

# Someone has to give in: theta oscillations correlate with adaptive behavior in social bargaining

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**During social bargain, one has to both figure out the others' intentions and behave strategically in such a way that the others' behaviors will be consistent with one's expectations. To understand the neurobiological mechanisms underlying these behaviors, we used electroencephalography while subjects played as proposers in a repeated ultimatum game. We found that subjects adapted their offers to obtain more acceptances in the last round and that this adaptation correlated negatively with prefrontal theta oscillations. People with higher prefrontal theta activity related to a rejection did not adapt their offers along the game to maximize their earning. Moreover, between-subject variation in posterior theta oscillations correlated positively with how individual theta activity influenced the change of offer after a rejection, reflecting a process of behavioral adaptation to the others' demands. Interestingly, people adapted better their offers when they knew that they were playing against a computer, although the behavioral adaptation did not correlate with prefrontal theta oscillation. Behavioral changes between human and computer games correlated with prefrontal theta activity, suggesting that low adaptation in human games could be a strategy. Taken together, these results provide evidence for specific roles of prefrontal and posterior theta oscillations in social bargaining.**

**Keyword:** social interaction; game theory; ultimatum game; theta oscillations; EEG; strategic behavior

## INTRODUCTION

To conduct a successful social interaction, people not only have to figure out their partners' intentions but also have to plan strategic behaviors to achieve their goals. Thus, people behave in such a way that their partners will be able to understand their intentions and adapt to them. The most used approach to study strategic behavior in social exchanges is game theory. In these games, players have to take into account the possible strategies of other participants to make more accurate decisions (Camerer, 2003; Colman, 2003). The degree of deep reasoning in these games (e.g. 'what you think the others think about what you think', and so on) has been related to dorsomedial prefrontal cortex activity (Coricelli and Nagel, 2009). In this line, other studies have compared games where opponents are able to punish their partners' unfair behaviors with those where it is not possible to do so. The behavioral change in these games, such as behaving fairer whenever punishing is possible, indicates strategic behavior. Neurobiological studies have reported that such behavior correlates with dorsolateral prefrontal cortex activity (Spitzer *et al.*, 2007) and that the thickness of this area is related to the implementation of this behavior in childhood (Steinbeis *et al.*, 2012). Accordingly, the inhibition of this area by transcranial magnetic stimulation alters the capacity to build a good reputation (Knoch *et al.*, 2009).

A common game used in these studies is the ultimatum game (UG) (Güth *et al.*, 1982). This game involves two players, the proposer and the responder. The proposer makes an offer as to how to split a certain

amount of money between the two players. 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. In both cases, the game usually finishes after one trial. Only few experimental studies have considered the repeated version of the game (Slembeck, 1999). Once the game is repeated for the pair, it becomes a reputation game. A rational proposer, by being unwavering at the beginning of the game, on the later rounds could benefit from his unbending stance (Avrahami *et al.*, 2013). Thus, proposers not only adjust their decisions according to immediate results but also elaborate long-term strategies to achieve their goals. To study how people implement these long-term strategies and what their neurobiological underpinnings are, we studied the electroencephalographic (EEG) activity of proposers in a repeated version of the UG.

In non-social settings, several studies have shown that oscillatory brain activity in theta range (4–8 Hz) over medial frontal cortex plays a key role in conflict monitoring and reinforcement learning (Cohen *et al.*, 2007, 2008; Cavanagh *et al.*, 2010). Thus, an increase in theta power occurs when people receive a negative feedback or a monetary loss (Kamarajan *et al.*, 2008; Marco-Pallares *et al.*, 2008; Lucchiarri and Pravettoni, 2010; Van Driel *et al.*, 2012). Interestingly, theta power is modulated by both the magnitude of monetary loss and its probability of occurrence (Cohen *et al.*, 2007; Cavanagh *et al.*, 2012) and is correlated with the subsequent action adjustment (Van de Vijver *et al.*, 2011). As frontal theta activity has also been associated to strategic control and conflict monitoring in social contexts (Billeke *et al.*, 2013; Cristofori *et al.*, 2013), we hypothesized that this activity might be a candidate for the neural implementation of long-term strategies for social bargaining. To evaluate whether this strategic behavior is specifically social, we carried out two tasks. In the main task, people played with a simulation believing that they were playing with other human, while in the control task, subjects played with the same simulation but during the game they were instructed that they were playing against a computer. Thus, in the main task, we expected the subjects to

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play strategically, for instance, changing less their offers with the expectation that their partners would change their behavior too. On the other hand, in the control task, where bargaining is not possible, people would learn quickly the more advantageous offer. Therefore, we propose that people with more prefrontal theta activity will behave in a more strategic way in the games with other humans.

**METHODS**

The data of the main task reported in this article were originally re-collected for Billeke et al. (2013). All the analyses presented in this work are new.

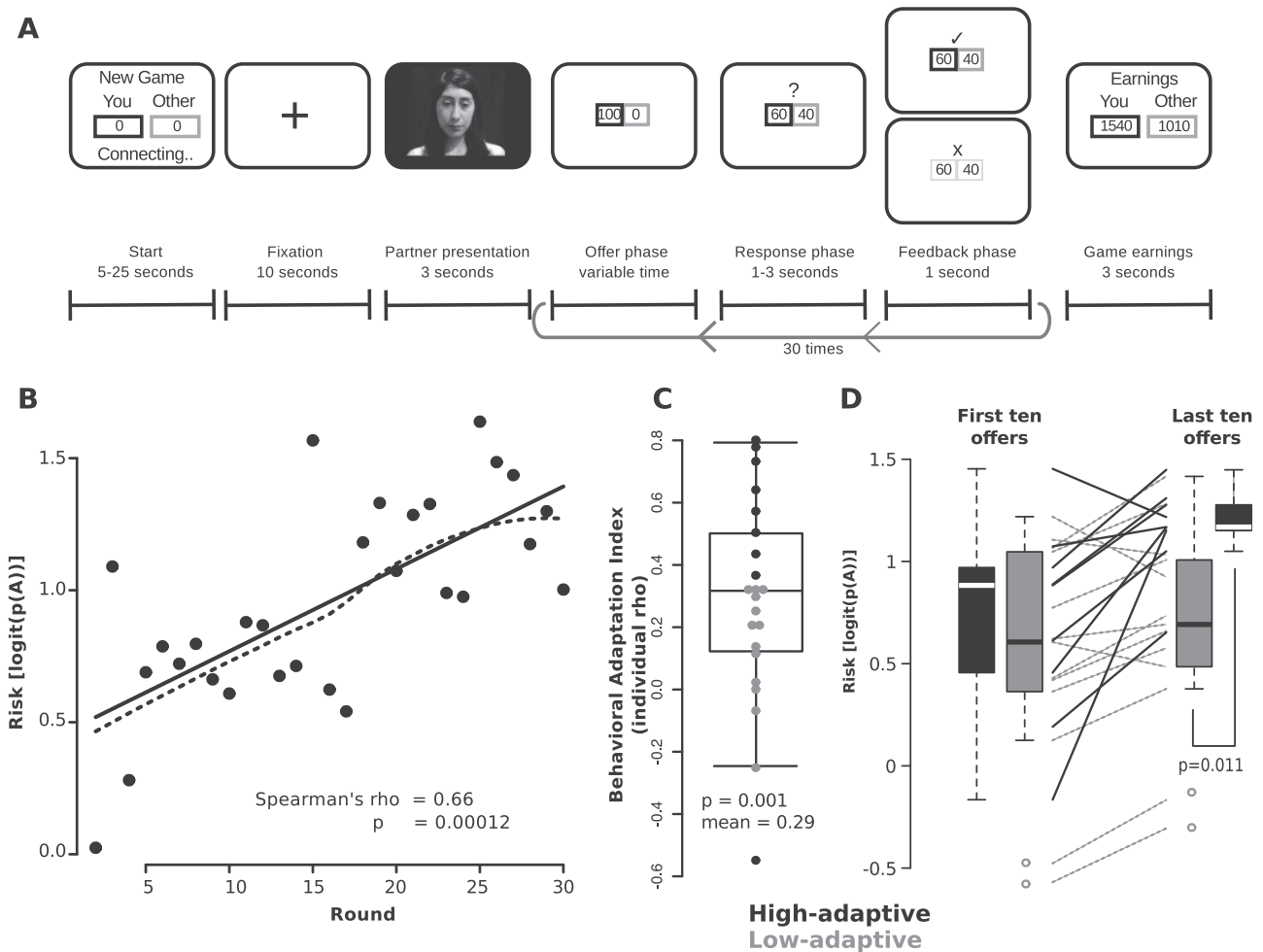
**Participants**

Thirty-nine individuals (22 with 7 women for the main task and 17 with 6 women for the control task) participated for monetary compensation after recruitment online. All participants were right-handed Spanish speakers, aged from 18 to 25 years (24.31, s.e.m. = 0.41). All participants had normal vision, no color-vision deficiency, no history of neurological diseases and no current psychiatric diagnosis prescriptions. All participants gave informed consent and the Ethics Committee of the Pontificia Universidad Católica de Chile approved

the experimental protocol. All experiments were performed at the Cognitive Neuroscience.

**Main task**

Participants played as proposers in a repeated version of the UG (Figure 1A). Subjects believed they were playing with a human partner, but they were actually playing with a simulated partner (see below). Together with the experimenter, participants read the instructions describing the game. Then, 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. At the beginning of each game, participants watched the fixation cross (fixation phase) and then a video of their partner. All videos showed full faces of participants in color on a black background. Each game consisted of 30 rounds and each participant played as a proposer eight times with different simulated responders. Each round defined a trial. Each trial had three phases as follows: in the first (offer phase), the proposer had to make the offer. In the second (response phase), the offer was revealed to the responder who had to decide whether to accept or reject it. In the last phase (feedback phase), the response was revealed to the proposer. At the end of each game, the



**Fig. 1** (A) Timeline of a game. Proposers (black box) and responders (gray box, computational simulations, see 'Methods' section) played an iterated UG. The proposer makes an offer on how to split 100 Chilean pesos between the responder and himself/herself (offer phase). The responder decides to either accept or reject it (response phase). If the responder accepts the offer, the money is split as proposed, and if he/she rejects it, the money is lost. The response is shown on the screen during 1 s (feedback phase). Each game consists of 30 iterated offers. In the main task, to make the interaction more realistic, the proposer watches a video of the responder at the beginning of each game (partner presentation). In the control task, the proposer sees a cue that indicates if his/her partner is a human ('H') or computer ('PC'). (B) Group correlation between the risk of the offer (logit transforms of the probability of acceptance) and game round. The solid line represents the fitted linear regression, and the dashed line represents the fitted local regression (LOESS). (C) Distribution of the individual correlation coefficients (between the risk of the offer and the round of the games) across subjects (BAI). (D) Mean of the offer risk in the first and last 10 offers per subject. (C and D) Subjects were divided as high adaptive (black) and low adaptive (gray) according to their BAI (see 'Results' section).

earnings each player had made in the game were revealed. After the set of games concluded, the experimenter interviewed each participant individually to check whether they had understood the game correctly. The amount of money each participant received depended on his/her performance with a minimum of 6000 and a maximum of 12 000 Chilean pesos (~12.6–25.2 USD). The task was programmed and presented using Presentation (Neurobehavioral Systems).

### Control task

This task was similar to the main task, although participants were informed that they were playing with another human (four games) or with a computer simulation (four games, randomly distributed). At the beginning of each game, participants watched a cue that indicated if they played with a human ('H') or a computer ('PC'). The experimenter explained to the participant that the computer simulation assigns a probability to accept or reject the offer given the amount of money offered, and that this probability might change among the different games but not during a game. The simulation used in human and computer games was the same as that used in the main task.

### Simulation

Simulations used in the tasks were based on a mixed logistic modeling of 33 people playing as receptors with other people (for more details, see Billeke *et al.*, 2013). Using this model, we were able to create different virtual players. All participants (in both tasks) played with the same simulated partners in random order and with a random assignment to 'human' or 'computer' in the control task. Specifically, the simulation assigns a probability to reject or accept the offer given the following two equations:

for round  $(x) = 1$ ,

$$\text{logit}(R_x) = (b_0 + r_0^i) + (b_1 + r_1^i)O_x,$$

and for round  $(x) > 1$ ,

$$\begin{aligned} \text{logit}(R_x) = & (b_0 + r_0^i) + (b_1 + r_1^i)O_x \\ & + (b_2 + r_2^i)\Delta O_x + b_2 Pr_x + b_3 \Delta O_x Pr_x \end{aligned}$$

where  $\text{Logit}(A_x)$  is the logit transform of the probability of acceptance for the round  $x$ ,  $O_x$  the offer,  $\Delta O_x$  the change of offer in relation to the preceding offer and  $Pr_x$  the preceding response. The coefficients estimated for each regressor were composed by a population parameter ( $b_y$ ) and a random effect for each simulated responder ( $r_{y,i}$ ,  $y$  = regressor and  $i$  = simulated partner, see [Supplementary Material](#) for a more extended explanation). That the simulation and setting generated a credible human interaction was verified by: (i) the distributions of acceptances and rejections, and the offering behaviors related to a rejection in the simulation game were similar to those obtained in a real human game (see Billeke *et al.*, 2013), suggesting that simulated responders elicited comparable behaviors in proposers and (ii) in the *post hoc* interview, experimenters asked the participant whether they believed that they had played against a human counterpart. All participants indicated that they actually believed that they had played against another human (in the main task), and that they felt the human games different from the computer games (in the control task).

### Psychological tests

Participants were evaluated with a battery of neuropsychological tests that were administered during a different session. The battery included the continuum performance test (Cornblatt *et al.*, 1988) to evaluate sustained attention, the trait-making test (Gaudino *et al.*, 1995) to evaluate speed of processing, the Wechsler Memory Scale III (e.g. Tulsky, 2004) to evaluate working memory, the Tower of

London (e.g. Phillips *et al.*, 2001) to evaluate reasoning and problem solving and the Baron-Cohen's Face Emotion Recognition Test (Baron-Cohen *et al.*, 2001) to evaluate social cognition.

### Electrophysiological recordings

Continuous EEG recordings were obtained with a 40-electrode NuAmps EEG System (Compumedics Neuroscan). All impedances were kept below 5 k $\Omega$ . 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 four electrodes. All recordings were acquired using Scan4.3 and stored for off-line treatment. At the end of each session, electrode position and head points were 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  $\pm 100 \mu\text{V}$ , and their contribution was removed from each dataset using principal component analysis by singular value decomposition and spatial filter transform. Other remaining artifacts (e.g. muscular artifacts) were detected by visual inspection of the signal and the trials that contained them were removed. Thus, we obtained  $220 \pm 20$  artifact-free trials per subject. For the frequency analysis at the sensor levels, epochs were transformed to current source density (CSD; Kayser and Tenke, 2006). CSD computes the second spatial derivative of voltage between nearby electrode 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. Induced power distribution was computed using Wavelets transform, with a 5-cycle Morlet wavelet, in  $-1$  to  $1$  s windows around the feedback release (padding to 0.5 s). For all analysis, we used the dB of power related to the fixation phase as baseline (at the beginning of each game, see [Figure 1](#)). This was done to avoid contamination by expectation before the feedback (e.g. theta suppression during reward anticipation, Bunzeck *et al.*, 2011).

### Source estimations

The neural current density time series at each elementary brain location was estimated by applying a weighted minimum norm estimate inverse solution (Baillet *et al.*, 2001) with unconstrained dipole orientations in single-trials per condition per subject. A tessellated cortical mesh template surface derived from the default anatomy of the Montreal Neurological Institute (MNI/Colin27) warped to the individual head shape (using  $\sim 300$  headpoints per subject) was used as a brain model to estimate the current source distribution. We defined  $3 \times 5005$  sources constrained to the segmented cortical surface (three orthogonal sources at each spatial location), and computed a three-layer (scalp, inner skull, outer skull) boundary element conductivity model and the physical forward model (Clerc *et al.*, 2010). The measured electrode level data  $X(t) = [x_1(t), \dots, x_{m_{\text{electrode}}}(t)]$  is assumed to be linearly related to a set of cortical sources  $Y(t) = [y_1(t), \dots, y_{m_{\text{source}}}(t)]$  ( $3 \times 5005$  sources, see above) and additive noise  $Y(t) = WX(t) = RLT(LRLT + \lambda 2C) - 1X(t)$ , where  $L$  is the physical forward model. The inverse solution was then derived as  $Y(t) = WX(t) = RLT(LRLT + \lambda 2C) - 1X(t)$  where  $M$  is the inverse operator,  $R$  and  $C$  are the source and noise covariances, respectively, and  $\lambda$  is the regularization parameter.  $R$  was the identity matrix that was modified to implement depth-weighting (weighting exponent: 0.8; Lin *et al.*, 2006). 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. In this source space, we computed frequency decomposition using the Wavelets transform. Since we used a small number of electrodes and no individual anatomy for head model calculation, the spatial precision of the source estimations is limited. To provide more information about the localization procedure, we show, for all source estimations, the scalp distribution of activity calculated separately from the CSD of the electrode space. Finally, 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 multiple comparison correction.

### Statistical analysis

For individual and global correlations, we used Spearman's rho. To evaluate whether the individual rho values were other than zero, we used the Wilcoxon signed rank test. To compare between groups of subjects, we used the Wilcoxon sum rank test. For the theta activity modeling, we used the robust linear model with MM-estimation and the Spearman partial correlation. To compare two correlations we used the Fisher  $z$ -transformation. To correct for multiple comparisons in time–frequency charts and source analysis, we used the Cluster-based permutation test (Maris and Oostenveld, 2007). Here, clusters of significant areas were defined by pooling neighboring bins that showed the same effect ( $P < 0.05$  in the statistical test carried out in each bin of either the time–frequency chart or the sources, e.g. Spearman correlation in Figure 2B). The cluster-level statistics was computed as the sum of the statistics of all bins within the corresponding cluster. We evaluated the cluster-level significance under permutation distribution of the cluster that had the largest cluster-level statistics. Then, a permutation distribution of the cluster-level statistics was obtained by randomly permuting the original data. After each permutation, the original statistical test was computed (e.g. Spearman correlation), and the cluster-level statistics of the greatest cluster was calculated. After 2000 permutations, the cluster-level significance of each observed cluster was estimated as the proportion of elements of the permutation distribution greater than the observed cluster-level statistics.

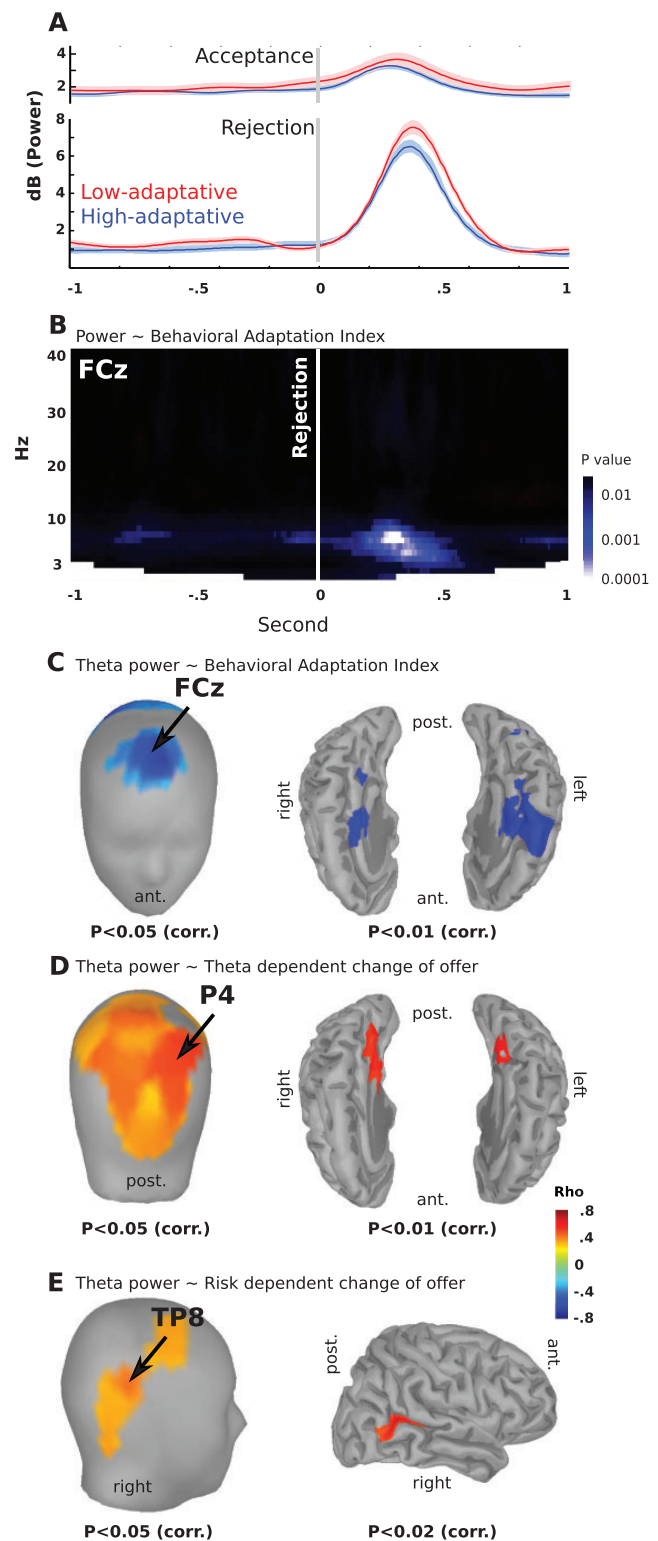
### Software

All behavioral statistical analyses were performed in R. The EEG signal processing was implemented in MATLAB using CSD toolbox (Kayser and Tenke, 2006), and in-house scripts (available online <http://lantoolbox.wikispaces.com/>). For the source estimation and head model, we used the BrainStorm (Tadel et al., 2011) and openMEEG toolboxes (Gramfort et al., 2011)

## RESULTS

### Behavior

Throughout the game, subjects offered a mean of  $42.6 \pm 1\$$  to receptors (modal offer: 50%) and obtained  $0.34 \pm 0.03$  rejection rates. We evaluated whether proposers performed strategic evolutions of their offers across the rounds of the games, analyzing how the risk of the offers changed across each game. The risk of the offers was calculated using the logit transform of the probability of the simulation accepting the offer. The simulation is different for each responder and is given by a model of real people behavior (Billeke et al., 2013). Our model takes into account the sum of money offered, the change of offer related to the preceding offer and the preceding responder's response (see 'Methods' section). Using the mean of the risk across subjects



**Fig. 2** (A) Time course of theta power related to rejections (lower panel) and related to acceptances (upper panel) per both high-adaptive (blue) and low-adaptive subjects (red). Areas represent the s.e.m. of each curve. (B) Time–frequency chart of the time windows when proposers receive a rejection. The color represents the  $P$ -value of Spearman's correlation between the power spectrum and the behavioral adaptive index across all subjects (see 'Results' section). (C) Spearman's partial correlation between theta power and the behavioral adaptive index. (D) Spearman's partial correlation between theta power and theta dependent change of offer. (E) Spearman's partial correlation between theta power and risk dependent change of offer. (B–D) Only significant clusters are shown (corrected by the cluster-based permutation test). See also Supplementary Figure S2.

per round, we evaluated the global tendency (Figure 1B). We found a strong positive correlation between the risk and the round number (Spearman's  $\rho = 0.66$ ,  $P = 1e-4$ ). Similar results were obtained using the amount of money offered ( $\rho = 0.44$ ,  $P = 0.01$ ) and the acceptance rates ( $\rho = 0.40$ ,  $P = 0.02$ ).

The overall trend was to make risky offers at the beginning of each game, and safer offers in the last rounds. To evaluate individual differences in this tendency, we carried out the same analysis for each subject by computing the individual correlation coefficient. Interestingly, in spite of the global tendency to positive values (Wilcoxon sign rank test,  $P = 0.001$ , Figure 1C), there was great dispersion of the individual correlation coefficients. Since each value reflects how each subject adapts her/his behavior to her/his partners' behaviors, we will call this value a behavioral adaptation index (BAI). Accordingly, we separated proposers into two groups depending on how they compared to the global tendency. Those subjects whose BAIs were not significant (i.e. their correlation coefficients were not statistically significant,  $P > 0.05$ ) were classified as low adaptive ( $n = 13$ ), while those whose BAIs were significant were classified as high adaptive ( $n = 9$ ). The high-adaptive subjects obtained higher earnings than the low-adaptive subjects (Wilcoxon rank sum test,  $P = 0.025$ ). In addition, high-adaptive subjects had a marginal tendency to have less variation of their offers across each game ( $P = 0.06$ ). The first 10 offers (out of 30) of low-adaptive subjects were undistinguishable from those of high-adaptive subjects ( $P > 0.5$ ; Figure 1D). In spite of the great inter-individual dispersion in the first 10 offers, the offer risks of the high-adaptive group converged in the last 10 rounds. Here high-adaptive subjects made offers with a high probability of acceptance (mean logit = 1.15, probability = 0.76) that were higher than that of low-adaptive subjects ( $P = 0.011$ ).

Finally, we assessed for demographic or cognitive differences between groups. There were no differences in either age ( $P = 0.26$ ) or socio-economic status ( $P = 0.68$ ). In the general, non-social cognition tests (attention, memory, executive functions and planning; see Supplementary Table S1), we did not find differences between groups. However, the low-adaptive group presented a higher score in the face emotion recognition test ( $P = 0.02$ ), which measures social cognition. In all subjects, this test's score correlated with the BAI ( $\rho = -0.57$ ,  $P = 0.005$ ).

## EEG

We evaluated whether the degree of adaptive behavior correlates with frontal oscillatory activity. We used the BAI (the individual correlation between the offer risk and the round) as an indicator of individual long-term adaptive behavior. First, we explored differences in theta activity elicited by the feedback between subjects with high BAI (high-adaptive subject) and those with low BAI (low-adaptive subjects). Only upon rejections did low-adaptive subjects present more theta activity (4–8 Hz). Notably, we found a specific correlation between the amplitude of theta oscillatory activity elicited by rejections (4–8 Hz, 0.3–0.5 s after negative feedback, fronto-medial electrodes) and the BAI (Figure 2B,  $P < 0.01$ , Wilcoxon sign rank test and cluster-based permutation test). This means that people with lower prefrontal theta power elicited by a rejection, adapted their offers obtaining more acceptances in the last round of each game. In a previous study, we showed that theta power was related to the change of offer after a rejection in a within-subject analysis (Billeke *et al.*, 2013). People tended to increase their offers after a rejection. This offer increase was correlated positively with the risk of the offer and negatively with the theta activity elicited by the rejection. Thus, to obtain an individual measure of this tendency, we calculated, per each subject, the Spearman's correlation between pre-frontal theta power elicited by

**Table 1** Multiple robust regression of prefrontal theta power after a rejection

Regressor	Beta (s.e.)	t-Value	P-value
Intercept	−12.8 (2.8)	−4.6	0.0003
BAI	−8.4 (2.0)	−4.3	0.0007
Change of offer in the next round	−0.4 (0.1)	−3.1	0.0074
Theta-dependent change of offer	9.1 (3.1)	2.9	0.0095
Risk-dependent change of offer	0.2 (2.5)	0.1	0.9
Rejection rate	−12.7(9.3)	−1.3	0.19
Risk of the rejected offers	12.1 (10.3)	1.1	0.25

a rejection and the next change of offer (theta-dependent change of offer, using FCz electrode where our previous analysis had identified the peak of this correlation (Billeke *et al.*, 2013), mean  $\rho$  value =  $-0.13$ , Wilcoxon sign rank test,  $P = 2e-4$ ). In the same way, we calculated the individual correlation between the risk of the offer and the change of the offer after a rejection (risk-dependent change of offer, mean  $\rho$  value =  $-0.53$ ,  $P = 4e-5$ ).

Then, to clarify the meaning of the between-subject variations of theta power, we first performed a multiple robust regression of theta power in the FCz electrode (Table 1) with several regressors as follows. First, we used the BAI to evaluate the relation between theta and the tendency to make safer offers in the last round of each game. Second, to evaluate the relation between the variation of theta power and how each subject reacted to a rejection, we used the mean of the change of offer after a rejection per each subject, the individual theta-dependent change of offer and the individual risk-dependent change of offer (see above). As theta power depends on the risk of the rejected offer, people who make risky offers have less theta power; hence people with greater BAI (who make risky offers at the beginning of the games) may have as a consequence less theta power. To rule this out, we included in the model the risk of the rejected offer and the rate of rejected offers per subject as control variables. Interestingly, the correlation between theta power and the BAI remained negative and significant (Table 1). In this model, the relation between theta power and the change of offer is also negative and significant, whereas the relation between theta power and theta-dependent change of offer is positive and significant.

We next computed the Spearman's partial correlation among the preceding variables for each electrode (Figure 2B–D) and each cortical source, to obtain an approximation of the cortical localization of these activities. We found a negative correlation between theta activity and BAI in the FCz and Fz electrode. The probable sources of this activity were located in the dorsal anterior cingulate cortex (dACC) and in the superior frontal gyrus (Brodmann's areas 8 and 24). In addition, the correlation between theta power and the theta-dependent change of offer was found at electrodes P4, Pz and P3. The source for this correlation was located in the precuneus/posterior cingulate cortex (PCC, Brodmann's areas 23 and 31). The correlation between theta and the risk-dependent change of offer was found at electrode TP8; its source was in the posterior temporal region.

Interestingly, the partial correlation also shows that BAI correlated positively with the theta-dependent change of offer ( $\rho = 0.6$ ,  $P = 0.009$ , FCz electrode) and negatively with the change of offer after a rejection ( $\rho = -0.65$ ,  $P = 0.004$ , FCz electrode). These results indicated that people with more theta power tend to maintain their offer across the game, in spite of the responders' rejections. Finally, we evaluated the relation between social cognition capacity, adaptive behavior and the oscillatory activity. We carried out a partial correlation between emotion recognition test, BAI, prefrontal theta and the individual earnings. BAI was correlated with both emotion recognition test ( $\rho = -0.58$ ,  $P = 0.005$ ) and theta activity ( $\rho = -0.56$ ,  $P = 0.007$ ),

although theta activity was not correlated with emotion recognition test ( $\rho = -0.12$ ,  $P = 0.14$ ). We did not find any significant correlation with the individual earnings.

### Control task

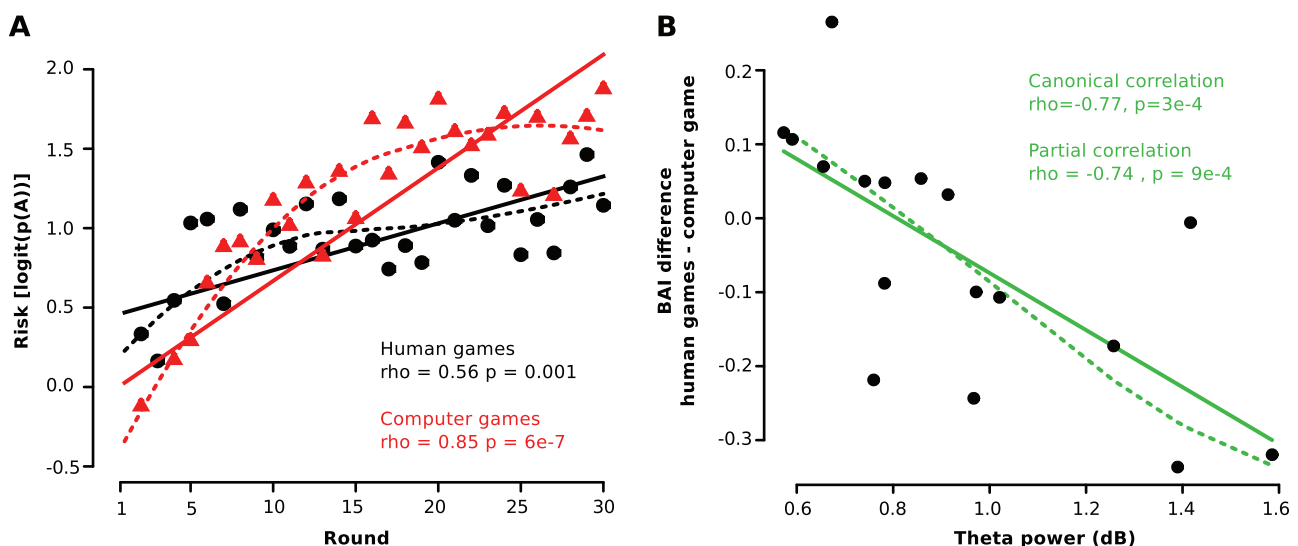
The above results indicated that subject with less theta activity adapted less their offers throughout the game. This can be due either to a poor learning of the game dynamics, or to a strategy based on the expectation that the other player will change his/her behavior before one does. To evaluate this, we carried out a control task where people believed they played four games against human partners and four games against computer simulations (see 'Methods' section). Crucially, human and computer games were both simulations, but in the computer games subjects knew that the computer would not change the rejection probability during each game. In both games subjects offered similar amount of money (human:  $42.0 \pm 1.4$ , PC:  $39.6 \pm 1.2$ , Wilcoxon test,  $P = 0.14$ ) and obtained similar rejection rates (human:  $0.36 \pm 0.04$ , PC:  $0.44 \pm 0.6$ ,  $P = 0.4$ ). They also had the global tendency to make safer offers toward the end of each game (PC:  $\rho = 0.85$ ,  $P = 6e-7$ ; human:  $\rho = 0.56$ ,  $P = 0.001$ ; difference:  $Z = 2.39$ ,  $P = 0.016$ ), although in the computer games the slope was greater during the first rounds and reached a plateau in the last rounds (Figure 3A). Then, we calculated the difference between the risk offer made in computer games and that made in human games, per round. In accordance with the preceding results, this difference had a significant correlation with the round number ( $\rho = 0.76$ ,  $P = 2e-6$ ).

Next, we evaluated the relation between BAI and prefrontal theta oscillation in both computer and human games during the control task. In both cases, we used a partial correlation to control for a possible effect of the risk of the rejected offers. Notably, in human games the correlation was significant ( $\rho = -0.73$ ,  $P = 5e-5$ ), while it was not significant in computer games ( $\rho = -0.19$ ,  $P = 0.4$ ; differences:  $Z = -2$ ,  $P = 0.045$ ). This difference was apparent mainly for the behavioral change in the human game, as there was a significant correlation between the change in the BAI (human game BAI - computer game BAI) and the theta power in human game (canonical correlation:  $\rho = -0.77$ ,  $P = 3e-4$ ; partial correlation controlled by the risk of the rejected offer in human games:  $\rho = -0.74$ ,  $P = 9e-4$ ).

### DISCUSSION

When people become involved in a social negotiation, they have to infer other people's intentions from their behavior and signal their own intentions back to them. In our study, subjects played as proposers with simulated responders, believing that they were interacting with other humans. These simulated responders did not change or adapt their 'intentions' during successive iterations of the game (e.g. the threshold for accepting/rejecting the offers). Therefore, subjects had to adapt their offers to the simulation's behavior to obtain higher earnings. In fact, behavioral results show that, at the group level, proposers adapt their offers toward the last round of the game (Figure 1). People who do not fit this tendency have increased prefrontal theta activity when compared to those that do. Previous studies have associated prefrontal theta activity with reward-based learning, where theta power is related to behavioral adaptations (Cavanagh et al., 2010). However, we found that people who adapt their offers to their partners' behaviors had less prefrontal theta power. At the within-subject level, theta activity is related to both unexpected results and subsequent adaptive behaviors during a social negotiation (Billeke et al., 2013). Prefrontal theta activity is probably originated in the ACC, an area that has been related to conflict monitoring between competing responses (Botvinick et al., 1999), prediction error (Brown and Braver, 2005) and linking reward information to action (Hayden and Platt, 2010). Recently, the ACC has been related to competitive efforts in social context (Hillman and Bilkey, 2012), and theta oscillations in this area increase amplitude when a social rejection occurs (Crowley et al., 2010; Cristofori et al., 2013).

Our results indicate that people who do not adapt their behaviors present more prefrontal theta activity evoked by a rejection. In a negotiation, people will not only adjust their own intentions but will also expect that their partners do so to achieve a mutual agreement. Interestingly, in the control task, when people played with computer partners and were informed that these would not change the rejection probability during a game, the BAI did not correlate with prefrontal theta oscillation. Thus, when change in others' behavior is ruled out, there is no correlation between BAI and prefrontal theta. Indeed, in this context, people adapt their offer in order simply to maximize their profit. Thus, the greater prefrontal theta activity in low-adaptive players seems not to be related with poor learning; it could rather



**Fig. 3** (A) Correlation between the offer risk (logit transform of the probability of acceptance) and the round number for both human (black) and computer (red) games. (B) Correlation between the differences in the BAI in human and computer game and the theta power in FCz electrode. (A and B) Solid lines represent the fitted linear regression, and dashed lines represent the fitted local regression (LOESS).

represent the tendency to expect others to accommodate to their own intentions regardless of the behavioral feedback. In addition, we found that people with this tendency score highly in a social cognition test measuring the capacity to understand the others' mental state. However, the score in this test did not correlate with prefrontal theta activity. This may suggest that these subjects read accurately the others' intentions and may use this information to behave strategically, expecting the others to give up to their whims. However, prefrontal theta activity is related to the strategy and not directly to this social cognition skill. An alternative interpretation would be that low-adaptive subjects pay less attention to the task. Nonetheless, we believe this is not the case for the following reasons: first, low-adaptive subjects did not differ from high-adaptive subjects on attention, memory and planning tests. Second, people tend to behave less adaptively when they believe that they are facing a human (in contrast to a simulation), suggesting that this change is a strategy to engage in human bargaining. Finally, low-adaptive subjects present more frontal theta activity. Several studies have shown that theta activity increases with conflict detection, prediction error (Cavanagh *et al.*, 2010), attention (Missonnier *et al.*, 2006) and task difficulty (e.g. Gomarús *et al.*, 2006), and decreases with distraction (Zhang *et al.*, 2013). Therefore, if subjects were paying less attention to the task, they should have had less theta activity.

In addition to prefrontal theta, posterior theta activity is related to how people change their offers after a rejection. Interestingly, this activity probably originates from the medial parietal region that includes the precuneus and the PCC. These regions are related to perspective taking, autobiographic memory (Maddock *et al.*, 2001) and empathy processes (Zaki and Ochsner, 2012). Recently, the PCC has been related to both the implementation of novel behavior responses to diverse environmental demands and the adaptive use of these behaviors in response to environmental change (Pearson *et al.*, 2011). Thus, people playing with a partner that does not change her/his behavior need to adjust their own strategy (e.g. offer more money than they originally intended) to increase their profits. Therefore, the posterior theta activity could reflect the implementation of a change in behavioral policy.

The results presented here provide novel evidence of the role of theta oscillations in social interactions, showing specific functions for anterior and posterior theta activity. On one hand, anterior theta (and probably ACC) activity reflects error signaling concerning the others' behaviors, but not necessarily the adaptation to them. Moreover, this error signal reflects the expectancy that the other will adapt his/her behavior to one's needs. On the other hand, posterior theta (and probably PCC/precuneus) activity reflects the process of behavioral adaptation to the others' demands. Thus, these two activities could reflect the neurobiological processes underlying the trade-off between giving in to others' demands and the expectation that others give in to ours.

## SUPPLEMENTARY DATA

Supplementary data are available at SCAN online.

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