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Neurocircuits underlying cognition–emotion interaction in a social decision making context☆

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ABSTRACT

Decision making (DM) in the context of others often entails complex cognition–emotion interaction. While the literature suggests that the ventromedial prefrontal cortex (vmPFC), striatum, and amygdala are involved in valuation-based DM and hippocampus in context processing, how these neural mechanisms subserve the integration of cognitive and emotional values in a social context remains unclear. In this study we addressed this gap by systematically manipulating cognition–emotion interaction in a social DM context, when the participants played a card game with a hypothetical opponent in a behavioral study (n = 73) and a functional magnetic-resonance-imaging study (n = 16). We observed that payoff-based behavioral choices were influenced by emotional values carried by face pictures and identified neurocircuits involved in cognitive valuation, emotional valuation, and concurrent cognition-emotion value integration. Specifically, while the vmPFC, amygdala, and ventral striatum were all involved in both cognitive and emotional domains of valuation, these regions played dissociable roles in social DM. The payoff-dependent responses in vmPFC and amygdala, but not ventral striatum, were moderated by the social context. Furthermore, the vmPFC, but not amygdala, not only encoded the opponent's gains as if self's losses, but also represented a "final common currency" during valuation-based decisions. The extent to which emotional input influenced choices was associated with the functional connectivity between the value-signaling amygdala and value integrating vmPFC, and also with the functional connectivity between the context-setting hippocampus and value-signaling amygdala and ventral striatum. These results identify brain pathways through which emotion shapes subjective values in a social DM context.

Introduction

Decision making (DM) is context-dependent (Kahneman and Thaler, 2006). The presence of other agents creates a social context that may be particularly important in human decision making and illustrates contextual effects. An agent may actually choose a less preferred option for the self in the presence of a partner (Kelley, 1979) and the presence of another can lead to emotional shaping of cognitive processes (Niedenthal et al., 2009), even in the absence of another person's actions. These findings suggest that the presence of another person may influence how the decision maker evaluates options at hand and such influence is likely to be experienced in emotional rather than cognitive terms. For example, when domestic partners co-decide whether to buy a car or to renovate the kitchen, they evaluate the outcomes not only cognitively (costs and benefits), but also emotionally, e.g., how "my partner and I will feel". Here, especially when seeing the other person's face in a social context, emotions can arise and consequently influence or even reverse one's original self-regarded preference.

Indeed, emotional face pictures can assign positive or negative incentive value to an object (Winkielman et al., 2005) and elicit approach or avoidance behaviors (Chen and Bargh, 1999). In a social context, seeing a happy face when experiencing an unfavorable outcome or seeing an angry face when experiencing a favorable outcome may more or less reverse one's evaluation of the outcome. Note that the emotional values carried by faces are very different from emotions that have been postulated to affect DM in the literature. While the former can be arbitrarily juxtaposed with cognitive payoff congruently or incongruently in general, the latter were derived from, and therefore intrinsically dependent on, certain preexisting payoff-related knowledge, such as guilt derived from returning less-than-expected money to an original investor (Battigalli and Dufwenberg, 2009; Chang et al., 2011), fear derived from a large monetary loss (Damasio, 1994), anxiety derived from uncertainty (Loewenstein et al., 2001), and regret derived from counterfactual thinking about gains or losses (Coricelli et al., 2005). Thus, the roles of face-based emotional values in a social DM context are virtually unknown.

In this study, we aimed to provide behavioral and neurobiological evidence to corroborate our working hypothesis that facial expressions,

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which signal another person's emotions, should carry "values" that can be integrated as part of a final common currency that determines actual decisions. Accordingly, it is inferred that a) behaviorally, incongruent emotional values should compromise preference based on cognitive values in a social context, b) neurobiologically, cognitive and emotional values are independently encoded in neurocircuits underlying valuation, described below, and c) the integration of cognitive and emotional values in these valuation-dependent neurocircuits is associated with the extent to which emotional values influence actual choice behaviors. To test these predictions, we conducted a behavioral study (Study 1) and a functional magnetic resonance imaging (fMRI) study (Study 2). In both studies, we utilized a novel paradigm that encompassed the key elements necessary for testing the working hypothesis, i.e., social context, independent domains of cognitive and emotional values, and valuation-based DM.

In this paradigm, a social context was created by having participants play a card game with a hypothetical partner. The participants first learned the relative values of four decks of cards that were differentially paired with probabilistic cognitive values (positive or negative points) and emotional values (happy or angry face pictures) in a value encoding stage (Learning Task). The purpose of the Learning Task was to allow the participants to observe all possible outcomes that each deck of cards can bring to the two players ("Self" and "Other"). During the Learning Task, we manipulated the relationship between the encoded cognitive and emotional values: In a neutral control condition (NEU), all decks of cards were paired with neutral faces and therefore possessing cognitive values only; in two experimental conditions, the decks of cards were paired with angry or happy faces that are either congruent (CON) or incongruent (INC) with the expected values of cognitive payoff.

Subsequently, in a DM task that involved value retrieval the participants made decisions about the same decks of cards without immediate feedback. The purpose of the DM Task was to examine the impact of congruent and incongruent emotional information provided in the preceding Learning Task on cognitive payoff-based choices in pair-wise decisions involving both "Self" and "Other" (Joint-Comparison) and single-deck decisions involving separate evaluations of each option (Separate-Evaluation). Notably, though the hypothetical player did not actively perform any actions, the participants constantly engaged the social context of "Self" and "Other" for the following reason: By design all the decks were equal in terms of total payoff pooling across the two players, but they differed in their differential player-dependent outcomes, i.e., each deck is either probabilistically favorable to "Self" *and* therefore unfavorable to "Other" or *vice versa*. Thus, without paying attention to the social context, which served as the only discriminative cue, the participants would not learn the player-dependent knowledge of which deck can probabilistically increase or decrease which player's payoff and therefore should fail to consistently make optimal payoff-based decisions to maximize their own payoff.

Specifically, we have the following predictions. Behaviorally (Study 1), we predicted that both congruent and incongruent conditions would cause interference during the conjunction of independent cognitive and emotional domains as compared to the neutral condition (the *conjunction cost effect*, CON and INC < NEU) (Gray et al., 2005). However, compared to the congruent condition, valuation signals should be compromised and decision making hindered in the incongruent condition (the *congruency effect*, CON > INC).

In Study 2, we examined underlying neural mechanisms in an fMRI environment. In light of the literature implicating cortical and limbic valuation-dependent neurocircuits that encompass the ventromedial prefrontal cortex (vmPFC), dorsal and ventral striatum (Chang et al., 2011; Fehr and Camerer, 2007; Kable and Glimcher, 2007; Lee, 2008; Montague and Berns, 2002; Rangel et al., 2008; Rushworth et al., 2011), we predicted that the cognitive and emotional values would be encoded independently in the vmPFC and striatum, which can integrate concurrent multi-domain values on a "common currency" (Hare et al., 2009, 2010; Izuma et al., 2008; Kable and Glimcher, 2009; Levy et al., 2011). The amygdala should also be involved in cognitive and emotional value integration as well, since the amygdala is a key substrate of social emotions (Adolphs, 2010) that represents external and internal state salience across physiological, emotional, and cognitive domains (Morrison and Salzman, 2010) and valuation-based DM (Jenison et al., 2011; Levy et al., 2011). Moreover, the social context should engage the hippocampus for context-setting (Schmajuk and Buhusi, 1997) that may enable multi-domain information processing necessary for social DM (Shohamy and Wagner, 2008).

Experimental procedure

The procedures for both studies were similar and they will be described jointly, highlighting key differences where appropriate.

Participants

Seventy three college students (41 males, mean age = 19.23, range: 18–25 years old) participated in Study 1, as part of a course requirement. The participants were randomly assigned to three conditions that varied in the relationship between cognitive and emotion domains: Congruent (n = 23), Incongruent (n = 27), and Neutral Control (n = 23). Sixteen new right-handed healthy participants (eight males, eight females; age range 18–27 years, mean age 20.9 years) without current or prior history of head injury, psychiatric illness or substance abuse/dependence participated in Study 2 (fMRI). All 16 participants underwent Incongruent and Neutral Control (baseline) conditions on two different days, ~7 days apart, in a randomized cross-over design. All participants received verbal and written explanation of the study and provided IRB approved, written, informed consent. Subjects received credit (Study 1) or compensation (Study 2) for their participation, without linkage to task performance.

Experimental design

Overview

In both Study 1 and 2, participants played a card game with four decks of cards and were instructed that "there is a hypothetical opponent (Other) in this game and you should learn the payoffs (points) of the cards and pay attention to which decks favor you and which decks favor your opponent in the Learning Task. Then, you should try to maximize your own points in the Decision Making Task. In the Decision Task, when you see two decks of card, you will pick one deck for yourself and automatically the other deck will be assigned to the opponent; when you see one deck and a "no" button, you will decide to pick this deck or reject it to keep the status quo. Only during the Learning Task the point outcomes and face pictures were presented trial by trial such that the participants can associate the cognitive and emotional values with the decks by associative learning. During the DM Task, no more point outcomes or face pictures were presented such that the decisions were made completely based on the participants' subjective valuation. In Study 2 only, a control task (Face Task) was added to independently measure neural responses associated with face pictures.

The values and probabilities of the decks of cards were programmed based on the following rules applied throughout the experiment. Unbeknown to the participants, there were the same number of positive cards and negative cards in each of the four decks, but they were rigged so that each deck distributed payoffs unevenly between the participant (Self) and the opponent (Other), with varying probabilities, such that each deck's conditional expected values to Self (EV_{Self}) plus its conditional expected values to Other (EV_{Other}) was equal to zero. Two of the decks were highly or moderately favorable to the participant (Self-Favorable Decks, i.e., $EV_{Self} > 0$ and $EV_{Other} < 0$) and two other decks were highly or moderately favorable to the counterpart (Other-Favorable Decks, i.e., $EV_{Other} > 0$ and $EV_{Self} < 0$).

This design ensured that the decks all appeared equally appealing if ignoring which player received the outcome, and therefore the Self/Other social context served as the only discriminative cue to discriminate the differences between the decks. For example, keeping the recipient in mind allowed the participant to discern that when a deck usually yielded a gain to the other player, it usually caused a loss to Self (and therefore it would be an Other-Favorable deck) and *vice versa*.

Note that while the social context (Self or Other) serves as the critical discriminative factor in determining the player-dependent values of card decks, the participants' choices did not depend on another person's actions. Thus, the meaning of "social DM" in this study is very different from that in multi-agent games wherein one agent's actions and outcomes are dependent on another agent's, such as Trust Game (Chang et al., 2011; Delgado et al., 2005) and Ultimatum Game (Fehr and Schmidt, 1999; Henrich et al., 2006; Yamagishi et al., 2009). Nevertheless, by design, our paradigm retained the key elements, i.e., social context and independent cognitive and emotional values, that are necessary for testing the working hypothesis without introducing other social DM processes, e.g., mentalizing other's goals and emotions such as guilt or regret, that are irrelevant to this goal.

Learning Task

In the Learning Task (Fig. 1a), participants observed all possible payoff (in points) that each deck of cards can bring to the two players to learn the respective player-dependent expected values. In each trial, two (from the set of four) decks of cards, face down, were presented on the screen. Participants were asked to choose a card from one deck for him/herself (Self), leaving the card from the other deck for the partner (Other) and instructed to learn the resulting outcomes with respect to Self and Other.

The Learning Task had two blocks, with 30 trials per block and an ITI jittered between 4 and 6 s. Two decks were presented simultaneously on each trial for up to 4 s, until the participant chose one for Self and one for Other (choice period). The border of the chosen Self card was highlighted thereafter throughout the trials. Cues "To You" or "To Other" were then presented for 0.5 s (social context cue period), followed by the payoffs to the corresponding recipients, sequentially presented for 3 s each (outcome period). The order of the "Self" and "Other" outcome presentation was pseudo-randomized to reduce the temporal collinearity between them. During the 3 s outcome period, a face picture (further specified below) was presented briefly

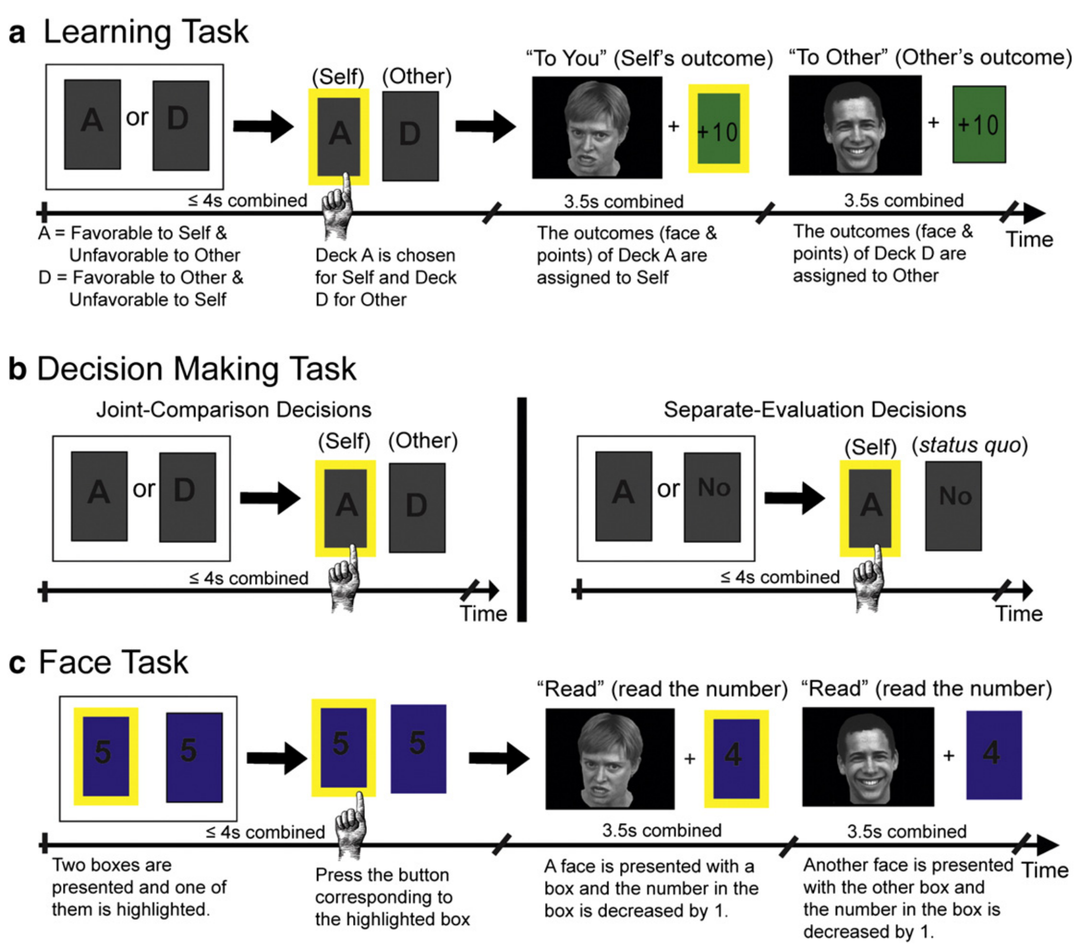

Fig. 1. The task designs: a) Learning Task: In each trial, two decks (e.g., decks "A" and "D") were presented for up to 4 s until the participant chose one for him or herself (Learning choice period, which is not analyzed) and subsequently viewed the recipient (social context) cues ("To Self" or "To Other", 0.5 s) and then the deck's probabilistic outcomes ("+10" or "−10" points) applied to the participant "Self" (3 s) and the other deck's probabilistic outcomes applied to the hypothetical partner "Other" (3 s), in a pseudorandom order. During the outcome presentation, angry, happy, or neutral face pictures were presented briefly (16 or 32 ms). The relationship between the deck's overall cognitive values (probabilistically self-favorable or other-favorable) and their emotional values (faces) were manipulated as congruent, incongruent, or neutral. b) Decision Making Task: The participants made two types of decisions, Joint-Comparison and Separate-Evaluation decisions. Each trial was self-paced (up to maximum duration of 4 s). For the Joint-Comparison decisions, two decks were presented and the participant chose one deck for "Self" and the other for "Other" to receive the decks' probabilistic outcomes, respectively. For the Separate-Evaluation decisions, one deck and a "No" box were presented and the participant chose the deck to receive its probabilistic outcome or the "No" to keep status quo. There were no immediate feedback in this task. c) Face Task: This task served as an independent probe of neural bases of emotional value encoding in a context similar to that of the Learning Task (fMRI experiment only). In each trial, two boxes were presented and one of them had the borders highlighted for up to 4 s (control choice period, which is not analyzed). The participants pressed a button corresponding to the highlighted box and then, after a brief control cue "read" (0.5 s), the boxes had a number presented in the center with the angry, happy, or neutral face pictures co-presented for (3 s) in a pseudorandom order similar to that in the Learning Task.

(16 ms) twice, in the beginning and middle of the period. Face pictures were not masked and therefore barely visible with a16 ms duration. Participants were instructed to ignore these flashing pictures and attend to the outcomes. A similar protocol has been shown to make objects associated with happy faces more desirable than those associated with angry faces (Winkielman et al., 2005).

Cognitive value specification. By design, the participant experienced the player-dependent probabilistic outcomes with the rule of expected values for Self and Other $EV_{Self} + EV_{Other} = 0$ in each deck. For Study 1, the four decks rendered +10 points to the participant with probabilities of 1, 0.67, 0.33, and 0 (and −10 points otherwise) and rendered −10 points to the partner with probabilities of 1, 0.67, 0.33, and 0 (and +10 points otherwise), resulting in the expected values $EV_{Self} = (10, 3.33, -3.33, -10)$ and $EV_{Other} = (-10, -3.33, 3.33, 10)$, respectively. For Study 2, the four decks rendered +10 points to the participant with probabilities of 0.8, 0.6, 0.4, and 0.2 (and −10 points otherwise) and rendered −10 points to the partner with probabilities of 0.8, 0.6, 0.4, and 0.2 (and +10 points otherwise), resulting in $EV_{Self} = (6, 2, -2, -6)$ and $EV_{Other} = (-6, -2, 2, 6)$, respectively. The probability increments were slightly reduced in Study 2 (from 0.33 to 0.2) in an attempt to maintain task difficulty across two sessions in the within-subject design. As rank-ordered by conditional expected value to Self (EV_{Self}), deck #1 was highly favorable to the participant, #2 was moderately favorable to the participant, #3 was moderately favorable to the partner, and #4 was highly favorable to the partner. The #1 and #2 decks were referred to as self-favorable decks, and #3 and #4 as other-favorable decks.

Emotional value specification. In addition to the point outcome information (which we interpret as cognitive), an emotion domain was added by pairing each deck with emotional face pictures carrying a particular valence (angry, happy, or neutral). When the paired facial expressions were emotionally positive (happy) or negative (angry), it became a multi-domain game that added emotional loading to the cognitive values by linking each deck to a positive or negative incentive value (Winkielman et al., 2005) that should increase the tendency of choosing or not choosing the deck (Chen and Bargh, 1999).

Manipulation of cognition–emotion interaction. We manipulated the relationship between the point outcomes and facial expressions during the Learning Task, which allowed us to examine how final common currency were formed based on the cognitive and emotional values associated with the decks during the DM Task. In the congruent condition (CON), self-favorable decks were paired with happy faces and other-favorable decks were paired with angry faces; in the incongruent condition (INC), the pairing rule was reversed; in a neutral control condition (NEU), all the decks were paired with neutral faces and it was reduced to just a cognitive-domain game about point information.

Sampling constraints. A use limit, indicated by a counter under each deck, was imposed during this Learning Task to ensure the participants comprehensively observed all possible player-dependent outcomes of each deck, with exactly one half of cards in each deck were dealt to each player. Constrained by the use limit, the choices made during the Learning Task were independent of the participants' preference, because when the use limit was met (i.e., the counter = 0) for one deck, the participants were forced to pick the other deck on the screen. Thus, the data related to these choices were not reflecting subjective valuation and therefore not analyzed.

Decision Making Task

In a two-block Decision Making (DM) Task (Fig. 1b), we examined the subjective valuation of the decks as a result of the Learning Task. Participants made two types of decisions—Joint-Comparison and Separate-Evaluation (see below)—presented in a pseudo-random order (ITI = 2 s), with 4 s allowed for responses. To prevent changes in valuation during the DM Task, all decisions were made without immediate feedback of cognitive and emotional outcomes, and the total points earned by both players were not displayed until the end of experiment. In the *Joint-Comparison Decisions*, two decks were again presented together, face down; participants were asked to choose one for Self and by doing so they assigned the remaining deck to Other, paralleling the social context of the Learning Task. There were 24 trials for each of six possible pairwise combination.

In the *Separate-Evaluation Decisions* only one deck was presented and participants could either accept the potential outcome of this deck for the Self or reject it by pressing a "No" button to keep the status quo. These decisions were used to probe subjective valuation of individual decks, assuming that accepted decks possessed higher subjective value than rejected ones. There were 24 trials for each deck.

Face Task (Study 2 only)

This task (Fig. 1c) was added to examine neural responses associated with the social emotional values of the faces and to control for the visual and motor activity during the Learning Task. It had 2 blocks with 12 trials per block. A trial started with a 2 s fixation, followed by display of two boxes with numerical labels. One box had its border highlighted and the participant was instructed to choose the highlighted box as quickly as possible. Then a word "Read" was presented as a control non-social cue period, which was followed by a control outcome period. In each control outcome period, one box was presented with its numerical label counting down and face pictures were presented in the beginning and middle of the period. The cues, faces, and numbers in the Face Task were presented for the same durations as their counterparts in the Learning Task.

Materials

Studies were conducted with E-Prime (Psychological Software Tools, Inc., Pittsburgh, PA) on Windows XP computers. For the behavioral experiment, four decks of cards (1.5″ by 2″ in each) labeled on one side as A, B, C, and D were positioned from left to right. For the fMRI experiment, the decks were labeled as A, B, C, and D in one session and O, P, Q, and R in the other, order counter-balanced. Positive and negative outcome points were presented on the flip side of cards on green and red backgrounds, respectively. Pictures of happy, angry, or neutral facial expressions (8 individuals each) were adopted from Gur's battery (Gur et al., 2002) and displayed on the monitor at 700 × 525 pixels. Each picture used in the task was briefly displayed 12 times. Pictures used in the Learning Task differed from those used in the Face Task in the fMRI experiment, though all of them were matched for gender, age, race, and arousal level based on an independent sample of participants (Britton et al., 2006).

Behavioral data analyses

We hypothesized that a) the addition of the emotion domain to the cognitive domain (with CON and INC conditions combined), when compared to the cognitive domain only (neutral faces) condition, would tax more mental resources to properly juxtapose values across domains (conjunction cost) (Gray et al., 2005) and b) the total valuation integrated across cognitive and emotion domains would reveal a congruency effect, i.e., overall values of options would be greater in the CON than INC condition (Winkielman et al., 2005). We tested these hypotheses on two dependent variables, payoff-based decision rate and reaction time (RT), measured in the DM Task.

Payoff-based decision rate

Decision performance was indexed using payoff-based decision rates, where a payoff-based decision, which is optimal in terms of maximizing points, is defined as the choice leading to higher (in points) expected value for the Self. Joint-Comparison decisions were expected to be shaped by not only the cognitive values, but also the congruent or incongruent emotional loading imparted to each deck by its paired emotional face valence (angry or happy). To examine the effects of differential emotional values, only trials with one self-favorable deck and one other-favorable deck (i.e., #1 and #4, #1 and #3, #2 and #4, or #2 and #3) were included in the analyses of emotional manipulation, because only these trials entailed a happy vs. angry contrast to signal differential emotional values in the CON and INC conditions. Thus, a payoff-based decision in a Joint-Comparison decision was to choose the self-favorable deck and avoid choosing the other-favorable deck. However, trials that had two self-favorable decks or two other-favorable decks would also reflect emotional responses induced by a specific expression (either happy-happy or angry-angry pairs) in the CON and INC conditions. These trials were analyzed separately to study differential effects of emotional faces and results are reported in the supplement. For the Separate-Evaluation decisions, we computed an acceptance rate as the percentage of trials in which a deck was accepted, and converted this to a payoff-based decision rate by defining a payoff-based Separate-Evaluation decision as acceptance of a self-favorable deck or rejection of an other-favorable deck.

Reaction time

RT was measured as the median interval between the trial onset and the button press during the decision making phase.

Emotional influence index

To quantify the extent to which emotional values affected DM within each participant in Study 2, we defined an emotional influence index as the difference between the payoff-based decision rates in the INC vs. NEU conditions. The more INC faces reduced payoff-based decisions relative to NEU faces, the more negative this emotional influence index became.

Data quality control

To ensure data quality, in Study 1 we used fixed criteria applied to all participants based on responses in the most obvious decisions: only participants who had greater than 25% payoff-based decision rates in the #1 vs. #4 Joint-Comparison decisions and greater than 12.5% payoff-based decision rates in the Separate-Evaluation decisions on the #1 and #4 decks were retained in data analyses. We did not use chance level decision making (50%) as cutoff for either type of decision, because, by design, we expected that incongruent emotional values would reduce payoff-based decisions to below chance levels. The cutoff was used to screen out outliers and was based on a prior pilot study, where we found more participants failed to meet this low cutoff if the tasks were conducted in sessions with a large group and diminished experimenter monitoring (10 participants or more), as compared to the results obtained in sessions with 1–2 participants. The chosen cutoffs eliminated two participants in the INC and three in the NEU condition in Study 1. No subjects were eliminated in Study 2 due to cutoff exclusions, but two (1 male and 1 female) were excluded from data analyses due to missing data.

Statistical analysis

Data were analyzed using SPSS 17.0 (Chicago, IL, U.S.A) with a mixed-effect general linear model, using the pairing condition as a between-subject factor and deck-pairs or decks as within-subject factors when applicable, and the payoff-based decision rate and RT as dependent variables. For Study 1, we used two mutually orthogonal contrasts to test the conjunction cost effect (CON = 1, INC = 1, NEU = −2) and the congruency effect (CON = 1, INC = −1, NEU = 0). For Study 2, INC and NEU were tested, one-tailed, as a within-subject factor.

MRI data acquisition

MRI scanning occurred on a 3-Tesla General Electric signa scanner (Milwaukee, WI). Structural standard T1 images (T1-overlay) for anatomic normalization and alignment, whole brain functional T2*-weighted image volumes, with reverse spiral formation sequence, (repetition time (TR) = 2000 ms; echo time (TE) = 30 ms; flip angle = 90°; field of view (FOV) = 22 cm; 40 slice; thickness/skip = 3.0/0 mm, matrix size = 64 × 64) were acquired and first four volumes in each run before thermal equilibrium of the MRI signal were discarded. This T2*-sensitive formation sequence was specifically designed to recover signal loss in ventral medial frontal regions, in which susceptibility artifact often impairs the T2* signal (Yang et al., 2002). After formation of functional volumes, a high-resolution T1 three-dimensional spoiled gradient-recalled formation in a steady state (SPGR) image (FOV = 24 cm; thickness/skip = 1.0/0 mm) was scanned for anatomic normalization.

The functional blood-oxygenated-level-dependent (BOLD) images were slice-time corrected using sinc interpolation of the eight nearest neighbors in the time series and realigned to the tenth image in the time series using McFlirt of FSL (Jenkinson et al., 2002). Additional preprocessing and image analysis of the BOLD signal were performed using the in-house batch mode of Statistical Parametric Mapping (SPM2) (Wellcome Institute of Cognitive Neurology, London, UK; www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB 7.0 (The Mathworks Inc. Natick, MA). The functional images and the high-resolution SPGR T1 image were co-registered with a T1 overlay structure image. This T1 overlay image was then spatially normalized to the scalped T1 brain template provided by SPM2. The co-registered functional volumes and the SPGR T1 image were normalized using the same transformation matrix before they were resliced and spatially smoothed by an isotropic 7 mm full-width-half-maximum (FWHM) Gaussian kernel to minimize noise and residual differences in gyral anatomy. High pass filter (128 s) was applied on the image time series to eliminate low frequency signals (Ashburner et al., 1997; Friston et al., 1995).

MRI data analysis

The pre-processed MRI data were analyzed using the general linear model (GLM) framework in SPM2 and MATLAB 7.0 (The Mathworks Inc. Natick, MA). The onsets and durations of events during the tasks were convolved with a canonical hemodynamic response function (HRF) to create the event regressors, in addition to covariates of six image realignment parameters to reduce movement induced artifacts. In the first-level analysis for each participant, the parameter estimates of event regressors were computed at each voxel. Appropriate linear contrasts, as described below, were applied to the parameter estimates to produce contrast images and statistical parametric maps (SPM t map). The contrast images of interest in these first-level models were used as subject-specific dependent variables in the corresponding second-level random-effect models (Friston et al., 2005). The results in these second-level models were corrected for multiple comparison using false-discovery rate (FDR) at $p = 0.05$ (Genovese et al., 2002) across the whole brain. The amygdala and NAc were delineated based on the anatomy as a priori regions-of interests (ROIs) for additional small volume corrections (s.v.c.), if required. The regressors and contrasts used in the first-level GLMs are described below.

Learning Task

To examine the effects of learning choice outcomes, we adopted a GLM in which the regressors of interest included four event regressors for the outcome periods in a two-by-two factorial design in terms of the valence of value and the receiving agent (Positive to Self, Negative to Self, Positive to Other, Negative to Other). Additionally, a regressor of no interest to model the choice periods across all trials was included in the model. The effects of cognitive outcome encoding were examined using the Positive to Self vs. Negative to Self contrast. The effects of face pictures were controlled by two face-related parametric regressors (Happy = 1, Angry = −1, Neutral = 0) and (Happy = 1, Angry = 1, Neutral = −2) for each event regressors described above.

We used a different model to separate the effects of social context setting and cognitive and emotional outcomes during the Learning

Task. While the social context cues ("To Self"/"To Other") and the outcomes (positive/negative) were presented successively with a fixed interval, it is still possible to separate these two events in this model. Based on the literature (Ollinger et al., 2001), for two successive components in a compound trial (A + B) that have a fixed interval between them, their BOLD responses can be uniquely estimated if at least one of them is also presented in a partial trial (A only or B only). In principle, this approach can be extended to a factorial design where each component is presented in multiple kinds of compound trials. In this case, the Learning Task used a 2-by-2 factorial design where four possible combinations of cues ("Self" or "Other") and outcomes (positive or negative values) were presented pseudo-randomly, i.e., Self-Positive, Self-Negative, Other-Positive, and Other-Negative. We can separate the neural responses associated with cues and outcomes without variable intervals between them because for any particular type of cue-outcome compound, say Self-Positive, the same cue (Self) was also presented with a different outcome, i.e., Self-Negative. Similarly, the relevant outcome (Positive) was also presented with a different cue, i.e., Other-Positive. In this first-level model, the Learning Task and Face Task were modeled as separate sessions (two per task). For the Learning Task sessions, we used four different regressors to model the cue periods based on the four types of cue-outcome compounds: 1) cues in the Self-Positive, 2) cues in the Self-Negative, 3) cues in the Other-Positive, and 4) cues in the Other-Negative compounds, and additionally one regressor each for 5) all the outcome periods and for 6) all the choice periods (six regressors total). Likewise, for the Face Task sessions, we used three regressors for 1) cues preceding Happy, 2) cues preceding Angry, and 3) cues preceding Neutral Faces and additionally one regressor each for 4) all the control outcome and 5) all the control choice periods (five regressors total). Notably, we pooled the trials across all cue-outcome compounds in the outcome regressor but maintain the cues separation based on the compound types. Thus, each cue regressor contained only a proportion of trails (e.g., ¼ in the Learning Task) modeled in the outcome regressor and the model was uniquely specified in SPM. We then tested specifically the contrast of social cues ("To You"/"To Other" during the Learning Task) vs. the non-social cues ("Read" during the Face Task) for the social context setting effects the contrasts of all social cues combined vs. outcomes and vice versa for the specific effects of social cues and outcomes, respectively.

DM Task

The regressors of interest were the Joint-Comparison and Separate-Evaluation decisions and several GLMs were tested. To examine the DM based on cognitive valuation free of influences of emotion values, we used the data in the NEU session only to test the main effects of DM, i.e., Joint-Comparison and Separate-Evaluation decisions vs. fixation, and the main effects of differential valuation, i.e., accepted vs. rejected cards within the Separate-Evaluation decisions. To test the effects of DM based on concurrent cognitive and emotion valuations, we contrasted the Joint-Comparison and Separate-Evaluation decisions in INC against those in NEU. To examine final valuation across cognitive and emotional values, we contrasted the differential valuation (accepted vs. rejected cards) in INC against those in NEU.

Face Task

Trials of the same emotion types (Angry, Happy, or Neutral) were modeled separately and the effects of all faces vs. fixation and emotional vs. neutral faces were tested using the corresponding contrasts.

Functional connectivity analysis

Functional connectivity analysis was performed by extracting the time series of the first eigenvariate of a seed region during a task of interest, e.g., the vmPFC in the DM Task, adjusting for effects of all psychological conditions in the model. We used the psychological–physiological interaction (PPI) analysis (Friston et al., 1997) to test the interaction between functional connectivity (physiological variable) and the between-session manipulation of INC and NEU (psychological variable). We first modeled all sessions from the INC and NEU days individually in a single-subject first-level GLM. In each session, we modeled all events (e.g., decision making) in that session as regressors and the physiological variable of the seed (across all trials and resting periods) as a covariate. In this model, the two levels of psychological variable (INC and NEU) were defined by the sessions and the PPI can be tested by contrasting the parameter estimates of the physiological variables in the INC sessions against those in the NEU sessions, i.e., delta functional connectivity. The null hypothesis was the parameter estimates of the physiological variable (ROI brain time-series) were the same between the INC and NEU sessions. Similar procedures were performed to examine condition-specific functional connectivity during Separate-Evaluation and Joint-Comparison conditions, by using the respective condition-specific physiological variables of the seed as separate covariates. In this case, the physiological variable (ROI brain time-series) was first devolved with the canonical HRF to generate activity-related time-series, which was then sorted into multiple activity-related time-series according to the Separate-Evaluation and Joint-Comparison conditions, and each condition-specific activity-related time-series was re-convolved with the canonical HRF to generate the condition-specific brain time-series as the condition-specific physiological variables. The PPI (delta functional connectivity) was tested by contrasting the parameter estimates of a condition-specific variable (e.g., Joint-Comparison) between the INC and NEU sessions.

To examine the influence of emotion on choices as a function of change in functional connectivity at the group level, we used the emotional influence index described above. The first-level contrast images of delta functional connectivity (INC vs. NEU) were then used as the group-level dependent variable in a simple regression model to be regressed against the subject-specific emotional influence index (INC–NEU payoff-based decision rates). The null hypothesis is that when contrasting between INC and NEU sessions, the change in payoff-based decision rates was not associated with the change of functional connectivity.

Results

Behavioral results

Study 1

In Joint-Comparison decisions, there was a significant main effect of the cognition-emotion manipulation on the payoff-based decision rate ($F_{(2,65)} = 6.207$, $MS_{error} = 0.299$, $p = 0.003$, Fig. 2a). Specific linear contrasts were tested post-hoc to examine the congruency effect (CON vs. INC) and conjunction cost effect (CON and INC vs. NEU). These linear contrasts revealed that the payoff-based decision rate was greater in the CON than INC condition (CON vs. INC, contrast estimate = 0.084, s.e. = 0.037, $p = 0.026$), suggesting that the cognitive value and emotional inputs were qualitatively "additive", such that the value differences were greater when cognitive value and emotional inputs were congruent than when they were incongruent (congruency effect). The payoff-based decision rate in NEU was greater than that averaged for the CON and INC conditions (the CON & INC vs. NEU contrast, contrast estimate = −0.178, s.e. = 0.068, $p = 0.011$), suggesting that when emotional values are incorporated in the decisions, the added emotion domain by itself can interfere with decisions (conjunction cost effect). There was also a significant main effect of the cognition-emotion manipulation on RT ($F_{(2,65)} = 3.469$, $MS_{error} = 455{,}440.409$, $p = 0.037$, Fig. 2b) and the linear contrasts showed a significant conjunction cost effect, i.e., the RT was longer in the CON and INC conditions combined than in the NEU condition (the CON and INC vs. NEU contrast, contrast estimate = 495.281, s.e. = 207.451, $p = 0.020$), but there was no

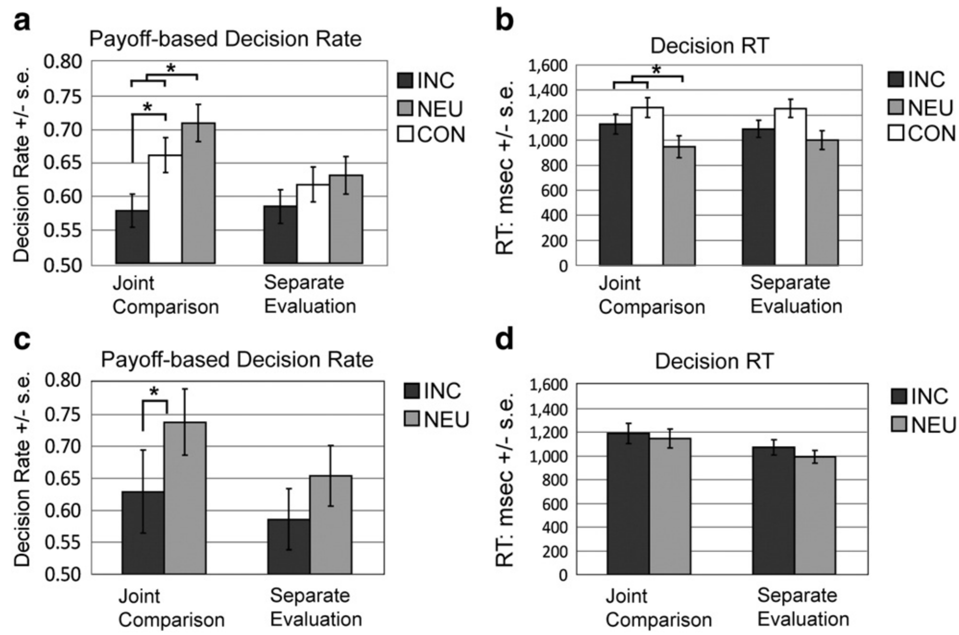

Fig. 2. The behavioral performance during the DM Task, i.e., the payoff-based decision rate and reaction time of the Joint-Comparison and Separate-Evaluation decisions: Mean payoff-based decision rate of all participants (+/− 1 standard error) for the behavioral and fMRI experiments are shown in a) and c), respectively. Mean of the median reaction time (ms) of all participants (+/− 1 standard error) for the behavioral and fMRI experiments are shown in b) and d), respectively. *: $p<0.05$.

difference between CON and INC conditions (INC vs. CON, contrast estimate = 131.353, s.e. = 112.575, $p = 0.248$). Pair-specific behavioral results as a function of time are reported in the supplemental materials (Supplemental Fig. 1).

In Separate-Evaluation decisions, the acceptance rate of the decks was predicted by their probabilistic values, suggesting that participants accurately differentiated the probabilistic values of the decks and in general accepted self-favorable decks and rejected other-favorable decks appropriately (the main effect of the values is significant $F_{(3,\ 195)} = 28.634$, $MS_{error} = 0.193$, $p<0.001$, with a significant linear trend $p<0.001$). However, in contrast to the Joint-Comparison decisions, there were no main effects of congruent or incongruent emotions ($F_{(2,65)} = 0.086$, $MS_{error} = 0.010$, $p = 0.918$, Fig. 2a). Similarly, there was a significant value main effect on RT, which decreased in responding to a deck with increasing self-favorable values, following the ordering of the card decks (the main effect $F_{(3,\ 195)} = 6.512$, $MS_{error} = 64365.201$, $p<0.001$, with a significant linear trend based on the cognitive values, $p<0.001$). The RT in the Separate-Evaluation condition was marginally affected by the cognition-emotion relationship manipulation (CON, INC, or NEU) ($F_{(2,65)} = 3.018$, $MS_{error} = 1{,}426{,}931.645$, $p = 0.056$, Fig. 2b). The post-hoc tests showed that there was a marginal conjunction cost effect (the CON and INC > NEU contrast, contrast estimate = 342.649, s.e. = 183.063, $p = 0.066$) and an insignificant congruency effect (the CON > INC contrast, contrast estimate = 162.229, s.e. = 99.341, $p = 0.107$). Deck-specific behavioral results as a function of time and specific emotions are reported in the supplemental materials (Supplemental Fig. 1 and 2).

Thus, as predicted, adding an emotion domain in social DM led to conjunction cost (CON and INC vs. NEU) and congruency (CON vs. INC) effects, as manifested in differences in payoff-based decision rates and prolonged RT in the Joint-Comparison decisions, wherein the participants chose one deck for the self and left the other deck for the partner. However, the emotions only marginally affected the Separate-Evaluation decisions, wherein the participants decided only to accept or reject the potential payoff of a deck. Note that, as reported in the supplemental materials (Supplemental Fig. 3), the mere presence of a specific retrieved emotion did not affect the Joint-Comparison decisions, when both decks were paired with the same emotional expressions (angry-angry or happy-happy). Thus, the conjunction cost and congruency effects observed in the Joint-Comparison decisions most likely resulted from the differential emotional signals provided by the contrast between happy vs. angry expressions.

Study 2

In light of the results of Study 1, we adapted the paradigm for the fMRI setting, focusing on the INC and NEU conditions. We predicted that INC as compared to NEU would show behavioral impairment resulting from a combination of conjunction cost and congruency effects (INC < NEU). We did not include the CON condition because CON did not differ from NEU in payoff-based decision rate in Study 1, and our focus in the fMRI study was on the neural pathways through which emotional values influenced the final common currency in valuation-based DM.

Replicating the behavioral findings in Study 1, incongruent emotional values (INC as compared to NEU) lowered the payoff-based decision rate in the Joint-Comparison decisions ($F_{(1,13)} = 3.750$, $MS_{Error} = 0.022$, $p = 0.037$) but not in the Separate-Evaluation decisions ($F_{(1,13)} = 1.192$, $MS_{Error} = 0.032$, $p = 0.295$) (Fig. 2c). The RT was not significantly different, in this smaller sample, between the INC and NEU in either the Separate-Evaluation decisions ($F_{(1,13)} = 2.805$, $MS_{Error} = 44{,}790.001$, $p = 0.118$) or the Joint-Comparison decisions ($F_{(1,13)} = 0.164$, $MS_{Error} = 13{,}039.931$, $p = 0.692$) (Fig. 2d).

fMRI results

Neurocircuits underlying value encoding in cognitive and emotion domains

Cognitive domain only: Learning Task. The neurocircuits involved in cognitive valuation were probed using the contrast of Self positive vs. negative outcomes in the Learning Task. The results (summarized in Table 1) revealed that cognitive valuation in a social context activated brain regions associated with a) reward circuitry (Diekhof et al., 2008; Hein et al., 2010), including the NAc, amygdala, orbitofrontal cortex (OFC), and vmPFC (Fig. 3a), b) social cognition networks, including the vmPFC, posterior cingulate cortex (PCC), and superior/middle temporal gyrus (STG/MTG) (Northoff et al., 2006; Van Overwalle, 2009), and c) executive control networks, including the dorsolateral PFC (dlPFC) and parietal lobe. Furthermore, in the absence of emotional

Table 1
Neurocircuits underlying cognitive value encoding in the Learning Task.

Brain region	Side	MNI coordinates			No. of voxels	Z score
		X	y	z		
Self's positive > negative cognitive outcomes						
lPFC	L	−36	45	0	208	4.52
OFC	L	−21	39	−9	140	4.08
Parietal lobe	R	27	−72	39	380	4.37
	L	−27	−51	48	194	4.29
Precuneus	R/L	−12	−78	54	427	4.24
dlPFC	L	−45	21	42	79	4.09
MTG/STG[a]	R	69	−15	−12	312	4.02
	L	−69	−42	−9	341	4.24
PCC	R/L	−3	−39	24	53	3.82
MFG/BA8[a]	L	−27	21	60	103	3.72
Nucleus accumbens (NAc)[b]	R	15	21	−18	74	3.62
	L	−15	21	−12	75	3.51
vmPFC[b]	R	12	45	−18	51	3.62
	L	−6	51	−21	53	3.19
Amygdala[a]	R	36	3	−24	20	3.07
Self's positive < negative cognitive outcomes						
None						
Self's > other's positive vs. negative outcomes						
Parietal lobe	R	30	−78	30	301	4.98
	L	−30	−69	45	319	4.62
Precuneus	R	12	−42	9	134	4.39
SFG	R	39	54	18	21	3.71
	L	−18	66	18	89	3.69
Amygdala[b]	R	36	0	−21	27	3.62
Caudate[a]	L	−12	21	9	56	3.57
	R	18	30	0	57	3.37
STG	L	−66	−9	0	63	3.56
ITG	L	−60	−6	−24	87	3.54
	R	57	−9	−33	29	3.39
dmPFC	L	−6	36	36	43	3.47
	L	−15	39	45	27	3.45
MFG/BA8[a]	R	33	12	48	31	3.22
dlPFC	R	42	36	33	36	3.22
PCC	R	6	−45	24	38	3.10
vmPFC[b]	R/L	0	60	−12	24	3.08
Self's < other's positive vs. negative outcomes						
None						

[a] Overlapping regions between the Learning and DM Tasks.
[b] Overlapping regions between the Face, Learning, and DM Tasks.

faces, neural responses to positive vs. negative outcomes during the NEU session were moderated by the social context (players) in many of these brain regions (summarized in Table 1), including the vmPFC and right amygdala, but not NAc (Fig. 3b). Notably, the effect size of Negative–Positive outcomes to Other was close to zero in the amygdala and NAc, but almost equivalent to the Positive–Negative outcomes to Self in the vmPFC.

Emotional domain only: Face Task. The neurocircuits associated with social emotional stimuli were examined using the Face Task. All three types of faces vs. fixation differentially activated the vmPFC, NAc, amygdala, and hypothalamus, suggesting that these regions were sensitive to the brief face presentations. Furthermore, the amygdala and NAc were differentially activated by the emotional expressions (happy and angry vs. neutral) and vmPFC was differentially activated by differential emotional values as probed by Angry vs. Happy faces, suggesting its role in emotional valuation (Fig. 3c). The results are summarized in Table 2.

Neurocircuits underlying DM based on only the cognitive-domain

We examined the neurocircuits underlying decision making based on cognitive valuation only during the DM Task condition with no emotional values (NEU). The brain regions activated across Joint-Comparison and Separate-Evaluation decisions include the midbrain, striatum (caudate, putamen, and NAc), right amygdala, posterior hippocampus, thalamus, precuneus, parietal lobe, anterior cingulate cortex (ACC), anterior insula, OFC, supplemental motor area (SMA), and dlPFC (Table 3). To further examine the neural regions involved in final valuation during DM, we examined Separate-Evaluation decisions, as presumably the accepted decks possess higher final values than unaccepted decks. Indeed, the contrast of accepted vs. rejected cards in the Separate-Evaluation decisions revealed that the midbrain, NAc, caudate, anterior insula, and vmPFC were related to final valuations (Table 3 and Fig. 3d).

Neurocircuits underlying emotional influences on valuation learning and DM

The effect of adding emotional signals to valuation learning and DM was examined by contrasting the INC condition (involving cognitive and emotional valuation concurrently) vs. NEU (involving cognitive valuation only). In these analyses, we focused on the vmPFC, NAc, and amygdala using small volume correction, since those regions mediated cognitive and emotional value encoding and decision making, and additionally explored other regions in a whole brain analysis.

With regard to the Learning Task, we examined the main effect of presenting emotional faces on cognitive valuation by contrasting the parameter estimates of the positive > negative outcomes in the INC vs. NEU conditions. We found that, as compared to the NEU, the incongruent emotional faces in the INC marginally reduced the valuation-related differential neural responses in the right NAc ($x, y, z = 12, 6, -12$, $Z = 3.68$, 12 voxels, $p = 0.054$, *s.v.c.*, Fig. 4a), but not those in the amygdala or vmPFC.

With regard to the DM Task, we examined the main effect of retrieved emotional values on DM by contrasting the parameter estimates of INC vs. NEU conditions in Joint-Comparison and Separate-Evaluation decisions. We found emotional value during the INC, as compared to NEU, reduced neural responses across both types of decisions in the right amygdala ($x, y, z = 33, 0, -27$, $Z = 3.35$, 34 voxels, $p < 0.05$, *s.v.c.*, Fig. 4b) and left hippocampus ($x, y, z = -33, -9, -21$, $Z = 3.29$, 44 voxels, $p = 0.001$, Fig. 4c). Amygdala, but not hippocampus, was activated during "cognitive only" DM, so the reduced amygdala activity that resulted from retrieved emotional values during the incongruent condition suggests that signal cancellation occurred in the right amygdala during *concurrent* cognitive and emotional valuations. Conversely, the differential responses in the left hippocampus may result from cognition–emotion interaction in a social context (discussed below).

Since the behavioral results suggest that emotion may preferentially affect the Joint-Comparison Decisions but not Separate-Evaluation Decisions, we sought potential neural mechanisms underlying this decision-by-emotion interaction by examining INC vs. NEU conditions in a Joint-Comparison vs. Separate-Evaluation contrast. However, there were no brain areas that were differentially activated in this decision-by-emotion interaction contrast.

We further examined the neurocircuits underlying integration of cognitive and emotional values on a "common currency". Presumably the "common currency" signal should be lower in INC than NEU because incongruent emotional input should decrease the overall values of cognitive based signal. We operationally defined the *neural* subjective value signal as the differential neural responses measured by the accepted vs. rejected cards contrast, and we predicted that such neural signal should be decreased in INC (due to value cancellation across incongruent cognitive and emotion domains) as compared to the baseline cognitive value signal in NEU. In light of the literature implicating vmPFC in a common valuation system (Hare et al., 2009, 2010; Kable and Glimcher, 2009; Levy et al., 2011), we defined the vmPFC ROI functionally based on the vmPFC cluster showing significant differential activation in the accepted vs. rejected cards contrast, pooled across the INC and NEU conditions ($x, y, z = -3, 51, 0$, $Z = 4.58$, 196 voxels, $p < 0.001$). This same ROI was also identified using the NEU condition only (see Table 3).

The null hypothesis is that, for this vmPFC ROI related to valuation, the differential neural responses in the accepted vs. rejected decks in the Separate-Evaluation conditions should not differ between the INC and NEU sessions, i.e., the interfering emotional signals in the INC

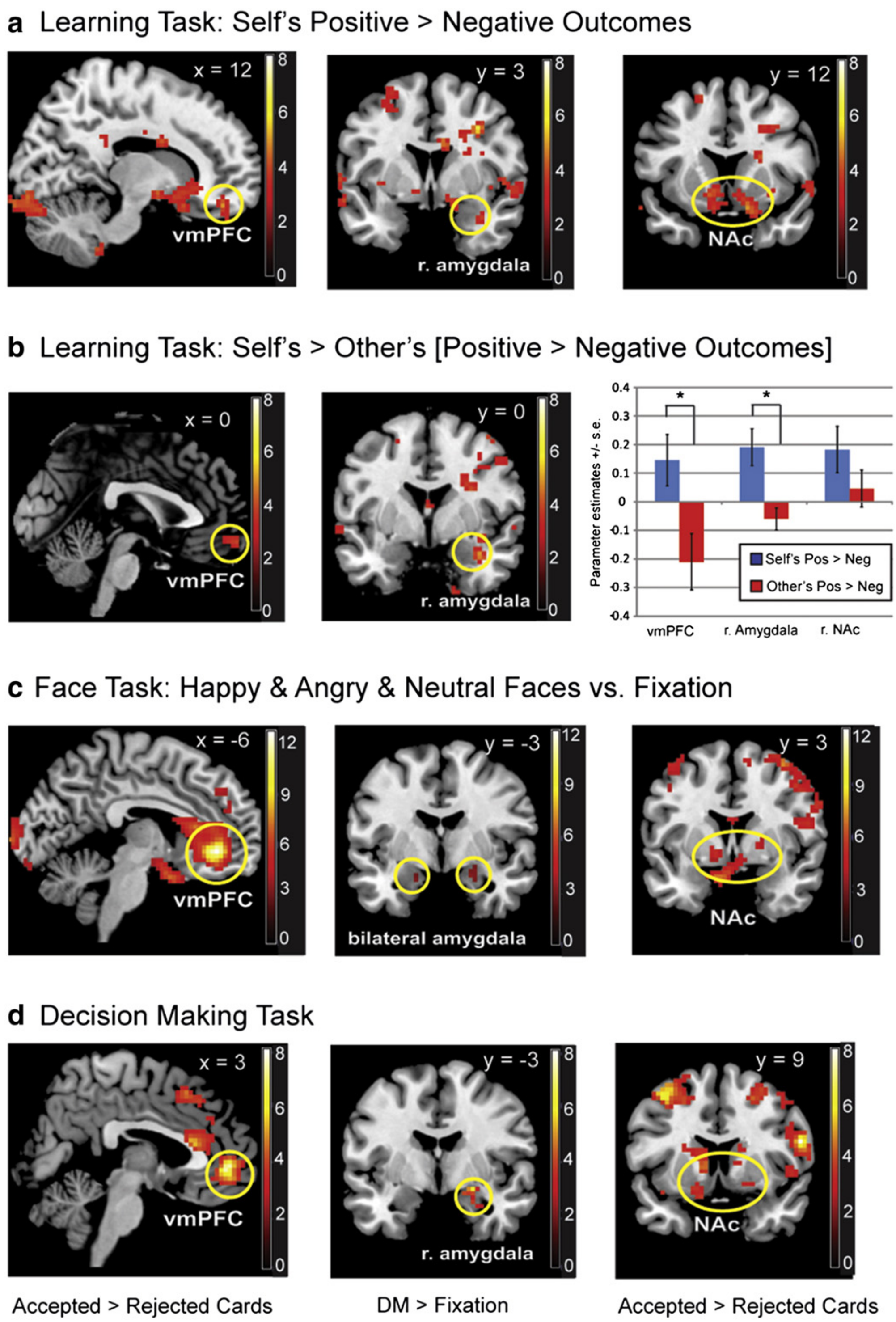

Fig. 3. The vmPFC, amygdala, and NAc were related to a) cognitive value encoding during the Learning Task (positive > negative outcomes for the Self), b) social context moderation of cognitive valuation (Self's > Other's [positive > negative outcomes]), except NAc, c) emotional face encoding during the Face Task, and d) cognitive value retrieval during the DM Task (NEU only) the subjective valuation of the decks (accepted > rejected cards in the Separate-Evaluation decisions). The statistical maps are illustrated at $p = 0.005$, uncorrected.

should not change the final common currency represented in the vmPFC. As predicted, the results rejected this null hypothesis, i.e., the accepted vs. rejected differential activation in the vmPFC was reduced in INC as compared to NEU ($x, y, z = 6, 45, -6$, $Z = 3.18$, 120 voxels, $p < 0.05$, *s.v.c.*, Fig. 4d).

Functional connectivity between vmPFC and amygdala in social DM

The INC vs. NEU results in the DM Task described above suggested dissociable roles of the vmPFC and amygdala in *concurrent* cognitive and emotional valuation in social DM. Specifically, while the right amygdala, but not the vmPFC, was sensitive to both cognitive and emotional values during the encoding stages of "state value" (the Learning and Face Tasks), the vmPFC appeared to mediate differential subjective value signals ("common currency") during the actual DM stage (the DM Task), as probed by the accepted vs. rejected cards contrast.

To further investigate the vmPFC–amygdala relationship during social DM, we performed functional connectivity analysis to examine whether the *concurrent* emotional input altered the vmPFC–amygdala

Table 2
Neurocircuits underlying emotional face encoding in the Face Task.

Brain region	Side	MNI coordinates			No. of voxels	Z score
		x	y	z		
Happy + angry + neutral face > fixation						
vmPFC[a]	L/R	−6	39	−6	42	5.76
OFC	L	−21	33	−21	144	4.79
Inferior parietal lobule	R	60	−45	39	167	4.77
Visual cortex	L/R	−9	108	3	396	4.73
Fusiform gyrus	L	−42	−81	−15	92	4.68
	R	42	−84	−18	11	4.05
Temporal lobe	L	−60	−33	0	314	4.13
	R	51	−27	−18	131	3.72
Hypothalamus	L/R	−6	0	−15	135	3.96
NAc[a]	L	−12	3	−3	223	3.77[b]
	R	6	3	−9	144	3.39[b]
Amygdala[a]	L	−18	0	−21	38	3.07[b]
	R[a]	21	3	−18	47	3.00[b]
Happy + angry + neutral face < fixation						
None						
Happy + angry face > neutral face						
Amygdala	L	−15	3	−21	43	3.42[b]
NAc[a]	R	18	9	−15	6	3.38[b]
Happy + angry face < neutral face						
None						
Happy face < angry face						
vmPFC[a]	L	−12	45	−3	32	3.63[b]
Happy face > angry face						
None						

[a] Overlapping regions between the Face, Learning, and DM Tasks.
[b] With small volume correction.

Table 3
Neurocircuits of cognitive valuation in DM Task (NEU only).

Brain region	Side	MNI coordinates			No. of voxels	Z score
		x	y	z		
Decision making > fixation						
SMA	R/L	0	21	48	859	6.9
Precuneus	R/L	−9	39	27	1752	5.95
Insula, anterior	R	36	27	0	457	5.03
	L	−33	27	−9	714	4.92
MFG	L	−51	21	27	796	5.67
	R	45	33	24	701	5.67
Superior parietal lobule	R	9	−72	54	210	5.77
	L	−33	−54	54	224	5.49
Inferior parietal lobule	L	−46	−54	54	506	5.56
	R	36	−54	54	351	5.12
Striatum (including NAc[a])	R	12	12	6	300	5.15
	L	−21	0	9	369	4.83
Hippocampus, posterior	R	33	−36	−9	82	4.99
	L	−21	−33	−3	72	4.5
OFC	R	24	60	−18	50	3.73
	L	−30	54	−12	99	3.84
Amygdala[a]	R	27	3	−15	22	3.55
Decision making < fixation						
None						
Accepted > rejected cards in separate-evaluation decisions						
lPFC	R	57	9	21	176	4.74
vmPFC[a]	R/L	0	51	0	124	4.66
MFG/BA8[b]	L	−36	12	48	377	4.26
Frontal pole/BA10	R	24	60	15	36	4.07
Thalamus	R	3	−18	3	60	4.03
	L	−21	−18	3	27	3.5
Midbrain	R/L	−3	−24	−24	13	3.97
dlPFC	R	48	45	18	90	3.97
	R	45	15	45	28	3.26
	L	−39	42	3	47	3.07
Insula, anterior	R	30	27	−21	48	3.75
	L	−27	24	−3	21	3.41
dACC[2]	R/L	6	27	15	42	3.78
Caudate[b]	L	−9	12	3	221	3.69
Hippocampus, posterior	R	36	−36	−9	42	3.67
	L	−30	−36	−9	14	3.43
MTG/STG[b]	L	−57	−12	−15	43	3.6
Precuneus/PCC[b]	R/L	0	−39	27	262	3.55
dmPFC/PreSMA	R/L	3	21	51	74	3.45
NAc[a]	L	−12	9	−18	16	3.03
	R	21	6	−9	32	2.99
Accepted < rejected cards in separate-evaluation decisions						
None						

[a] Overlapping regions between the Face, Learning, and DM Tasks.
[b] Overlapping regions between the Learning and DM Tasks.

coupling and actual behavioral choices, i.e., the change in corresponding payoff-based decision rates in the INC vs. NEU conditions (emotional influence index). Here decreased payoff-based decision rating in INC as compared to NEU should indicate increased emotional interference. We defined the seed for functional connectivity analysis as the peak in vmPFC (*x, y, z* = 6, 45, −6, 6 voxels) that was associated with differential final common currency (INC < NEU for the accepted vs. rejected cards). We found that higher functional coupling between the vmPFC and right amygdala (*x, y, z* = 27, −6, −15, *Z* = 3.00, 7 voxels, $p < 0.05$, *s.v.c.*, Fig. 5a) was associated with decreased payoff-based decision rates in INC vs. NEU, indicating that the ability of concurrent incongruent emotional input to reduce cognitive value-based decisions was linked to right amygdala–vmPFC connectivity during decision making.

Interestingly, similar association between vmPFC–amygdala connectivity and the influences of emotional value on actual choices was also found during the Learning Task. That is, higher functional coupling between the vmPFC and right amygdala (*x, y, z* = 24, −3, −27, *Z* = 3.28, 22 voxels, $p = 0.001$, Fig. 5b) in INC vs. NEU during the Learning Task was associated with greater reduction of *subsequent* payoff-based choices during the DM Task.

The role of hippocampus in social context setting

As reported earlier, neural response in the left hippocampus was reduced during DM in INC vs. NEU. However, unlike the right amygdala, the left hippocampus was not engaged by cognitive valuation during DM Task in NEU, nor by emotional face pictures during the Face Task. In light of the literature suggesting that the hippocampus is involved in context setting (Schmajuk and Buhusi, 1997) and *concurrent* multi-domain information processing (Shohamy and Wagner, 2008), the observed emotional influences on the hippocampus signal (INC < NEU) during the DM Task could come from the interaction between the social context (Self and Other) and emotional influences on cognitive processing (Niedenthal et al., 2009). To examine potentially dissociable roles of the left hippocampus, which is hypothesized to subserve social-context setting, and the right amygdala, which is hypothesized to subserve cognitive and emotional valuations, we built a GLM model to isolate the social context processing, which was related to processing the verbal social context cues “To You” or “To Other” prior to the presentation of outcomes during the Learning Task. We contrasted the social context cues (combining all “To You” or “To Other” cue regressors) in the Learning Task vs. non-social control cues (combining all “Read” non-social cue regressors) in the Face Task to examine the social context setting responses. We also examined the contrasts of the all social context cues vs. outcomes for cue-specific effects, and *vice versa* for outcome-specific effects, in the Learning Task.

Indeed, the left hippocampus (*x, y, z* = −30, −6, −15, *Z* = 3.92, 16 voxels, $p < 0.001$, FDR whole-brain corrected, Fig. 6a) was differentially activated in the contrast of social context cues vs. the non-social cues, but not in the social cues vs. outcomes or outcome vs. social cues contrasts, which suggests that the left hippocampus continued to be involved during the outcome periods. Conversely, the right amygdala (*x, y, z* = 39, 0, −24, *Z* = 3.84, 7 voxels, $p < 0.001$, FDR whole-brain corrected, Fig. 6b) and vmPFC (*x, y, z* = −6, 39, −12, *Z* = 5.59, 228 voxels, $p < 0.001$, FDR whole-brain

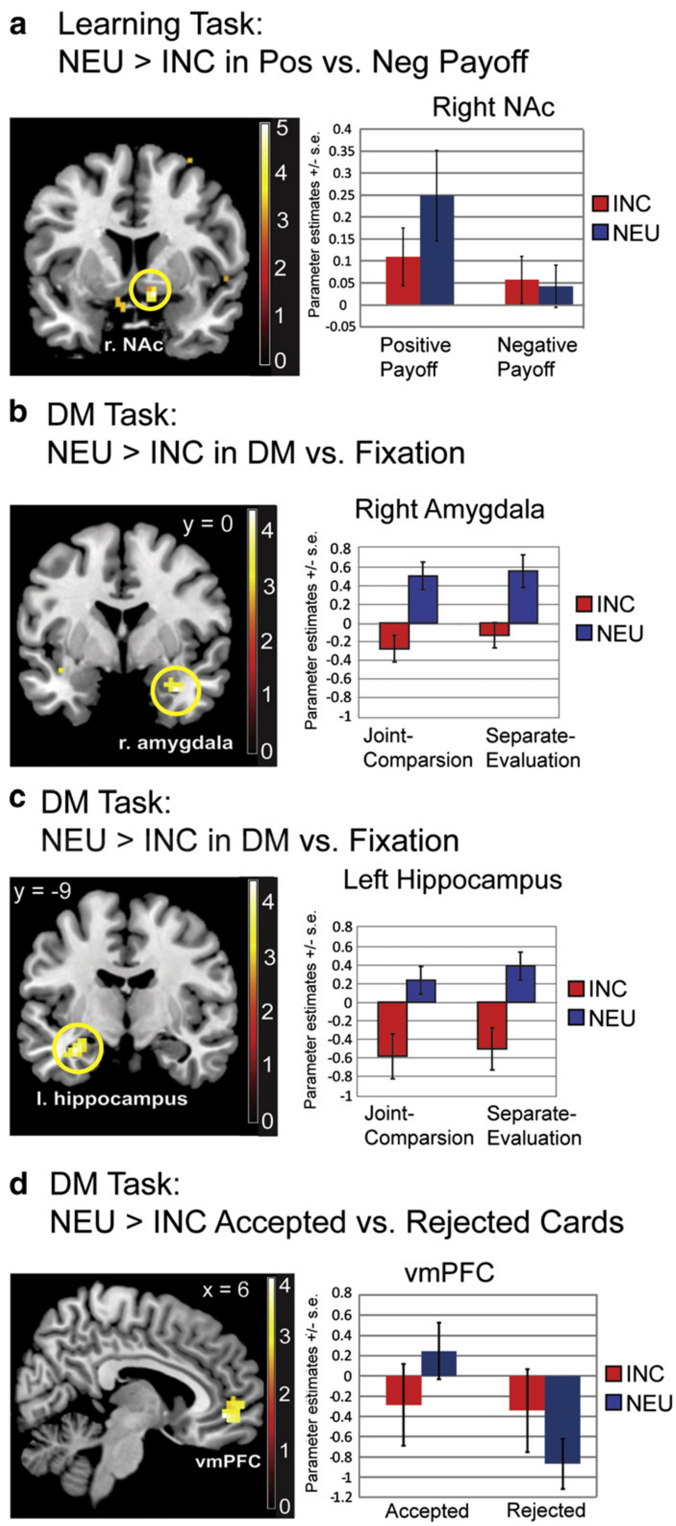

Fig. 4. The incongruent emotional values affected the valuation-related brain regions during the Learning and DM Tasks: The INC vs. NEU condition decreased the differential responses related to a) positive > negative outcomes (across players) contrast in the right NAc during the Learning Task, b) DM vs. fixation contrast in the right amygdala and c) the left hippocampus across the Joint-Comparison and Separate-Evaluation decisions, and d) accepted > rejected cards contrast in the vmPFC during the DM Task. The statistical maps are illustrated at $p = 0.005$, uncorrected.

corrected, Fig. 6c) were differentially activated in the outcomes vs. all social cues combined contrast, but not the social context cues vs. non-social control cues. These outcome-specific neural responses in the right amygdala and vmPFC were consistent with their roles in the cognitive and emotional valuation, as reported in Tables 1–3. Notably, these consistent results also suggested that the effects of cues and outcomes components had been successfully separated in this model, despite the fixed intervals between them, and hence the social cue vs. control cue results in the hippocampus should be reliable.

Functional connectivity underlying social context and valuation in social DM

Given the results suggesting that a part of the left hippocampus was involved in both social context setting (Fig. 6a) and cognition–emotion interaction in social DM (Fig. 4b), we postulated that emotional influences on social DM may depend on functional coupling between the left hippocampus and regions related to cognitive and emotional valuations. Thus, we performed a functional connectivity analysis using the left hippocampus cluster as the seed, searching for brain regions in which functional connectivity with the left hippocampus differed between the INC and NEU conditions as a function of behavioral emotional influence index (the INC–NEU difference in payoff-based decision rate). We found that, during the Joint-Comparison decisions, emotional influences on the payoff-based decision rates were associated with increased functional connectivity between the left hippocampus and bilateral amygdala ($x, y, z = -24, 3, -18$, $Z = 2.78$, 8 voxels, $p < 0.05$, *s.v.c.*, Fig. 7a, and $x, y, z = 27, -9, -15$, $Z = 2.78$, 40 voxels, $p < 0.05$, *s.v.c.*, Fig. 7b) and right NAc ($x, y, z = 15, 12, -12$, $Z = 3.82$, 66 voxels, $p < 0.05$, *s.v.c.*, Fig. 7c). Similarly, during the Separate-Evaluation decisions emotional influences on the payoff-based decision rates were also associated with the difference in hippocampal functional connectivity with bilateral amygdala ($x, y, z = -21, 0, -12$, $Z = 2.91$, 28 voxels, and $x, y, z = 27, -6, -15$, $Z = 3.27$, 9 voxels, *both* $p < 0.05$, *s.v.c.*), but not with NAc.

Discussion

We designed a novel paradigm to study behavioral and neural mechanisms underlying cognitive and emotional valuations when values were learned and decisions were made in a social context. Participants played a card game in which cognitive and emotional values were paired with decks of cards and encoded during a Learning Task, while the relationship between the cognition and emotion values was manipulated by systematically juxtaposing cognitive payoffs (points) and emotional values (emotional faces) in Congruent (CON), Incongruent (INC), and Neutral Control (NEU) conditions. In a DM Task, the participants made social (Joint-Comparison) and self-focused (Separate-Evaluation) decisions, and the influence of emotional valuation on actual choices was indexed by computing the difference between payoff-based decision rates in the INC and NEU conditions. We observed that the retrieved emotional values significantly impacted payoff-based decision making, reducing the payoff-based decision rate and slowing the decision process (conjunction cost). Incongruent emotion produced the largest reduction in payoff-based decisions, but these effects were only present when participants were making Joint-Comparative decisions involving both self and another agent. Emotional influences on the Joint-Comparative decisions were not observed when only positive or only negative emotional values (angry–angry or happy–happy) were juxtaposed with the pair of decks (see supplemental materials), suggesting that the interference effect was particularly linked to incongruent emotional values in a social context and was not caused by a general effect of angry or happy faces alone. These results are consistent with the literature (Hsee et al., 1999; Niedenthal et al., 2009) and suggest that research examining emotional modification of cognitive valuation might benefit from the presence of a social context.

In Study 2, we first examined neurocircuits underlying cognitive and emotional value encoding separately and found that the vmPFC, amygdala, and ventral striatum (NAc) were involved in the encoding of differential cognitive values (positive > negative

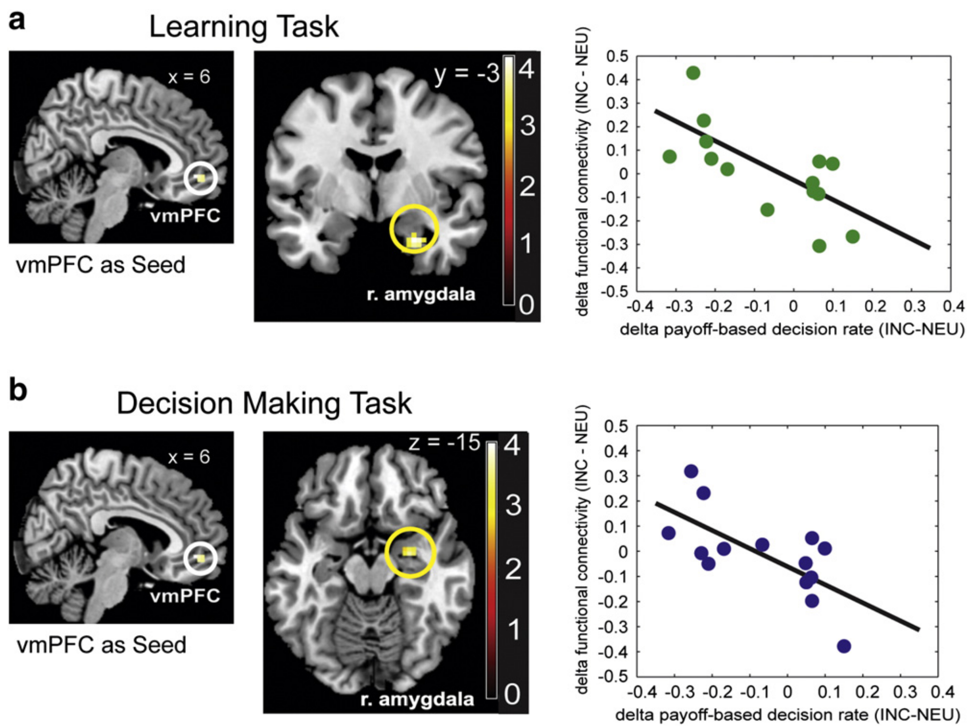

Fig. 5. The emotional influences (INC vs. NEU) on actual payoff-based decision rates across the Joint-Comparison and Separate-Evaluation decisions were inversely associated with the emotional influences on the functional connectivity between the vmPFC and right amygdala during a) Learning Task and b) DM Task. The scatter plots inside the sub-panels depict the subject-specific INC vs. NEU difference in the mean parameter estimate of vmPFC-right amygdala functional connectivity on the y-axis and the INC vs. NEU delta payoff-based decision rates on the x-axis.

outcomes for Self) and emotional values (emotional > neutral faces or angry > happy faces); the valuation-related neural responses in the vmPFC and amygdala, but not NAc, were moderated by the social context; while the NAc and amygdala did not differentiate the other's gains and losses, the vmPFC responded to the other's gains as if they were the Self's losses (Table 1 and Figs. 3a,b,c). In examining neurocircuits underlying DM based on cognitive values only in the NEU condition, we found that the right amygdala was activated by DM across Joint-Comparison and Separate-Evaluation decisions, while the vmPFC and NAc were sensitive to differential subjective values (probed by accepted > rejected cards in Separate-Evaluation) (Table 3 and Fig. 3d). Notably, we found that the emotional values provided in the INC condition seemed to cancel out cognitive value signals in the right NAc during the Learning Task (Fig. 4a) and the right amygdala and vmPFC during the DM Task (Figs. 4b,d).

These results corroborated that the vmPFC, NAc, and amygdala are involved in processing both cognitive and emotional domains of valuation, as parts of a common valuation system (Hare et al., 2009, 2010; Izuma et al., 2008; Kable and Glimcher, 2009; Levy et al., 2011). However, these three brain regions also played dissociable roles in social DM. The vmPFC appeared to represent the *final* common currency as a combination of social, cognitive, and emotional domains, i.e., cognitive valuation moderated by the social context during Learning (Fig. 3b) and integrating cognitive and emotional values that were directly related to differential choices (accepting or rejecting a deck) during DM (Figs. 3d and 4d). The NAc encoded cognitive and emotional values during Learning (Figs. 3a,c and 4a) and mediated cognitive value signals shaping behavioral choices (accepting vs. rejecting a deck) (Fig. 3d). In contrast to the vmPFC, the NAc value signals were independent of the social context (Fig. 3b) and not influenced by retrieved emotional values during DM. The amygdala showed self-regarded value signals (positive vs. negative outcomes during Learning), though it did not respond to the other's gains and losses differently (Fig. 3b), and also showed salience-related responses (DM vs. fixation) that were reduced by incongruent emotional values (NEU > INC) (Fig. 4b). In contrast to the vmPFC and NAc, the

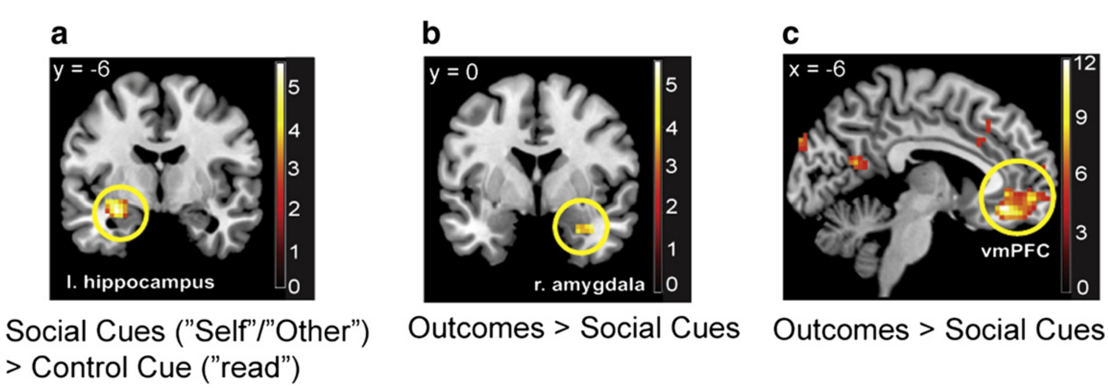

Fig. 6. a) the left hippocampus was differentially activated by the social context cues ("To You"/"To Other") during the Learning Task as compared to the control cues ("Read") during the Face Task. b) The amygdala and c) vmPFC were differentially activated by the outcomes vs. social context cues during the Learning Task.

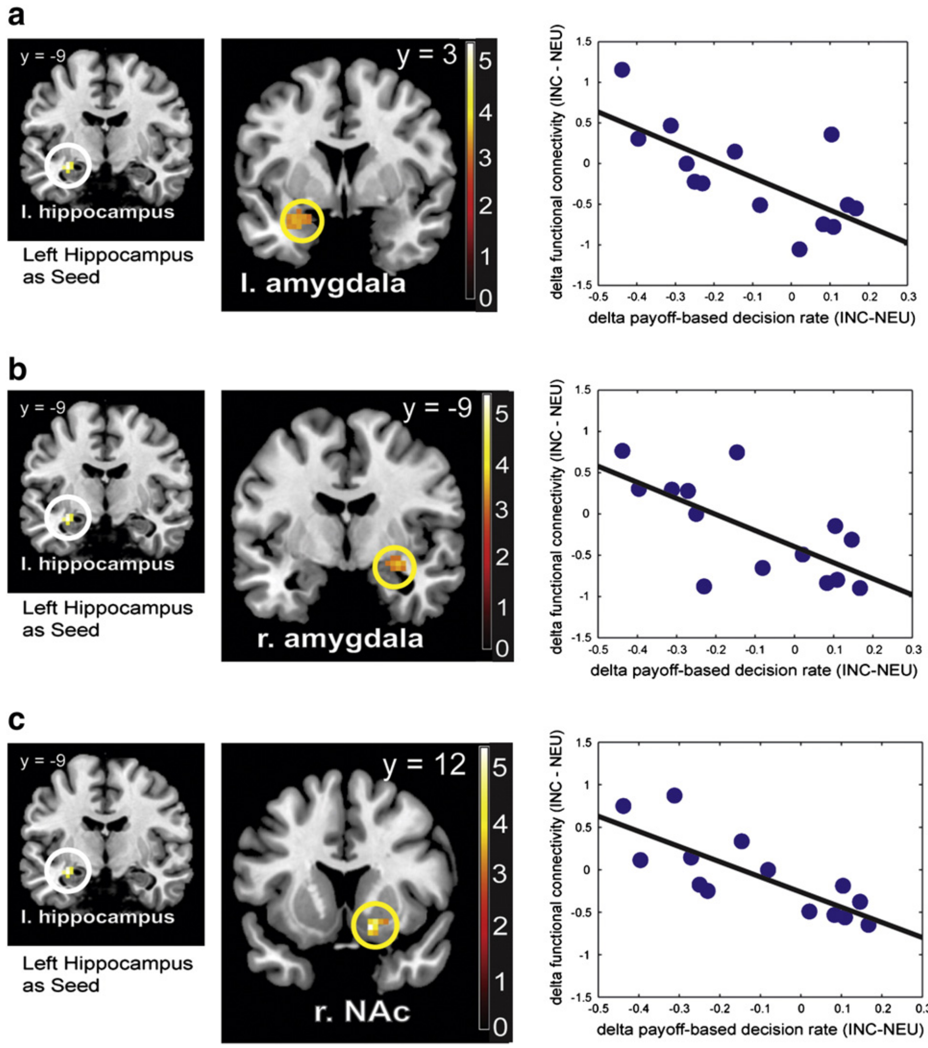

Fig. 7. The emotional influences (INC vs. NEU) on actual payoff-based decision rates in the Joint-Comparison were inversely associated with the INC vs. NEU delta functional connectivity between the left hippocampus and a) left amygdala, b) right amygdala, and c) NAc during the DM Task. The scatter plots inside the sub-panels depict the subject-specific INC vs. NEU difference in the mean parameter estimate of vmPFC-right amygdala functional connectivity on the y-axis and the INC vs. NEU delta payoff-based decision rates on the x-axis.

amygdala signal was unrelated to final choices (accepted vs. rejected) based on subjective valuation during DM.

The results that the vmPFC responded to Other's gains as if Self's losses, during the Learning Task, indicate social context can totally "flip over" the higher-order value representations in the vmPFC, but not the value-dependent signals in the amygdala and NAc (Fig. 3b). Alternatively, one may argue that regret-like counterfactual thinking (Camille et al., 2004; Coricelli et al., 2005), e.g., "had I chosen that card instead, I would've earned or lost that many points", can also explain the same results in the vmPFC. However, this alternative interpretation cannot explain how the vmPFC can represent subjective valuation (final common currency) during the DM task, which provided no immediate feedback at all and therefore no counterfactual thinking could occur.

Compared to the vmPFC, the amygdala clearly processed the cognitive and emotional values at a more "up-stream" stage of information processing. During the DM Task, cognitive and emotional value signals are both mediated by the amygdala to form self-regarded salience signals based on retrieved memory of "state valence" (Morrison and Salzman, 2010), and these retrieved salience signals are integrated down-stream in the vmPFC, possibly with additional social inputs from other sources to form a *final* common currency across social, emotional, and cognitive domains for actual behavioral choices. Indeed, this interpretation may explain a body of literature suggesting that while individuals may have some social preferences for equity in payoffs—potentially represented in the vmPFC—they care about others' payoffs considerably less than their own, potentially due to the lack of the amygdala's salience signals with regard to others (Fehr and Schmidt, 1999; Henrich et al., 2006; Yamagishi et al., 2009).

This interpretation was further supported in our study by the psychological–physiological interaction analysis of functional connectivity between the vmPFC and right amygdala. We found that increased functional connectivity between these two regions during processing of concurrent emotional and cognitive signals (INC vs. NEU) was associated with the extent to which incongruent emotion reduced the payoff-based decision rates (INC<NEU). If the information flow is from the upstream amygdala to the downstream vmPFC, these results suggest that the more the vmPFC received signals from the right amygdala, the more the choices were negatively influenced by incongruent emotional values. Notably, the same pattern was found in different stages of information processing, i.e., value encoding stage (Learning Task) and value retrieval stage (DM Task) (Fig. 5). These results suggest that these two regions of the common valuation system act as a concerted network in both value encoding *and* retrieval. Thus, our results suggest specific roles of the amygdala–vmPFC pathway in the construction of subjective values in social decision making.

Likely, such “funneling” of value information processing toward final common currency allows incorporation of other meaningful contextual information—such as internal drive states (e.g., hunger) and social situations (e.g., peer evaluations)—that may be relevant for the final behavioral choices. Indeed, we found clear influences of social contexts on cognition–emotion interaction in the present study. In concert with the notion that social context enables emotional influences on cognitive functioning (Niedenthal et al., 2009), we observed behaviorally that social context indeed moderated the impacts of emotional values on decision making. Neurobiologically, we found that the left hippocampus, but not right amygdala or vmPFC, was sensitive to social context cues vs. non-social cues (Fig. 6a). Conversely, the right amygdala and vmPFC, but not left hippocampus, were preferentially responding to the outcomes vs. cues (Figs. 6b,c). This suggests that the left hippocampus was involved in social context setting while the right amygdala and vmPFC were preferentially involved in cognitive and emotional valuations (common valuation system). Notably, the neural response in the left hippocampus did not decline during the outcomes following social context cues, which probably allowed the hippocampus to contribute to the social context modulation of cognition–emotion interaction. Indeed, we also found that the decision-related (DM vs. fixation) neural responses in this social context-setting left hippocampus area were decreased in the incongruent condition during DM (Fig. 4c) and the increasing INC vs. NEU delta functional connectivity between the left hippocampus, as the seed, and both bilateral amygdala and right NAc (Figs. 7a,b and c) was associated with the extent to which the incongruent emotions reduced the payoff-based decision rates (INC<NEU). These results suggest that the hippocampus-amygdala-NAc networks may underlie the cognition-emotion interaction in social DM.

Further work is required to address a number of questions raised by the current findings. For example, when social decisions (Joint-Comparison) were being made, emotional input exerted corresponding effects on both behavior and the brain responses. However, similar emotional effects on brain were found when decision making involved only the self (Separate-Evaluation did not differ from Joint-Comparison in brain findings) despite the absence of significant emotional effects on behaviors in the Separate-Evaluation condition in Study 1. One explanation is that the social context was still implicitly retrieved in the Separate-Evaluation conditions, but the emotional effects resulting from the implicit social context were obscured by a behavioral floor effect. Thus, future research is needed to further clarify the effects of added emotional valuation on behavior in non-social decision making, without any social context. Furthermore, it remains to be tested whether the neuroimaging results presented here generalize to conditions with congruent cognitive and emotional values as well.

In summary, the present study provides compelling evidence to corroborate the hypothesis that facial expressions can carry emotional values as part of final common currency and reveal the dissociable roles of vmPFC, amygdala, NAc, and hippocampus in integrating cognitive payoff and social emotional values carried by facial expressions in a social DM context. Our results corroborate and expand on the role of vmPFC as a critical node in a *final* common valuation system across social, cognitive, and emotional domains. They suggest that the amygdala acts as a preliminary value integration system in integrating concurrent salience signals across cognitive and emotional domains. We also demonstrated that the NAc was sensitive to both cognitive values and emotional inputs, but not social context, whereas the hippocampus was sensitive to social context but not cognitive values and emotional inputs. Furthermore, functional coupling linking the final common value site of vmPFC to the amygdala, and linking the context-setting hippocampus to the value signaling amygdala and NAc, were associated with emotional influences on actual choices.

Theoretically, the construction of values from salience signals to final common currency for the purpose of decisions making can be considered a special case of a psychological constructionist theory of emotion, which postulates that an emotional episode and its resulting instrumental actions are produced after core affects are attributed to an object with potential modifications based on appraisal of circumstances (Russell, 2003). Consistent with this constructionist view, we found in the present study that influences of emotions on overt decision making stem from core salience signals (mediated by the amygdala) that are subject to social contextualization (mediated by hippocampus) before experiences/actions arise based on final valuation signals (mediated by the vmPFC). While the psychological constructionist account is receiving wide attention in the affective neuroscience literature (Lindquist et al., 2012), our findings offer neural evidence for its potential applicability to valuation and shed light on the fundamental psycho-neurobiological mechanisms underlying the cognitive–emotional interactions that shape decision making in a social context.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2012.07.017.

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