et al., 2012). Since ERN and FRN are supposed to reflect the same error processing system it is plausible that the first

negative deflection, that we call early negative wave, in the time range of the ERN, evoked by an error or a loss in gambling and complex decision-making tasks, could also reflect an error processing system as it is the case of FRN in speeded tasks.

A second component of the feedback-related potentials is a frontal positive wave peaking around 180-280 ms (P200). This wave could represent an early processing of several stimulus parameters (predictability, valence, salience) that may be relevant in the decision-making process and in subsequent choices (Polezzi, Lotto, Daum, Sartori, and Rumiati, 2008; San Martín, Manes, Hurtado, Isla, and Ibáñez, 2010; Schuermann, Endrass, and Kathmann 2012). The P200 component has been interpreted as indicative of an early processing of reward feedback signals, with larger amplitudes to losses compared to gains (Polezzi et al., 2008; Schuermann et al., 2012) and, thus, sharing some of the characteristics of the FRN, although some authors relate the P200 component to the P300 component (Endrass, Klawohn, Gruetzmann, Ischebeck, and Kathmann, 2012; Falkenstein, Hoormann, Christ, and Hohnsbein, 2000).

Regarding long-latency potentials, it has been suggested that P300 and late ERP components might reflect the same process (e.g., Sailer et al., 2010; San Martín et al., 2010), and that they indicate a greater allocation of processing resources to motivational or significant stimuli and therefore to be of importance for guiding behavior in subsequent choices. Only a few studies report late-potential data with latencies of 500 ms or longer on gambling tasks. Polezzi et al. (2008; 2010) report a late negative potential (N500) that is higher to unpredictable and negative outcomes (Polezzi et al., 2008; 2010). Goyer et al. (2008) found a late wave in the window 400-600 ms after feedback that was more negative to losses than to gains, and proposed that this slow component may respond to an emotional appraisal of

the outcome influencing the following choices in the task.

Since decision-making, as studied in the IGT, depends in part on the feedback signals resulting from each decision, and this feedback provoke several ERP components -related to the neural activity involved in the processing of those feedback signals-, the goal of this research was to study the time course of the cortical activity to wins and losses in the IGT through the ERP components, **in the 80-350 ms time window (early negativity, P200, FRN) and P300 and late potentials in the 400-600 ms time window**, and the relationship of this activity with the performance in the task. A characterization of the course of neural responses in the IGT, as revealed by ERPs, would show the processing steps involved in the task that may have influence in the performance. To our knowledge this is the first study covering the five different components that may appear in response to gain and loss feedback in the IGT.

According to the literature reviewed above, ERPs elicited in the time window 80-350 ms are thought to reflect an initial analysis of the consequences of the choices, and ERPs with latencies in the 400-600 ms time range would reflect a more complete analysis of gain and losses, including motivational and emotional processes. The complexity of the IGT requires a great involvement of cortical activity, including the dorsolateral and ventromedial prefrontal cortices and, presumably, a more detailed and slow processing reflected in the ERPs in the time window of 400-600 ms, that might be more related to performance, than those elicited in the 80-350 ms time window.

Regarding short-latency components, following previous research we expected that the **early negativity** would be sensitive to both gains and losses,

whereas losses would provoke larger P200 amplitudes than gains. These components were expected to be followed by an FRN wave with larger amplitudes to losses than to gains. Finally, P300 and late potentials were expected to be differentially affected by both gains and losses, and also by the amount of money earned or lost, with higher amplitudes to losses than to gains, especially to high losses. In addition, we also analyzed the relationship of each of these ERP components with the task performance, since previous research has suggested that some feedback ERPs are related to the performance in the IGT. We also expected some similarities between the early negativity and FRN in terms of amplitude to gains and losses and also in terms of performance. In the same line, and according to previous research, P200 would be also similar to P300 in the same parameters, amplitudes to gains and losses and relationship with performance.

Additionally, we studied the source of the ERPs in order to compare the results of the study with source analysis data obtained from different types of decision-making tasks. In this line, FRN has been reported to be originated in or near the cingulate cortex, and also to be the result of a transient decrease in dopaminergic input to the midbrain (Holroyd and Coles, 2002). If the FRN has the same features in the IGT and in other decision-making tasks, this would indicate a certain similarity in the brain mechanisms involved. Source analysis would provide a more complete picture of the underlying processes in decision-making.

2. Method

2.1. Participants

Twenty-five female volunteer psychology students, aged between 20 and 32 (mean age 22.4 ± 3.39 years) participated in this research. Each student received a course credit for her participation. All participants underwent an extensive medical and psychological interview, including assessment of clinical characteristics through self-report questionnaires and a standardized neuropsychological test battery. All [participants](#) were strongly right-handed as measured by the Edinburgh handedness inventory (EHI; mean 21.2 ± 4.5) (Oldfield, 1971), they had no significant neurological history, and they were not receiving psychiatric or pharmacologic treatment. The study was in accordance with the Declaration of Helsinki (World Medical Association, 1991), with written informed consent from all [participants](#). The protocol was approved by the committee of [the University of Balearic Islands](#).

2.2. Iowa Gambling Task

We employed a computerized version of the IGT ([Bechara, Damasio, Damasio, and Anderson, 1994](#)) that was modified for ERP recordings (see [Figure 1](#)). The IGT was programmed to award different amounts of play money (wins) after each card selection and to deliver monetary losses of different amounts in specified trials. High amounts of monetary gains and losses were associated with two decks (disadvantageous decks), whereas low amounts of monetary gains and losses were associated with the other two (advantageous decks). Thus, the participants could receive four different outcomes: high gain (175€ or 200 €), low gain (25€ or 50€), high loss (-1000€ or -1200€) or low loss (-25€ or -50€). The task is designed in such a way that the high reward decks give higher levels of punishments than the low reward decks. Regarding the frequency of punishments, one of the high reward decks and one of the low reward decks have a high

frequency of punishments (5 in 10 trials), whereas in the other two decks the frequency of punishments is lower (1 in 10 trials). At the start of each trial, a fixation cross slide was presented for 2000 ms. Then, the four decks of cards (A, B, C and D) were displayed and kept on the screen until the participant pressed one button to select one of the decks. Next, a fixation cross slide was presented for 2000 ms and participants were presented with the feedback. Two feedback could be showed to participants: only win outcomes or win-loss outcomes. In only win outcomes a happy yellow face was showed with the message "WIN" and the positive value of the earned amount (e.g., +120€) for 2000 ms, followed by a 1000 ms fixation cross slide. In win-loss outcomes a happy yellow face was showed with the message "WIN" and the positive value of the earned amount (e.g., +120€) for 2000 ms, and followed by a 1000 ms fixation cross slide (outcome XXXXXX). Next, an unhappy yellow face with the message "LOSS" and the negative value of the lost amount (e.g., -50€) for 2000 ms was displayed followed by a fixation cross slide for 1000 ms (outcome XXXXXX).

INSERT FIGURE 1 HERE

In the long run, decks A and B were disadvantageous and decks C and D were advantageous. The payoff scheme as well as the task instructions followed those used in other IGT experiments (e.g., Bechara, Damasio, Damasio, and Anderson, 1994). Participants had to choose in total 100 cards, one at each trial and they were told that the goal of the task was to gain and to avoid losing as much virtual money as possible.

2.3. Procedure

Data were collected within a single session that lasted 90 min. Participants were verbally informed about the details of the study. A specifically designed,

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information leaflet was also given to all participants and, after their agreement to participate, a written consent was obtained. The volunteers answered several questionnaires to confirm the inclusion criteria. They then were seated comfortably ~1 m in front of a computer screen in a dimly lit, electromagnetically shielded room and EEG electrodes were applied. Participants were instructed on how to carry out the IGT and they were given twenty-six practice trials. Finally, the experimental session started.

2.4. EEG recording

Brain electrical activity was recorded with an electrode cap from 60 sites placed according to the international 10–20 system plus two bipolar channels to record electrooculography and two electrodes in earlobes. Eye movements and blinks were monitored via bipolar recordings with electrodes placed above and below the right eye (vertical EOG). Ground was placed anteriorly to the location of the FCz electrode. All impedances were kept below 10 k Ω . The signals were registered by a BrainAmp MR amplifier at a sampling rate of 1000 Hz, with high and low pass filter settings at 0.10 Hz and 70 Hz, respectively. A 50 Hz notch filter was also applied. EEG recordings were analyzed by means of the EEGLAB Toolbox 6.01b (Delorme and Makeig, 2004), running in a MATLAB 2008 environment (Mathworks, Natick, MA, USA). Separate EEG epochs of 1000 ms (with 100-ms pre-Outcome) were extracted offline, for the Outcome (wins and losses) for each trial on each electrode. In order to match the number of win and loss epochs, we selected the trials with both outcomes, and thereby a mean of 27,4 trials per participant were selected. All channels were re-referenced with a common average. Vertical and horizontal EOG correction was applied using the Gratton method (Gratton, Coles, and Donchin, 1983), which was done with Ocular

[Correction plugin available for EEGLAB, with a time window for detection of 20 ms and a criterion for blink detection of 25 \$\mu\$ Volts.](#) Then, trials with amplitudes outside a range of ± 70 μ V were automatically excluded. Finally, trials were visually inspected and excluded if EOG artifacts were still observable.

2.5. Data analysis

[Behavioral data analysis](#)

For analysis purposes, the task was divided in five blocks of 20 trials (trials 1-20, 21-40, 41-60, 61-80, 81-100). [Behavioral performance was analyzed by calculating the number of choices for the advantageous and disadvantageous decks. Next, we calculated the net scores for each block by subtracting the number of disadvantageous choices from the number of advantageous ones.](#) The performance was analyzed by a repeated-measures analysis of variance, [ANOVA](#) with the factor Block (5 blocks) as within-subjects [variable](#).

[The amount of money earned was established by calculating the number of wins and losses obtained by each subject, and analyzed by a 2x5 ANOVA, with one between-group factor Outcome \(Wins/Losses\) and one repeated-measures factor Block \(5 blocks\).](#)

[Time course of ERPs to wins and losses](#)

The evoked potentials elicited by [win and loss](#) outcomes were included in the statistical analysis of the physiological data. Firstly, the Grand Average from all participants for each outcome was inspected visually in Fz, Cz, Pz in order to detect standard ERPs. Relevant [ERPs](#) after win and loss onset were [found](#) at latency ranges of 80–180 ms, [corresponding to the early negativity](#), 180-280 ms [to P200](#).

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and 360–480 ms to P300. For components later than 480 ms, no clear peak could be identified; therefore, the time-window from 480 to 800 ms after outcome onset was selected. The range between 280-360 ms was identified as corresponding to the FRN potential, however previous studies (Cui et al., 2013; Toyomaki and Murohashi, 2005; Hajcak et al., 2006; Polezzi et al., 2008) have reported that the amplitude of the FRN is affected by P200 (Hajcak et al., 2006; Polezzi et al., 2008). Thus, we considered the difference between the amplitude mean of P200 and amplitude mean of 280–360ms as the amplitude of the FRN for each ERP and electrode in accordance with the procedure suggested by Hajcak et al. 2006.

Since we were interested the “region” effects but not in the individual “electrode” effects, the electrodes were nested within regions. Thus, 33 electrodes were selected to represent six brain regions following the procedure described by Kamarajan et al., (2010): frontal (F3, Fz and F4), central (FC3, FCz, FC4, C3, Cz, and C4), Parietal (P3, Pz, P4, C3P, CPz and C4P), occipital (O1, Oz, O2, Po3, Poz and Po4), left temporal (FT7, T7, TP7, CP5, P7 and P5) and right temporal (FT8, T8, TP8, CP6, P8 and P6). Multiple simple ANOVAS for each brain regions were computed to compare mean amplitude of Outcome (wins versus losses) for early negative wave, P200, FRN, P300 and late potential.

Relation between ERP and performance measures

Bivariate Pearson correlations were computed relating ERP outcomes on Fz, Cz and Pz to performance (net scores and number of advantageous and disadvantageous choices) and amount of money.

Source regions analysis

All of the statistical analyses were performed using the Statistical Package for Social Sciences (SPSS) 15 software. Greenhouse-Geisser corrections were

[applied when necessary, and post-hoc pairwise comparisons were performed using Bonferonni test with a significant level of \$p < 0.05\$. The reported significance results are presented with the original degrees of freedom and a measure of effect size.](#)

Source reconstruction of the ERP [grand average across participants for Outcomes was](#) applied to each temporal interval using the BrainStorm 3.1 software (Tadel, Baillet, Mosher, Pantazis, and Leahy, 2011). [The analysis was conducted on the ensemble averaged data from each of the 60 electrodes clean of artifacts. The source localization maps were obtained for each Outcome \(wins/losses\) at ERP. The average EEG data for each channel, win and losses outcomes, were imported into Brainstorm. The inverse problem solution was calculated by the Standardized Low Resolution Electromagnetic Tomography \(sLORETA\) method.](#) The head was modeled using the MNI-Colin25 high-resolution T1-weighted MR images, and a 3-shell sphere Berg approximation representing the brain. The cortical surface was parsed, represented as a high-density mesh of vertices, and subsequently down-sampled to 1516 vertices and electrode positions were approximated based on a template electrode position file. Current source density estimates were z-score normalized relative to the baseline (-100 to 0 ms prior to Outcome onset). Each source map was [thresholded](#) at $p < 0.05$ value relative to the post-outcome distribution of all vertices in each time interval, and a cluster threshold (ten vertices connected) was applied.

3. Results

3.1 Performance in the Iowa Gambling Task

[The analysis showed that subjects improved their performance \(i.e., they](#)

selected more advantageous than disadvantageous decks) as the task progressed (see Figure 2). The statistical analyses yielded a significant main effect of Block, $F(4,96) = 6.44$, $p = .003$, $\eta^2 = .21$. When the Bonferroni post-hoc test was carried out, significant differences were found in task performance between block 5 and block 1 ($p = .034$), block 2 ($p = .004$) and block 3 ($p = .009$).

These results were confirmed when we compared the amount of money earned with the amount lost in all five blocks. The ANOVA (2×5) on the amount of money earned showed significant differences in the Outcome factor $F(1,23) = 417.75$, $p < .001$, $\eta^2 = .94$. Overall, participants obtained more wins than losses during the task. No significant differences between blocks nor in the interaction Outcome by blocks were found (all $ps > .05$).

INSERT FIGURE 2 HERE

3.2 Time course of ERPs to wins and losses

Figure 3 shows grand average waveforms for outcome condition in the 60 electrodes and according to interval and electrode site. Mean values of mean amplitude and electrode localization can be seen in Table 1.

INSERT FIGURE 3 HERE

Early negative wave (80-180 ms)

ANOVAs revealed that early negativity had a smaller amplitude for win feedback than for loss feedback, as indicated by a significant effect of the Outcome factor for parietal ($F(1,24) = 7.83$, $p = .02$, $\eta^2 = .24$), temporal left ($F(1,24) = 18.87$, $p < .001$, $\eta^2 = .44$) and temporal right ($F(1,24) = 33.69$, $p < .001$ partial $\eta^2 = .58$) (see Table 1).

P200 (180-280 ms interval)

ANOVAs revealed that P200 was smaller for win feedback than for loss feedback as indicated by a significant effect of Outcome factor for frontal ($F(1,24) = 69.91, p < .001, \eta^2 = .74$) and central localizations ($F(1,24) = 42.83, p < .001, \eta^2 = .64$) (see Table 1).

FRN (280-360 ms)

ANOVAs revealed that the Outcome effect was significant for central ($F(1,24) = 63.88, p < .001, \eta^2 = .72$), occipital ($F(1,24) = 24.01, p < .001, \eta^2 = .50$), temporal left ($F(1,24) = 53.29, p < .001, \eta^2 = .68$) and temporal right ($F(1,24) = 25.25, p < .001, \eta^2 = .51$). Win trials were more negative than loss trials in central electrodes, while in temporal and occipital localizations win trials were less negative than loss trials.

When we considered the difference between the mean amplitude of P200 and the mean amplitude of 280–360ms as the amplitude of the FRN, a t-test indicated that the difference between a win and loss was largest in the Fz ($t=2.60, df=24, p = .016, one-tailed$). Non-significant differences were found in FCz and Cz (all $ps > .05$) (see Figure 3).

INSERT FIGURE 4 HERE

P300 (360-480 ms)

Follow-up ANOVAs revealed that the Outcome effect was significant for central ($F(1,24) = 44.42, p < .001, \eta^2 = 0.64$), parietal ($F(1,24) = 48.58, p < .001, \eta^2 = 0.66$), occipital ($F(1,24) = 11.84, p < .001, \eta^2 = 0.33$), and temporal right ($F(1,24) = 9.07, p < .001, \eta^2 = 0.27$). Loss trials were more positive for all

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electrode localization (see Table 1).

Late potential (450-800 ms)

ANOVAs revealed that the Outcome effect was significant for frontal ($F(1,24) = 14.55, p < .001, \eta^2 = 0.37$), central ($F(1,24) = 31.80, p < .001, \eta^2 = 0.57$), occipital ($F(1,24) = 13.58, p < .001, \eta^2 = 0.36$), and temporal left ($F(1,24) = 6.39, p = .018, \eta^2 = 0.21$). Win trials were less negative for frontal and central electrodes while loss trials were less negative for occipital and temporal left electrodes (see Table 1).

INSERT TABLE 1 HERE

3.3 Correlations between ERP mean amplitudes and performance measures.

Significant positive correlations were found between mean amplitude of early negative wave to win feedback and the number of advantageous selections in the IGT for Fz ($r = 0.43, p = .029$), and Cz ($r = 0.50, p = .011$). The early negative mean amplitude to loss trials at Cz correlated positively with the number of advantageous selections ($r = 0.45, p = .024$).

Significant positive correlations were found between the amplitude of P200 to loss feedback and the number of disadvantageous selections at Fz ($r = 0.52, p = .007$) and Cz ($r = 0.44, p = .024$). The amplitude of FRN in wins trials showed a positive correlation with the number of advantageous selections at Pz ($r = 0.56, p = .004$). Finally, the mean amplitude of the late potential to win feedback positively correlated at Pz with the number of advantageous selections ($r = 0.41, p < .038$).

No significant correlations were found between net scores and amount of money earned.

3.4 Source localization

SLORETA t-test maps for comparisons among wins and losses are depicted

in Figure 4. Regarding the early negative wave a greater source activity was observed to loss feedback in the Supplementary motor area ($t[44]=6.67$; MNI: 1.94 - 8.65 69.87) extending to middle cingulum (MNI: 1.67 -7.89 48.84) (Figure 3.A).

For the FRN component, we found significantly higher activation in the anterior cingulate cortex (ACC) ($t[44]=1.0$; MNI: 6.13 35.50 11.22), inferior frontal gyrus, corresponding to Brodmann area 47 (BA 47) ($t[44]=3.22$; MNI: -56.42 26.07 - 3.40), and right middle orbito-frontal gyrus ($t[44]=3.87$ MNI: 29.84 50.97 -3.68) (see Figure 4.B and 4.C).

INSERT FIGURE 5 HERE

4. Discussion

_____ We studied the whole range of ERPs to wins and losses in the IGT in the time window 80-800 ms and their relations with task performance. Since previous literature has found most outcome feedbacks to gains and losses in medial fronto-central (early negative wave, P200, FRN) and parietal (P300) regions, and for comparison reasons, this discussion will deal mainly on the ERPs obtained at Fz, Cz and Pz electrodes (e.g., Hajcak et al., 2005; Hewig et al., 2011).

Initially, the processing of the feedback resulted in an early negative wave, indicating that the evaluation of the consequences of a given choice starts very early after the feedback stimulus, but this wave was not sensitive to wins or losses. The processing of the loss feedback started at the time window of P200 that was larger for losses than gains. The FRN showed the well-known effect of increased magnitude to losses than to wins, followed by the P300 component, also with larger amplitudes for losses than for gains that can be interpreted as reflecting the

greater motivational significance of losses in comparison to wins. In addition, greater processing resources were allocated on losses, as reflected by the larger amplitude of the late ERP components beyond P300.

Our prediction that ERPs in the 400-600 ms time window would be more related to performance than those ERPs with shorter latencies was not fulfilled. In fact, all ERPs, with the exception of P300, were related to performance in the task in terms of the numbers of wins and losses, but unrelated to net scores.

We examine next with more detail, and in order of appearance, the five ERPs, their relationships with win and loss feedback, the source analysis of each component, and their relationship with the task performance.

Early negative wave

An early fronto-central negativity, that we have called the early negative wave, was found after feedback for both wins and losses, corresponding to an early negativity in the visual N1 range (Luck, 2005). Loss feedback elicited more negativity than win feedback at parietal, left and right temporal electrodes, but no significant differences between win and loss feedback in wave amplitude were found at frontal and central regions. Wave amplitudes and correlation analyses are indicative of an early brain response that, as predicted, does not differentiate between outcomes and that reflects a general evaluative process rather than a loss related processing. A source for this ERP response to loss feedback was found at the supplementary motor area, reaching the medial cingulate cortex in agreement with previous data (Roger, Bénar, Vidal, Hasbroucq, and Burle, 2010).

The amplitude of this early negative wave correlated with the number of wins at FCz and with both the number of wins and losses at Cz, and also with the number of advantageous selections, what is in partial agreement with Frank,

Woroch, and Curran (2005) who also found a relationship between the amplitude of an early negative wave and good decisions in a reinforcement learning task. This short-latency wave may appear after every behaviorally relevant stimulus related to the task and it is compatible with the idea of an initial process of evaluation of the consequences of the choices without a clear distinction between wins and losses.

P200

The first positive wave, P200, with larger amplitude to losses than to wins was located in frontal and central regions. This is in accordance with previous studies in decision-making tasks (Polezzi et al., 2008; Schuermann et al., 2012). The amplitude of P200 to losses at FCz and Cz positively correlated with the number of losses, thus reinforcing the idea of P200 as an early component mainly related to the processing of negative feedback signals and of error awareness and also to that of gathering error-related information (Steinhauser and Yeung, 2010, 2012). Polezzi et al. (2008) found this component as directly related to the predictability of the outcomes, with higher amplitudes to unpredictable outcomes. In this line, the uncertainty of the IGT results in higher P200 amplitudes to losses.

In contrast with the early negative wave, P200 represents an early differentiation between gain and loss feedback, and its amplitude is related with the selection of the disadvantageous decks.

FRN

A negative deflection, similar to the FRN, in the time window 280-360 ms that interrupted an ongoing positive wave was observed in frontal, central, occipital and right and left temporal electrodes to both types of feedback. Negativity was higher to loss trials in occipital and both left and right temporal

electrodes. However, and contrary to our predictions, loss feedback components were more positive than win feedback components in frontal and central electrodes. When differential measures between the previous P200 and the FRN were taken into account, losses resulted in a more negative wave than wins in frontal electrodes but not in central electrodes, which is in agreement with Cui et al. (2013) who found larger effects on FRN between win and loss at Fz, and in partial agreement with Bianchin and Angrilli (2011) who reported larger FRN components to loss than to win at both Fz and FCz during the performance of the IGT.

Significant positive correlations were found between FRN amplitudes to win feedback at Pz and the number of advantageous selections, indicating that the larger the amplitude of the gain feedback potential, the better the performance in the IGT. Interestingly, source analysis revealed higher activation in the ACC, inferior frontal gyrus (BA 47) and right middle orbito-frontal gyrus. The ACC is the region where the FRN is supposed to be generated, thus confirming previous research (Gehring and Willoughby, 2002). These data are in accordance with functional imaging studies during performance of the IGT that point to a cluster of brain regions involved in the processing of the consequences of the choices: ACC, the ventromedial prefrontal cortex and its orbitofrontal section, and the inferior frontal gyrus (Fukui, Murai, Fukuyama, Hayashi & Hanakawa; Li et al., 2010; Ma et al., 2015; Northoff et al., 2005; Wang et al., 2017).

P300

Loss feedback elicited larger P300 magnitudes than wins for all electrode localizations. This is in accordance with previous reports that have found higher wave amplitudes in this component to loss trials (Cohen, Elger, and Ranganath,

2007; Frank et al., 2005; San Martín et al., 2010; Schuermann et al., 2012), and especially in accordance with Cui et al. (2013) who found in the IGT larger P300 amplitudes to losses. Other authors, however, have found larger P300 amplitudes for gains than for losses in gambling tasks other than the IGT (e.g., Hajcak et al., 2005). Since P300 amplitude is related to the motivational significance of the result of the choice, this positive wave could reflect a late evaluation process more sensitive to losses than to gains in the IGT.

Late potential

Lastly, in accordance with some researchers (Polezzi et al., 2008; 2010) a late negative component in the 450-800 ms time window, similar to N500, appeared as a response to loss trials at frontal and central regions, while less negativity dominated in the reaction to win trials. More negativity to losses than to wins has also been reported by Goyer et al. (2008). In addition, the amplitude of this late component to wins at Pz positively correlated with the number of wins.

Similarities between P200 and P300

P200 and P300 were more sensitive to losses and behaved in a parallel way. This result gives support to the hypothesis suggesting that P200 shares some features with the classic stimulus-locked P300, and that these two feedback-related positive waves reflect the same processes related to the conscious recognition or the motivational significance of the error (Arbel & Donchin, 2009; Endrass et al., 2012; Falkenstein et al., 2000; Steinhauser & Yeung, 2010). P200 seems to be mainly indicative of an early reaction to losses or worse than expected outcomes and associated to increased attention and greater arousal levels, while P300 would be indicative of additional information processing and of the motivational significance of the loss (San Martín et al., 2010; Schuermann et al., 2012). In the IGT, P200 would

appear as an early component reflecting an initial processing of mainly negative feedback signals, while P300 would reflect a conscious processing of either the motivational significance of losses or of the relative frequency of the different outcomes.

Conclusions

Our study extends previous results on the ERPs evoked by feedback signals in decision-making tasks to the whole range of electrocortical activity. The processing of loss feedback seems to be an important feature in the performance of the IGT. Interestingly, the amplitude of the three negative waves (early negative wave, FRN and the long-latency wave) correlated with the number of wins, and two of them, early negativity and FRN, had the same source in or near the ACC, suggesting a similar origin and function, as well as the involvement of the medial prefrontal cortex, especially the anterior cingulate, in decision making. These data lead to a better knowledge of the brain activity that takes place during decision-making tasks, and particularly on its electrocortical signature and source.

This characterization of the ERP components associated to feedback may be helpful in order to discriminate the processing steps of the feedback received after an option is chosen, and that might be necessary to guide the behavior in subsequent choices. Further research is needed in order to test whether a failure in some of these processing steps, as revealed by ERPs, may result in a deficit in decision making, as may be happening in individuals with several pathological conditions (e.g., drug addiction, etc). A limitation of the study that should be addressed in further works is that only female participants were studied. Gender differences in the performance of the IGT have been reported by several authors,

with the consistent finding that men generally tend to choose the advantageous decks more frequently and outperform women (Byrne & Worthy, 2016), and this calls for the need to include male participants in further studies.

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Tables

Table 1. Means and standard deviations (in parentheses) of area under curve of the event related potentials according to interval and cerebral regions.

Figure Captions

Figure 1. Schematic depiction of the Iowa Gambling task as used in the present study.

Figure 2. Participants' performance in the Iowa Gambling Task along the 100 trials. Net scores were calculated by subtracting the number of advantageous choices from the number of disadvantageous ones. Error bars represent the standard error of the mean.

Figure 3. Grand averaged ERPs to feedback of wins and losses in all electrode sites. Right column shows average responses in Fz, Cz and Pz .

Figure 4. Mean amplitudes of feedback related negativity (FRN) at Fz, FCz and Cz, calculated as the difference between the mean amplitude the 180-280 milliseconds interval and the mean amplitude in the 280-360 milliseconds interval. Error bars represent the standard error of the mean.

Figure 5. Graphical representation of the sLORETA t-statistics comparing the ERPs for Win and Loss at the time point of the individual peak over 80-180 sec interval. Red color indicates local maxima of increased electrical activity for loss compared to win responses in an axial, a sagittal and a coronal slice through the reference brain.