Oscillatory Brain Activity Correlates with Risk Perception and Predicts Social Decisions

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In social interactions, the perception of how risky our decisions are depends on how we anticipate other people’s behaviors. We used electroencephalography to study the neurobiology of perception of social risk, in subjects playing the role of proposers in an iterated ultimatum game in pairs. Based on statistical modeling, we used the previous behaviors of both players to separate high-risk [HR] offers from low-risk [LR] offers. The HR offers present higher rejection probability and higher entropy (variability of possible outcome) than the LR offers. Rejections of LR offers elicited both a stronger mediofrontal negativity and a higher prefrontal theta activity than rejections of HR offers. Moreover, prior to feedback, HR offers generated a drop in alpha activity in an extended network. Interestingly, trial-by-trial variation in alpha activity in the medial prefrontal, posterior temporal, and inferior parietal cortex was specifically modulated by risk and, together with theta activity in the prefrontal and posterior cingulate cortex, predicted the proposer’s subsequent behavior. Our results provide evidence that alpha and theta oscillations are sensitive to social risk and underlie a fine-tuning regulation of social decisions.

**Keywords:** EEG, social neuroscience, decision-making, mediofrontal negativity, ultimatum game

**Introduction**

The consequences of the decisions we make during social interactions depend on how others react to our behavior. For example, if the owner of a property decides to raise the house rent, the lessee could decide to accept the proposal, negotiate (bargain for a better offer), or simply leave the house. To achieve our goals, we evaluate the risk of our proposals by anticipating the others’ most probable behaviors. In this anticipation, we predict the others’ intentions based (among other factors) on what we know about their previous behaviors. For instance, if the lessee has consistently rejected the owner’s proposals in the past, there is a high chance he/she will reject future attempts to raise the rent. In trying to figure out how others will react, however, we must also consider what they perceive our intentions to be. In the example above, if the owner raises the rent too often, the lessee may perceive that the intention is to take advantage of him/her and likely reject the proposal. Therefore, risk perception in social interactions must integrate other people’s intentions, how others perceive our intentions, and how these intentions change as decisions are made. In spite of the fact that risk perception is critical for social behavior, it remains unclear how the integration of these factors occurs and what its neurobiological mechanism is.

Lay people commonly identify risk as the possibility of negative or dangerous consequences (Slovic 1987). In contrast, traditional economic and financial models of risk often assume that this is a context-independent function of the variability of possible outcomes (Markowitz 1952; see also Mohr et al. 2010; Schonberg et al. 2010). However, research on risk perception indicates that it is neither context independent nor a pure measure of outcome variability (Tversky and Kahneman 1986; Weber et al. 2002). In non-social contexts, neuroscientists have studied how risk changes both anticipatory and evoked activity related to monetary reward. Anterior insular (AI) and thalamic activity have been related to emotional reward anticipation under risk (Kuhnen and Knutson 2005; Knutson and Greer 2008; Mohr et al. 2010), while medial prefrontal cortex (mPFC) activity has been related to cognitive reward anticipation (Mohr et al. 2010). In frontal areas, an anticipatory activity characterized by a decrease in low frequencies (delta and theta) and an increase in high frequencies (alpha and beta) of the electroencephalography (EEG) has been observed (Cohen et al. 2009). However, the relationship between oscillatory brain activity and risk remains unclear. On the other hand, it has been shown that risk modulates outcome-evoked brain activity. For example, the mediofrontal negativity (MFN), an event-related potential (ERP) elicited by error prediction (Holroyd and Coles 2002) and monetary loss (Gehring and Willoughby 2002), is stronger when the loss is unexpected (Potts et al. 2006; Hajcak et al. 2007). Interestingly, both anticipatory (Kuhnen and Knutson 2005; Hampton and O’doherty 2007) and evoked (Yeung and Sanfey 2004) activity correlates with the risk taken in subsequent behavior.

In contrast to non-social settings, during social exchanges, the evaluation of risk and reward depends on other people’s behavior. Indeed, brain activity in reward-related areas changes when one is aware of the other participants’ gains, even when one’s gains do not change (Fliessbach et al. 2007). Moreover, the MFN elicited by someone else’s loss is modulated by the nature of the social interaction (computer or human partner, competitive or cooperative partner; Fukushima and Hiraki 2009; Marco-Pallarés et al. 2010; Rigoni et al. 2010). A way of recreating social exchange situations in laboratory settings is through game theory-based tasks (Camerer and Fehr 2006; Lee 2008), such as the ultimatum game (Güth et al. 1982). In this game, 2 players split a certain amount of money. One player (the proposer) makes an offer as to how the money should be split between the 2. The other player (the responder) can either accept or reject the offer. If the offer is accepted, the money is split as proposed, but if it is rejected, neither player receives any money. Previous studies using functional magnetic resonance imaging (fMRI) and EEG have shown an increase in the activity of both the AI and the anterior cingulate cortex (ACC; Sanfey et al. 2003) as well as a larger MFN (Polezzi et al. 2008; Boksem and De Cremer 2010; Campanha et al. 2011; Alexopoulos et al. 2012) when the re-
sponder receives an unfair offer. However, little is known about how the proposer evaluates his/her own decisions in these situations. This is important because, when faced with a recurrent interaction, the proposer has to consider both his/her and the responder's previous behavior in order to estimate the most probable outcome of his/her current decision. Thus, focusing on the proposer in an iterated ultimatum game allows us to study the neurobiology of risk perception of social decisions.

In order to address this issue, we performed 2 separate studies, one behavioral and the other using EEG, while participants played an iterated version of the ultimatum game (Fig. 1). In the behavioral study (Experiment 1), participants played both as proposers and as responders in different games (see the Materials and Methods section). We fitted a mixed-effects logistic model to predict the responders' behavior. Using this model, we determined the most stable predictors among responders (Table 1). Based on these results, we propose a classification for separating high-risk [HR] offers from low-risk [LR] offers. We subsequently performed an EEG study (Experiment 2) where each participant played only as proposer, but against different simulated responders. Using the proposed classification, we indentified brain activity associated with the perception of HR and LR social decisions. Moreover, we found that trial-by-trial variation in specific bands of the EEG can predict the proposer's next behavior.

Materials and Methods

Participants
Fifty-five individuals participated for monetary compensation after recruitment online, 32 in the behavioral study (18 women) and 23 in the EEG study (7 women). Participants in the behavioral study were right-handed Spanish speakers, aged from 18 to 30 years (M = 23.71, SEM = 0.57). EEG participants were right-handed Spanish speakers, aged from 18 to 25 years (M = 21.31, SEM = 0.37). All participants had normal or corrected-to-normal vision, no color-vision deficiency, no history of neurological diseases, and no current psychiatric diagnosis or psychotropic prescriptions. All participants gave informed consent and the Ethics Committee of the Pontifica Universidad Católica de Chile approved the experimental protocol. All experiments were performed at the Cognitive Neuroscience Laboratory of the Department of Psychiatry of the university.

Behavioral Study Task
Participants were divided into groups of 3 or 4 persons. None knew the identity of the other participants. Together with the experimenter, participants read the instructions describing the iterated ultimatum game (Fig. 1). Each game consisted of 30 rounds. Each participant played both as a proposer and as a responder in 2 or 3 games. Each player played in a different room viewing different monitors which were connected to the same computer. At the beginning of each game, both players where presented with the color that represented him/her on the screen. Each round defined a trial. Each trial had 3 phases as follows. In the first (offer phase, variable duration), the proposer had to make the offer. In the second (response phase, variable time), the offer was revealed to the responder who had to decide whether to accept or reject it. In the last phase (feedback phase, 1 s duration), the response was revealed to the proposer. At the end of each game, the earnings each player had made in the game were revealed. After the set of games concluded, the experimenter interviewed each participant individually in order to gather the general impression the participants had on the experiment and check whether they had understood the game correctly. The amount of money each participant received depended on his/her performance with a minimum of 3000 and a maximum of 6000 Chilean pesos (~US$6.37–12.74). Participants were recorded with a digital video camera during the games. These video recordings were then used in

Figure 1. Timeline for a game. Proposers (black box) and responders (gray box) played an iterated ultimatum game in different rooms. The proposer made an offer on how to split $100 Chilean pesos between the responder and himself (offer phase). The responder saw the offer and he/she decided to either accept or reject it (response phase). If the responder accepted the offer, the money was split as proposed, and if he/she rejected it, the money was lost. The response was shown on the screen during 1 s (feedback phase). Each game consisted of 30 iterated offers. In the EEG study, proposers believed that they were playing with a human partner, but they were actually playing with a simulation based on the behavioral study (see the Materials and Methods section and Table 1). To make the interaction more realistic, the proposer watched a video of the responder at the beginning of each game (partner presentation). The original screens were in Spanish.
the EEG Study (see below). The task was programmed and presented using Presentation (Neurobehavioural Systems™).

**Behavioral Statistical Analysis**

Responders’ responses were analyzed with logistic regression and mixed-effects logistic regression, treating responders as a grouping factor for random effects. Nagelkerke’s $R^2$ was computed comparing each full model against the fixed-effect intercept model. Mixed logistic models were compared using the likelihood ratio test (Baayen et al. 2008). Reaction probability ($p(R)$) was calculated per proposer using the rate between the number of rejected offers and the total number of offers. Shannon entropy was calculated in each proposer using the rejection and the next change of offer were analyzed with the Fried-uncorrected Wilcoxon signed-rank test. The offer behavior related to a fixation probability and Shannon entropy were analyzed across proposers (behavioral study (Table 1). We used the following 2 equations.$$
\text{Logit}(A_e) = \frac{-4.15 + n_0 + (0.11 + r_1) \times O_x}{1},
$$
and for round $(y) > 1$,
$$
\text{Logit}(A_e) = \frac{-14.01 + n_0 + (0.32 + r_{11}) \times O_y + 0.06 \times \Delta O_x + (1.22 + r_3) \times PR_e - 0.07 \times PR_e \times \Delta O_y}{1},
$$
where Logit($A_e$) is the logit of the probability of acceptance for the round $x$, $O_y$ the offer, $\Delta O_x$ the change of offer, and $PR_e$ the preceding response. The coefficients estimated for each regressor were composed by a population parameter (the number in the equations) and a random effect for each simulated responder ($r_{11}$, $y$ = parameter and $i$ = simulated partner). At the beginning of the experiment, participants were recorded with a digital video camera for a few seconds and the experimenter informed them that the recordings would be shown to the other players during the games. Each game consisted of 30 rounds and each participant played as a proposer 8 times with different simulated responders. The procedure was similar to that described in the Behavioral Study Task. At the beginning of each game, participants watched the fixation cross (10 s, fixation phase) and then a video of their partner. All videos showed full faces of participants in color on a black background (Xvid 1.2.1, 720 x 486, 29.97 fps, 1.78 Mbps). The duration of each response phase was randomized with a uniform distribution (1–4 s). The amount of money participants received depended on their performance, with a minimum of 6000 and a maximum of 12 000 Chilean pesos (~US$12.74–25.48).

**Electrophysiological Recordings**

Continuous EEG recordings were obtained with a 40-electrode NuAmps EEG System (Compumedics Neuroscan). All impedances were kept below 5 kΩ. Electrode impedance was retested during pauses to ensure stable values throughout the experiment. All electrodes were referenced to averaged mastoids during acquisition and the signal was digitized at 1 kHz. Electro-oculogram was obtained with 4 electrodes. All recordings were acquired using Scan 4.3 (Compumedics Neuroscan) and stored for off-line treatment. At the end of each session, the electrode position was digitalized using a 3D tracking system (Polhemus Isotrak).

**EEG Data Analysis**

EEG signals were preprocessed using a 0.1–100 Hz band-pass filter. Eye blinks were identified by a threshold criterion of ±100 μV, and their contribution was removed from each dataset using principal component analysis by singular value decomposition and spatial filter transform. Other remaining artifacts were detected by visual inspection of the signal and the trials that contained them were removed. In ERPs and frequency analyses, epochs were transformed to current source density (CSD; Kayser and Tenke 2006a, 2006b). CSD computes the second spatial derivative of voltage between nearby electrodes, sites, acting as a high-pass spatial filter. The CSD transformation highlights local electrical activities at the expense of diminishing the representation of distal activities (volume conduction). ERPs were computed as the mean of the current density for each electrode and each participant over trials (the feedback release mark the time zero). Induced power distribution (Tallon-Baudry and Bertrand 1999) was computed using a sliding-window fast Fourier transform (Melloni et al. 2007). In the exploratory analysis, we computed power in $\sim$1–1 s windows around both the offer release (which marks the zero time in the expectancy phase) and the feedback release (which marks the zero time in the feedback phase). We used sliding time windows (Hamming) that were moved in steps of 0.01 s. This initial exploratory analysis was performed on frequencies between 1 and 30 Hz using fixed windows of 0.4 s, with a frequency resolution of 1 Hz. In the time–frequency regions that showed statistical differences, we adjusted the length of the analysis window to an integer number of cycles per frequency (3 cycles for theta band and 5 cycles for alpha band) for the subsequent analysis. Plots show the differences between conditions, using dB unit ($10 \times \log_{10}(\text{condition} / \text{condition})$). Following a previous work that studied theta band (Kaplan et al. 2012), a 5-cycle morlet wavelet time-frequency analysis ranging from 3 to 30 Hz with a frequency resolution of 1 Hz was also conducted in order to control for possible differences due to the analytical method (see Supplementary Figs 4–6). Lower delta frequencies (below $3$ Hz) were not measured because of the limited number of possible cycles in the short trial length and border effects.

**Source Estimations**

The neural current density time series at each elementary brain location was estimated by applying a weighted minimum norm estimate inverse solution with unconstrained dipole orientations in both single trials per condition per subject (for the time–frequency analysis) and the average per condition per subject (for ERP analysis). In both cases, we re-referenced the data to the average. A tessellated cortical mesh template surface derived from the default anatomy of the Montreal Neurological Institute (MRI/Colin27) was used as a brain model to estimate the current source distribution. We defined $3 \times 5005$ sources constrained to the segmented cortical surface (3 orthogonal sources at each spatial location) and computed a 3-layer (scalp, inner skull, outer skull) boundary element conductivity model and the physical forward model (Clerc et al. 2010). To estimate neural activity at the cortical source level, we used the weighted minimum

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Fixed effects</th>
<th>Random effects</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Coefficients (SE)</td>
<td>P-values</td>
</tr>
<tr>
<td>Intercept</td>
<td>−14.01 (1.54)</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Sum of money offered ($O_x$)</td>
<td>0.32 (0.03)</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Change of offer ($\Delta O_x$)</td>
<td>0.06 (0.01)</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Preceding response ($PR$)</td>
<td>1.22 (0.24)</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Interaction $\Delta O_x \cdot PR$</td>
<td>−0.07 (0.01)</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

n = 32 subjects; 84 games, with 29 analyzed trials per game (2nd to 30th offer). Responders were used as grouping factor for random effects. Nagelkerke’s $R^2 = 0.591$. See also Supplementary Tables 1 and 2.
norm approach (Baillet et al. 2001). The measured electrode level data \( X(t) = [y_1(t), ... , y_m(t)] \) is assumed to be linearly related to a set of cortical sources \( Y(t) = [y_1(t), ... , y_m(t)] \) (3 \( \times \) 5055 sources constrained to the cortical surface, 3 orthogonal sources at each spatial location, see above) and additive noise \( N(t) = X(t) - Y(t) \), where \( I \) is the physical forward model (the gain matrix). A noise covariance matrix \( C \) was estimated from the raw EEG data (fixation phase). These two matrices, along with the source covariance matrix \( R \), were used to calculate the depth weighted minimum-norm estimate inverse operator: \( W = R^{+}C^{-1} \). \( R^{+} \) was modified to implement depth weighing (weighing exponent: 0.8; Lin et al. 2006), and the regularization parameter \( \lambda \) was set to 1/3. To estimate cortical activity at the cortical sources, the recorded raw EEG time series at the sensors \( X(t) \) were multiplied by the inverse operator \( W \) to yield the estimated source current, as a function of time, at the cortical surface: \( Y(t) = WX(t) \). Since this is a linear transformation, it does not modify the frequencies of the underlying sources. It is therefore possible to undertake time–frequency analysis on the source space directly (Jerbi et al. 2007; Supp et al. 2011; Alvenin et al. 2012). We then computed frequency decomposition using the Fourier transform and hamming windows. In this analysis, we explored the time–frequency windows that showed statistical differences in the electrode space and adjusted the length of the windows to an integer number of cycles per frequency. For early expectancy alpha (8–12 Hz), we used a 0.5 s length time window (five 10 Hz cycles) centered at 0.55 s after the offer. For late expectancy alpha (8–12 Hz), we used a 0.5 s length time window (five 10 Hz cycles) centered at –0.45 s before feedback. For feedback high alpha (10–15 Hz), we used a 0.4 s length time window (five 12.5 Hz cycles) centered at 0.35 s. In this case, we used a higher frequency range in order to avoid contamination with theta activity (see Fig. 3 and Supplementary Fig. 2 for a comparison between different alpha ranges). Finally, for feedback theta, we used a 0.6 s length time window (three 5 Hz cycles) centered at 0.4 s. Additionally, per each frequency band, we recollected a window in the fixation phase with the same durations of the window of interest that we used as a baseline in the models (see below). To control for possible bias due to the choice of windows with a different number of cycles, we replicated these analyses using a wavelet transform (see Supplementary Figs 4–6).

Since we used a small number of electrodes (40) and a standard template for head model calculation, the spatial precision of the source estimations is limited. In order to provide more information about the source localization procedure, we show, for all estimations, the scalp distribution of activity (current, power, or t-value of the model) calculated separately from the CSD of the electrode space. Finally, in order to minimize the possibility of erroneous results, we only present source estimations if there are both statistically significant differences at the electrode level and the differences at the source levels survive a conservative multiple comparison correction (see below).

EEG Statistical Analysis

For all ERP analyses, we conducted paired comparisons (Wilcoxon signed-rank tests, 2-tailed) across the means of trials of each subject per condition in both the expectancy phase (HR and LR offers) and the feedback phase (unexpected rejection [UR] and expected rejection [ER]). Since the frequency of each condition depends on the subject’s behavior, the average number of trials per condition was variable among subjects (UR = 38.7 ± 4.1, ER = 62.3 ± 6.9, HR = 100.5 ± 7.8, LR = 187.9 ± 10.3). However, we controlled for this factor in the statistical analysis (see below). Continuous clusters of significant areas were identified using a cluster-based permutation test (Maris and Oostenveld 2007): The data were transformed into a 3D space (2D plane of electrode positions and time) and clusters of significant areas were defined by pooling neighboring bins showing the same effect (P < 0.05). The cluster-level statistics was computed by the sum of the statistics of all bins within the corresponding cluster. We controlled the false alarm rate for the complete cluster (set of electrodes and time bins) by evaluating the cluster-level significance under permutation distribution of the cluster that had the largest cluster-level statistics. Permutation distribution was obtained by randomly permuting the 2 conditions for each subject, thereby eliminating any systematic difference between the conditions. In order to control for possible statistical bias due to a different number of trials per condition, in each permutation, we used the same proportion of trials as in the original data (for each condition per subject) to construct the random distributions. After each permutation, a Wilcoxon signed-rank test was computed. After 1000 permutations, the cluster-level significance was estimated as the proportion of elements of the permutation distribution greater than the observed cluster-level significance.

For the power spectrum exploratory analysis, we used the same method as for the ERPs, but the data were transformed to a 4D space (2D plane of electrode positions, time, and frequency). In the source space, we conducted paired comparisons (Wilcoxon) across the means of trials of each subject per condition and used false discovery rate (FDR < 0.01) for multiple comparison correction. Trial-by-trial analysis was computed using mixed-effects linear regression with subjects as a grouping factor for random effects. For each time–frequency window of interest, the power spectrum was calculated from the time series of the single trial, both for each electrode CSD and for each source. Thus, the regressions were calculated separately in each electrode and each source. The average number of trials per subject was 257.2 (SEM = 15.2). In all models, we used dB of power related to a baseline in the fixation phase. We corrected the model P-values with FDR (< 0.01).

Software

All behavioral statistical analyses, the models of the time–frequency windows-of-interest, and the behavioral performances were performed in R software. The EEG signal processing was implemented in MATLAB using fieldtrip toolbox (Oostenveld et al. 2011), CDS toolbox (Kayser and Tenke 2006b), and in-house scripts (available online http://lntoolbox.wikispaces.com/). For the source estimation and head model, we used the BrainStorm MEG and EEG Toolbox (Tadel et al. 2011) and openMEG (Glamfort et al. 2011).

Results

Experiment 1

Behavior

The distributions of rejections and acceptances as a function of the offer are shown in Figure 2A. The $50 offer (out of $100) was the most frequently made and 86% of offers below $40 were rejected. We used simple logistic models to evaluate parameters that might predict the acceptance of an offer. The sum of money offered \((O_x, \beta = 0.168, P < 0.001, R^2 = 0.437; \text{Fig. 2C})\), the change of offer related to the preceding offer \((\Delta O_x, \beta = 0.058, P < 0.001, R^2 = 0.194; \text{Fig. 2D})\), and the responder’s preceding response \((\text{PR, } \beta = 0.92, P < 0.001, R^2 = 0.062)\) resulted in significant predictors. These parameters, together with the interaction between the change of offer and the preceding response, also remained significant when we evaluated them in a multiple logistic model (see Supplementary Table 1).

Post hoc interviews revealed that participants were able to distinguish between responders who accepted low offers and those who accepted only offers close to $50. To assess this interindividual variation in the responses, we used a mixed logistic model with the same predictors as in the multiple logistic model. The best-fit model included random effects in the intercept, the offer, and the preceding response (Table 1 and see Supplementary Table 2). In other words, the change of offer and its interaction with the preceding response were the parameters that showed less variation across responders.
Based on this result, we performed the following classification for separating HR offers (offers with high likelihood of rejection) from LR offers (offers with low likelihood of rejection).

**HR offer**: An offer that is either 1) lower than the preceding offer or 2) equal to the preceding offer when this has been rejected.

**LR offer**: An offer that is either 1) higher than the preceding offer or 2) equal to the preceding offer when this has been accepted.

From the proposer's point of view, the rejection probability resulting from HR offers and that resulting from LR offers were significantly different (0.7 and 0.17, respectively; Wilcoxon's signed-rank test, \( P<0.001 \); see Supplementary Fig. 1). On the other hand, the Shannon entropy (as a measure of the variability of the responses) of these 2 sets of offers also resulted significantly different (HR: 0.88, LR: 0.64; \( P<0.001 \); see Supplementary Fig. 1). According to this, we separated HR offer rejections (which we will call ERs; 71.2% of all rejections) from LR offer rejections (URs; 28.7% of all rejections). Similarly, we separated LR offer acceptances (expected acceptances, EAs, 83% of all acceptances) from HR offer acceptances (unexpected acceptances, UAs, 16.9% of all acceptances).

We first focused on rejections, since 1) the difference between the number of UR trials and that of ER trials resulted less than the corresponding difference in the case of acceptances, and 2) neither URs nor ERs received any money. Interestingly, the offering behavior around an ER was different from that related to a UR (Fig. 2). Before an ER occurred, the proposer had tried to increase his/her profits by lowering his/her offer. But when this offer was rejected, the proposer returned to the original (higher) offer in the following rounds. In contrast, when a UR occurred, the proposer had made a smaller offer in the preceding round and had increased it in the next round, but it got rejected. Interestingly, in this case, the proposer maintained the last offer over the rounds after the rejection. When taking into account all conditions (ERs, URs, EAs, and UAs), we found that the next change of offer was different among conditions (Friedman's rank-sum test, \( P<0.001 \); Fig. 2).

![Figure 2. Behavior in games with human partners (behavioral study). (A) Histogram of offers in games with human partners (behavioral study). (B) Offering behavior related to a rejection. The x-axis indicates round numbers relative to a rejection round "R". The right y-axis indicates the absolute offers. In the extreme right, the black bar represents URs and the gray bar the ERs. The left y-axis indicates offers relative to a rejected offer. (C) logit of the acceptance probability, logit(A), as a function of the offers. (D) logit(A) as a function of the change of offer. (E) logit(A) as a function of the acceptance probability. (A) and (B) Error bars are 95% confidence interval of the mean by bootstrapping distributions (left bars indicate the intraindividual variations and right bars the interindividual variations; see the Materials and Methods section). P-values: *0.01 \( \leq P \leq 0.05 \), **0.001 \( \leq P < 0.01 \), ***P < 0.001. ERs, expected rejections; UAs, unexpected acceptances; URs, unexpected rejections; EAs, expected acceptances. See also Supplementary Figure 1.](https://academic.oup.com/cercor/article-abstract/23/12/2872/465333/2876)
**Experiment 2**
Concerning the EEG data, we first explored the feedback phase because there are well-known electrophysiological activities of error prediction that allow us to test our classification. We next explored the electrophysiological activity of the anticipatory phase, and finally, we analyzed the relation of these activities with the decision taken in the next round.

**Behavior**
In the EEG study, subjects played as proposers against simulated partners whom they believed were human. We used the coefficients of the logistic mixed model to simulate responders (see the Materials and Methods section). The distributions of acceptances and rejections, and the offering behaviors related to a rejection were similar to the corresponding ones in the behavioral study (Fig. 2 and see...
Supplementary Fig. 1), suggesting that simulated responders elicited comparable behaviors in proposers.

**Brain Activity in the Feedback Phase**

If our risk classification was consistent with the risk perceived by the proposer, the error-related activity evoked by the unexpected responses should be larger than that evoked by the expected responses. Specifically, when proposers perceive LRs for their offers, rejections should elicit a higher MFN than when they perceive HRs. To test this hypothesis, we analyzed the time window when a proposer received a rejection. As conjectured, we found a significant difference between the MFN component of URs and that of ERs in fronto-medial electrodes (main peak in FCz electrode, $P=0.00003$ uncorrected, and $P<0.001$ corrected by the cluster-based permutation test, see Fig. 3 and Supplementary Table 3 and Fig. 3 for the time course of the evoked response over all scalp electrodes). To rule out the possibility that this difference was due to differences arising from neighboring positive components (mainly p2 and p3), we carried out 2 control analyses. In one we computed the MFN amplitude relative to neighboring positive components ($\frac{(p3+p2)}{2}$–MFN, $\text{UR} = 0.253 \mu \text{V/cm}^2$, $\text{ER} = 0.173 \mu \text{V/cm}^2$, $P = 0.0012$). In the other analysis, we fixed the most negative point occurring in the time window 250–300 ms per subject to compute the mean across subjects ($P<0.001$). In both analyses, the MFN difference remained significant. In accordance with previous studies, the significant differences in the estimated cortical sources of this component were located in the mPFC and in the medial posterior region (Miltner et al. 1997; Gehring and Willoughby 2002; Luu et al. 2003; Polezzi et al. 2010).

We then explored the time–frequency dynamics during the feedback phase and found that risk modulated activity in 2 frequency bands (Fig. 5). In frontal regions, between 240 and 400 ms after the feedback, URs presented a greater upper alpha band power (10–15 Hz) than that of ERs (main peak in FCz electrode, $P=0.0001$ uncorrected, and $P<0.001$ corrected by the cluster-based permutation test, Fig. 3 and see Supplementary Table 4). In a more extended time window (250–700 ms), theta band activity (4–7 Hz) was characterized by a stronger increase in power after URs (main peak in FCz electrode, $P=0.00004$ uncorrected, and $P<0.001$ corrected by the cluster-based permutation test, Fig. 3 and see Supplementary Table 4). We therefore focused on these time–frequency windows of interest for further analysis (see the Materials and Methods section). In agreement with previous reports (Christie and Tata 2009), the differences in the estimated cortical sources of theta activity were located in the mPFC, mainly on the right hemisphere, and in the medial posterior region. The sources of high alpha activity were located in the mPFC and lateral prefrontal cortex (IPFC; see also Supplementary Fig. 3 for comparison between different alpha ranges).

Since expectations changed theta activity, we evaluated whether the degree of risk modulated activity in these frequency bands. For this end, we carried out a trial-by-trial analysis using a mixed linear regression. We estimated the degree of risk using both the probability of acceptance (using the logit transform of the probability of acceptance, logit($A$)) and the Shannon entropy of the possible responses (logit($E$)). In both cases, we used the coefficients of the logistic mixed model of the behavioral study (Table 1). Due to the fact that theta activity may correlate with both responses and expectations, we separated activity related to rejections from that related to acceptances and included the response as a factor in the model. In this analysis, logit($A$) significantly predicted theta power in rejections (main peaks in Fz and FCz electrodes, $P<0.01$ corrected by FDR, Fig. 5 and see Supplementary Table 5). Interestingly, when we added the logit ($E$) (as a measure of the variability of the possible outcomes), it did not turn out to be a significant predictor. The source estimation of the logit($A$) coefficient in rejections was located in the right IPFC, mPFC, and medial posterior region and the source of the responses (as a factor) was located in mPFC and IPFC. In the case of acceptances, logit($A$) sources were placed in mPFC, but these did not survive the multiple comparison correction. All of these results were replicated using a wavelets transform, suggesting that our results are not an artifact of the analytical method (see Supplementary Fig. 4). None of these analyses was significant for upper alpha band activity.

**Brain Activity in the Anticipatory Phase**

Since feedback-related brain activity changed under different risk perceptions, proposers should have had different anticipatory-related brain activity according to the way they estimated how risky the proposal they had just made was. In order to study this, we explored the period after proposers sent their offers but prior to receiving the corresponding answer from the responder. As in the feedback phase, we first made an exploratory analysis of brain oscillatory activity. In right-central electrodes, we found clear differential anticipatory activity in alpha bands. Alpha activity presented a significant right-lateralized drop in HR offers in the 400–800 ms window after the offer was made (mean peaks in TP8 and FC4 electrodes, $P<0.001$ uncorrected, and $P<0.001$ corrected by the cluster-based permutation test, Fig. 4 and see Supplementary Table 6). Brain sources estimated for this difference were distributed and included temporo-parietal regions, the left IFPC and the right insular cortex. We therefore focused on these time–frequency windows of interest in order to evaluate whether alpha power depended on risk. For this, we used logit($A$) and logit($E$) as measures of risk. Interestingly, trial-by-trial alpha power correlated positively with logit ($A$) (using a mixed linear model, main effect in FT8 and TP8 electrodes, $P<0.01$ corrected by FDR, Fig. 4 and see Supplementary Table 7). Notably, unlike feedback theta activity, when we added the logit($E$) to the model, it also resulted in a significant predictor (see Supplementary Tables 8 and 9).

Previous studies have shown specific temporal dynamics of mesolimbic dopaminergic neurons related to the probabilistic reward anticipation. Some neurons present a transient activation that correlates with the probability of the reward, whereas other neurons present a tonic activation (increasing over the time interval), which is related to the variability or uncertainty of the reward (Schultz 1998; Schultz et al. 2008). To evaluate whether alpha activity has a similar temporal dynamics, we examined an additional late time window (late alpha, −700 to −200 ms before the feedback). Interestingly, early alpha fitted best with the probability, while late alpha correlated better with the entropy (see Supplementary Table 9). In the brain source space, the correlation between early alpha and logit($A$) included the temporo-parietal regions and the insular cortex of the right hemisphere. Interestingly, the correlation between late alpha and logit($E$) included sources in the bilateral medial frontal cortex (Fig. 4).
Like in the case of brain activity during the feedback phase, these results were also replicated using a wavelets transform (see Supplementary Fig. 5).

**Brain Activity and the Next Decision**

As discussed previously, the proposer’s behavior was influenced by both the risk of the preceding offer and the corresponding responder’s feedback. This became evident in the change of the next offer in both experiments (Fig. 2E and see Supplementary S1). Thus, each risk–response combination was followed by a particular change of offer (ER: $+8.1, UA: $+4.3, UR: $−2.1 and EA: $−4.5; P < 0.001). Due to the fact that theta and alpha bands showed specific risk modulations, they could underlie fine behavioral adaptation processes in social interactions. For example, prior reports suggest that frontal theta band signals error prediction in the context of behavioral adaptation (Cavanagh et al. 2010).

To look into this possibility, we analyzed whether the power of these frequency bands predicted the next change of offer (see Supplementary Fig. 5).
negotiating attitude, we found a strong negative correlation between the current change of offer and the next change of offer (Spearman’s $\rho = -0.41$, $P < 0.001$). In other words, after an HR offer, the proposers were willing to make an LR offer and vice versa. This prompted us to include the current change of offer in the model. We were thus able to evaluate whether oscillatory activity underlies behavioral regulation necessary for this social negotiation and is not just an epiphenomenon of it. Interestingly, in this model, late alpha and feedback theta were significant predictors for the next change of offer. In the brain source space, late alpha prediction was associated with activity in the right temporo-parietal region and left insular cortex, and theta prediction was related to activity in IPFC, mPFC, and posterior cingulate cortex (PCC) for rejections. In the case of acceptances, the sources in mPFC did not survive the multiple comparison correction. As in previous analyses, results were replicated using wavelets transform (see Supplementary Fig. 6), confirming that our results where not biased by the use of the windowed fast-Fourier transform approach.

Theta band activity, thereby, seems to reflect brain mechanisms that sense the prediction error: After an acceptance, proposers tend to decrease their offers and, indeed, in this case, theta activity correlated negatively with risk and predicted a smaller decrease in the next offer (Fig. 5; see Supplementary Table 11). In contrast, after a rejection, proposers tend to increase the offer. In this case, theta correlated positively with risk and predicted a smaller increase in the next offer. On the other hand, the fall in alpha band seems to reflect a preparatory activity for a possible rejection. Accordingly, it correlated with risk and predicted, only when a rejection occurred, an increase in the next offer.

**Discussion**

People participating in social interactions are able to distinguish safe from risky decisions. In making this distinction, people integrate others’ intentions and the way others perceive their own intentions. In order to investigate how this integration occurs both at the behavioral and the neural levels, the current study examined individuals playing the iterated ultimatum game in a behavioral and an EEG experiment.

The behavioral results indicate that responders reject offers that are far from the social norm of 50%, although there are important interindividual variations. In our iterated version of the ultimatum game, prior behaviors of both players are the only way to infer both the other’s intentions and how the other perceives his/her partner’s intentions. Notably, previous behavior influences significantly the responders’ responses, showing less interindividual variations than the influence of the absolute offer made. We conjecture that within the social norm compliance generated whenever punishment is possible (Fehr and Fischbacher 2004; Spitzer et al. 2007), prior behavior exerts a fine-tuning regulation on both risk perception and the expectation of subsequent behavior in an iterated interaction. Accordingly, we have proposed a classification based on preceding behavior in order to separate HR offers from LR offers. This classification not only distinguishes offers with high rejection probability and high variability (both criteria that define risk), but also particular situations in a social interaction that generate distinct subsequent behaviors.

We used the MFN, an ERP component that has been related to error predictions (Holroyd and Coles 2002), as a neuronal marker of the expected other’s behavior. As predicted, URs elicited a larger MFN than that of ERs. Several studies have shown that differences in this component can also be attributed to monetary losses (Gehring and Willoughby 2002). We rule out this possibility because the offers of URs were higher, or in other words, the potential absolute reward of URs was smaller than that of ERs. In spite of the limitation due to the reduced number of electrodes (see the Materials and Methods section) to provide a precise localization of underlying sources of EEG activity, our results are in accordance with previous work. Indeed, several studies have located the brain sources corresponding to this component over the mPFC/ACC and PCC (Miltner et al. 1997; Gehring and Willoughby 2002; Luu et al. 2003; Nieuwenhuis et al. 2005). These areas are related to conflict monitoring and mediate the relationship between the previous action-reinforcement history and the next action choice (Rushworth et al. 2007). Since MFN has been proposed to reflect theta power enhancement over the medial frontal cortex (Cohen et al. 2007; Bernat et al. 2008; Marco-Pallares et al. 2008), we looked for risk modulation of oscillatory activity in the feedback phase. In our social interactive task, the generation of expected outcomes depends on how one anticipates the others’ behaviors on the basis of preceding interactions. Interestingly, feedback theta activity correlated trial-by-trial with the probability of obtaining a response different from the expected one and not with the entropy of possible responses. In other words, and in agreement with its proposed role in error prediction (Cavanagh et al. 2010), the increase in the theta power reflects the degree of unanticipatedness of the response. The estimated sources of feedback theta activity were located in medial frontal regions, including the mPFC/ACC (Gehring and Willoughby 2002; Luu et al. 2003; Christie and Tata 2009; Martin et al. 2009). These cortical regions have been related to social cognitive tasks and social behavior (Amadio and Frith 2006; Van Overwalle 2011). For example, the ACC is activated when 2 people play interactive games, such as the trust game and the prisoner’s dilemma task (Rilling et al. 2002; Tomlin et al. 2006; De Vico Fallani et al. 2010), and the paracingulate area activates when making judgments about others (Mitchell et al. 2006). Moreover, these areas have been related to how one believes that others perceive one’s own self (Ochsner et al. 2005). Recently, the ventral mPFC has been related to how one evaluates the other players’ intentions and their compliance with social norm (Cooper et al. 2010). In our experiments, participants tended to increase the offer after a rejection. However, theta activity in the prefrontal cortex and in the medial posterior region parametrically opposed this tendency, predicting a small increase in the next offer or its maintenance. Thus, our results extend the pervious literature that relates MFN and prefrontal theta activity in the behavioral adaptation through reinforcement learning (Cohen and Ranganath 2007; Cavanagh et al. 2010; Chase et al. 2011). Interestingly, theta activity is also generated in the medial posterior regions, which has been recently associated with the change of strategy when the environment changes (Pearson et al. 2009, 2011). Thus, this activity could participate in mechanisms of fine behavioral regulation during social interactions by integrating the other’s actual behavior with the expected one.
In the expectancy phase, the alpha power modulation is located in areas that are known to participate in social processes, such as the medial frontal region and the temporo-parietal region (Saxe 2006; Zaki and Ochsner 2009). More specifically, we surmise that the drop in alpha may be related to social risk identification or an anticipatory activity to a possible negative response to one’s actions. Previous studies have shown that the identification of personal risk situations generates a fall in alpha band, more salient in the right hemisphere (Qin et al. 2009). In our experiment, during the expectancy phase, the correlation between alpha power and the probability for acceptance was higher in the early time window than in the late time window. This earlier activity includes the right temporo-parietal region which is an area related to the perception of others’ intentions and of the inconsistency between others’ behaviors and one’s expectations (Saxe and Wexler 2005). Interestingly, the correlation between alpha and the entropy of the possible response was higher in the late time window (see Supplementary Table 4). This late activity is mainly medial, including areas related to mental state attributions (Saxe and Powell 2006; Dödell-Feder et al. 2010). It is worth noting that the temporo-parietal region has been associated with a low-level processing in the social-cognitive computations, with shared activation in tasks requiring reorienting attention and the sense of agency (Decety and Lamm 2007; Mitchell 2008). This would be compatible with the earlier activation related to the outcome probability. In contrast, late activity in medial regions could reflect a more complex computation related to the inference of the other’s mental state. Indeed, these areas correlated with uncertain offers that require a more complex mental state attribution process in order to anticipate the other’s response. Notably, this dynamics resembles the dopaminergic mesolimbic neuron activity described in monkeys (Schultz 1998; Schultz et al. 2008), suggesting a strong relation between the cortical representation of social interactions and subcortical reward regions.

It has been proposed that alpha power shows a negative correlation with cortical activity, in particular in occipital and frontal areas (Laufs et al. 2003; Gonçalves et al. 2006; Laufs et al. 2006; Cosmelli et al. 2011). Several studies have found that frontal asymmetric decreases in alpha band power are related to motivational directions (approach/withdrawal; Harmon-Jones 2004; Balconi et al. 2009; Peterson et al. 2011) where a right-lateralized alpha power decrease reflects behavioral inhibition and a predisposition to respond with negative affects (Sutton and Davidson 2000; Schmidt and Hanslmayr 2009). In a task with monetary rewards, the right-lateralized frontal activity decreases when loss is possible (Miller and Tomarken 2001). In our experiment, subjects presented a decrease in right alpha power, possibly representing anticipation to negative affect elicited by an upcoming rejection. This would be in line with fMRI experiments where negative affect anticipation has been associated with AI activation (Knutson and Greer 2008) that can modulate the risk of the next financial decision (Kuhnlen and Knutson 2005). Next, the alpha decrease in the temporo-parietal region predicted trial-by-trial the change of offer in the next round only when a rejection occurred. Taken together, these results indicate, on the one hand, that a network of alpha oscillatory activity in brain areas related to social cognition is recruited in order to evaluate the risk of one’s social decisions. This network involves, first, a low-level process related to the probability distribution of others’ behavior, which is associated with right temporo-parietal region. Next, it involves a more complex process related to the uncertainty of the others’ behavior in medial frontal region. On the other hand, theta activity in the prefrontal cortex and medial posterior regions contrasts the expected with the actual behavior of the other in order to adapt subsequent behavior. Thus, both alpha and theta dynamics reflect evaluation and adaptation of the behavior necessary to participate and maintain an ongoing social interaction.

Successful social interaction crucially depends on our capacity to anticipate how others will react to our decisions and, therefore, on our capacity to estimate how risky our actions might be in a given situation. Here, we have shown that in an ultimatum game designed to study monetary social exchange, participants take into account the history of prior interactions to evaluate the risk of their decisions. Such evaluation is dependent on the recruitment of an extended brain network oscillating in the alpha range that includes key social brain regions. This network could underlie our capacity to integrate what we think the other’s intention is and how he/she perceives our intentions in order to predict effectively the other’s choices. Once we learn the other’s decision, we contrast it with our expectations and update our impressions. Here, we have provided evidence that such a process correlates with medial theta band activity, which, together with activity in the alpha band, determines our next decision.

Supplementary Material
Supplementary material can be found at: http://www.cercor.oxfordjournals.org/.

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