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Learning from other people's experience: A neuroimaging study of decisional interactive-learning

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ABSTRACT

Decision-making is strongly influenced by the counterfactual anticipation of personal regret and relief, through a learning process involving the ventromedial-prefrontal cortex. We previously reported that observing the regretful outcomes of another's choices reactivates the regret-network. Here we extend those findings by investigating whether this resonant mechanism also underpins interactive-learning from others' previous outcomes. In this functional-Magnetic-Resonance-Imaging study 24 subjects either played a gambling task or observed another player's risky/non-risky choices and resulting outcomes, thus experiencing personal or shared regret/relief for risky/non-risky decisions. Subjects' risk-aptitude in subsequent choices was significantly influenced by both their and the other's previous outcomes. This influence reflected in cerebral regions specifically coding the effect of previously experienced regret/relief, as indexed by the difference between factual and counterfactual outcomes in the last trial, when making a new choice. The subgenual cortex and caudate nucleus tracked the outcomes that increased risk-seeking (relief for a risky choice, and regret for a non-risky choice), while activity in the ventromedial-prefrontal cortex, amygdala and periaqueductal gray-matter reflected those reducing risk-seeking (relief for a non-risky choice, and regret for a risky choice). Crucially, a subset of the involved regions was also activated when subjects chose after observing the other player's outcomes, leading to the same behavioural change as in a first person experience. This resonant neural mechanism at choice may subserve interactive-learning in decision-making.

Introduction

Real-world decision-making in the social context is very likely to be influenced by other people's experience, in particular by what other individuals experience as a result of their choices. Yet, this factor has been rarely considered by studies on the neural correlates of *learning* in decision-making.

Up to date, the latter topic has been investigated from two main complementary perspectives. The first view emphasizes the role of affective experience. Choices are regarded as driven by learning to anticipate *regret or relief*, the complex counterfactual emotions arising from reasoning on "what might have been". That is, from the awareness that, compared with the chosen option, the unchosen one would have produced, respectively, a better or a worse outcome (Mellers et al., 1999). Clinical and neuroimaging studies employing gambling-tasks showed the role of ventromedial prefrontal cortex (vmPFC) along with the Anterior-Cingulate-Cortex (ACC), amygdala and hippocampus (Camille et al., 2004; Coricelli et al., 2005) in such process. These studies also highlighted the crucial difference between the counterfactual emotions of regret/relief and the basic feelings of disappointment/satisfaction, with the former entailing a sense of responsibility for the counterfactually negative outcomes, and thus eliciting higher autonomic responses and inducing a stronger disposition to behavioural change (see also Chua et al., 2009; Zeelenberg et al., 1998).

The second view is rooted in the framework of Reinforcement Learning Theory, and emphasizes the role of the computation of a "reward prediction-error". At the neural level, different portions of the caudate nucleus are involved in reward-related processing and learning (Schultz, 2002). The ventral striatum updates predictions about future rewards, by computing the difference between expected and obtained rewards (i.e. a "reward prediction-error"), while the dorsal striatum maintains action-values to guide future decisions (Kahnt et al., 2009).

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The two aforementioned approaches, however, are not mutually exclusive. Recent developments in computational neuroscience consider both the role of prediction error and of affective consequences of choice. In this extended view, the difference between factual and counterfactual outcomes (i.e. a “fictive” prediction-error) is an additional learning signal that increases the explanatory power of reinforcement learning models (Lohrenz et al., 2007; Chiu et al., 2008; see Sommer et al., 2009). While the processing of a fictive prediction-error by the striatum, devoid of affective content, is in itself sufficient to account for the behavioural adaptation resulting from past experience (Sommer et al., 2009), the emotional consequences of evaluating alternative outcomes (Camille et al., 2004; Coricelli et al., 2005) contribute to such learning process, by strengthening anticipatory regret and relief, via the involvement of the vmPFC and related structures.

As we mentioned, such accounts have so far largely neglected the role of the *social domain*. Yet, behavioural studies showed that the subjective experience of regret is influenced by others' similar experiences, and that people seek relevant information to validate their decisions (van Harreveld et al., 2008). Experimental evidence unambiguously suggests that one's own decisions may be socially influenced by what *other* individuals experience as a result of their choices (i.e. by some sort of interactive learning). Neural-networks modeling of decision-making extends this idea at the computational level, showing that predictions about the behaviour of two interacting players are significantly improved by incorporating the feeling of regret experienced by the other player throughout the game (Marchiori and Warglien, 2008).

One might then wonder how such learning occurs, i.e. how the other's regretful outcomes are coded in the player's brain. Does this process involve the mere encoding of numerical quantities, as in neural-networks and computational modeling? Behavioural studies rather point to the fact that, when observing the negative outcome of another's choices, individuals react as if they were personally involved in that situation (Girotto et al., 2007), a finding that is further supported by recent event-related-potentials (ERPs) evidence (Bellebaum et al., 2010).

These results fit with neuroimaging evidence, showing that a mirroring-mechanism previously described for pain (Singer et al., 2004) and disgust (Wicker et al., 2003) also involves counterfactual emotions. Indeed, observing the regretful outcomes of another's choices activates a subset of the regions associated with a first-person experience of regret, including the vmPFC, hippocampus and ACC (Canessa et al., 2009). Overall, the available data suggest that knowing the regretful outcomes of others' choices leads to the same counterfactual emotions, and to the reactivation of a subset of the related brain regions, as in a direct experience.

Building on these premises, here we address whether such a crucial resonant emotion also impacts on the behavior of a 3rd-person as in the case of 1st-person decision-making. Based on the reviewed literature, we predict that personal decisions are also shaped by the counterfactual outcomes of another's choices (*interactive-learning*). We further predict that this process involves regions in which activity, at choice, reflects the difference between factual and counterfactual outcomes (i.e. level of regret or relief) in the preceding trial *both* as a 1st and a 3rd-person experience (*neural interactive-learning*). Such a resonant mechanism is likely to involve the vmPFC and, based on our previous data (Canessa et al., 2009), it is likely to be stronger in females, than males, participants.

Materials and methods

Subjects

Twenty-four right-handed (Oldfield, 1971) healthy subjects (12 females; mean age = 21.61 years, standard deviation [s.d.] = 2.75) participated in the study. All subjects had normal or corrected-to-normal visual acuity. All reported no history of psychiatric or neurological disorders, and no current use of psychoactive medications. They gave their written informed consent to the experimental procedure, that was approved by the local Ethics Committee.

Task

The subjects performed a classical gambling-task (Mellers et al., 1999). In every trial, they chose one of two gambles depicted as “wheels of fortune”, where different probabilities of financial gain or loss are represented by the size of colored sectors of a circle. The gambles are then played and the results shown. Subjects could thus evaluate not only the financial consequences of their decision, but also the outcome they might have obtained had they selected the alternative gamble. This evaluation gave subjects the sense of being *responsible* for their choices, i.e. the main hallmark of regret, when decisions produce relatively negative outcomes.

There were 2 basic experimental conditions (Fig. 1). In the “I play” (IP) condition, subjects chose one of two gambles, leading to a financial gain or loss for themselves. The gambles were shown for 4.5 s, during which they could evaluate them and make a decision. Next, the appearance of an asterisk in the centre of the screen prompted them to choose, by pressing one of two buttons on a keyboard with their right index or middle fingers. Subjects had 2 s to choose the gamble, otherwise they received an “out of time” message, and a new trial started. Once selected, the chosen gamble was highlighted by a yellow contour, that would remain on the screen up to the end of the trial, and 2 s after the appearance of the asterisk a white arrow appeared in a random position within each wheel. One second later both arrows started spinning clock-wise, with different and random initial speeds, and stopped after exactly 4 s, indicating the final outcomes of both gambles, that remained on the screen for 3 s. In the “She/he plays” (SHP) condition, subjects were shown the same sequence of events (gambles evaluation, decision and outcome, with the same timings), which were referred to another individual, playing the same task in a nearby room.

Crucially, the experience of regret/relief (as opposed to mere disappointment/satisfaction) has to be generated by a sense of choice-responsibility for the obtained outcomes (Coricelli et al., 2005). Therefore, as a baseline, two further conditions were used: in the “I follow” (IF) and “She/he follows” (SHF) conditions, subjects were informed that the computer would randomly choose one of the gambles for themselves or for the other player, respectively. The order and length of each sub-event within IF and SHF trials was the same as in IP and SHP ones. These trials still resulted in the same overall pattern of visual stimulation (the outcome of both gambles) and in financial gains or losses for the subjects or the actor, yet eliminated the sense of being responsible for one's own choices, which is a crucial determinant of the emotion of regret (Coricelli et al., 2005). Each trial started with its specific instructions (1.5 s), which remained on the bottom of the screen throughout its length.

In order to focus subjects' attention on the decision made by either the other player or the computer in the SHP, IF and SHF conditions, when the yellow contour appeared they had to indicate whether the choice made was the riskier or the less risky, by pressing one of the two buttons of the keyboard (2 s). Moreover, it was crucial that subjects attended the outcomes in all conditions. Therefore, on 10% of the trials within each run, after outcome presentation they were asked to report whether it was a win or a loss. They were informed that this question might follow a trial belonging to any condition. Indeed, it followed an equal number of trials for each condition. We used such a question, rather than a judgment concerning the experienced feeling at outcome, to prevent the induction of an “empathic” response for the other player's emotional reactions when her/his counterfactual outcomes are shown. Indeed, to provide the

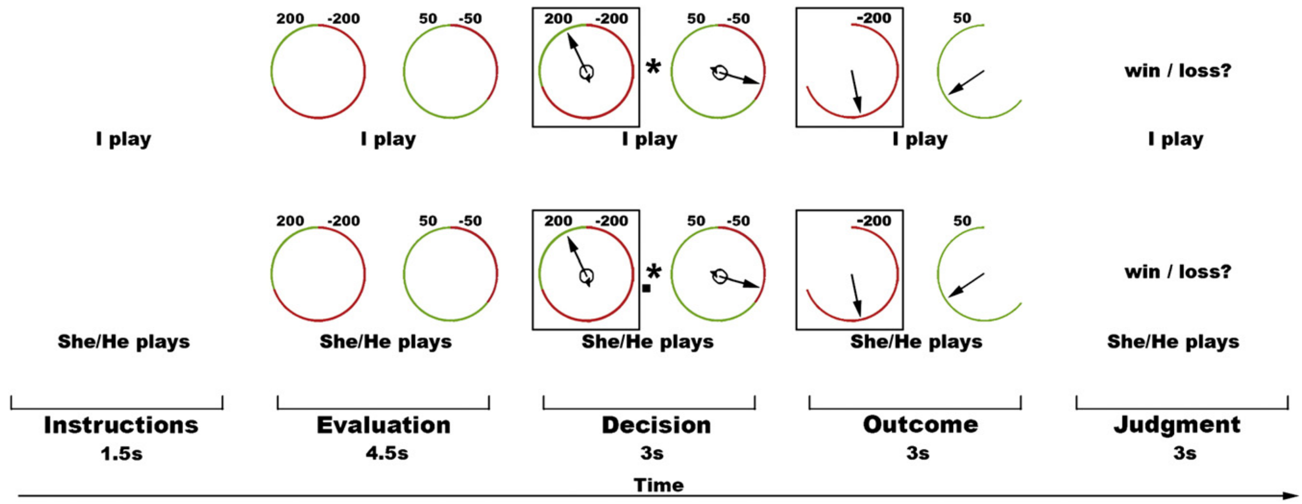

Fig. 1. Experimental conditions. From left to right, schematic depiction of the sequence of events in the two main experimental conditions "I play" (top) and "She/he plays" (bottom). Within each condition there are the same 5 phases: instruction, evaluation, choice, outcome and judgment. The length in seconds of each sub-event is shown in the inferior part of the figure.

correct answer required subjects to focus on just the obtained outcome, rather than the non-obtained (that would induce regret or relief via a counterfactual comparison) one. Therefore, if an effect of such response on cerebral activity underlying outcome evaluation actually does occur, this is supposed to be *against* the counterfactual comparison that elicits the experience of regret/relief.

Gambles structure

All subjects participated in 2 separate scanning sessions, each including 8 functional runs whose order was individually randomized. 256 trials were distributed among the 4 conditions in a pseudo-random order so that, in each run, the complete list of trials was predetermined and identical for all subjects. In each gamble, the 4 possible outcomes resulted from paired combinations of 200, 50, −50 and −200 (arbitrary units), associated with 3 different levels of probability (25–75, 50–50 and 75–25). Thus, the possible counter-factual combinations of wins and losses gave four potential levels of regret and relief (±100, ±150, ±250 and ±400). Both the possible combinations of payoffs and the levels of probability were equally balanced across all experimental conditions. In each trial, payoffs and probabilities were associated so that one of the gambles was riskier than the other, and in order to minimize as much as possible the difference between them with regard to expected-value (i.e. the sum of the probability of the two possible outcomes of the gamble, each multiplied by the corresponding outcome value). In order to compare the effects of different experienced vs. attended amounts of regret/relief, it was crucial that the number of events of interest across the different conditions was comparable. Therefore, unbeknownst to the subjects, in SHP, IF and SHF conditions every trial was pre-determined to result in a given pair of outcomes (and thus in a pre-specified amount of either regret or relief in the SHP condition). In the IP condition, every trial was pre-determined to result in a variable amount of either regret or relief by means of a feedback-routine depending on subject's choice. This procedure allowed to obtain an overall equal number of events of interest (variable amounts of regrets and relieves) across the different conditions. For every condition, the thereby obtained "regret" and "relief" trials were then assigned to the different runs, to get a variable proportion of regrets and relieves within each run. Thus, every condition equally represented the 4 possible types of counterfactual outcome (Relief for a risky decision [RL-R], Regret for a risky decision [RG-R], Relief for a non-risky decision [RL-NR], Regret for a non-risky decision [RG-NR]) and, within them, the 4 possible counterfactual levels of regret and relief (±100, ±150, ±250 and ±400). In all conditions, we ensured that the least probable outcome of each of the presented gambles would occur in a proportion equal or inferior to 25%. Indeed, as witnessed by a post-scanning debriefing session, all subjects were unaware of the experimental control on the probabilistic occurrence of wins and losses at the end of the study.

The trials within each run were presented in a pseudo-random order, so that those of specific conditions would follow each other (e.g., a IP trial would follow a SHP, IF or a SHF trial) according to a pre-defined manner. This procedure allowed to obtain a pre-specified and equal number of trials in which the subject chose (IP) after observing the outcomes in a trial belonging to the different conditions: the IP condition itself, the other player's outcome (SHP), or an outcome resulting from a random choice by the computer (IF or SHF). Moreover, each of these types of event equally represented the 4 possible outcomes (RL-R, RG-R, RL-NR, and RG-NR) and, within them, the 4 possible counterfactual levels of regret and relief (±100, ±150, ±250 and ±400). Finally, gamble-parameters were specified so that anticipated regret/relief and disappointment/satisfaction in a given trial (Coricelli et al., 2005) were not significantly correlated with experienced regret/relief and disappointment/satisfaction in the previous trial.

Instructions and procedure

Subjects underwent a training session, and were introduced to an unknown actor, before the beginning of the study. Half male, and half female, subjects played with a male actor, the other half with a female actor. The two actors were the same throughout the whole study. Subjects were informed that both their and the actor's performance in IP/IF and SHP/SHF conditions, respectively, would have resulted in a financial gain or loss with respect to an initial endowment, that was delivered with one-week advance to prevent the "house-money" effect (i.e. the greater risk-seeking behaviour sometimes exhibited by subjects receiving "windfall" gains). Importantly, they were explicitly informed that their potential gains/losses were completely independent of those of the other player. Subjects were informed about their cumulative earnings after the second session, when the difference with respect to the initial endowment was given (in case of win) or asked (in case of loss) to them in cash.

In order to desynchronize the timings of event-types with respect to the acquisition of single slices within functional volumes, interstimulus intervals (ISIs) between successive trials were presented in different ("jittered") durations across trials (2.3, 4.7 and 7.1 s in the proportion of 4:2:1) (Dale, 1999). The software

Presentation 11.0 (Neurobehavioral systems, Albany, CA, http://www.neurobs.com) was used both for stimulus presentation and subjects' answers recording.

After the scanning, subjects were asked to report any personal impression about the task. Then, one month later, they were asked to complete an Italian version (Meneghini et al., 2006) of the Balanced-Emotional-Empathy-Scale (BEES; Mehrabian and Epstein, 1972), a 30-items questionnaire measuring individual tendency to empathize with others' emotional experiences.

Behavioural data analysis

At the *behavioural level* we examined, on a trial-by-trial basis, whether and how subjects' risk-aptitude was influenced by a specific type of outcome resulting from a choice made, in the preceding trial, by either the subject her-himself, the other player, or randomly by the computer. To this purpose, at the individual level we computed the average deviation from subject's mean risk-aptitude (overall proportion of risky choices) as a function of a) the *outcome* of the preceding trial (RL-R, RG-R, RL-NR, and RG-NR) and b) the *agent* of the choice that determined it (the subject, the other player, or the computer). In order to isolate the "absolute" strength of the behavioral effects, we reversed the direction of those associated with risk-seeking decrease. All data were then entered into a group-level ANOVA for repeated measures, with the deviation from mean risk-aptitude as dependent variable and, as factors: a) the *agent* of the choice in the preceding trial (the player her-himself, the other player, or the computer), b) the *outcome* of that choice (Regret or Relief), c) its *cause* (a risky or a non-risky decision), d) the *gender* of the subject, and e) the *gender* of the other player.

Functional-Magnetic-Resonance-Imaging (fMRI) data acquisition and statistical analysis

Magnetic-Resonance images were acquired with a 3-Tesla Philips Achieva scanner (Philips Medical Systems, Best, NL), using an 8-channels Sense head coil (sense reduction factor = 2). Functional images were acquired using a T2*-weighted gradient-echo, echo-planar (EPI) pulse sequence (34 interleaved coronal slices, Repetition-Time (TR) = 2038 ms, Echo-Time (TE) = 30 ms, flip-angle = 85°, Field-Of-View (FOV) = 240×240 mm^2, inter-slice gap = 0.5 mm, slice thickness = 4 mm, in-plane resolution = 2.5×2.5 mm^2). We also acquired a high-resolution T1-weighted anatomical scan (150 slices, TR = 600 ms, TE = 20 ms, slice thickness = 1 mm, in-plane resolution = 1×1 mm^2).

Image pre-processing and statistical analysis were performed using SPM5 (http://www.fil.ion.ucl.ac.uk/spm). The first 5 volumes of each subject were discarded to allow for T1 equilibration effects. All volumes were spatially realigned to the first volume of the first session, unwarped, normalized to a grey-matter probabilistic map (http://Loni.ucla.edu/ICBM/ICBM_TissueProb.html), resampled in $2 \times 2 \times 2$-mm^3 voxels after normalization, spatially smoothed with a 10-mm full-width half-maximum (FWHM) isotropic Gaussian kernel and globally scaled to 100. The resulting time series across each voxel were then high-pass filtered to 1/128 Hz, and serial autocorrelations were modeled as an Auto-Regressive AR(1) process.

In the statistical analysis we employed a parametric approach to highlight the regions where, during the evaluation of the gambles when making a decision in the IP condition, changes in cerebral activity were positively and linearly related to the difference between factual and counterfactual outcomes in a previous trial that may belong to different conditions (IP, SHP, IF or SHF). Therefore, all the functional results described here are parametric in nature, and related to a discrete parameter that previous studies have interpreted in terms of level of regret or relief (Coricelli et al., 2005). Statistical maps were generated using a random-effect model, implemented in a 2-levels procedure.

The effects of previous outcomes were first classified, as already explained, in Relief for a risky decision [RL-R], Regret for a risky decision [RG-R], Relief for a non-risky decision [RL-NR], and Regret for a non-risky decision [RG-NR]. The behavioural results did not show any significant difference between the effects on the current choice of either a previous RL-R or RG-NR (increased risk-seeking) and RL-NR or RG-R (reduced risk-seeking). Therefore, due to the paucity of some event-types in some subjects, we collapsed the two types of outcomes eliciting the same behavioural change when modeling at the first-level their effects on the cerebral activity underlying choice. Accordingly, at the single-subject level the evaluation phase was partitioned in sub-conditions based on: a) the *agent* of the previous choice (3 levels: the subject her/him-self [IP], the other player [SHP], and the computer [IF-SHF]), b) the type of *outcome* in the immediately preceding trial (2 levels: "RL-R or RG-NR" and "RL-NR or RG-R"), and c) the final *decision* made by the subject in the current trial (2 levels: risky and non-risky). This procedure gave 12 sub-conditions that were separately modeled as mini-epochs lasting 4.5 s. Crucially, for each of them one additional regressor modeled a linear parametric modulation of the evaluation-related activity by the difference between the factual and counterfactual outcomes (i.e. level of regret/relief) experienced/attended in the immediately preceding trial. All the within-trial events other than the evaluation of the gambles, as well as those trials in which a wrong response or no response was given, were modeled in a single regressor of no interest. We did not model separately winning and losing trials, since a key feature of counterfactual comparisons is that also positive outcomes can result in regret, and negative ones can result in relief, if compared to an even more positive or negative outcome, respectively. Regressors modeling events were convolved with a canonical Haemodynamic Response Function (HRF), and parameter estimates for all regressors were obtained at each voxel by maximum-likelihood estimation.

Since regret and relief require a personal responsibility upon the outcome of a deliberate choice (Coricelli et al., 2005) it was crucial to isolate the effects of the previous outcome of a *human* decision from the effects that were merely due to satisfaction/disappointment, i.e. the generic reaction to the outcome of a non-deliberate, devoid of responsibility, choice. Therefore, the parametric effect of the outcome of a preceding random choice by computer, either for the subject or the other player, was used as an explicit-baseline, and subtracted out from the parametric effect of a preceding choice made either by the subject her/him-self or the other player. Accordingly, the parameter estimates corresponding to the *parametric* regressors in each of the 12 modeled sub-conditions were used to produce 1st-level "contrast images" for each of the contrasts of interest. For instance, "Non-Risky-Decision after RG-R in the IP condition *minus* Non-Risky-Decision after RG-R in the IF or SHF conditions" to isolate the parametric effect of a previous 1st-person experience of "regret for a risky decision" when making a non-risky decision.

At the group-level the resulting 1st-level contrast-images were entered into a $2 \times 2 \times 2$ factorial design with sphericity-correction for repeated measures (Friston et al., 2002) with factors: a) the *agent* of the previous choice (the subject vs. the other player — after subtracting the effects of the random choice by the computer), b) the type of *outcome* ("RL-R or RG-NR" vs. "RL-NR or RG-R") and c) the final *decision* in the current trial (risky vs. non-risky). The number of events for the different sub-conditions was modeled as a covariate. Direct comparisons were performed to assess specific linear parametric effects of previous outcome-types, or the effects of decision-types, on choice-related cerebral activity. To ensure that the observed activations did not result from relative deactivations, the resulting statistical maps were inclusively masked at $p < 0.05$ (uncorrected) by those associated with the conditions of interest minus the baseline. In order to assess, at choice, *common* activations across the parametric effects of a previous 1st and 3rd-person outcome driving to opposite behavioural changes ("RL-R or RG-NR": risk-seeking increase; "RL-NR or RG-NR": risk-seeking decrease), we carried out a conjunction analysis (Friston et al., 2005) on the corresponding 1st-person *and* 3rd-person statistical maps. Based on a-priori hypotheses from previous studies (Coricelli et al., 2005; Canessa et al., 2009), the results were thresholded at $p<0.001$ uncorrected for multiple comparisons, and only clusters larger than 5 voxels were considered.

The location of the activation foci was determined in the stereotaxic space of Talairach and Tournoux (1988) after correcting for differences between the latter and the MNI space by means of a nonlinear transformation (http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispace.shtml). The regions for which maps are provided were localized with reference to cytoarchitectonical probabilistic maps of the human brain, using the SPM-Anatomy toolbox (http://www.fz-juelich.de/inm).

Results

Behavioural results

At the *behavioural level* we examined whether and how subjects' risk-aptitude was influenced by the type of outcome in the previous trial, i.e. by the emotions arising from the counterfactual comparison between the outcomes of chosen and unchosen gambles. Such outcomes may result from a choice made, in the immediately preceding trial: a) by the subject her–himself; b) by the other player; or, c) randomly, by the computer. Previous studies showed that choices are significantly shaped by anticipated regret, but not by anticipated disappointment (Zeelenberg et al., 1998; Camille et al., 2004; Coricelli et al., 2005). Accordingly, we predicted a change in subjects' risk-aptitude coherent with the outcomes of regret/relief of her/his previous decision. That is, increased risk-seeking after "relief for a risky choice" (RL-R) and "regret for a non-risky choice" (RG-NR), and reduced risk-seeking after "relief for a non-risky choice" (RL-NR) and "regret for a risky choice" (RG-R). Moreover, based on the results of behavioural studies on counterfactual reasoning in a 1st or 3rd-person situation (Girotto et al., 2007), as well as our previous imaging evidence on a mirror-like resonant response for regret (Canessa et al., 2009), we predicted a similar influence also from the outcomes of regret and relief consequent from the other player's choices. In contrast, we expected weaker effects of disappointment/satisfaction (i.e. behavioural change after the outcome of a random choice by the computer).

In order to test these hypotheses, we assessed deviations from the individual mean risk-aptitude (overall proportion of risky choices in the whole study) as a function of: a) the *agent* of the choice in the preceding trial, b) the *outcome* of that choice (regret or relief), c) its *cause* (a risky or a non-risky decision), d) the *gender* of the subject, and e) the *gender* of the other player. Since no significant interaction was observed [$F(2,40)=0.29$; $p=0.74$], we focused on the main effects of the principal factors (see Supplementary Fig. 1).

Concerning the effect of the 4 different outcome-types, descriptive statistics showed a stronger effect of "regret for a risky decision" than of the other outcomes. However, when assessing statistically their net effect (using the absolute strength of the effect, regardless of its direction) we did not find a significant main effect of either the *outcome* (regret vs. relief; [$F(1,20)=1.61$; $p=0.21$]) or its *cause* (a risky vs. a non-risky decision; [$F(1,20]=2.99$; $p=0.099$), nor a significant interaction between the two factors [$F(1,20)=0.54$; $p=0.47$] or a significant interaction between *outcome*, *cause* and *agent* of the preceding choice [$F(2,40)=0.08$; $p=0.92$]. By and large, the 4 outcomes were equally effective in producing a behavioural change coherent with their emotional consequences (increased risk-seeking after RL-R or RG-NR; reduced risk-seeking after RL-NR or RG-R), independent of whether the subject had experienced it in a 1st or a 3rd-person situation. Instead, observing the outcomes of random choices by the computer elicited weaker effects.

Indeed, we observed a significant main effect of the *agent* of the previous choice on risk-aptitude [$F(2,4)=7.56$; $p=0.002$]. Post-hoc tests showed no significant difference between the effects of previous experienced (1st-person, IP) or attended (3rd-person, SHP) outcomes [$p=0.87$], both significantly stronger than the effects of the outcome of a random choice by the computer (IF or SHF, which did not significantly differ from each other [$p>0.05$]). There was a significant interaction between the *agent* of the preceding choice and the *gender* of the subject [$F(2,40)=3.39$; $p=0.043$]: although the gender of the subject was not significant *per se* [$F(1,20)=1.46$; $p=0.24$], female subjects were more prone than males to an influence from the other player's outcomes. This difference may be related to the higher empathic aptitude observed in females than males, as assessed with the Balanced-Emotional-Empathy-Scale (BEES; Mehrabian and Epstein, 1972; Meneghini et al., 2006). Mean scores were 53.83 (s.d. = 11.67) for females and 23.08 (s.d. = 27.11) for males, and revealed a significant difference, females being more empathic than males (Kolmogorov–Smirnov test for normality: $d=0.19$, $p>0.2$; two-sample *t*-test, $N=24$, $t(22)=3.62$, $p=0.007$).

Imaging results

Based on behavioural results, in the *f*MRI-data analysis we first aimed at investigating the cerebral regions in which activity, when making a new decision, reflects the difference between factual and counterfactual outcomes (i.e. level of regret or relief) in the previous trial, in a way that is consistent with their effect on subjects' risk-aptitude (i.e. *learning*). Moreover, we examined regions where this effect also arises from others' outcomes, besides one's own ones (i.e. *interactive-learning*). Since behavioural results (see above) did not show any significant difference between the effects on the current choice of either a previous "RL-R or RG-NR" (increased risk-seeking), or "RL-NR or RG-R" (reduced risk-seeking), and due to the paucity of some event-types in some subjects, we collapsed the two types of outcomes eliciting the same behavioural change when modeling at the first-level their effects on cerebral activity underlying choice. Therefore, we employed a parametric approach to investigate the cerebral regions where, *at choice in the IP condition*, activity was linearly and positively related to the difference between factual and counterfactual outcomes in the previous trial, as a function of: a) the *type* of outcome itself ("RL-R or RG-NR", or "RL-NR or RG-R"), b) the *agent* of the choice that determined it (the subject her/him-self, the other player or the computer), and c) the final *decision* (risky or non-risky) that the subject is about to make in the current trial.

Crucially, we aimed at isolating the neural effects of the previous outcome of a *human* deliberate decision (regret or relief) from the effects of the generic reaction to the outcome of a random, non-deliberate, choice (disappointment or satisfaction). Therefore, the parametric effect of a preceding choice randomly made by computer was used as an explicit-baseline, and subtracted from the parametric effect of the same type of outcome resulting from a preceding choice made by either the subject her/him-self or the other player. For the sake of clarity, we report the results of the main comparisons separately.

The effect of previous outcomes on activity underlying new choices

First, we focused on the general influence of past choice-related experience on cerebral activity associated with decision-making. Therefore, we examined the main effects of the *type* of outcome, independent of both the agent of the decision that produced it in the previous trial and of the final decision in the current trial (Fig. 2, Table 1).

Direct comparisons between behaviourally opposite parametric effects revealed that the previous outcomes that increased risk-seeking, compared with those that reduced it ("RL-R or RG-NR" vs. "RL-NR or RG-R"), elicited stronger activity at the subsequent choice in the subgenual ACC, right posterior insula and superior parietal lobule, bilateral hippocampus and left cerebellum. At the subcortical

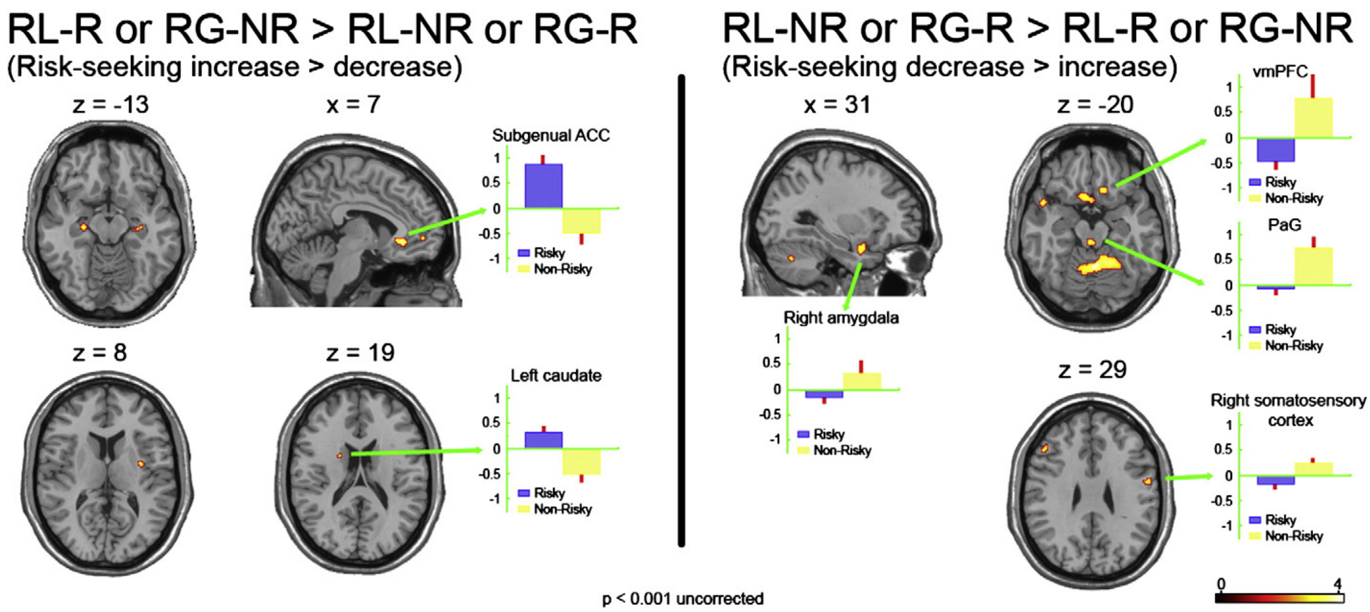

Fig. 2. The parametric effect of previous outcomes on neural activity underlying subsequent choices. The cerebral regions where, at choice in the "I Play condition", the parametric effect of the difference between factual and counterfactual outcomes (i.e. level of regret or relief) in the previous trial is stronger for those outcomes that behaviourally increase risk-seeking compared with those that reduce risk-seeking (left), and vice versa (right). For the regions where activity showed significant differences according to the subject's final choice, histograms represent the size of the statistical effect (risky-choice = blue; non-risky-choice = yellow). The error-bars represent the standard error of the mean. ACC = Anterior-Cingulate-Cortex, vmPFC = ventromedial PreFrontal Cortex, PaG = Periaqueductal Grey-matter, RL-R = Relief for a risky choice, RL-NR = Relief for a non-risky choice, RG-R = Regret for a risky choice, RG-NR = Regret for a non-risky choice.

level, the left dorsal caudate nucleus was activated. In contrast, the outcomes that reduced risk-seeking, compared with those that increased it ("RL-NR or RG-R" vs. "RL-R or RG-NR"), elicited stronger activity at choice in the vmPFC, middle cingulate cortex, right somatosensory cortex, right parahippocampal gyrus and amygdala, brainstem periaqueductal grey matter and bilateral cerebellum.

The link between activity reflecting previous outcomes and current choice

Together with behavioural data, the above results suggest a functional link between a given outcome, resulting from a deliberate choice, and the subsequent decision. Is it possible, then, that activity in the regions reflecting the effect of previous outcomes consistently act as a neural marker of the upcoming decision? In order to answer this question, we extracted the parameter estimates in the peak-voxels of the regions that, at choice, reflect the outcomes that either increased or decreased risk-seeking, and compared them according to whether subjects were about to make a final risky vs. non-risky decision. Results showed that some of these regions were differently activated according to subjects' actual choices, consistently with the predictions resulting from behavioural data (Fig. 2). In particular, the subgenual ACC, caudate nucleus and cerebellum, whose activity reflected a previous emotional outcome of RL-R or RG-NR, were significantly more activated by a final risky, compared with a non-risky, decision. On the other hand, the vmPFC, middle cingulate and somatosensory cortex, parahippocampal gyrus and amygdala, periaqueductal-gray-matter and cerebellum, whose activity reflected a previous emotional outcome of RL-NR or RG-R, were significantly more activated by a final non-risky, compared with a risky, decision. These results were further supported by whole-brain analyses specifically assessing the cerebral regions where activity predicts a risky vs. non risky choice (see supplementary text and supplementary Table 1 for additional details).

Conjunction analyses: shared effect of previous outcomes on activity underlying new choices

After exploring the functional role of the observed regions in adaptive learning from past emotional experiences, we finally investigated those underpinning neural *interactive-learning*. Therefore, we employed conjunction-analyses to assess whether the regions where activity, at choice, correlates with the difference between factual and counterfactual outcomes (i.e. level of regret or relief) resulting from a decision of the subject her/him-self also correlates with the same outcome resulting from someone else's choice (Fig. 3, Table 2).

Common activations reflecting, at choice, both a 1st and 3rd person experience of an outcome that increased risk-seeking (RL-R or RG-NR) were observed in the left caudate nucleus, right inferior and superior parietal lobuli, and right parahippocampal gyrus. Moreover, both a 1st and 3rd-person experience of an outcome that reduced risk-seeking (RL-NR or RG-R) elicited common activations in the vmPFC, and bilaterally in the somatosensory cortex, cerebellum and periaqueductal grey matter.

Discussion

Optimal decision-making requires learning, i.e. the ability to flexibly adapt choices to recent outcomes. Computational modeling within reinforcement learning theory indicates the difference between expected and obtained rewards (a "reward prediction-error"), as well as the difference between factual and counterfactual outcomes (a "fictive prediction-error"), as the basis for adaptive-learning, signaling the need to adjust future choices (Chiu et al., 2008; Daw and Doya, 2006; Lohrenz et al., 2007). This process involves the mesolimbic dopaminergic pathway, as well as the prefrontal cortex, anterior cingulate cortex and insula (Cohen and Ranganath, 2005). Importantly, upcoming risky vs. non-risky choices are predicted by specific activations in some of the same structures, such as caudate nucleus and insula, respectively (Cohen and Ranganath, 2005; Kuhnen and Knutson, 2005).

In addition to these computational effects, the processing of counterfactual outcomes in the striatum is considered to be associated with the complex emotions of regret and relief (Lohrenz et al., 2007; Sommer et al., 2009). Due to a sense of *responsibility* for the obtained outcomes, these emotional responses induce more intense feelings and exert a stronger effects on future choices than disappointment

Table 1
The parametric effect of previous outcomes on cerebral activity underlying new choices.

H	Anatomical region	K	x	y	z	Z-score
RL-R or RG-NR>RL-NR or RG-R						
R	Subgenual cortex	59	8	30	−6	3.84
R	vmPFC (mid orbital gyrus)	8	6	50	−4	3.22
R	Posterior insula	11	34	−6	8	3.2
R	Superior parietal lobule/precuneus	34	18	−58	46	3.71
L	Hippocampus (CA/SUB)	13	−26	−18	−14	3.29
R	Hippocampus (SUB/CA)	83	24	−22	−8	3.93
L	Caudate nucleus	54	−18	2	24	3.72
L	Cerebellum	62	−20	−54	−46	3.46
RL-NR or RG-R>RL-R or RG-NR						
L	vmPFC (rectus gyrus)	98	−10	16	−16	3.50
R	vmPFC (rectus gyrus)	59	8	24	−22	3.70
R	vmPFC (mid orbital gyrus)	24	14	48	−12	3.25
L	vmPFC (mid/superior orbital gyrus)	12	−20	50	−10	3.35
L	IFG pars triangularis	20	−48	28	28	3.34
L/R	Middle cingulate cortex/SMA	195	−4	8	48	3.25
	Middle cingulate cortex		8	14	42	3.83
R	Middle cingulate cortex	38	12	−14	40	3.29
L	Temporal pole	73	−48	10	−20	3.49
R	Parahippocampal gyrus/amygdala	84	32	4	−26	3.74
R	Superior temporal gyrus	70	54	−12	2	3.55
R	Postcentral gyrus	42	56	−4	30	3.54
R/L	Paracentral lobule/Precuneus	91	10	−42	62	3.67
	Precuneus		−12	−44	62	3.24
R	Lingual gyrus	193	16	−80	−2	3.61
L/R	Periaqueductal grey-matter	28	−2	−30	−18	3.08
L/R	Cerebellum (vermis)	622	−2	−58	−10	4.23
L/R	Cerebellum		4	−54	−18	4.12
R	Cerebellum		12	−56	−22	3.96
L	Cerebellum		−10	−58	−20	3.39
R	Cerebellum crus1	35	28	−66	−34	3.49

The cerebral regions where, at choice in the "I play condition", the parametric effect of the difference between factual and counterfactual outcomes (i.e. level of regret or relief) in the previous trial is stronger for those outcomes that behaviourally increase risk-seeking compared with those that reduce risk-seeking (top), and vice versa (bottom).
H = Hemisphere, L = Left, R = Right, K = cluster-extension in number of voxels ($2\times2\times2$ mm^3), RL-R = Relief for a risky choice, RL-NR = Relief for a non-risky choice, RG-R = Regret for a risky choice, RG-NR = Regret for a non-risky choice, vmPFC = ventromedial Prefrontal Cortex, CA = Cornu-Ammonis, SUB = Subiculum, IFG = Inferior Frontal Gyrus, SMA = Supplementary-Motor-Area.

and satisfaction for factual outcomes (Camille et al., 2004; Coricelli et al., 2005; Chua et al., 2009; Zeelenberg et al., 1998).

Assuming the driving role of emotions on choice entails one important consequence. Emotions are shared, through mechanisms of empathy (Preston and de Waal, 2002) and emotional contagion (Barsade, 2002) associated with resonant neural mechanisms (Singer et al., 2004; Wicker et al., 2003). Thus, any evidence that emotions shape decision-making raises the issue of potential *social* influences on choice, as suggested by behavioural (van Harreveld et al., 2008) computational (Marchiori and Warglien, 2008) and imaging (Canessa et al., 2009) studies.

Here we investigate this hypothesis using *f*MRI and a gambling-task. First, behavioural data confirmed the importance of emotions resulting from a sense of responsibility. Subjects' choices were affected by their previous outcomes of regret and relief, an effect that does not merely result from the association between a given choice-type and its outcome *per se*. Indeed, a significantly weaker influence was exerted by random-choices by the computer that, being devoid of responsibility for the outcome, could only result in satisfaction or disappointment. Crucially, our results extend these observations to the *social* domain, by showing that an influence is also exerted by the outcomes of another's choices. Such social influence may arise from the activation, at choice, of regions specifically reflecting the outcomes not only experienced as a 1st-person, but also attended as a 3rd-person, in the preceding trial. This account is supported at the behavioural level by the larger influence from others' outcomes in females, who also obtained higher empathy-scores than males, and at the neural level by results showing the influence of previous outcomes on the activation associated with subsequent choices.

Indeed, previous outcomes that oppositely influence behaviour engaged different regions. The effect of the outcomes increasing risk-seeking involved the subgenual ACC, a target of the midbrain-dopaminergic pathway (Haber et al., 2006) heavily connected with the nucleus-accumbens (Johansen-Berg et al., 2008), and the subiculum. The latter structure, by connecting the hippocampus and the reward-circuitry, activates the dopamine system to highlight the reinforcing properties of rewarding stimuli (Cooper et al., 2006). Importantly, these regions were also more strongly activated by final risky, compared with non-risky, decisions (Fig. 2; see supplementary text and supplementary Table 1 for additional details). Their activation is then likely to reflect the motivational drive arising from the outcomes that increase risk-seeking (Daw and Doya, 2006), thus highlighting the reward-value of risky options. The engagement of the dorsal caudate nucleus may be considered to underpin the processes leading from reward-value mapping to guiding actions toward their expected outcomes (Kahnt et al., 2009; Lohrenz et al., 2007).

It is noteworthy that the subgenual ACC is a critical hub in a network mediating depressive symptoms (Seminowicz et al., 2004), which have been associated with increased regret and risk-aversion (Leahy, 2001). A dysfunction of the neural system involved in learning from the experiences that drive to risk may facilitate the opposite system, representing the experiences *reducing* risk-seeking.

This latter system comprises the vmPFC, assessing the emotional value of the level of regret potentially resulting from the choice (Coricelli et al., 2005), as well as the amygdala, somatosensory cortex and periaqueductal grey-matter. All these regions, along with the anterior insula, were more strongly activated while making non-risky vs. risky choices (see supplementary text and supplementary Table 1 for additional details). These data suggest a model in which the vmPFC reflects adaptive-learning from past emotional experiences reducing risk-seeking. Its activation then involves the anterior-insula, that is reciprocally connected with both vmPFC (Augustine, 1996) and amygdala (Reynolds and Zahm, 2005; Yacubian et al., 2006), and that represents the negative bodily states associated with risky options, thus driving to non-risky ones (Kuhnen and Knutson, 2005; Preuschoff et al., 2008). A crucial role is also played by periaqueductal gray-matter, a key-structure, in connection with the amygdala, for inhibitory mechanisms modulating defensive behaviour (Brandao et al., 2008; Peyron et al., 2000). Their conjoint activation thus underpins the negative feelings associated with the anticipation of risk, driven by the vmPFC (Coricelli et al., 2005).

Are these brain regions involved in learning from others' experiences? Crucially, we observed a common set of regions reflecting both 1st and 3rd-person previous outcomes when making new choices, a finding that fits with the influence from others' outcomes highlighted by behavioural data. This result extends for the first time the concept of emotional resonance to the decisional domain, where such a shared response might act as the neural mechanism underlying social-learning. This is a mechanism that, to date, had been only postulated at the computational level (Marchiori and Warglien, 2008). In this view, the emotional consequences of others' choices are mapped onto the same emotional states that are experienced as a 1st-person, through the reactivation of the same cerebral regions that are involved in their direct experience, paralleling the behavioural effects of learning from others' emotions. However, different neural mechanisms seem to underpin social influences towards oppositely directed behavioral changes (risk-seeking increase vs. decrease). Previous results suggest a distinction between the computational processing of a "fictive prediction-error" in the striatum (particularly in its dorsal component; Lohrenz et al., 2007), and the engagement of a "second-level" reward processing which involves the vmPFC, where such a learning signal elicits regret

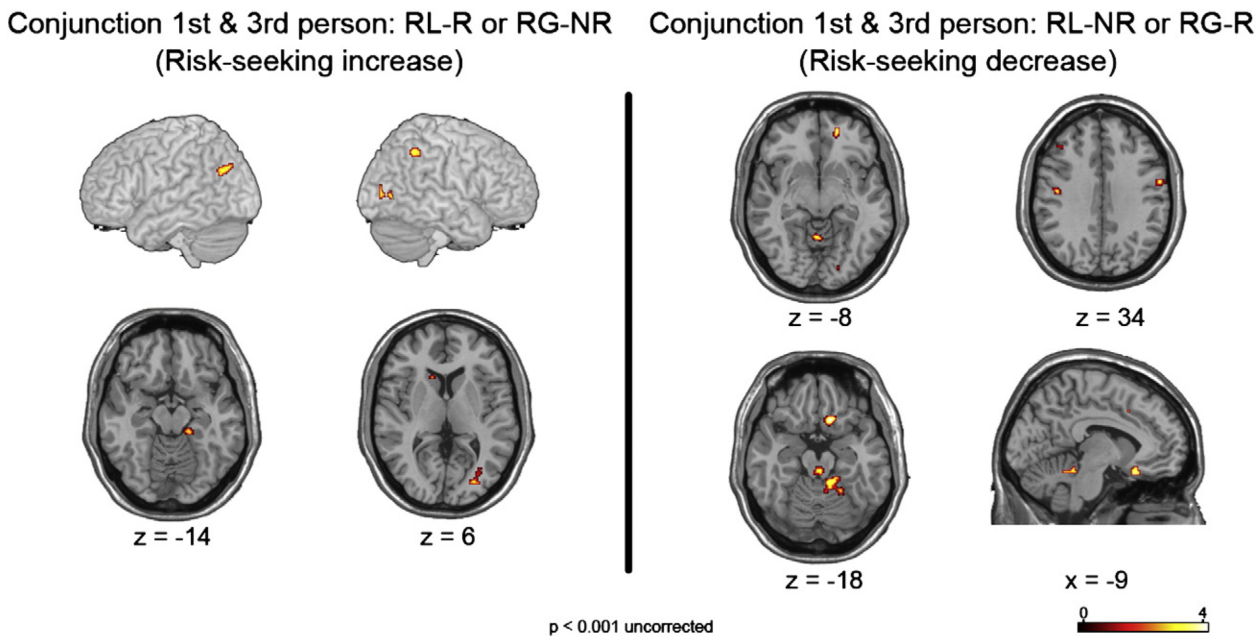

Fig. 3. Conjunction analysis: shared parametric effect of previous outcomes on neural activity underlying subsequent choices. The cerebral regions where activity, at choice in the "I play condition", reflects the parametric effect of the difference between factual and counterfactual outcomes (i.e. level of regret or relief) in the previous trial *both* when they are experienced (1st-person) and when they are attended (3rd-person). The shared parametric effects of previous outcomes that behaviourally increase (left) or reduce (right) risk-seeking are shown. RL-R = Relief for a risky choice, RL-NR = Relief for a non-risky choice, RG-R = Regret for a risky choice, RG-NR = Regret for a non-risky choice.

and relief (Coricelli et al., 2005), the affective facet of counterfactual evaluation of outcomes (Sommer et al., 2009). In light of this hypothesis, it is worth noting that only the outcomes that reduce risk-seeking are the subject of a genuine resonance mechanism involving emotion-related regions (vmPFC, somatosensory cortex and periaqueductal gray-matter), while those increasing risk-seeking exert their effect through the dorsal striatum and the inferior parietal cortex, involved in coding expected-value (Platt and Glimcher, 1999). This differentiation is further supported by the significant correlation between individual empathy scores (measured with the BEES; Mehrabian and Epstein, 1972; Meneghini et al., 2006) and activity in the portion of vmPFC reflecting those attended outcomes that reduce risk-seeking (RG-R or RL-NR; $p < 0.001$; Fig. 4). Indeed, this was the only region showing a significant gender effect. Namely, its activity was stronger in females than males, a result that is in agreement both with previously reported gender effects in a resonant mechanism for regret involving the vmPFC (Canessa et al., 2009), and with behavioral data showing females to be more prone than males to an influence from the other player's outcomes, particularly those reducing risk-seeking.

Table 2
Conjunction analysis: shared parametric effect of previous outcomes on cerebral activity underlying new choices.

H	Anatomical region	*K*	*x*	*y*	*z*	*Z*-score
Conjunction 1st and 3rd person: RL-R or RG-NR						
R	Inferior parietal lobule	37	46	−50	46	3.60
R	Superior/inferior parietal lobule	153	22	−54	46	4.05
L	Middle occipital gyrus	53	−34	−68	30	3.51
R	Parahippocampal gyrus (SUB)	19	16	−32	−14	3.37
L	Caudate nucleus	9	−14	22	6	3.23
Conjunction 1st and 3rd person: RL-NR or RG-R						
R	vmPFC (rectus gyrus)	78	12	22	−20	3.67
R	Orbitofrontal cortex (mid/superior orbital gyrus)	26	16	50	−8	3.46
R	Postcentral gyrus	93	56	−4	30	3.38
L	Postcentral gyrus	26	−44	−12	34	3.22
L	Middle occipital gyrus	21	−36	−68	18	3.34
R	Middle occipital gyrus	40	48	−80	0	3.45
L/R	Periaqueductal grey-matter	23	2	−30	−18	3.30
L/R	Cerebellum	19	−2	−56	−10	3.22
R	Cerebellum	106	10	−40	−18	3.38
R/L	Cerebellum	39	2	−44	−46	3.39

The cerebral regions where activity, at choice in the "I play condition", reflects the parametric effect of the difference between factual and counterfactual outcomes (i.e. level of regret or relief) in the previous trial *both* when they are experienced (1st-person) and when they are attended (3rd-person). The shared parametric effects of previous outcomes that behaviourally increase (top) or reduce (bottom) risk-seeking are reported. H = Hemisphere, L = Left, R = Right, K = cluster-extension in number of voxels ($2 \times 2 \times 2$ mm^3), RL-R = Relief for a risky choice, RL-NR = Relief for a non-risky choice, RG-R = Regret for a risky choice, RG-NR = Regret for a non-risky choice, SUB = Subiculum, vmPFC = ventromedial Prefrontal Cortex.

Notably, regret experience in real-word learning tasks such as stock-market investments predicts changes in subjects' behaviour (Lohrenz et al., 2007). Thus, the evidence for a resonant mechanism biased towards risk-aversion suggests that even counterfactual learning in the financial domain might be reinforced by observing someone else's investments returns, thus triggering an exponential effect which provides a cue for the formation of financial bubbles.

An interpretation of the data in terms of neural resonance of others' emotional experiences does not exclude the possible involvement of different complex emotions, as envy and gloating for others' outcomes, as suggested by behavioural (Bault et al., 2008) and neuroimaging (Takahashi et al., 2009) data. In particular, Bault et al. (2008) observed that in a direct social confrontation, when individuals played *simultaneously* on the same trials, their choices were more strongly affected by envy and gloating than by regret or relief. The activations observed here could then relate to envy or gloating for the other's outcomes, rather than to shared relief or regret. However, those studies were designed to elicit direct social comparisons between individuals, by either manipulating subjects' information or by having individuals playing on the same trials. In the present study, instead, subjects played on different trials to minimize the effect of possible social comparisons. Moreover, outcomes producing the feelings of regret and relief were counterbalanced, thus further reducing the effect of envy and gloating also when SHP and IP followed each other. Finally, we also predict the idea of possible different emotions, than regret or relief, arising from the awareness of someone else's outcomes. Still, our data show that when direct social comparison is minimized, and when individuals are aware of others' regret or relief, they

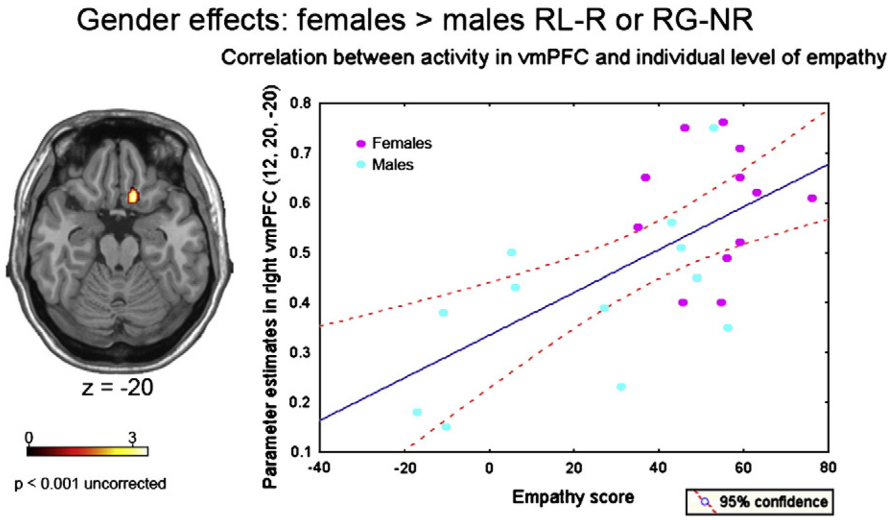

Fig. 4. Gender differences in the parametric effect of previous outcomes on neural activity underlying subsequent choices. The stronger activation of the vmPFC, reflecting the effect of previous outcome that behaviourally decrease risk-seeking, in female than male participants (stereotaxic coordinates $x = 12$, $y = 22$, $z = -20$). Activity in the vmPFC was significantly correlated with individual empathy scores, measured with the Balanced-Emotional-Empathy-Scale (BEES).

behaviourally and neurally respond as in a 1st-person situation. The common activation of the *same* cerebral regions that reflect both one's own and the other player's emotional states when making a new choice, coherently with their behavioural effect, supports an interpretation in terms of an automatic understanding of the feelings experienced by others. It is also worth noting that experiencing envy and gloating for another's fortunes or misfortunes is likely to require the understanding of her/his positive and negative, respectively, emotional state. In line with the suggested role of a mirror-like response in social cognition (Gallese et al., 2004), then, such a resonant mechanism for the experiential understanding of others' choice-related emotions may even represent a prerequisite upon which envy and gloating can develop, and exert their influence on decision-making in social settings.

Conclusions

Our data provide novel evidence on the neural bases of social influences in decision-making, by showing that adaptive learning to the outcomes of previous choices can be also elicited by the observation of other people's outcomes. Such a "shared" effect of previous experience is underpinned by neural mechanisms specifically reflecting the influence of past experiences driving to risk or not to risk. These mechanisms, indeed, exert an opposite influence on risk-aptitude both when they are experienced *and* when they are observed in others. However, only the attended outcomes that reduce risk-seeking elicit a resonant affective response centered in the vmPFC and related limbic regions, while those that increase risk-seeking seem to exert their shared effect only via computational learning signals devoid of affective components. This neural mechanism may be crucial for learning in social decision-making, at least when inter-subject competition is not elicited.

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Author contributions

Study concept and design: NC MM FA DP SFC. Acquisition of data: NC FA. Analysis of data: NC. Drafting of the manuscript NC. Critical revision of the manuscript for important intellectual content: NC MM DP SFC.

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References

Augustine, J.R., 1996. Circuitry and functional aspects of the insular lobe in primates including humans. Brain Res. Brain Res. Rev. 22, 229–244.

Barsade, S.G., 2002. The ripple effect: emotional contagion and its influence on group behavior. Adm. Sci. Q. 47, 644–675.

Bault, N., Coricelli, G., Rustichini, A., 2008. Interdependent utilities: how social ranking affects choice behavior. PLoS ONE 3, e3477.

Bellebaum, C., Kobza, S., Thiele, S., Daum, I., 2010. It was not MY fault: event-related brain potentials in active and observational learning from feedback. Cereb. Cortex 20, 2874–2883.

Brandao, M.L., Zanoveli, J.M., Ruiz-Martinez, R.C., Oliveira, L.C., Landeira-Fernandez, J., 2008. Different patterns of freezing behavior organized in the periaqueductal gray of rats: association with different types of anxiety. Behav. Brain Res. 188, 1–13.

Camille, N., Coricelli, G., Sallet, J., Pradat-Diehl, P., Duhamel, J.R., Sirigu, A., 2004. The involvement of the orbitofrontal cortex in the experience of regret. Science 304, 1167–1170.

Canessa, N., Motterlini, M., Di Dio, C., Perani, D., Scifo, P., Cappa, S.F., Rizzolatti, G., 2009. Understanding others' regret: a FMRI study. PLoS ONE 4, e7402.

Chiu, P.H., Lohrenz, T.M., Montague, P.R., 2008. Smokers' brains compute, but ignore, a fictive error signal in a sequential investment task. Nat. Neurosci. 11, 514–520.

Chua, H.F., Gonzalez, R., Taylor, S.F., Welsh, R.C., Liberzon, I., 2009. Decision-related loss: regret and disappointment. Neuroimage 47, 2031–2040.

Cohen, M.X., Ranganath, C., 2005. Behavioral and neural predictors of upcoming decisions. Cogn. Affect. Behav. Neurosci. 5, 117–126.

Cooper, D.C., Klipec, W.D., Fowler, M.A., Ozkan, E.D., 2006. A role for the subiculum in the brain motivation/reward circuitry. Behav. Brain Res. 174, 225–231.

Coricelli, G., Critchley, H.D., Joffily, M., O'Doherty, J.P., Sirigu, A., Dolan, R.J., 2005. Regret and its avoidance: a neuroimaging study of choice behavior. Nat. Neurosci. 8, 1255–1262.

Dale, A.M., 1999. Optimal experimental design for event-related fMRI. Hum. Brain Mapp. 8, 109–114.

Daw, N.D., Doya, K., 2006. The computational neurobiology of learning and reward. Curr. Opin. Neurobiol. 16, 199–204.

Friston, K.J., Glaser, D.E., Henson, R.N., Kiebel, S., Phillips, C., Ashburner, J., 2002. Classical and Bayesian inference in neuroimaging: applications. Neuroimage 16, 484–512.

Friston, K.J., Penny, W.D., Glaser, D.E., 2005. Conjunction revisited. Neuroimage 25, 661–667.

Gallese, V., Keysers, C., Rizzolatti, G., 2004. A unifying view of the basis of social cognition. Trends Cogn. Sci. 8, 396–403.

Girotto, V., Ferrante, D., Pighin, S., Gonzalez, M., 2007. Postdecisional counterfactual thinking by actors and readers. Psychol. Sci. 18, 510–515.

Haber, S.N., Kim, K.S., Mailly, P., Calzavara, R., 2006. Reward-related cortical inputs define a large striatal region in primates that interface with associative cortical connections, providing a substrate for incentive-based learning. J. Neurosci. 26, 8368–8376.

Johansen-Berg, H., Gutman, D.A., Behrens, T.E., Matthews, P.M., Rushworth, M.F., Katz, E., Lozano, A.M., Mayberg, H.S., 2008. Anatomical connectivity of the subgenual

cingulate region targeted with deep brain stimulation for treatment-resistant depression. Cereb. Cortex 18, 1374–1383.
Kahnt, T., Park, S.Q., Cohen, M.X., Beck, A., Heinz, A., Wrase, J., 2009. Dorsal striatal-midbrain connectivity in humans predicts how reinforcements are used to guide decisions. J. Cogn. Neurosci. 21, 1332–1345.
Kuhnen, C.M., Knutson, B., 2005. The neural basis of financial risk taking. Neuron 47, 763–770.
Leahy, R.L., 2001. Depressive decision-making: validation of the portfolio theory model. J. Cogn. Psychother. 15, 341–362.
Lohrenz, T., McCabe, K., Camerer, C.F., Montague, P.R., 2007. Neural signature of fictive learning signals in a sequential investment task. Proc. Natl Acad. Sci. USA 104, 9493–9498.
Marchiori, D., Warglien, M., 2008. Predicting human interactive learning by regret-driven neural networks. Science 319, 1111–1113.
Mehrabian, A., Epstein, N., 1972. A measure of emotional empathy. J. Pers. 40.
Mellers, B.A., Schwartz, A., Ritov, I., 1999. Emotion-based choice. J. Exp. Psychol. Gen. 128, 1–14.
Meneghini, A.M., Sartori, R., Cunico, L., 2006. Adattamento e validazione su campione italiano della Balanced Emotional Empathy Scale di A. Mehrabian. Ricerche Psicol. 29, 123–152.
Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh Inventory. Neuropsychologia 9, 97–113.
Peyron, R., Laurent, B., Garcia-Larrea, L., 2000. Functional imaging of brain responses to pain. A review and meta-analysis (2000). Neurophysiol. Clin. 30, 263–288.
Platt, M.L., Glimcher, P.W., 1999. Neural correlates of decision variables in parietal cortex. Nature 400, 233–238.
Preston, S.D., de Waal, F.B., 2002. Empathy: its ultimate and proximate bases. Behav. Brain Sci. 25, 1–20 (discussion 20-71).
Preuschoff, K., Quartz, S.R., Bossaerts, P., 2008. Human insula activation reflects risk prediction errors as well as risk. J. Neurosci. 28, 2745–2752.
Reynolds, S.M., Zahm, D.S., 2005. Specificity in the projections of prefrontal and insular cortex to ventral striatopallidum and the extended amygdala. J. Neurosci. 25, 11757–11767.
Schultz, W., 2002. Getting formal with dopamine and reward. Neuron 36, 241–263.
Seminowicz, D.A., Mayberg, H.S., McIntosh, A.R., Goldapple, K., Kennedy, S., Segal, Z., Rafi-Tari, S., 2004. Limbic-frontal circuitry in major depression: a path modeling metanalysis. Neuroimage 22, 409–418.
Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R.J., Frith, C.D., 2004. Empathy for pain involves the affective but not sensory components of pain. Science 303, 1157–1162.
Sommer, T., Peters, J., Glascher, J., Buchel, C., 2009. Structure–function relationships in the processing of regret in the orbitofrontal cortex. Brain Struct. Funct. 213, 535–551.
Takahashi, H., Kato, M., Matsuura, M., Mobbs, D., Suhara, T., Okubo, Y., 2009. When your gain is my pain and your pain is my gain: neural correlates of envy and schadenfreude. Science 323, 937–939.
Talairach, J., Tournoux, P., 1988. Co-Planar Stereotactic Atlas of the Human Brain. Thieme, Stuttgart.
van Harreveld, F., van der Pligt, J., Nordgren, L., 2008. The relativity of bad decisions: social comparison as a means to alleviate regret. Br. J. Soc. Psychol. 47, 105–117.
Wicker, B., Keysers, C., Plailly, J., Royet, J.P., Gallese, V., Rizzolatti, G., 2003. Both of us disgusted in My insula: the common neural basis of seeing and feeling disgust. Neuron 40, 655–664.
Yacubian, J., Glascher, J., Schroeder, K., Sommer, T., Braus, D.F., Buchel, C., 2006. Dissociable systems for gain- and loss-related value predictions and errors of prediction in the human brain. J. Neurosci. 26, 9530–9537.
Zeelenberg, M., van Dijk, W.W., van der Pligt, J., Manstead, A.S.R., van Empelen, P., Reinderman, D., 1998. Emotional reactions to the outcomes of decisions: the role of counterfactual thought in the experience of regret and disappointment. Organ. Behav. Hum. Decis. Process. 75, 117–141.