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Original Article

Neural bases of loss aversion when choosing for oneself versus known or unknown others

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Despite the ubiquitous interdependence between one's own decisions and others' welfare, and the controversial evidence on the behavioral effect of choosing for others, the neural bases of making decisions for another versus oneself remain unexplored. We investigated whether loss aversion (LA; the tendency to avoid losses over approaching equivalent gains) is modulated by (i) choosing for oneself, other individuals, or both; (ii) knowing or not knowing the other recipients; or (iii) an interaction between these factors. We used fMRI to assess the brain activations associated with choosing whether to accept or reject mixed gambles, either for oneself, for another player, or both, in 2 groups of 28 participants who had or had not briefly interacted with the other players before scanning. Participants displayed higher LA for choices involving their payoff compared with those affecting only the payoff of other, known, players. This "social" modulation of decision-making was found to engage the dorsomedial prefrontal cortex and its inhibitory connectivity to the middle cingulate cortex. This pattern might underpin decision-making for known others via self-other distinction processes associated with dorsomedial prefrontal areas, with this in turn promoting the inhibition of socially oriented responses through the downregulation of the midcingulate node of the empathy network.

Key words: dorsomedial prefrontal cortex; loss aversion; social cognitive intervention; fMRI; social decision.

Introduction

The ubiquity of social cognition is well shown by us being constantly immersed in a social context (Tomasello 2014; Arioli, Crespi, et al. 2018; Holt-Lunstad 2018; Snyder-Mackler et al. 2020), be it real or represented, to the extent that, even in the latter case, cognitive processing is biased toward interpersonal relationships (Yeshurun et al. 2021). Being interconnected components of a collective context, rather than its separate units, entails a remarkable interdependence between one's own decisions and others' welfare. A prototypical example of such dependence is when one's outcomes directly reflect the choices made by somebody else who is accountable for their impact. The social implications of these decisions are typical of structured societies in which—for instance—parents, physicians, or politicians make decisions on behalf of their loved ones, patients, or citizens, respectively (Wonderling et al. 2005; Garcia-Retamero and Galesic 2012; Nicolle et al. 2012; Jung et al. 2013; Ruff and Fehr 2014; Vlaev et al. 2017).

Due to its emotional impact, being aware of the "social" consequences of one's own choices is expected to modulate the cognitive biases that have been invoked to explain humans' deviations from economic models (Colman 2003; Lieder and Griffiths 2020). Two prototypical examples of such biases are "risk aversion" (i.e. preferring certain compared with probabilistic outcomes; Tversky and Kahneman 1981; De Martino et al. 2006; Lilleholt 2019) and "loss aversion" (LA; i.e. overweighing the negative choice consequences over the positive ones; Kahneman and Tversky 1979; Tom et al. 2007; Canessa et al. 2013, 2017; Sokol-Hessner and Rutledge 2019). Neuroimaging evidence suggests that these decision patterns reflect the interplay between neural responses underlying appetitive drives (ventral tegmental area, nucleus accumbens, and medial prefrontal cortex) and aversive drives (amygdala and insula) via mechanisms of cognitive control involving the posterior fronto-medial cortex alongside dorsolateral prefrontal regions (Kouneiher et al. 2009; Canessa et al. 2013; Hayes et al. 2014; Sokol-Hessner and Rutledge 2019). It is thus surprising, in the light of the "ultra-social" nature of human beings (Tomasello 2014), that limited evidence exists on the neural bases of incorporating, in these evaluations, the social dimension that is inherent in choosing on behalf of others. Moreover, the few published studies on this topic did not provide conclusive evidence concerning the effect of choosing on behalf of others on LA and risk aversion (Polman 2012a; for a recent review, see Polman and Wu 2020). Deciding for another person, compared with oneself, has been shown to decrease LA (Polman 2012b; Mengarelli et al. 2014; Andersson et al. 2016) and the appetitive drive inherent in evaluating prospective outcomes (Albrecht et al. 2011, 2013; Civai et al. 2012). However, there is opposite evidence showing increased LA when making decisions for others (Eriksen and Kvaløy 2010; Hermann et al. 2019) but not when choosing for both oneself and the other (Füllbrunn and Luhan 2015; Andersson et al. 2016).

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A modulation by choosing for someone else, whatever its direction, has been also investigated for risk attitude but again with mixed results. Some studies have found no difference in risk preference when deciding for someone else versus oneself (Barrafrem and Hausfeld 2020) or both (Andersson et al. 2016), while others have reported either decreased risk-taking (Pahlke et al. 2015; Eriksen et al. 2020) or increased risk-taking and less patience (Vlaev et al. 2017) when choosing for others. Such inconsistencies reflect not only considerable individual differences across participants (Charness and Jackson 2009; Füllbrunn and Luhan 2015) but also varying behavior within the same individuals (Eriksen et al. 2020) when choosing for another. Importantly, all these studies focused on economic decisions made for unknown others. However, large individual differences have been also observed when participants are asked to make decisions on behalf of a friend, concerning both economic (e.g. Liu et al. 2017) or noneconomic (e.g. security or romantic relationships) issues, resulting both in decreased (Stone et al. 2013) and increased (Beisswanger et al. 2003) risk-taking.

To further complicate this picture, the only 2 studies investigating the neural correlates of risk attitude when choosing for another versus oneself (Jung et al. 2013; Zhang et al. 2019) reported different results. Only the former study highlighted the specific engagement of the medial prefrontal sector of the mentalizing network (Arioli et al. 2021) for social, compared with individual, decisions, which, however, was not replicated by the latter. Moreover, these studies suggested alternative interpretations of the dorsomedial prefrontal cortex (dmPFC) role in choice-related evaluations, which was considered to support either individual (Zhang et al. 2019) or social (Jung et al. 2013) decision-making. Moreover, none of these neuroimaging studies has assessed the neural bases of a possible modulation of LA when choosing for another, which remains an unexplored topic.

This inconsistent picture of the neuro-cognitive mechanisms underlying social decisions may reflect difficulties in simulating others' preferences and choices (Suzuki et al. 2012), which are generally deemed as different from one's own ones (Hsee and Weber 1997). The social distance between the decision-maker and the outcome recipient might represent another modulating factor of risk attitude. Again, however, distinct studies reported either decreased (Fareri et al. 2022) or increased (Sun et al. 2017) risk aversion when choosing for a friend when compared with an unknown person. Overall, these data suggest that further evidence is required to assess the effect of choosing for another compared with oneself, the possible modulation by social distance, and their neural bases.

To fill this gap, a novel decision-making paradigm was developed to assess behavioral LA for monetary outcomes and was administered during fMRI to 56 healthy participants who made decisions either for themselves, or for another player, or both. We also aimed to assess whether a possible effect of the outcome recipient was additionally modulated by social distance. To this purpose, we compared LA and the associated neural responses across the 2 subgroups of 28 participants who had versus did not have a brief interaction with the other individuals before fMRI scanning.

Based on the available literature, we predicted a modulation of behavioral LA when choosing on behalf of other individuals, particularly after having interacted with them, reflecting in a specific pattern of activity and connectivity involving frontomedial regions, which was associated both with social cognitive processing (Arioli et al. 2021) and cost–benefit economic evaluations (Hayes et al. 2014).

Materials and methods

Participants

Fifty-six right-handed, healthy volunteers (28 females and 28 males; mean age = 25.4 years; SD = 3.64; age range = 18–40) participated in the study. All subjects had normal or corrected-to-normal visual acuity, and none of them reported a history of neuropsychiatric conditions or substance abuse nor was currently taking any medication interfering with cognitive functioning. They gave their written informed consent to the experimental procedure, which was approved by the local Ethics Committee.

Task

Subjects performed the same task used in previous studies addressing the effect of LA when weighing the prospective positive and negative consequences of choices (e.g. Sokol-Hessner et al. 2009). In each trial, they were asked to choose between a certain "0" outcome (i.e. the status quo) and a mixed gamble (i.e. a gamble involving both positive and negative possible outcomes) that might result in variable amounts of gains or losses with equal 50% probabilities (Fig. 1). In different fMRI runs, subject were asked to: (i) make decisions for oneself (1a), or for another player (1b), or both (1c) and (ii) to attend the decisions made by the other player (other than that involved in the former condition), while knowing that such choices will influence one's own (2a), the other player's (2b), or both players' (2c) final payoff.

This experimental paradigm therefore entails 2 macroconditions, i.e. "I decide" versus "Other decides" (macroconditions 1 and 2, respectively), each including 3 different subconditions concerning the outcome recipient, i.e. the subject oneself, the other player, or both players (a/b/c). As detailed below, the 3 "I decide" and the 3 "Other decides" subconditions were blocked within a triplet of consecutive fMRI runs, with both macrocondition order ("I decide" and "Other decides") and subconditions (a, b, c) being counterbalanced across subjects. Each of the 6 experimental subconditions included 49 trials.

Experimental procedure

To calibrate stimuli to participants' individual level of LA, 1 week before the MRI session, they were asked to perform 49 trials of subcondition 1a (i.e. choosing only for themselves) of the task described above. The gain-loss values of this task, sampled from a 7 × 7 matrix, were centered to a LA level of 2, which is representative of the general population (Kahneman and Tversky 1979; Ruggeri et al. 2020). To estimate both LA and risk aversion, participants performed 49 "mixed" (or "gain-loss") gambles requiring to choose between a gain and an equally probable loss and 30 "gain-only" gambles that required to choose between a 100% guaranteed amount and 50% chances of a larger gain (Sokol-Hessner et al. 2009, 2013, 2015). Then, for the fMRI session, we created multiple sets of 49 mixed gambles for each 1 of 8 possible levels of LA ranging from $\lambda = 0.5$ to $\lambda = 4$ in steps of 0.5. To equalize the probability of accepting/rejecting a gamble across participants, and to maximize the number of trials in which the gain/loss ratio was close the subject's indifference point, we selected the sets of stimuli that were adapted to the participant's LA to be used for the subconditions of the "I decide" and "Other decides" macroconditions. The order of subconditions within each macrocondition was counterbalanced across subjects, and the order of trials within each subcondition was randomized for each subject.

Immediately before the fMRI scan, participants received detailed instructions about the task and completed a training

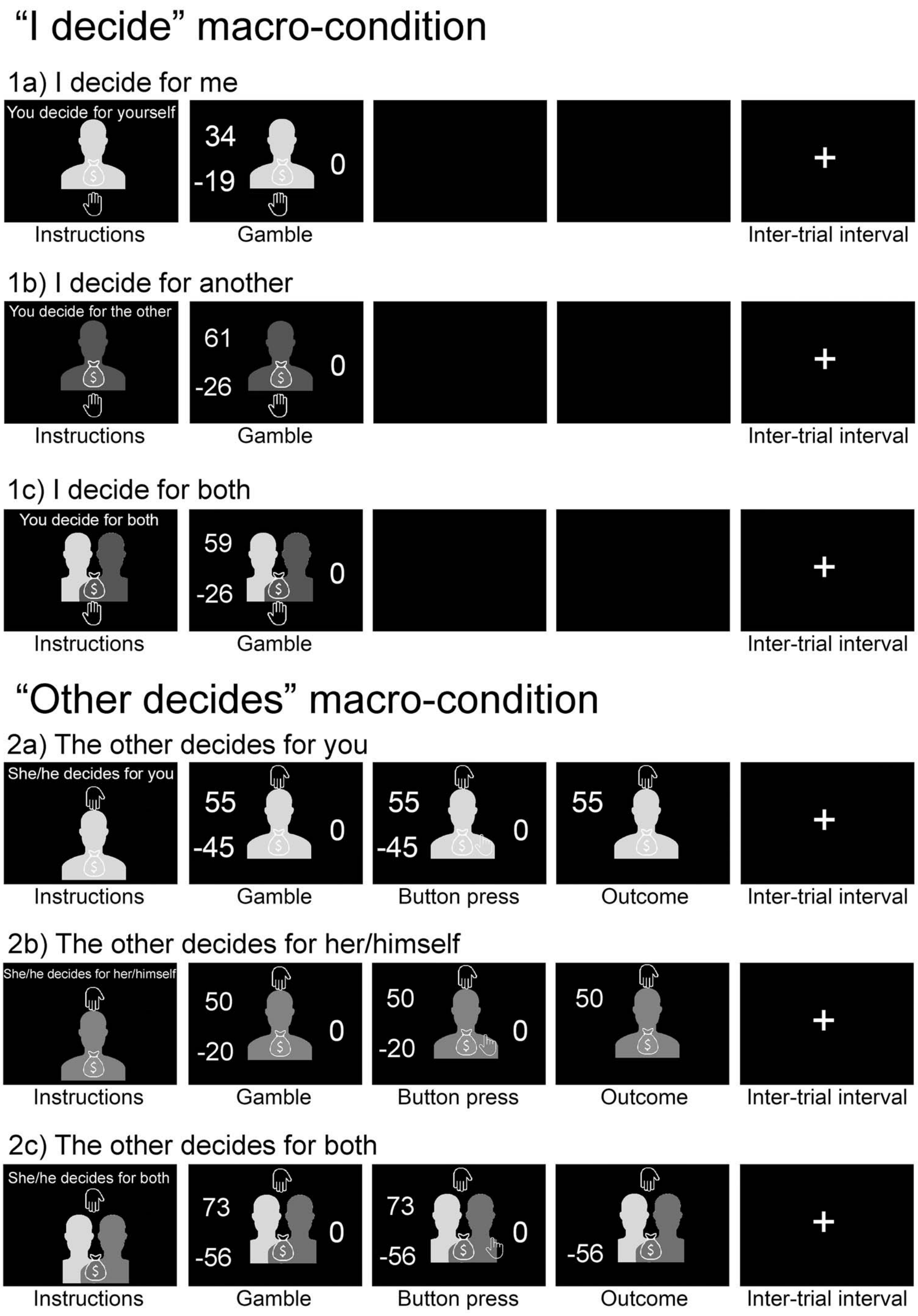

Fig. 1. Experimental procedure. The figure displays the timeline of events for all the 6 subconditions ("I decide" or "Other decides," for "oneself," "another," or "both"). All subconditions started with written instructions lasting for 4 s. the instructions included a picture depicting the avatar(s) indicating the recipient(s) of the choice outcome, and a hand, oriented so as to indicate the decision-maker. In all subconditions, gambles were then shown for 4 s during which a choice could be made by pressing 1 of 2 buttons of a response box, corresponding to the left–right position of the gamble and certain outcome. To prevent learning effects, participants received no feedback about the outcomes of their own choices in the "I decide" macrocondition. In the "Other decides" macrocondition, they attended to the gambles that were being presented to another player and were informed that she/he had made a choice via a screen (lasting for 0.5 s) displaying an index finger pressing a button ("button-press"). To equate the presence of a motor response, at this stage, they had 2 s to press any of the 2 available buttons in order to be shown the outcome of the choice which remained on the screen for 2 s.

session to familiarize with the task. They were provided with a monetary endowment, were asked to place it in their wallet (Sokol-Hessner et al. 2009, 2013), and were told that the sum would increase or decrease, at the end of the experiment, based on their actual performance. Namely, the final monetary payoff was based on the outcome of a single trial (randomly extracted from the set of accepted gambles) from the 4 experimental subconditions other than "I decide/She-he receives" and "She/he decides/She-he receives." Before being positioned in the scanner, half participants (14 females and 14 males) were introduced to their 2 companion players (always 1 male and 1 female, aged 18–40 years as the participant) and were told that they would take part in the same task via an ethernet connection; they were not told, however, who of 2 companion players would participate in the “I decide” and “Other decides” macroconditions. The other half of participants (14 females and 14 males) were only informed about the presence of 2 additional participants who would take part in the same task in a nearby room. There was no difference, across such “interaction” and “no-interaction” groups, concerning the level of LA before MRI ($t(54) = 1.399$, $P = 0.167$), or the individual empathy level as assessed with the Interpersonal Reactivity Index (Davis 1980; Larson et al. 2010; $t(54) = 1.32$, $P = 0.192$). Participants were also informed that their own final payoff would be independent from those of the companion players and that they would not meet the other players after the MRI session. Before entering the scanner, they chose an avatar, among several available options differing in color, which was aimed to help distinguishing themselves from the other players during the experimental task (Fig. 1). We ensured that participants and their companion players were associated with differently colored avatars.

To avoid a continuous switch among subconditions, which might blur behavioral effects, each of the 6 subconditions corresponded to a fMRI run. Moreover, the 3 “I decide” and the 3 “Other decides” subconditions were blocked in a series of 3 consecutive runs. The “I decide” and “Other decides” macroconditions were separated by a resting-state fMRI scan lasting 8 min, and their order was counterbalanced across female and male subjects: namely, 28 subjects (14 females and 14 males) played the “I decide” macrocondition before the resting-state scan, while the other 28 (14 females and 14 males) played it after the resting-state scan.

In the 3 “I decide” subconditions (i.e. 1a, 1b, and 1c), gambles were shown for 4 s during which participants could make their choice by pressing 1 of 2 buttons of a response box, corresponding to the left–right position of the gamble and certain outcome. To prevent learning effects, they received no feedback about the outcome of the accepted gambles; instead, they were informed that the outcome would be shown to the other player, as described below. In the 3 “Other decides” subconditions (i.e. 2a, 2b, and 2c), indeed, subjects attended the gambles that were being presented to the other player and were informed that she/he had made a choice via a screen (lasting 0.5 s) displaying an index finger pressing a button. To equate the presence of a motor response, at this stage, subjects had 2 s to press any of the 2 available buttons in order to be shown the outcome of the choice made by the other player, which remained on the screen for 2 s. Subjects were informed that (i) both the 2 partners (the decision-maker in “Other decides” condition, and the recipient in the “I decide” condition) aimed to maximize their monetary payoff; (ii) only the accepted gambles would contribute to the final monetary payoff; (iii) in both the “I decide” and “Other decides” macroconditions, a missed press would result in a financial penalty; and (iv) the other player had been instructed to follow the same procedure.

All subconditions started with written instructions (e.g. “You decide for yourself,” “She/he decides for both,” etc.), lasting for 4 s. The instructions included a picture depicting (i) the colored avatar(s) indicating the recipient(s) of the choice outcome and (ii) a hand, oriented so as to indicate the decision-maker (Fig. 1). This picture remained visible throughout each trial alongside the values associated with gain, loss, and certain out comes.

Within each fMRI run, visual stimuli were shown at the center of the screen and they were temporally separated by a black screen. The duration of this implicit baseline was varied (“jittered”) at every trial to desynchronize the timings of event types with respect to the acquisition of single slices within functional volumes and thus to optimize statistical efficiency (Dale 1999). We used the OptSeq2 Toolbox (http://surfer.nmr.mgh.harvard.edu/optseq/) to estimate the optimal interstimulus intervals (ISIs; mean ISI = 5 s, range = 1.5–19 s). Subjects viewed visual stimuli via an MRI-compatible LCD screen located behind the scanner and a mirror placed on the head-coil and gave their response with the right hand via an MRI-compatible response box. We used the software Presentation 20.1 (http://www.neurobs.com) both for presenting stimuli and for recording subjects’ answers.

To assess whether having interacted, or not, with the partners might have shaped the participants’ impressions about them, all participants from both groups completed a survey after fMRI. They were asked to provide a sincere assessment on the companion players and were reassured that it would be kept secret from them. Namely, they were asked to judge (i) their impression about valence, fairness, and trustworthiness of the partner who made decisions for them and (ii) the impression they felt they had generated, with respect to the same dimensions, in the partner who was the recipient of their decisions. In particular, they were asked to evaluate their partners via 5-point Likert scales for (i) general valence (from −2 [very negative] to +2 [very positive]), (ii) fairness (from −2 [very unfair] to +2 [very fair]), and (iii) trustworthiness (from −2 [very untrustworthy] to +2 [very trustworthy]).

fMRI data acquisition

We collected anatomical T1-weighted and functional T2∗-weighted MRI images with a 3 Tesla General Electrics Discovery MR750 scanner (GE Healthcare), which was equipped with a 16-channel head coil. Participants were positioned comfortably on the scanner bed and were fitted with soft ear plugs; foam pads were used to minimize the head movements. Functional images were acquired using an echo-planar imaging sequence (42 continuous ascending transverse slices covering the whole brain, tilted 30°downward with respect to the bicommissural line to reduce susceptibility artifacts in orbitofrontal and inferior temporal regions; TR = 2,000 ms, TE = 30 ms, flip-angle = 78°, field of view (FOV) = 192 × 192 mm, slice thickness = 3.4 mm, interslice gap = 0.2 mm, in-plane resolution = 3 × 3 mm), preceded by 5 “dummy” functional volumes covering the amount of time required by T1-equilibration effects. A high-resolution, 3D, T1-weighted, IR-prepared FSPGR (BRAVO) brain scan was also acquired along the AC-PC plane (152 slices, FOV = 256 mm, in-plane resolution = 1 × 1 mm, slice thickness = 1 mm).

LA estimation

Participants’ choices in the gambling tasks were assessed under the assumption that both gain-loss and gain-only trials are required to isolate LA from risk attitude since both are involved in anticipatory valuation processes (Sokol-Hessner et al. 2015). Following Prospect theory-inspired models (Kahneman and Tversky 1979), the probability of accepting a gain-loss or a gain-only gamble was

$$p\left(\textbf{accept gamble}/G, L, B\right) = \frac{1}{1 + e^{-\mu \times \left(p_G \times (G)^{\rho} - \lambda \times p_L \times (-L)^{\rho} - B^{\rho}\right)}},$$

where G is the gain ($G > 0$), L is the loss ($L < 0$ for gain-loss gambles and $L = 0$ for gain-only gambles), B the guaranteed gain ($B = 0$ for gain-loss gambles and $B > 0$ for gain-only gambles), $p_G = 0.5$ is the probability of a gain, and $p_L = 1 - p_G = 0.5$ is the probability of a loss. The free parameters of the model are: (i) the LA lambda (λ), i.e. the multiplicative weight associated with anticipated losses compared with gains; (ii) the risk attitude rho (ρ), i.e. the curvature of the value function $u(x) = x^{\rho}$ that embodies the diminishing sensitivity to increasing outcome; and (iii) the choice consistency or "softmax temperature" (μ), i.e. a measure of noisiness versus systematicity in choices. They were estimated via maximum likelihood estimation with MATLAB (MathWorks, Natick, MA) for each subject and session separately. Because of time constraints, we could only include gain-loss trials in the fMRI session. We therefore used the gain-only trials obtained in the calibration session (see Experimental procedure section) to estimate the model parameters in each subcondition of the fMRI session. The reliability of this procedure was ensured by (i) the high correlation between rho estimated in the calibration session and during fMRI subconditions (always >0.92, with $P < 0.00001$); (ii) the lack of significant differences across rho values from the 4 sessions ($F(3, 165) = 0.569$, $P = 0.636$). Since λ is positively skewed, $\log(\lambda)$ was modeled in the statistical analyses. A lack of convergence after 50,000 iterations—suggestive of a lack of fit for the model and thus representing a possible indicator of inconsistent choices—represented an exclusion criterion.

Behavioral statistical analysis

In keeping with our aims and hypotheses (see Introduction), we used a 2-way repeated-measure Analysis of Variance (ANOVA) to assess whether the degree of LA, when choosing between the mixed gamble and the certain outcome, was modulated by (i) the recipient of the choice outcome (3-level within-subject factor: the subject oneself, the other player, or both); (ii) having interacted with the other player before fMRI (2-level between-subject factor: yes and no); and (iii) a statistical interaction between these factors. We used Greenhouse–Geisser corrections to adjust the degrees of freedom for violation of sphericity condition in tests involving the 3-level within-subject factor. Participants' gender, and the order of the "I decide" and "Other decides" blocks, were also modeled in separate analyses.

Based on behavioral results (see Behavioral LA section), we additionally tested a more parsimonious model comparing self-outcome with other outcome. To this purpose, we recomputed LA for self-outcome (average of LA for both and for oneself) and for other outcome (average of LA for both players and for another only). We then run a 2 × 2 repeated-measure ANOVA to test the main effects of recipient (self-outcome/other outcome) and the previous interaction (yes/no) and their interaction.

fMRI data preprocessing and statistical analyses

We performed image preprocessing with SPM12 (http://www.fil.ion.ucl.ac.uk/spm) (Worsley and Friston 1995). The first 5 volumes of each functional run were discarded to allow for T1 equilibration effects. All remaining volumes from each subject underwent a standard spatial preprocessing including slice-timing correction with the middle slice in time as a reference, spatial realignment to the first volume and unwarping, and spatial normalization into the standard Montreal Neurological Institute (MNI) space and resampling in 2 mm^3 voxels as well as spatial smoothing with a 8-mm full-width half-maximum isotropic Gaussian kernel. The resulting time series across each voxel were then high-pass filtered to 1/128 Hz, and serial autocorrelations were modeled as an AR(1) process. We used the MotionFingerprint toolbox (www.medizin.unituebingen.de) to compute, for each subject, a comprehensive indicator of scan-to-scan head motion (i.e. framewise displacement).

We then used SPM12 to perform statistical analyses assessing condition-specific regional changes of brain activity associated with contrasts of interest. Statistical maps were based on a random-effect model implemented in a 2-level procedure (Friston et al. 1999). At the first (single-subject) level, we modeled fMRI responses via a design matrix comprising the gamble onset for each trial of the different 6 subconditions (i.e. I decide for me [1a], for the other player [1b], for both [1c]; the other player decides for me [2a], for oneself [2b], for both [2c]), with duration equal to the response time (RT). Importantly, RTs did not differ significantly across the 3 "I decide" subconditions ($F(2, 110) = 0.621$, $P = 0.539$). To equate the duration of miniepochs at the single-subject level, and to ensure comparability between macroconditions, the duration of the 3 "Other decides" trials was modeled in SPM12 using the RT associated with the same mixed-gamble from the corresponding "I decide" subcondition. Instead, the time period in-between response and gamble offset was modeled as an event of no interest, alongside instructions, to remove their effect from the implicit baseline. We therefore implemented a mixed block-/event-related design (Petersen and Dubis 2012), allowing to investigate BOLD changes associated with miniepochs time-locked to gamble onset, while maintaining the 6 subconditions temporally separated. An additional regressor modeled the framewise head displacement resulting from the MotionFingerprint toolbox. We then convolved regressors modeling events with a canonical hemodynamic response function (HRF), and parameter estimates were obtained for all regressors by maximum-likelihood estimation.

In line with study aims and behavioral analyses (see Behavioral statistical analysis section), we focused on the "I decide" subconditions. At the second level, we therefore performed an initial random-effect group analysis with sphericity correction for repeated measures (Friston et al. 2002) by comparing the 2 macroconditions "I decide" and "Other decides" to highlight the brain regions showing stronger activity when evaluating a gamble to make a decision compared with observing another's gamble.

In a second group-level analysis, we modeled a 3 (outcome recipient: "the subject oneself," "the other player," and "both") × 2 (previous interactions with the companion players: "yes" and "no") factorial design with sphericity correction for repeated measures (Friston et al. 2002), which was based on the respective first-level contrast images. In keeping with our aims and hypotheses (see Introduction), we then assessed a modulation of choice-related brain activity by the main effect of social decision, i.e. evaluating the mixed gamble while knowing that its outcome would impact on one's own, the other player's, or both players' payoff. In particular, contrasts between these subconditions were aimed to highlight possible differential neural responses in social versus individual choices entailing real economic consequences and particularly the possible effect of a sense of social decision inherent in "choosing for the other player" compared with "choosing for oneself." Moreover, we assessed a statistical interaction between the "outcome recipient" and "previous interaction" factors to test whether possible activations associated with choosing for other individuals (compared with oneself) would be itself modulated by having (compared with not having) interacted with the companion players.

Behavioral analyses (see below) showed that the degree of LA was indeed significantly modulated by the statistical interaction between the outcome recipient and a previous interaction with the other companion players. On this basis, in a second group-level analysis of fMRI data, we modeled a parametric regressor coding a linear modulation of choice-related activity by the degree of condition-specific LA. The resulting statistical maps therefore highlighted the voxels in which the strength of activity tracked the different sensitivity to losses associated with making decisions for oneself, the other player, or both, after having or not having interacted with the companion players.

We reported as statistically significant only the voxels surviving a statistical threshold of $P < 0.05$, which was corrected for multiple comparisons based on cluster extent using topological false discovery rate (FDR; Chumbley et al. 2010), with $P < 0.005$ at the voxel level. Importantly, the combination of a cluster-level FDR correction with a forming threshold at $P < 0.005$ might produce more false-positive clusters than stated (Eklund et al. 2016), and represents a limitation to the present results, that therefore require further support from future studies. However, based on the available evidence on the neural bases of social decision-making, we had robust predictions concerning the engagement of the dmPFC (see Introduction and Results). We used the SPM Automated Anatomical Labeling (AAL) toolbox (v3.1; Rolls et al. 2020) to localize the activated brain regions in the MNI space.

Psychophysiological interaction analyses of functional connectivity

The results of standard fMRI analyses informed a subsequent psychophysiological interaction (PPI) analysis (Friston et al. 1997) aimed to unveil the functional neural interactions underlying the relationship with the different degree of LA associated with making decisions for oneself, the companion players, or both, after having or not having interacted with them.

The PPI approach highlights a significant increase/decrease of connectivity from a seed region to all other brain voxels, in association with a given context, by regressing the activity at any voxel on the activity of the seed. PPI represents an advancement with respect to functional connectivity analyses based on pairwise temporal correlation, which cannot disambiguate the context-specific connectivity from the resting-state connectivity or connectivity associated with a common neuro-modulatory input. To discount correlations due to shared task inputs, indeed, the PPI model also includes as nuisance covariates the activity of the seed region and an experimental context, i.e. the physiological and psychological factors, respectively. The resulting regression coefficient represents, at each voxel, the degree of change in activity per unit change in the seed region, or in simpler words, a measure of the influence one neural system has on another due to a psychological variable, here, represented by the condition-specific degree of behavioral LA. In particular, we aimed to isolate voxels in which such modulation reflected the interactive effect of outcome recipient ("subject oneself," "the other player," and "both") and previous interaction with the companion players ("yes" and "no").

We first defined our region of interest (ROI) as a 6-mm radius sphere centered on the coordinates of the dmPFC, which was found to track this interaction in standard fMRI analyses (see Brain activity underlying LA modulation by choice recipient and previous interaction in Results). The first eigenvariate of the BOLD time series from this ROI was then extracted, temporally filtered, mean-corrected, and deconvolved to generate the underlying neuronal signal. We then created: (i) the interaction factor (PPI regressor), i.e. the product of the mean-centered task time course and the demeaned seed ROI time course; (ii) the psychological factor (P regressor) representing the contrast for the interaction effect between the "outcome recipient" and "previous interaction with the companion players" factors; and (iii) the physiological factor (Y regressor) representing the ROI time course. These regressors were convolved with the canonical HRF and entered into a regression model also including a regressor coding framewise head displacement. This procedure was carried out for each subject, and the resulting images of contrast estimates were entered into a random-effect group analysis to isolate the voxels in which changes of connectivity from the seed region reflected the differential degree of LA according to the "outcome recipient" and "previous interaction" factors. We reported as statistically significant only the voxels surviving a $P < 0.05$ threshold that was corrected for multiple comparisons with FDR (Genovese et al. 2002).

Results

Behavioral results

Subjective assessment of the companion players

There was no significant difference, between the members of the "interaction" and "no-interaction" groups, concerning (i) their assessment of the partner who made decisions for them (general valence: $t(54) = 0.80$, $P = 0.42$; fairness: $t(54) = 1.63$, $P = 0.10$; trustworthiness: $t(54) = 0.70$, $P = 0.48$; sum of the 3 dimensions: $t(54) = 0.667$, $P = 0.501$) and (ii) their beliefs about the impression generated in the recipient of their own choices (general valence: $t(54) = 0.22$, $P = 0.82$; fairness: $t(54) = 1.82$, $P = 0.07$; trustworthiness: $t(54) = 0.39$, $P = 0.69$; sum of the 3 dimensions: $t(54) = 0.661$, $P = 0.509$). These findings seem to weaken the hypothesis that behavioral differences between the "interaction" and "no-interaction" groups might be driven by different psychological attitudes (e.g. in-group vs. out-group effect) toward the partners associated with this experimental manipulation.

Behavioral LA

The number of missing responses (leading to a financial penalty) was on average very low (<1 out of 147 total trials), with no significant difference across the three "I decide" subconditions, $F(2,110) = 1.12$, $P = 0.329$.

The main 3 × 2 ANOVA showed no significant main effect of the "outcome recipient" ($F(1.840, 95.658) = 0.097$, $P = 0.893$) or "previous interaction" ($F(1, 52) = 0.769$, $P = 0.385$) factors on behavioral LA, which was, however, significantly modulated by their interaction ($F(1.840, 95.658) = 3.767$, $P = 0.030$). As shown in Fig. 2A, Fisher Least Significant Difference (LSD) post hoc tests showed that this interaction results from a significant increase of LA when choosing for oneself ($P = 0.034$) or both ($P = 0.040$) when compared with choosing for the other player only, after having interacted with the companion players. None of the other post hoc comparisons were statistically significant (all $Ps > 0.05$). Moreover, no significant effect was found for the participants' gender ($F(1, 52) = 0.948$, $P = 0.335$) or the order of the "I decide" and "Other decides" blocks ($F(1, 52) = 2.726$, $P = 0.105$).

An additional statistical model, comparing self-outcome with other outcome, supported the equivalence, suggested by these data. A 2 × 2 ANOVA showed no significant main effect of the "outcome recipient" (self-outcome/other outcome) ($F(1, 54) = 0.542$, $P = 0.465$) or "previous interaction" ($F(1, 54) = 0.967$, $P = 0.330$) factors on behavioral LA, which was, however, significantly modulated by their interaction ($F(1, 54) = 4.600$, $P = 0.036$). As shown in Fig. 2A, Fisher LSD post hoc tests showed that this interaction results from a significant increase of LA for self-outcome ($P = 0.047$), compared with choosing for the other player only, after having interacted with the companion players. None of the other post hoc comparisons were statistically significant (all $Ps > 0.05$).

fMRI results

Neural bases of evaluating mixed gambles

Compared with observing another's gamble ("Other decides" macrocondition), making a decision ("I decide" macrocondition)

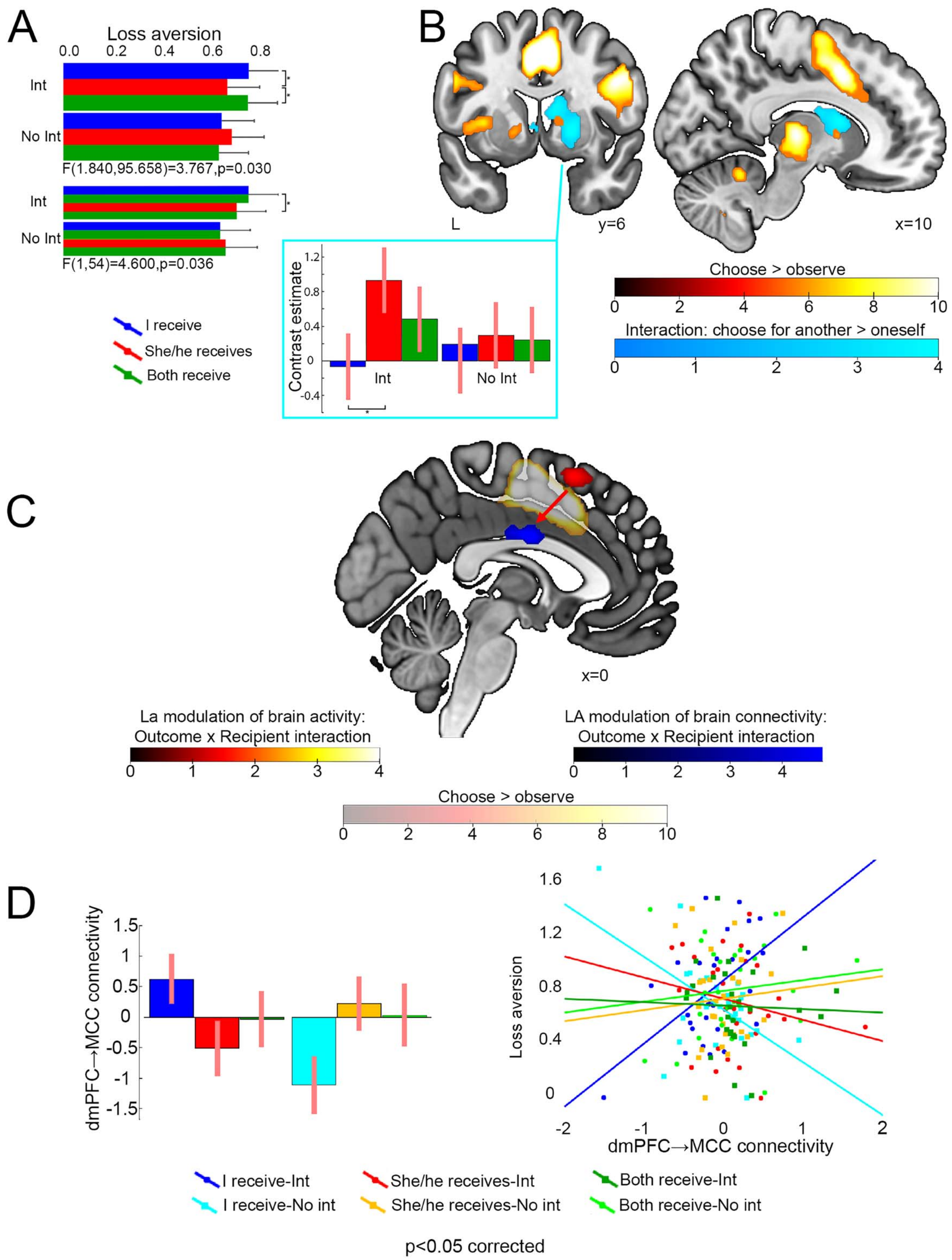

Fig. 2. Behavioral and neuroimaging results. A) Behavioral results. The top-left figure sector depicts the significant interacting effect of outcome recipient (the subject oneself, the other player, or both), and previous interaction (yes/no) with the other player, on behavioral LA. The inferior part of the figure shows the results of a more parsimonious model comparing self-outcome with other outcome. Vertical bars denote 0.95 confidence intervals. Asterisks denote significant pairwise comparisons across conditions, as shown by Fisher post hoc tests ($P < 0.05$). B) Neural bases of choosing on behalf of others. The top-right sector shows the brain regions that were significantly activated in association with (i) making a decision when compared with observing another's choice (yellow); (ii) choosing for others, compared with choosing for oneself, after having interacted with them (cyan). As shown by the histogram, the latter condition was associated with a significant engagement of the right striatum. The statistical threshold was set at $P < 0.05$, FDR was corrected for multiple comparisons. C) Condition-specific LA modulation of brain activity and connectivity. The middle figure sector depicts the clusters displaying changes of LA-related brain activity (red) and connectivity (blue), reflecting the interacting effect of outcome recipient and previous interaction with the other player. As shown by histograms and scatterplots displayed in D), this interaction was associated with higher dmPFC activity, and stronger inhibitory connectivity from the dmPFC to the MCC, when choosing either for oneself or both (compared with choosing for others) after having (compared with not having) interacted with them. The statistical threshold was set at $P < 0.05$, FDR was corrected for multiple comparisons. The posterior fronto-medial region associated with making a decision compared with observing another's choice is also depicted in transparency (opacity was set at 30%).

Table 1. Neural bases of evaluating mixed gambles.

Cluster size	Hem	Anatomical region	x	y	z	T score	Z score
8,926	Left	Medial superior frontal gyrus/SMA	−4	−4	50	17.72	>8
	Right	Medial superior frontal gyrus/SMA	2	6	48	16.16	>8
	Left	Middle cingulate cortex	−8	−28	42	8.94	>8
	Left	Supramarginal gyrus	−50	−24	16	12.65	>8
	Left	Superior parietal lobule	−14	−70	40	5.97	5.81
1,446	Left	Insula lobe	−30	14	6	12.62	>8
	Left	Precentral gyrus	−54	2	34	9.49	>8
	Left	Insula lobe	−38	−4	12	7.19	6.92
	Left	Rolandic operculum	−44	−2	8	7.02	6.77
2,074	Right	Insula lobe	32	18	4	11.32	>8
	Right	Precentral gyrus	50	4	32	10.36	>8
	Right	Superior frontal gyrus	28	−6	52	8.29	>8
187	Left	Middle frontal gyrus	−34	42	22	6.58	6.37
42	Right	Middle frontal gyrus	30	38	28	5.63	5.49
696	Left	Middle temporal gyrus	−46	−66	0	7.93	7.57
	Left	Fusiform gyrus	−38	−62	−14	6.39	6.20
77	Right	Superior temporal gyrus	52	−34	16	5.22	5.11
22	Right	Middle temporal gyrus	48	−60	0	4.99	4.89
1,386	Right	Postcentral gyrus	48	−26	42	8.86	>8
	Right	Supramarginal gyrus	44	−32	42	8.81	>8
	Right	Precuneus	16	−70	42	5.73	5.59
	Right	Angular gyrus	28	−60	42	5.46	5.33
1,005	Right	Cerebellum (VI)	22	−52	−24	13.37	>8
	Right	Cerebellum (VIII)	14	−60	−48	6.5	6.30
	Right	Cerebellar vermis (8)	4	−66	−34	6.22	6.04
	Right	Cerebellar vermis (6)	6	−62	−18	5.26	5.15
	Right	Cerebellar vermis (9)	2	−58	−32	5.15	5.04
148	Left	Putamen/pallidum	−16	6	−2	6.26	6.08
79	Right	Caudate nucleus	12	6	6	6.19	6.02
1,652	Left	Ventro-lateral thalamus	−12	−20	6	12.62	>8
	Right	Ventro-lateral thalamus	10	−18	4	10.25	>8
	Right	Medio-dorsal medial thalamus	8	−18	0	10.21	>8

From left to right, the table reports the extent (number of 2 × 2 × 2 mm^3 voxels), hemispheric lateralization (left/right), anatomical labeling based on the AAL3 Toolbox (Rolls et al. 2020), and stereotactic coordinates and statistical (*T* and *Z*) value for the clusters that were found to be significantly activated in association with making a decision compared with observing another's choice. SMA, supplementary motor area.

recruited a widespread network mainly involving the fronto-striatal and thalamic structures (Table 1 and Fig. 2B). Prefrontal regions included the posterior fronto-medial cortex (extending from the dorsal anterior cingulate cortex, through the midcingulate cortex, to the supplementary motor area) alongside the fronto-insular cortex (encompassing the anterior insula and the precentral gyrus) and middle frontal gyrus bilaterally. Further activations were found in the posterior sector of superior and middle temporal cortex bilaterally, plus in the right parietal cortex (extending from the postcentral gyrus to the angular and supramarginal gyri) and in the cerebellum. Subcortical activations involved the ventrolateral and mediodorsal sectors of the thalamus alongside the right caudate nucleus and left putamen and pallidum.

Modulation of brain activity by choice recipient and previous interaction

We did not find regions in which the changes of activity tracked an interaction between the "outcome recipient" and "previous interaction" factors, or a main effect of the latter. Instead, a right-hemispheric striatal cluster—encompassing the dorsal striatum, putamen, and pallidum—displayed a significant main effect of the "outcome recipient" factor (Table 2). Post hoc contrasts showed that this main effect reflected a stronger activation of these structures, alongside the ventral striatum and the dmPFC, when choosing for others when compared with oneself (Table 2). A further comparison showed that the right striatal cluster—including the dorsal striatum, ventral striatum, putamen, and pallidum—was selectively activated by choosing for others, compared with oneself, in participants who had interacted with them (Table 2 and Fig. 2B). This comparison was not statistically significant when this comparison was constrained to the subgroup of participants who had not met the other players.

Brain activity underlying LA modulation by choice recipient and previous interaction

The strength of activity in the dmPFC reflected the behavioral evidence of an interacting effect of the "outcome recipient" and "previous interaction" on the degree of LA (Table 3 and Fig. 2C). Namely, the relationship between LA and the activity of this region was stronger when choosing either for oneself or both, compared with choosing for other players, but only after having interacted with them.

Functional connectivity underlying LA modulation by choice recipient and previous interaction

The latter dmPFC region was modeled as seed for PPI analyses aimed to investigate a similar modulation of LA by the interacting effect of "outcome recipient" and "previous interaction" on whole-brain functional connectivity. Such modulation was found to engage the middle cingulate cortex (MCC). Namely, a stronger

Table 2. Neural bases of choosing for someone else.

A. Main effect of ‘Outcome recipient’

Cluster size	Hem	Anatomical region	x	y	z	F score	Z score
312	Right	Caudate nucleus/dorsal striatum	14	−4	20	10.43	3.87
	Right	Putamen/pallidum	20	8	0	9.86	3.74
	Right	Caudate Nucleus	10	8	14	9.29	3.61
	Right	Putamen	26	18	−2	7.18	3.08

B. Choosing for others vs. oneself

Cluster size	Hem	Anatomical region	x	y	z	T score	Z score
857	Right	Putamen/pallidum	20	8	0	4.40	4.27
	Right	Caudate nucleus/dorsal striatum	14	−4	20	4.26	4.14
	Right	Caudate Nucleus	12	10	14	4.18	4.07
	Right	Putamen	26	18	−4	3.66	3.58
	Left	Caudate Nucleus/ventral striatum	−2	2	4	3.29	3.23
	Right	Pallidum	22	−6	2	3.21	3.16
592	Left	Medial superior frontal gyrus	−8	26	54	4.03	3.93
	Right	Superior frontal gyrus	14	44	34	3.43	3.36
	Left	Medial superior frontal gyrus	−4	32	34	3.29	3.23

C. Previous interaction: choosing for others vs. oneself

Cluster size	Hem	Anatomical region	x	y	z	T score	Z score
1063	Right	Putamen/pallidum	20	8	0	4.19	4.07
	Right	Caudate Nucleus	8	2	12	4.17	4.06
	Right	Caudate Nucleus/dorsal striatum	14	−4	20	3.70	3.62
	Left	Caudate Nucleus/ventral striatum	−2	4	2	3.43	3.37
	Left	Putamen	−24	10	2	3.24	3.19
	Left	Caudate Nucleus/dorsal striatum	−4	−2	14	3.20	3.14
	Left	Putamen/pallidum	−18	4	−2	3.06	3.01

From left to right, the table reports the extent (number of $2 \times 2 \times 2$ mm^3 voxels), hemispheric lateralization (left/right), anatomical labeling based on the AAL3 Toolbox (Rolls et al. 2020), and stereotactic coordinates and statistical value for the clusters showing a significant main effect of the “outcome recipient” factor (top) as well as stronger activation when choosing for others compared with oneself (middle) and when choosing for others compared with oneself exclusively in participants who interacted with the other players (bottom).

inhibitory connectivity from the dmPFC to the MCC underpins LA-related activity when choosing either for oneself or for both, compared with choosing for other players, but only after having interacted with them (Table 3 and Fig. 2C and D).

Discussion

We coupled fMRI and a well-established mixed gamble task to address 2 gaps in the current literature on social decision-making under risk. Previous behavioral studies have provided largely controversial evidence on the behavioral effects of choosing on behalf of others (Polman 2012a), and such inconsistencies were not solved by the few neuroimaging studies that, to date, have investigated the neural bases of incorporating the social dimension in one’s own evaluation of risk (Jung et al. 2013; Zhang et al. 2019). We addressed both issues by leveraging the individual differences in the sensitivity to anticipated losses (i.e. LA; Kahneman and Tversky 1979) to investigate the neural bases of social decision in healthy individuals who—during fMRI—chose whether to accept or reject mixed gambles either for themselves, or for other players, or both, after having or not having interacted with them.

Regardless of these experimental manipulations, evaluating gambles to make a decision (compared with passively observing other’s ones) recruited the fronto-striatal, posterior temporal, and right parietal cortexes alongside thalamus and cerebellum. The involvement of these structures fits with the available evidence on their role in decision-making (e.g. Ho et al. 2009; Liu and Pleskac 2011) and in the modulation of evaluation processes by agency (e.g. Crivelli and Balconi 2017; Haggard 2017) and by the processing of perceived responsibility for the consequences of one’s actions (e.g. Frith 2014; Liang et al. 2021). Evaluating prospective choice outcomes indeed entails the processing and integration of distinct parameters (O’Doherty 2014), which in the case of mixed gambles mainly reflect the differential subjective value of anticipated losses and gains, coded by basal ganglia alongside the middle, medial prefrontal, and cingulate cortexes (Padoa-Schioppa and Assad 2006; Gold and Shadlen 2007; Tom et al. 2007; Rushworth et al. 2011; Canessa et al. 2013; Garvert et al. 2015). In particular, distinct medial prefrontal areas are considered to encode the subjective value of choice options (Canessa et al. 2009, 2011; Kahnt et al. 2010, 2011; Philiastides et al. 2010), thus allowing to weigh the prospective gains against their associated losses (Croxson et al. 2009; Hayes et al. 2014). The outcome of such a cost–benefit analysis supports the accumulation of evidence in favor of a specific decision by the parietal cortex (Basten et al. 2010), where the resulting appetitive drives translate into motor representations that are then released via the premotor and supplementary motor cortex (Tosoni et al. 2008).

This preliminary evidence on the neural bases of evaluating mixed gambles provided the ground for assessing their modulation by our 2 experimental factors. On this basis, we investigated the brain regions underlying the effects of choosing either for oneself, other players, or both, after having or not having interacted with them. We first observed that, compared with choosing for oneself, making decisions for other players recruited the right caudate and pallidum but only after having interacted with them. Both structures have been associated with the processing of economic and social rewards (Arsalidou et al. 2020), enhancing the motivational and emotional drives supporting the action-outcome associations and action selection based on the resulting reward expectations (Balleine et al. 2007; Balleine and O'doherty 2010). Extensive evidence indeed shows that the processing of rewards by these subcortical structures is further modulated by a variety of factors pertaining to the realm of social cognition (Bhanji and Delgado 2014). In particular, increased striatal activity has been reported in association with multiple facets of social interaction, e.g. cooperation (Rilling et al. 2002), desire for revenge (De Quervain et al. 2004), social comparisons (Fliessbach et al. 2007; Bault et al. 2011), fair offers at the Ultimatum game (Weiland et al. 2012), moral evaluations of interactive partners (Delgado et al. 2005), and attending the misfortune of previously envied people (i.e. experiencing Schadenfreude; Takahashi et al. 2009) as well as social learning during multiround trust game exchanges (King-Casas et al. 2005; Phan et al. 2010; Wardle et al. 2013; Bellucci et al. 2017; Fairley et al. 2019). Importantly, however, previous studies have also shown differential caudate responsiveness to (i) the processing of one's own and another's reward (Báez-Mendoza et al. 2016) and (ii) relevant others compared with unknown persons (Aron et al. 2005). Both these findings fit the present evidence that the activity of this structure is modulated by knowing that the consequences of one's own choices involve another, yet relevant, individual (Báez-Mendoza and Schultz 2013; Pfeiffer et al. 2014). Moreover, there is evidence of stronger striatal response to rewards resulting from own decisions compared with another's ones (Mobbs et al. 2015). Overall, these data suggest a role for the caudate nucleus in making decisions by anticipating outcomes that will involve one's utility compared with the utility of another known individual.

This pattern of striatal engagement appears to mirror the behavioral evidence of higher LA in participants who have interacted with the other players for decisions involving one's own final payoff, as opposed to those exclusively impacting another's one (Fig. 2A and B). This specific interaction of the "outcome recipient" and "previous interaction" factors is suggestive of greater emotional responsiveness (Wagner et al. 2012; Jung et al. 2013; Mengarelli et al. 2014; Andersson et al. 2016; Barrafrem and Hausfeld 2020; Sun et al. 2021), possibly reflecting greater consideration of negative outcomes (Beisswanger et al. 2003) when one's choice impacts on oneself in the presence of a known person. This pattern seems to rule out an interpretation of results based on social distance, which is known to reduce the emotional connotation of a situation (Sun et al. 2021), and that would therefore suggest higher LA when choosing for others after interacting (compared to noninteracting) with them. No such result was found in our data, which is, however, consistent with previous evidence that the effect of social distance when choosing for another only results from comparing "close" and "distant" friends and not "known" and "unknown" people (Sun et al. 2017), thus ruling out a mere familiarity effect. One possible interpretation of these behavioral data is that social interaction might enhance a competitive attitude mediated by social comparison (Garcia et al. 2013; Bocage-Barthelemy et al. 2018). As previously reported with different experimental paradigms (e.g. Bault et al. 2008), such an effect might be mediated by the higher emotional responsiveness, facilitating impulsive biases such as LA, associated with spontaneous comparisons between one's own and another's payoff (Li et al. 2017; Hu et al. 2021).

To ease the interpretation of these findings, we investigated the brain regions in which the strength of activation reflected the interaction between the "outcome recipient" and "previous interaction" highlighted by behavioral data. A pattern of stronger activity when choosing for oneself (compared with choosing for others), after having (compared with not having) interacted with them, was found in the dmPFC (Fig. 2C), i.e. 1 of the key nodes of social cognitive processing (Arioli et al. 2021). This region has been previously shown to extract social information even from minimal social material (Wagner et al. 2012), which might explain its involvement in performing rapid computations with real consequences in social interaction (Cooper et al. 2012), for instance, by driving altruistic and pro-social behavior (Waytz et al. 2012) or, conversely, by encoding social comparisons (Swencionis and Fiske 2014; Lindner et al. 2015) that support the implementation of advantageous strategies to defeat the competitor (McDonald et al. 2020). In the present study, behavioral data suggest that, despite a minimal level of interaction, participants adjusted their choices to avoid losses more for themselves than for the other players. From a computational standpoint, previous neuroimaging studies highlighted the involvement of the dmPFC in distinct processes that might support this type of behavioral adjustment to the social context, such as computing prediction errors for others' social behavior (Behrens et al. 2008; Hampton et al. 2008), the uncertainty about others' strategy (Yoshida et al. 2010), and the level of strategic reasoning in competitive games (Coricelli and Nagel 2009). In the present study, dmPFC activity might play a role in detecting the competitive facet of social context, and accordingly, in implementing behavioral adjustments aimed to maintain a desirable level of social comparison (see Bault et al. 2011). This interpretation fits with other neuroimaging findings highlighting a preferential mPFC activation for competitive (Le Bouc and Pessiglione 2013) and negatively valenced (Decety et al. 2004; Arioli et al. 2021) social interaction and in processing cues of social competition such as the discrepancy between self and others' preferences (Tamir and Mitchell 2010) and deceptive intentions toward oneself (Grezes et al. 2004). Importantly, these hypotheses on the dmPFC role in processing and guiding social interaction are also supported by studies based noninvasive brain stimulation, that—under specific conditions (Bergmann and Hartwigsen 2021)—can be considered to enable causal brain–behavior inferences. First, increasing evidence suggests that the dmPFC is involved in separating self-representation and other representations (Wittmann et al. 2021). Estimating one's own and others' abilities as separate is essential for improving one's sense of self (Toma et al. 2010). In this respect, neurostimulation studies provided causal evidence that the dmPFC is involved in tasks requiring an explicit distinction between self and other and in higher-order social cognitive task involving the integration of information pertaining to others (Martin et al. 2017; Lockwood et al. 2018). In particular, inhibiting dmPFC activity elicited more positive and slower judgments about other individuals (Ferrari et al. 2016, 2016), which supports its role in social perception (Iacoboni et al. 2004; Sliwa and Freiwald 2017; Arioli, Perani, et al. 2018) and inferring mental states (Moessnang et al. 2017; Arioli et al. 2021) and in modulating the actual outcomes of social interaction (Powers et al. 2016).

The possible role of dmPFC in mediating the influence of social comparison on decision-making was further supported by PPI analyses, showing that the interaction pattern highlighted by behavioral data reflected in a stronger inhibitory connectivity from this region to the MCC. Again, the strength of this connection reflected the higher LA associated with making decisions for oneself (compared with choosing for others) after having (compared with not having) interacted with them (Fig. 2D). The MCC is one of the main nodes of a network associated with empathic processing

Table 3. Neural bases of LA modulation by choice recipient and previous interaction.

Cluster size	Hem	Anatomical region	x	y	z	*T* score	*Z* score
A. Brain activity							
582		Medial superior frontal gyrus/SMA	0	16	58	4.29	4.16
	Left	Precentral gyrus	−32	−2	56	4.27	4.14
	Left	Superior frontal gyrus	−14	10	54	3.76	3.67
B. Brain functional connectivity							
193		Middle cingulate cortex	0	−4	24	4.77	4.61

From left to right, the table reports the extent (number of 2 × 2 × 2 mm^3 voxels), hemispheric lateralization (left/right), anatomical labeling based on the AAL3 Toolbox (Rolls et al. 2020), and stereotactic coordinates and statistical value for the clusters in which changes of LA-related brain activity (top) and connectivity (bottom) reflected the interacting effect of outcome recipient and previous interaction with the other player. SMA, supplementary motor area.

(Fan et al. 2011; Lamm et al. 2011) and compassion (Singer and Klimecki 2014) as well as motivational processes facilitating the so-called "empathic concern" (i.e. care for others in need) (Bellucci et al. 2020), in turn driving prosocial behavior (Lamm et al. 2019). Inhibiting its activity might therefore facilitate choices aimed to pursue "social" gains via a self-centered approach grounded in hyperthinking about oneself and/or reduced sharing of other's affective states, possibly to decrease the effect of anticipated guilt on decision-making (e.g. Zhu et al. 2019). Such an interpretation of the functional meaning of the dmPFC–MCC connectivity is supported by distinct findings. First, its strength has been reported to reflect the degree of trait positive empathy (Yue et al. 2021), as indexed by the Positive Empathy Scale (Morelli et al. 2015). Moreover, experiencing positive social emotions has been associated with "increased" top-down connectivity from the dmPFC to the amygdala via the cingulate cortex (Scharnowski et al. 2020). These data support the notion that inhibiting the MCC activity might mediate the influence of social comparison on decision-making through a decreased sharing of others' outcome-related affective states, thus releasing the "cautionary brake on behavior" inherent in LA (De Martino et al. 2010) when choosing for known others.

Importantly, this interpretation of our findings requires further supporting evidence. Although consistent with available knowledge of the role of dmPFC and MCC in social cognitive processing (Bellucci et al. 2020; Kogler et al. 2020; Berkay and Jenkins 2022), this interpretation is indeed limited by the lack of procedures that are capable of detecting the perception of social comparison with the other players and therefore requires further inquiry. Moreover, alternative interpretations should be considered, such as in-group and out-group biases (e.g. Saarinen et al. 2021) which are elicited by interacting and not interacting with the partners, respectively. The fact that this manipulation did not reflect in a different assessment of the other players seems, however, to rule out a possible modulation of choice behavior by personal attitudes. Behavioral findings might also be shaped by an enhanced "social facilitation" or "audience effect," i.e. behavioral changes caused by the mere presence of another individual (Zajonc and Sales 1966), or by the awareness of being observed by someone else (Triplett 1898), respectively, in participants engaged in a real interaction with the other players. Overall, the present data therefore suggest that further evidence is required to unveil the modulators of social decision-making for known versus unknown others. For instance, future studies might test whether the higher empathic concern elicited by choosing for a close other (e.g. Meyer et al. 2013) reflects in an enhanced inhibitory connectivity from the dmPFC to MCC.

Beyond their relevance for a lively sector of social cognitive neuroscience, the present findings might help in characterizing the socio-cognitive and behavioral disorders in several neurological and/or psychiatric populations that have been already associated with the alterations of social decision-making, such as Alzheimer's (Roheger et al. 2022) and fronto-temporal (Wong et al. 2017; Lichtenstein et al. 2022) dementia, Tourette syndrome (Albin 2018), Huntington's Disease (Mason et al. 2021), chronic pain (Timm et al. 2021), Parkinson's disease (Caballero et al. 2022), or depression (Zhang et al. 2012; Wang et al. 2014; see Lockwood and Wittmann 2018; Baez-Mendoza et al. 2021). Evaluating and treating social cognitive impairments is a relatively novel challenge in rehabilitative medicine, which might benefit from theoretical and methodological inputs from the "baseline" evidence collected in healthy individuals (Henry et al. 2016; Arioli, Crespi, et al. 2018; Arioli and Canessa 2019). Supporting the potential translational value of neuroeconomics findings (e.g. Sharp et al. 2012), the present results might thus represent a reference to evaluate the neural correlates of social cognitive deficits and the effects of evidence-based rehabilitative interventions.

Future studies might also address the relationship between socio-economic decisions and personality features, and particularly, the potential modulation by psychopathic and narcissistic traits on making decision with social consequences (Coleman et al. 2022; Gunschera et al. 2022) and social relationships (Scalabrini et al. 2017; Wright et al. 2017).

Limitations

There are some limitations to the present study. First, there are inherent differences between the 2 macroconditions "I decide" versus "Other decides" since the gamble outcome is not shown in the former condition to prevent "learning" effects possibly shaping participants' choices (e.g. Tom et al. 2007; Charpentier et al. 2016). Moreover, although a motor response was required in both macroconditions, it occurred at different times, and such response followed an evaluative process only when participants were choosing for themselves. Importantly, however, this study was mainly aimed at assessing the effect of choosing for different outcome recipients rather than the effect of choosing versus observing another's choices. Finally, the lack of in-depth metrics on the socio-affective bond established between players does not allow robust interpretations of the present behavioral data.

Conclusion

The present results provide novel insights into a debated literature on the effect of choosing on behalf of others, which reported mixed findings concerning the modulation of decision-making parameters by factors such as the outcome recipient or the familiarity with the individual for whom one is choosing (Polman 2012a). In keeping with studies reporting negative findings, neither factors were associated with a significant main effect on LA, which was instead modulated, both at the behavioral and neural levels, by their interaction. Possibly as a result of social comparisons elicited by interacting with the companion players, participants indeed displayed decreased LA—suggestive of a more cautionary behavior (De Martino et al. 2010)—for choices involving their profit compared with those affecting others' payoff (Zhang et al. 2019).

This "social" modulation of decision-making involved a circuitry centered on the dmPFC, possibly supporting the detection of social comparisons (Bault et al. 2011; Wen et al. 2017, 2019), thereby enhancing processes of self-other distinction (Wittmann et al. 2021) and social competition (Le Bouc and Pessiglione 2013; McDonald et al. 2020), which might in turn require the inhibition of empathic and prosocial responses (Bellucci et al. 2020; Yue et al. 2021) via the downregulation of the MCC node of the empathy network (Fan et al. 2011; Lamm et al. 2011). The lack of experimental procedures designed to detect the presence of social comparisons highlights, however, the need of further evidence supporting, or refining, this hypothesis. Still, the present findings provide a baseline reference for future studies investigating the social modulation of decision-making (e.g. Meier and Johnson 2022) even in microsocieties arising from minimal interaction.

Authors' contributions

Maria Arioli (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Writing—original draft), Gianpaolo Basso (Investigation, Methodology, Resources, Writing—review & editing), Gabriel Baud-Bovy (Formal analysis, Methodology, Software, Writing—review & editing), Lorenzo Mattioni (Investigation, Writing—review & editing), Paolo Poggi (Investigation, Resources), and Nicola Canessa (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Supervision, Writing—original draft).

Data availability

The datasets generated during the current study are available from the corresponding author on reasonable request.

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