Medial prefrontal cortex and striatum mediate the influence of social comparison on the decision process

Nadège Bault[a,b,1], Mateus Joffily[a,c], Aldo Rustichini[d], and Giorgio Coricelli[a,c,e,1]

[a]Cognitive Neuroscience Centre, Centre National de la Recherche Scientifique, Unité Mixte de Recherche 5229, 69675 Bron, France; [b]Center for Research in Experimental Economics and Political Decision-Making, and Cognitive Science Center Amsterdam, University of Amsterdam, 1018TV Amsterdam, The Netherlands; [c]Center for Mind/Brain Sciences, University of Trento, 38060 Mattarello, Italy; [d]Department of Economics, University of Minnesota, Minneapolis, MN 55455; and [e]Department of Economics, University of Southern California, Los Angeles, CA 90089-0253

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We compared private and social decision making to investigate the neural underpinnings of the effect of social comparison on risky choices. We measured brain activity using functional MRI while participants chose between two lotteries: in the private condition, they observed the outcome of the unchosen lottery, and in the social condition, the outcome of the lottery chosen by another person. The striatum, a reward-related brain structure, showed higher activity when participants won more than their counterpart (social gains) compared with winning in isolation and lower activity when they won less than their counterpart (social loss) compared with private loss. The medial prefrontal cortex, implicated in social reasoning, was more activated by social gains than all other events. Sensitivity to social gains influenced both brain activity and behavior during subsequent choices. Specifically, striatal activity associated with social gains predicted medial prefrontal cortex activity during social choices, and experienced social gains induced more risky and competitive behavior in later trials. These results show that interplay between reward and social reasoning networks mediates the influence of social comparison on the decision process.

Information on the outcome of actions that we did not choose may be useful in improving our future decisions. Emotions such as regret (1, 2) embody the painful lesson that circumstances would have been better if we had made a different choice (3, 4). Theoretical (5–10) and empirical (11–14) studies have shown that regret and fictive error signals (which consider the difference between the obtained outcome and the outcomes of alternative foregone actions) have an adaptive function—they constitute a way of evaluating past outcomes to adjust choices in the future. By the same logic, information regarding the outcome of actions chosen by others should also be useful. From social comparison theory (15), we derive the insight that individuals use information on outcomes of others to evaluate their own abilities, and therefore, social comparison allows efficient learning.

The neural response to fictive or counterfactual outcomes (that is, the outcomes of unchosen options) has been localized in the human orbitofrontal cortex (12, 16) and the anterior cingulate cortex both in humans (12) and nonhuman primates (17). In addition, the ventral striatum has been found to play an important role in encoding fictive error signals in dynamic decision-making settings (13). Hence, neural structures related to reward processing (18, 19) and learning (20–23) are involved in encoding counterfactual information in the private setting. Little is known about the neural responses to fictive social signals (24, 25), which refer to the comparison between the outcome from the action that we chose and the outcome of an alternative action chosen by someone else. Here, we directly compare the neural underpinnings of fictive signals in private relative to social settings. The first goal of this research was to investigate how individuals evaluate the outcome of their decision in private vs. social contexts to test the hypothesis that, for the same given outcome, social comparison will enhance brain activity related to social reasoning (26–31) in addition to eliciting a stronger response of the reward system (32–34). Second, the study was designed to investigate whether private and social evaluations of outcomes of risky choices differently influence subsequent decisions. Does the process of encoding counterfactual information in private and social settings share the same neural circuitry? How does the interplay between the reward-related brain areas and the social reasoning network mediate the effect of social comparison on the decision process?

To answer these questions, we designed a lottery choice task in which participants could compare the outcome of their choices with the outcome of the unchosen lottery and in one-half of the trials, with the outcome of choices made by another player. We combined functional MRI (fMRI) and skin conductance recordings to measure brain activity and autonomic responses while participants made a sequence of choices between pairs of lotteries that differed in their expected values and levels of risk (Fig. 1*A*). We manipulated the decision context: in the private context, the participant chose in isolation, whereas in the social context, the participant could see, after they had made their choice, a counterpart's independent and simultaneous choice for the same pair of lotteries. The actions of one of the players had no influence on the outcomes of the other. After the participant and counterpart had made their choice, three outcome contexts were possible: private (P), social same choice (SSC), when the participant and the counterpart had made the same choice, and social different choice (SDC), when they chose different lotteries (Fig. 1*B*). Trials were also categorized as relative gain (+) or relative loss (−) trials, depending on the sign of the difference between the outcomes of the chosen and unchosen lotteries. To summarize, we considered different events according to their outcome context and relative valence of the outcome (Fig. 1*B*).

After participants experience others' choices and outcomes as affecting the way they evaluate the outcome of their own choice, they may begin to anticipate this effect on future trials and adapt their decisions accordingly. Our experiment was designed to analyze this effect by randomly allocating participants to two environments that we call bold and prudent (*Methods*) based on the risk attitude of the controlled counterpart. In the bold environment, the counterpart selected lotteries with higher mean returns, whereas the prudent counterpart made safe choices, selecting lotteries with lower variance. In other words, the two groups of participants were facing two different competitors: one

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[1]To whom correspondence may be addressed. E-mail: nadege.bault@isc.cnrs.fr or giorgio.coricelli@usc.edu.

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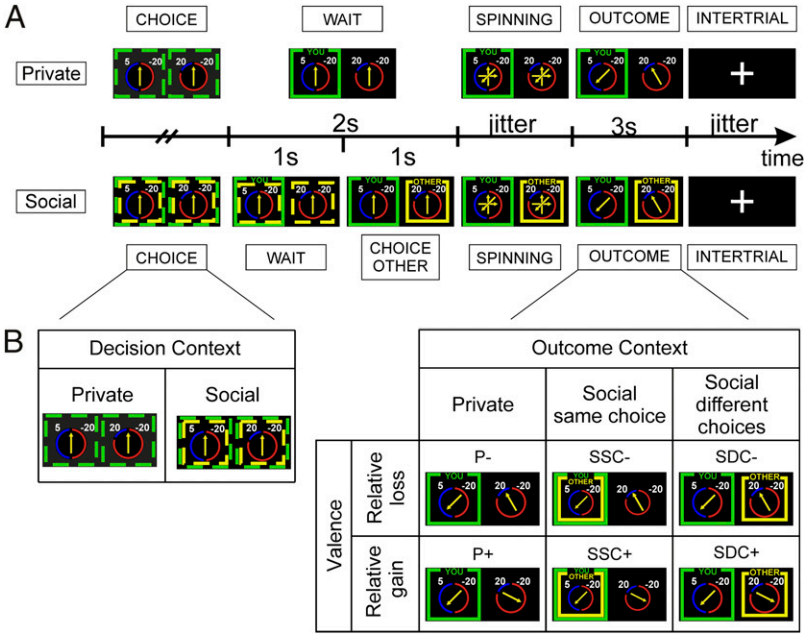

Fig. 1. Experimental paradigm. (*A*) Task and time course. The time courses of the private and social conditions are displayed above and below the time line, respectively. Pairs of lotteries were displayed, with numbers indicating the possible outcomes and probabilities represented by colored sectors of a circle. Lotteries were surrounded by green dotted squares representing the participant's possible choices, plus yellow dotted squares representing the counterpart, in the social condition only. The presence of the yellow dotted square, thus, indicated to the participant that they would see their counterpart's choice. (*B*) Experimental design. At the time of choice, the Blood-oxygen-level dependent (BOLD) signal was analyzed to test the effect of the decision context that could be private or social. During the outcome period, the BOLD signal and skin conductance data were analyzed to test the effect of two factors: valence and outcome context.

group had tough competitors, with high average payoff (bold environment), and the other group had weaker competitors, with relatively lower average earnings (prudent environment).

The theory we adopt (35) (*SI Methods*, *Theoretical Model of Choice*) predicts that sensitivity to relative social gains will motivate participants to outperform the other player, resulting in a more risky behavior, especially when playing with a competitive counterpart. Thus, a difference in participants' risky behavior in the two environments will reveal the effect of social comparison on choice; additionally, more risky behavior than their counterparts will indicate the participants' intent to outperform the others.

Results

Social Comparison Affects Choice Behavior. Participants took significantly longer to make their choice in the social context (3.97 ± 1.39 s) compared with the private context [3.82 ± 1.24 s; Wilcoxon signed rank test (WSRT), $z = 2.714$, $P < 0.01$]. The social or private nature of the comparison affects choice behavior as well. This finding is reflected in participants' attitude to risk. Regression analysis (*Methods*, Table S1, and *SI Methods*, *Logit Model*) on choice behavior over all participants ($n = 24$) and trials shows that participants chose by maximizing expected value ($dEV = 0.171$, $P < 0.001$) and were risk-neutral ($dSD = 0.003$, $P > 0.5$). We then tested whether participants' risk attitude differed between the two environments and found that there was an interaction between environment (bold and prudent) and risk attitude of participants (Environment × $dSD = 0.036$, $P < 0.05$). When the regression was run separately for the two environments, we found that participants in the prudent environment ($n = 12$) were risk-neutral ($dSD = 0.003$, $P > 0.5$), whereas participants in the bold environment ($n = 12$) were risk-seeking ($dSD = 0.039$, $P < 0.001$) (Table S1). The interaction between the variable risk and environment was not significant for the first 20 trials (Environment × $dSD = -0.041$, $P > 0.5$); thus, the two groups did not differ in risk attitude in early trials (Table S1). To control for the number of trials, we also ran the same regression on the last 20 trials. The results are very similar to those results of the regression including all trials, with a significant interaction between environment and risk (Environment × $dSD = 0.114$, $P < 0.005$). Participants adapted their choice behavior across the experiment to take into account that of their counterpart. In summary, as predicted (*SI Methods*, *Theoretical Model of Choice*), individuals in a more challenging environment became more risk-seeking.

Participants' behavioral adjustment to the behavior of their counterpart across the experiment was related to the social gains that they experienced in early trials. The difference between the participant's and their counterpart's payoffs, in early social gain events, was strongly correlated with the distance between the two players' risk behavior in late trials of the experiment ($r = 0.85$, $P < 0.001$) (Fig. 2). This distance was measured as the difference between the subject's and counterpart's dSD coefficients given by the logistic regression. In other words, participants who experienced greater amounts of social gain in early trials behaved in a more risk-seeking manner in subsequent trials, making choices that were likely to yield a relatively higher payoff compared with their counterpart. This relation did not hold for experienced social losses (Fig. 2) ($r = 0.34$, $P > 0.1$).

fMRI Results. ***Brain activity during outcome evaluation.*** Our hypotheses imply that both the counterfactual outcome (i.e. the outcome of the nonchosen lottery) and the outcome context (private or social) influence the way participants react to their obtained outcomes. We searched for brain regions where activity is modulated by (*i*) the comparison between the outcomes of the two lotteries, (*ii*) the outcome context, and (*iii*) the integration of these two signals. We conducted a two-way ANOVA with two factors: outcome context (three levels: P, SSC, and SDC) and valence at the time of outcome (two levels: relative loss and relative gain) (*Methods*, *Functional MRI Model*).

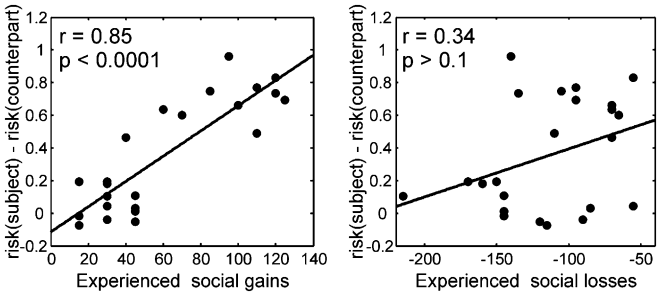

Fig. 2. Behavioral effect of experienced outcomes. (*Left*) The scatter plot represents the across-subjects correlation between the distance of subject's risk behavior to its counterpart (in sessions 2 and 3) and the cumulated experienced social gains in early trials (session 1). (*Right*) The plot shows the same correlation for the experienced social losses. The distance between the subject's and counterpart's risk attitude was computed as the difference between the subject's and counterpart's *dSD* individual coefficients given by the logit regression. In a single trial, experienced social loss and social gain were measured as the difference between the obtained outcome and the outcome of the lottery chosen by the other player. We then summed these differences to compute the total value of each experienced outcome. One data point was excluded from the two correlations analyses, because participant's risk difference score was >3 SD from the grand mean. When including the outlier, $r = 0.49$ and $P < 0.02$ for early social gains, and $r = 0.05$ and $P > 0.5$ for early social losses.

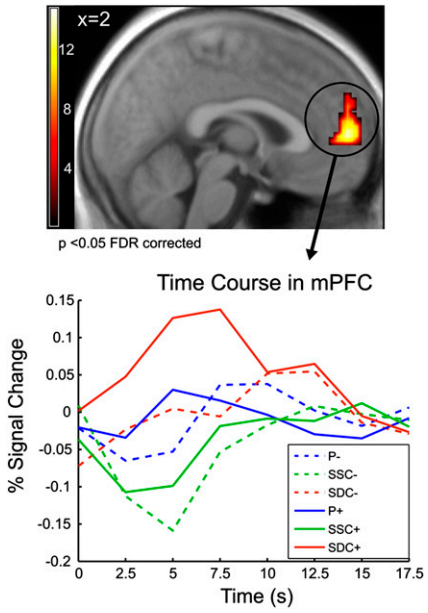

Fig. 3. mPFC activity related to social gains. (*Upper*) mPFC activity discriminates between the three outcome conditions (P, SSC, and SDC), when the outcomes of the two lotteries are revealed. *F* maps projected on the subjects' averaged brain. (*Lower*) Time course in the mPFC (0, 54, 9) for the six possible outcomes. The mPFC is more activated for social gain than for all other events.

Activity related to the valence of the relative outcomes was found (Fig. S1) in the bilateral ventral striatum [caudate and putamen; peak voxels Montreal Neurological Institute coordinates (x, y, z): left (−12, 9, −9) and right (21, 15, −3)] and the orbitofrontal cortex (0, 48, −12; Table S2 has a complete list of regions, coordinates, and statistics). In all reported clusters, activity was larger for relative gains than relative losses.

Looking at the effect of outcome context allows us to differentiate brain regions implicated in social comparison from regions involved in mere comparison of lottery outcomes. The main effect of outcome context revealed brain activity in the right ventral striatum (15, 21, −9), the medial prefrontal cortex (mPFC; 0, 54, 9), the dorsolateral prefrontal cortex (45, 21, 30), and the temporoparietal junction [TPJ; left (−45, −60, 27) and right (54, −54, 21)] (Fig. S1 and Table S2). Fig. 3 shows that activity in the mPFC (0, 54, 9) related to social gain events was greater than activity related to all other events. To test whether this difference was significant, we contrasted the social gain (SDC+) event with all five other events using an inclusive mask of the main effect of outcome context. This analysis revealed that activity related to SDC+ was indeed significantly higher than all other events in the brain regions reported above ($P < 0.001$, false discovery rate-corrected for all peak voxels). Because these regions are not activated in the SSC condition (Fig. 3), the current pattern of results suggests that they do not simply encode social vs. private context but rather, a competitive/strategic component of the interaction, with the favorable social comparison having the strongest activation.

To test whether some structures processed relative gains and losses differently in the three outcome contexts (P, SSC, and SDC), we looked at the interaction between the valence and outcome context. Several areas, including the bilateral striatum, showed an interaction between the factors valence and social context (Table S2). We extracted the percent of signal change from the striatum (*Methods*) to look at specific contrasts. The activity related to social loss (SDC−) in the ventral striatum was more intensively deactivated compared with private loss (P−) (Fig. 4*A*) [posthoc test: $F(1, 23) = 13.48$, $P < 0.001$ in left caudate and nucleus accumbens (−9, 9, −3); $F(1, 23) = 13.86$, $P < 0.001$ in right caudate and nucleus accumbens (9, 12, −3)]. Activity related to social gain (SDC+) was relatively higher compared with private gain [P+; $F(1, 23) = 4.29$, $P < 0.05$ in left caudate, not significant in right caudate]. Notably, the striatum was the only brain area that exhibited this particular pattern.

This pattern of activity closely resembles the pattern of skin conductance responses recorded during the fMRI experiment (Fig. 4*B*) and subjective ratings participants gave for each event in previous behavioral study using the same task (Fig. 4*C*). Skin conductance response (SCR) magnitudes (*Methods* and *SI Methods, Skin Conductance Recording*) in outcome evaluation depended on the outcome context (Fig. 4*B*) (Friedman test: $\chi^2 = 11.375$, $P < 0.005$); responses to relative gains and relative losses for the SDC events were more arousing than the SSC (WSRT: $z = 2.637$, $P < 0.05$) and the private events (WSRT: $z = 2.017$, $P < 0.05$). This finding suggests that the relatively larger activation (deactivation) related to social gain (loss) events compared with private gain (loss) events is associated with higher skin conductance responses.

Brain activity during choice period is influenced by outcome-related striatal activity. Our analysis of behavior has shown that past experience of outcomes in the social condition affects later behavior. We investigate the neural basis for this behavioral effect by first comparing the activity at the moment of choice in the two contexts and then examining the path from outcome-related striatal activity to choice making.

We found larger activity in mPFC in the social than private contexts during the choice period (−3, 42, 39 and 9, 54, 3). Superior temporal sulcus [left: (−63, −6, −21) and right: (54, −15, −12)], bilateral TPJ [left: (−60, −51, 21) and right: (57, −39, 18)], and precuneus (9, −48, 42) were also activated by the social condition relative to the private condition (Fig. S2 and Table S3) (no significant activity was found for the contrast private > social).

To determine whether outcome-related striatal activations influenced decision-related activity, we ran a connectivity analysis using beta seed correlations methods (*SI Methods* has a detailed description of the procedure). This analysis allowed us to find all brain voxels that had activity during the choice period correlated with the striatal activity during the previous outcome evaluation. We found that activity of the left (−9, 9, −3) and right (9, 12, −3)

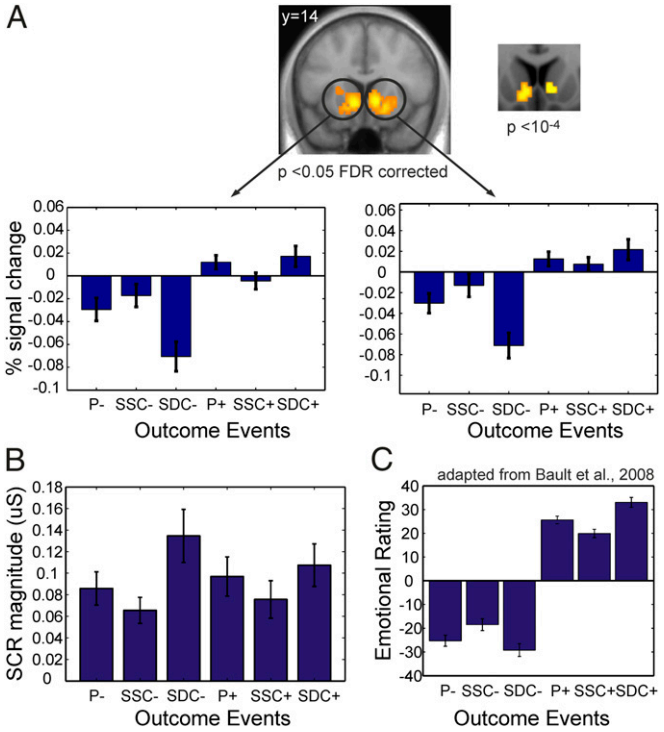

Fig. 4. (*A*) Striatal activity encoding outcomes' relative valence and outcome context during the outcome evaluation period. The coronal slice shows the interaction effect between the valence and outcome context factors. The bar graphs indicate the percent of signal change (± SEM) for the left (−9, 9, −3) and right (9, 12, −3) caudate (areas of interest defined from the interaction analysis). (*B*) Mean skin conductance responses (± SEM) for the six outcome events. Responses are reported in microsiemens. (*C*) Emotional evaluations [on a scale from −50 (extremely negative) through 0 (neither positive nor negative) to +50 (extremely positive)] given by 42 participants for the six outcome events in a previous behavioral study. Adapted from Bault et al. (41).

ventral striatum during the outcome phase correlated with activity in the mPFC during the decision phase (Fig. 5).

We also found a cross-subjects correlation ($r = 0.52$, $P = 0.01$) between activity of the mPFC (−1, 46, 30) at the time of choice and putamen activity (30, −12, −3) during outcome evaluation in social gain (SDC+) events. More specifically, participants with higher putamen activity during SDC+ events at outcome exhibited higher mPFC activity during social choices. The correlation between private gain events and private choices within the same two regions was not significant ($P > 0.05$).

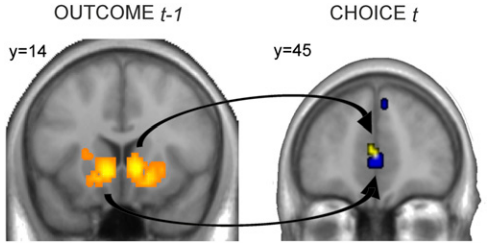

Fig. 5. Effect of experienced outcomes on choice-related brain activity. Functional connectivity analysis. The map shows the voxels where activity during the choice period *t* is correlated with activity of the striatum during the outcome evaluation of the previous trial *t* − 1. The seed regions are the left and right ventral striatum regions that showed an interaction between the factors valence and outcome context (Fig. 4*A*).

Discussion

We combined a choice task with functional brain imaging and physiological recordings to directly compare the brain activity underlying decision making in social and private contexts. More specifically, our goal was to understand how counterfactual and social comparisons influence choice. Our experimental design has two main advantages compared with previous studies. It enabled us to directly contrast private and social decision processes within a single task, and it also allowed us to study the effect of social comparisons made by subjects on their subsequent choices (hence, to study the effect of social loss and social gains on choice behavior and brain activity).

The striatum, a brain structure implicated in reward processing (18, 19), encoded both relative gains and losses and outcome context, showing amplified responses when social comparison was involved compared with the private context and same choice events. These findings support results from previous studies reporting that the ventral striatum encodes social rewards (34, 36), positive social comparison (33), social ranking (32), and emotional reaction to the misfortune of previously envied people (i.e., the feeling of Schadenfreude) (37).

In addition to the ventral striatum, we found evidence for the involvement of areas of the mentalizing network (a brain network associated with the attribution of mental states to others) (26–31), such as the mPFC and the TPJ, in relative social reward processing. Activity in these regions was driven by a favorable social comparison (social gain), signaling situations in which the participant had done better than her counterpart.

mPFC, superior temporal sulcus, TPJ, and precuneus were selectively activated during choices in the social context. Notably, in our experiment, participants interacted with their counterpart in a minimal way; it was made clear in the instructions that player's payoffs were completely independent. Despite the minimal level of interaction during decision making, the mentalizing network was strongly recruited. This finding is in accordance with the behavioral results: participants adjusted their choices to the choices of their counterpart, making choices that were likely to yield a relatively higher payoff compared with the other. Recent neuroimaging studies have suggested that the mPFC and other regions of the mentalizing network compute prediction errors of the expected behavior of others (24, 25), the uncertainty about other's strategy (38), and the level of strategic reasoning in competitive games (39). Thus, we suggest that mPFC activity at choice in our experiment is related to the strategic and competitive component of the social context and not simply to the presence of the other player.

The design of our study, in contrast to previous studies investigating social comparison (33, 37, 40), enabled us to investigate the neural underpinnings of the effect of social comparison on subsequent choices. We found that the mPFC was more activated in the social context than the private context, both at choice and outcome phases. First, mPFC activity during choice was correlated with activity in the ventral striatum during the outcome period of the previous trial. Second, mPFC activity during choice in the social context depends on how rewarding the social gain events are to the subjects, which was suggested by the across-subjects correlation between the activity of the striatum during social gains and the activity of the mPFC during choice. During outcome evaluation, mPFC activity was more specifically related to social gains. Finally, participants who experienced more social gains behaved in subsequent trials in a more competitive way, seeking more rewarding and risky options. We suggest that this coherent pattern of brain and behavior characterized the dynamical relationship between the experience and the anticipation of social rewards. Furthermore, there are some aspects of the current study that could be addressed in future work. We did not detect a significant dif-

ference between the brain activity involved in the two environments (bold and prudent). We believe that this indicates that the mental processes underlying the behavioral effect of social comparison in both environments are highly similar, but alternative hypotheses should be explored. Future work could also consider including a (nonsocial) computer condition. This condition would create nonsocial same and nonsocial different choices. These could be more directly compared with the SSC and SDC condition, because neither of these additional conditions should induce social comparison.

Crucial findings in our study are the role of the mPFC in signaling the events in which participants won more than their counterpart (social gain events) and the observation that mPFC activity was correlated with earlier activity in reward-related brain structures. These findings suggest that the brain is equipped with the ability to detect and encode social signals, make social signals salient, and then, use these signals to optimize future behavior. Specifically, the interaction between the reward and the mentalizing networks mediates the competitive component of evaluation of social outcomes and social decision making. Finally, it is important to note that such brain activity and behavior in a social context is driven more by the prospect of winning than by the prospect of losing.

Methods

Participants. Twenty-four subjects (12 females, 2 left-handed subjects, mean age = 23 ± 3.7 y) participated in the study. These volunteers gave fully informed consent for the project, which was approved by the French National Ethical Committee. Individuals with a history of psychiatric or neurological problems were not included in the study.

Experimental Procedure. Participants underwent 120 trials in three successive sessions (Table S4 has a complete list of trials). A lottery task adapted from the work of Bault et al. (41) was used with an event-related design, varying the magnitude and probabilities of potential gains and losses. Subjects repeatedly chose between two lotteries. Each lottery had two outcomes, each outcome from the set of values {−20; −5; +5; +20}. The probability of the first outcome was taken from the set {0.2; 0.5; 0.8}. The same pseudorandomized sequence of pairs of lotteries and outcomes was used for all participants. A trial could be private (60 trials) or social (60 trials). In social trials, participants were instructed that they would see the other player's choice and outcome. The order of the two types of trials was randomized inside each of the three fMRI runs. They were very similar regarding visual features and time course (Fig. 1*A*). At the beginning of the trial, two lotteries were displayed. A green dotted square surrounded the lotteries in private trials, and a yellow dotted square surrounded the lotteries in social trials, as depicted in Fig. 1*A*. The subject could choose one of the two lotteries at any time by pressing one of two buttons of an MR-compatible response box placed in the subject's right hand. After the choice, a continuous green line surrounded the lottery chosen by the individual during 2 s. In addition, in social trials, a continuous yellow line indicated the choice made by the other during 1 s. After a spinning period (4–6 s), the outcomes of both lotteries were displayed at the same time for 3 s. The participants could then compare their outcome to the outcome of the lottery not chosen (private counterfactual comparison) or to the outcome of the second player (social comparison). The outcome of a lottery chosen by both players was the same for both. The second player was a confederate of same sex as the subject. The confederate was introduced to the subject as another participant recruited in the same conditions as he had been. They went through the training part in the same room, and therefore, the participant was lead to believe that he would see the other's choice while inside the scanner. We ensured that the confederate played his role until the subject was installed in the scanner. During the experimental sessions, counterpart's choices were made by a computer algorithm. This procedure allowed us to first analyze the participant's behavior independently from the other player. It also allowed us to manipulate the environment created by the other player's choice behavior and the outcomes that the subject was facing. In one group of 12 participants (six females), the algorithm chose the lottery with the highest expected value in 90% of the trials (bold environment). This algorithm was very competitive, cumulating 206 Euros over the experiment for the given pseudosequence of outcomes, thus creating an environment in which the opponent was realizing large sums on average. In the second group of the remaining 12 participants (six females), the computer was selecting the lottery with the lowest SD in 90% of the trials (prudent environment). This second algorithm corresponded to a more prudent behavior, winning less (only 15 Euros over the 60 social trials) but with smaller variability. During debriefing at the end of the experiment, no participant reported any doubt about with whom they were playing (*SI Methods, Debriefing Questionnaires*). To avoid having participants mentally sum their earning and be able to treat trials independently, participants were told that the outcome from 20 randomly drawn trials would be sum at the end of the experiment and that they would receive this amount added to a 5 Euros show-up fee. For ethical reasons, all participants received 50 Euros, irrespective of their gains in the game.

Choice Behavior Analysis. Choice behavior was analyzed based on panel data analysis (*SI Methods, Logit Model* has more details) using the statistical software package Stata (Stata). We ran panel logit regressions, which take each participant as the unit and the trial as time, and we estimated both random and conditional fixed effects. We report the results for the random effects analysis. We estimate, with the logit regression, the probability of the participant choosing the first lottery ($c = 1$) as a function of the difference in expected value (*dEV*) and SD (*dSD*; i.e., risk) between the first and the second lottery (Eq. **1**):

$$\Pr(c = 1|dEV, dSD) = \frac{\exp[\alpha + \beta(dEV) + \gamma(dSD)]}{1 + \exp[\alpha + \beta(dEV) + \gamma(dSD)]}. \quad [1]$$

A positive and significant *dEV* coefficient indicates that subjects chose, everything else being equal, the lottery with highest expected value; a significant and positive (negative) *dSD* indicates choices of higher (lower) level of risk, and nonsignificant *dSD* indicates risk neutrality. The distance between the two players' risk behavior (Fig. 2) was measured by the difference between the subject's and the counterpart's *dSD* coefficients estimated in the logit regression.

Skin Conductance Responses. Skin conductance was continuously recorded and sampled at 50 Hz using a BIOPAC MP150 data acquisition unit (BIOPAC Systems) (*SI Methods, Skin Conductance Recording* has more details). The SCR amplitude was thresholded at 0.02 μS. SCR magnitude was calculated as the mean response amplitude computed across all trials, including trials without a measurable response. Nonparametric tests were applied on the datasets, because it violated several parametric assumptions.

fMRI: Data Acquisition, Preprocessing, and Statistical Analysis. fMRI data acquisition and preprocessing were carried out using standard procedures described in *SI Methods, fMRI Analysis*. Voxel-wide differences in BOLD contrast within the smoothed normalized images resulting from the different task conditions and trial types were examined using SPM5. Standard neuroimaging methods using the general linear model were used with the first level (individual subject analyses), providing contrasts for group effects analyzed at the second level (group analyses). No voxel showed significant activation when comparing the two environments (bold and prudent), neither during the choice period nor outcome period in the social context, even when applying a liberal threshold of $P < 0.001$, uncorrected. We, thus, merged the data from the two groups for the analyses. Two time periods were of interest for the fMRI analysis: choice and outcome. They were both preceded by a 4- to 6-s jittered period. The jitter periods and trial order were set to optimize estimation efficiency and detection power (42, 43). We introduced all four events of the trial (decision, button press, anticipatory, and outcome) in the same general linear model to attribute signal variance to all known sources of variance. The decision period was modeled as a variable epoch, time-locked to the onset of the trial, and ended with the button press indicating choice (self-paced). The button press was modeled as a δ-function. The anticipatory period was modeled with an epoch of duration of the spinning, and the outcome period started when the spinning stopped with 3-s duration. All regressors were convolved with the canonical hemodynamic response function.

fMRI Model. For choice, regressors came in two conditions: private and social (decision context) (Fig. 1*B*). For the anticipatory period, we modeled separately the P, SSC, and SDC trials. For the outcome period, trials were categorized into six events according to the condition and the relative gains (+, obtained outcome greater than outcome of the unchosen lottery) or relative loss (−, obtained outcome less than outcome of the unchosen lottery): private loss (P−), shared loss (SSC−), social loss (SDC−), private gain (P+), shared gain (SSC+), and social gain (SDC+). Eight trials could not be categorized as relative gain or loss, because the outcomes of the two lotteries were identical. These trials were not included in the analysis. Linear contrasts were

used to obtain subject-specific estimates for each regressor. These estimates were entered into a second-level analysis treating subjects as a random effect using a full factorial analysis. For the choice period, there was one factor, the decision context with two levels of private and social. For the outcome period, we tested a 3 × 2 factorial design (Fig. 1*B*), with the first factor representing the outcome context (P, SSC, and SDC) and the second factor representing the valence of the outcome (relative gain or loss). We report results from three contrasts, namely the main effect of the outcome context, the main effect of valence, and the interaction between the outcome context and the valence.

Activations Localization and Reported Statistics. Reported coordinates conform to the Montreal Neurological Institute space. Activations are reported as significant for clusters > 10 voxels with $P = 0.05$, corrected for multiple comparisons using voxel-wise control of the false discovery rate. Plots representing percent of signal change as well as cross-subject correlations of brain activity between brain regions were realized by extracting BOLD data for areas of interest. Areas of interest were functionally defined, based on main effect of decision and the interaction effect between outcome context and valence, for the choice and outcome period, respectively. Parameter estimates from the fitted model were extracted and averaged across all voxels in the cluster for each subject, and then, the percent of signal change was estimated. In the striatum, a small volume correction was applied using an anatomical mask to determine more precisely which parts of this region encoded the outcome context, the valence, and their interaction. For the cross-subject correlation, the mPFC area of interest was defined from the main effect of decision context, and the putamen area of interest was defined from the interaction analysis between outcome context and valence. These analyses were performed with the MarsBaR 0.41 SPM toolbox (http://marsbar.sourceforge.net/).

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1. Bell DE (1982) Regret in decision making under uncertainty. *Oper Res* 30:961–981.
2. Loomes G, Sugden R (1982) Regret theory: An alternative theory of rational choice under uncertainty. *Econ J* 92:805–824.
3. Ritov I (1996) Probability of regret: Anticipation of uncertainty resolution in choice. *Organ Behav Hum Decis Process* 66:228–236.
4. Zeelenberg M, Beattie J, van der Pligt J, de Vries NK (1996) Consequences of regret aversion: Effects of expected feedback on risky decision making. *Organ Behav Hum Decis Process* 65:148–158.
5. Coricelli G, Rustichini A (2009) Reward-based emotions: Affective evaluation of outcomes and regret learning. *Handbook of Reward and Decision Making*, eds Tremblay L, Dreher JC (Elsevier, Amsterdam), pp 427–439.
6. Coricelli G, Rustichini A (2010) Counterfactual thinking and emotions: Regret and envy learning. *Philos Trans R Soc Lond B Biol Sci* 365:241–247.
7. Foster DP, Vohra R (1999) Regret in the on-line decision problem. *Games Econ Behav* 29:7–35.
8. Hart S (2005) Adaptive heuristics. *Econometrica* 73:1401–1430.
9. Megiddo N (1980) On repeated games with incomplete information played by non-Bayesian players. *Int J Game Theory* 9:157–167.
10. Montague PR, King-Casas B, Cohen JD (2006) Imaging valuation models in human choice. *Annu Rev Neurosci* 29:417–448.
11. Chiu PH, Lohrenz TM, Montague PR (2008) Smokers' brains compute, but ignore, a fictive error signal in a sequential investment task. *Nat Neurosci* 11:514–520.
12. Coricelli G, et al. (2005) Regret and its avoidance: A neuroimaging study of choice behavior. *Nat Neurosci* 8:1255–1262.
13. Lohrenz T, McCabe K, Camerer CF, Montague PR (2007) Neural signature of fictive learning signals in a sequential investment task. *Proc Natl Acad Sci USA* 104: 9493–9498.
14. Marchiori D, Warglien M (2008) Predicting human interactive learning by regret-driven neural networks. *Science* 319:1111–1113.
15. Festinger L (1954) A theory of social comparison processes. *Hum Relat* 7:117–140.
16. Camille N, et al. (2004) The involvement of the orbitofrontal cortex in the experience of regret. *Science* 304:1167–1170.
17. Hayden BY, Pearson JM, Platt ML (2009) Fictive reward signals in the anterior cingulate cortex. *Science* 324:948–950.
18. Schultz W (1998) Predictive reward signal of dopamine neurons. *J Neurophysiol* 80: 1–27.
19. Schultz W (2002) Getting formal with dopamine and reward. *Neuron* 36:241–263.
20. O'Doherty JP (2004) Reward representations and reward-related learning in the human brain: Insights from neuroimaging. *Curr Opin Neurobiol* 14:769–776.
21. Schultz W (1998) The phasic reward signal of primate dopamine neurons. *Adv Pharmacol* 42:686–690.
22. Schultz W, Dayan P, Montague PR (1997) A neural substrate of prediction and reward. *Science* 275:1593–1599.
23. Seymour B, et al. (2004) Temporal difference models describe higher-order learning in humans. *Nature* 429:664–667.
24. Behrens TEJ, Hunt LT, Woolrich MW, Rushworth MFS (2008) Associative learning of social value. *Nature* 456:245–249.
25. Hampton AN, Bossaerts P, O'Doherty JP (2008) Neural correlates of mentalizing-related computations during strategic interactions in humans. *Proc Natl Acad Sci USA* 105:6741–6746.
26. Amodio DM, Frith CD (2006) Meeting of minds: The medial frontal cortex and social cognition. *Nat Rev Neurosci* 7:268–277.
27. Fletcher PC, et al. (1995) Other minds in the brain: A functional imaging study of "theory of mind" in story comprehension. *Cognition* 57:109–128.
28. Frith CD (2007) The social brain? *Philos Trans R Soc Lond B Biol Sci* 362:671–678.
29. Frith CD, Frith U (2006) The neural basis of mentalizing. *Neuron* 50:531–534.
30. Gallagher HL, et al. (2000) Reading the mind in cartoons and stories: An fMRI study of 'theory of mind' in verbal and nonverbal tasks. *Neuropsychologia* 38:11–21.
31. Gilbert SJ, et al. (2006) Functional specialization within rostral prefrontal cortex (area 10): A meta-analysis. *J Cogn Neurosci* 18:932–948.
32. Dvash J, Gilam G, Ben-Ze'ev A, Hendler T, Shamay-Tsoory SG (2010) The envious brain: The neural basis of social comparison. *Hum Brain Mapp* 31:1741–1750.
33. Fliessbach K, et al. (2007) Social comparison affects reward-related brain activity in the human ventral striatum. *Science* 318:1305–1308.
34. Izuma K, Saito DN, Sadato N (2008) Processing of social and monetary rewards in the human striatum. *Neuron* 58:284–294.
35. Maccheroni F, Marinacci M, Rustichini A (2011) Social decision theory: Choosing within and between groups. *Rev Econ Stud*, in press.
36. Izuma K, Saito DN, Sadato N (2010) Processing of the incentive for social approval in the ventral striatum during charitable donation. *J Cogn Neurosci* 22:621–631.
37. Takahashi H, et al. (2009) When your gain is my pain and your pain is my gain: Neural correlates of envy and schadenfreude. *Science* 323:937–939.
38. Yoshida W, Seymour B, Friston KJ, Dolan RJ (2010) Neural mechanisms of belief inference during cooperative games. *J Neurosci* 30:10744–10751.
39. Coricelli G, Nagel R (2009) Neural correlates of depth of strategic reasoning in medial prefrontal cortex. *Proc Natl Acad Sci USA* 106:9163–9168.
40. Zink CF, et al. (2008) Know your place: Neural processing of social hierarchy in humans. *Neuron* 58:273–283.
41. Bault N, Coricelli G, Rustichini A (2008) Interdependent utilities: How social ranking affects choice behavior. *PLoS One* 3:e3477.
42. Friston KJ, Zarahn E, Josephs O, Henson RN, Dale AM (1999) Stochastic designs in event-related fMRI. *Neuroimage* 10:607–619.
43. Liu TT, Frank LR, Wong EC, Buxton RB (2001) Detection power, estimation efficiency, and predictability in event-related fMRI. *Neuroimage* 13:759–773.