Affective evaluation of others' altruistic decisions under risk and ambiguity

Wei Xiong [a],

benefactor's kind intention from these contextual factors, which enables individuals to recognize high-quality benefactors and build cooperative relationships (i.e., the find-remind-bind theory) (Algoe, 2012). Therefore, the perceived kind intention behind help may be a crucial factor that links other appraisals, such as benefactor's cost and self-benefit, to the feeling of gratitude (Algoe, 2012; Algoe et al., 2008; Algoe and Stanton, 2012; Wood et al., 2008).

Consistently, at the neural level, previous studies have associated gratitude with the activation of ventral medial prefrontal cortex (vmPFC) (Fox et al., 2015; Kini et al., 2016; Yu et al., 2017, 2018; Zahn et al., 2009), a region implicated in value computation (Bartra et al., 2013; Rangel et al., 2008) and praiseworthy social intention representation (Izuma et al., 2008; Ruff and Fehr, 2014). Neural signals representing cognitive antecedents of gratitude (e.g., temporoparietal junction for the evaluation of benefactor-cost and ventral striatum for the evaluation of self-benefit), passed to vmPFC via effective connectivities, suggesting a potentially pivotal role of kind intention perception in generating gratitude (Yu et al., 2018).

In fact, a decision maker's attitude towards uncertainty is crucial for others to infer the hidden preference/intention behind his/her decision (Barasch et al., 2014; Capraro and Kuilder, 2016; Jordan et al., 2016; Van de Calseyde et al., 2014). Specifically, individuals dislike uncertainty; dealing with uncertainty can be unpleasant and accompanied with fear and anxiety (Grupe and Nitschke, 2013; Tanovic et al., 2018). As such, individuals are less likely to make altruistic decisions under uncertainty (Hu et al., 2017; Vives and FeldmanHall, 2018). Compared with individuals who attempt to eliminate uncertainty when making altruistic decisions, such as seeking more information or calculating costs and benefits, individuals who make altruistic decisions under uncertainty are considered to be more altruistic and trustworthy (Ames et al., 2004; Capraro and Kuilder, 2016; FeldmanHall and Shenhav, 2019; Jordan et al., 2016; Kappes et al., 2018; Pérez-Escudero et al., 2016). Given the importance of perceived kind intention in the generation of gratitude and the role of uncertainty in intention inference, we could hypothesize that the perceived kind intention may mediate the influence of uncertainty in benefactor's cost on the beneficiary's gratitude. Yet despite the observations of the role of uncertainty in favor-receiving contexts, little is known about the neurocognitive bases underpinning how individuals perceive other's altruistic decisions under uncertainty and respond with gratitude and reciprocity.

Neuroimaging studies regarding how individuals make their own decisions under uncertainty may contribute to the understanding of this issue. In social decision-making, a neuroimaging study (Hu et al., 2017) on altruistic behaviors demonstrated that, as the risk of being punished increased, participants' frequency to help others decreased. This increased uncertainty was associated with the increased activity in dorsomedial prefrontal cortex (dmPFC), a region implicated in the mentalizing process during social interactions (Corradi-Dell'Acqua et al., 2015; Koster-Hale and Saxe, 2013; Molenberghs et al., 2016; Nagel et al., 2018; Sanfey et al., 2015) and commonly observed in the uncertainty-related processing during non-social economic decision-making (Blankenstein et al., 2018; Hsu et al., 2005). Moreover, the decision on whether to trust or invest in another person is a type of decision-making under uncertainty, as this trust or investment might be reciprocated or betrayed (Vives and FeldmanHall, 2018). A series of works have investigated the neural responses underlying this uncertain social investment using economic games, such as trust game (Belfi et al., 2015; Tzieropoulos, 2013; for a meta-analysis, see Bellucci et al., 2017), prisoner's dilemma (Chen et al., 2016; Rilling et al., 2008), and ultimatum game (Sanfey et al., 2007; for a meta-analysis, see Feng et al., 2015). Results of these studies consistently linked the uncertainty-related processing with anterior insula (aINS), a region related to the processing of negative emotions or stimuli, indicating the aversive feelings evoked by uncertainty and unexpected outcomes (Chang et al., 2013; Rilling and Sanfey, 2011; Singer et al., 2009). Furthermore, social learning is an important way to reduce uncertainty during consecutive social interactions, in which individuals learn from the differences between current predictions and actual outcomes (i.e., prediction errors or expectation violations) to form more accurate predictions of others' attitudes and actions (FeldmanHall and Chang, 2018; FeldmanHall and Shenhav, 2019). Neuroimaging studies on social learning about others' probabilities to reciprocate (Delgado et al., 2005; De Luca, Emanuele, 2015; King-Casas et al., 2005; Phan et al., 2010; Smith-Collins et al., 2013; Vanyukov et al., 2019), norm compliance behaviors (Xiang et al., 2013), attitudes towards oneself (Jones et al., 2011; Will et al., 2017) and other traits (Hackel et al., 2015; Harris and Fiske, 2010; Zhu et al., 2012) revealed neural activities similar to those in non-social reward learning (for reviews see Chib et al., 2009; Kable and Glimcher, 2009; Ruff and Fehr, 2014). The processing of social expectation violation is mainly associated with the activity in striatum (especially ventral striatum), and the conflict monitoring process associated with expectation violation is mainly linked to the activity in dorsal anterior cingulate cortex (dACC, Heilbronner and Hayden, 2016; Shackman et al., 2011). Moreover, the experienced social reward associated with other's behaviors is linked to the activity in orbitofrontal cortex (including vmPFC), ventral striatum and amygdala (for reviews see Ruff and Fehr, 2014; Seo and Lee, 2012).

In non-social decision-making, economic studies have focused on two kinds of uncertainty: (1) risk, an uncertainty with known probabilities, and (2) ambiguity, an uncertainty with unknown probabilities, of which the latter is often considered as more uncertain and aversive (Camerer and Weber, 1992; Ellsberg, 1961; Hsu et al., 2005). Neurally, processing risk and ambiguity in one's own decision-making involves both shared and differential neural bases. On the one hand, lateral orbitofrontal cortex (lOFC) and aINS were found to be associated with aversive responses to both risk and ambiguity, i.e., general uncertainty processing (Hsu et al., 2005; Levy, 2017; Platt and Huettel, 2008). On the other hand, compared to decision under risk, decision under ambiguity was associated with greater activation in the dorsal part of prefrontal regions (Krain et al., 2006), including dmPFC and dorsolateral prefrontal cortex (dlPFC; Blankenstein et al., 2018; Hsu et al., 2005; Huettel et al., 2006). Compared to decision under ambiguity, decision under risk was more associated with the striatal system (Hsu et al., 2005) and parietal cortex (Huettel et al., 2005, 2006). However, questions remain as to whether these commonalities and differences in one's own decision-making could be generalized to explain how others' altruistic decisions under risk and ambiguity influence one's feeling of gratitude.

Here we developed an interpersonal interactive game based on previous studies on gratitude (Yu et al., 2017, 2018) to 1) investigate whether perceived kind intention mediates the relationship between uncertainty in benefactor's cost and beneficiary's gratitude, and 2) examine the neural commonalities and differences underlying gratitude responses to others' altruistic decisions under risk and ambiguity. We manipulated the uncertainty level associated with the cost of help (Certain vs. Risky vs. Ambiguous amount of pain) faced by the benefactor (the co-player), even though the beneficiary (the participant) knew that the final cost of the benefactor was the same across all conditions. Before scanning, participants made predictions of the co-players' helping rate in each condition. During scanning, participants made monetary allocation between themselves and the co-player after receiving help in each round, which was used as an index of gratitude-induced reciprocity. After scanning, participants rated their feelings of gratitude and perceived kind intention for each condition. Behaviorally, echoing the find-remind-bind theory (Algoe, 2012), we predict that as participants would predict that the co-players were less likely to help under uncertain cost, when the co-players did decide to help in uncertain situations, participants' perceived kind intention of the co-players would increase, leading to increase in their gratitude and reciprocity. Neurally, we predict that gratitude ratings would be related to the activity in vmPFC (Fox et al., 2015; Kini et al., 2016; Karns et al., 2017; Yu et al., 2017, 2018; Zahn et al., 2009). Inspired by the evidence on one's own decision-making under uncertainty reviewed above, we hypothesize that there would be both shared and differential neural bases for evaluating other's altruistic decisions under uncertainty. On the one hand, the simulation theory (Gallese and Goldman, 1998; Ondobaka et al., 2017) posits that individuals may infer others' decision-making process based on their own interoceptive experiences. Therefore, it is reasonable to assume that brain structures involved in representing general uncertainty (i.e., lOFC and aINS) and those involved in ambiguity-sensitive (e.g., dmPFC) and risk-sensitive (e.g., striatal system) processing for one's own decisions might play a role when participants evaluating others' decisions under risk and ambiguity. On the other hand, evaluating others' altruistic decisons might recruit conflict-monitoring (e.g., dACC) and mentalizing (e.g., dmPFC) processes, which enable individuals to monitor the discrepancy between actual outcome and prediction (e.g., actual help under uncertainty vs. predicted low possibility of helping) and to infer the benefactor's intention to generate gratitude.

2. Materials and methods

2.1. Participants

A total of 42 graduate and undergraduate students were recruited for the fMRI experiment (Experiment 1). Four participants were excluded due to excessive head motion (>3 mm) in the fMRI scanner, leaving 38 participants (18 female, mean age 22 years, range 19–25) for further analyses. All participants were right-handed with normal or corrected-to-normal vision and with no self-reported history of neurological and psychological problems. In addition, 33 and 34 graduate and undergraduate students were recruited for two additional behavioral experiments, respectively (Experiments 2 and 3, see Supplementary Materials for details). Four and five participants were excluded in Experiments 2 and 3 respectively due to their failure to pass the manipulation check, leaving 29 participants (14 female, mean age 21 years, range 19–23) in Experiment 2 and 29 participants (16 female, mean age 20 years, range 18–25) in Experiment 3 for further analyses. The experiments were carried out in accordance with the Declaration of Helsinki and were approved by the Ethics Committee of the School of Psychological and Cognitive Sciences, Peking University. Informed written consent was obtained from each participant before the experiment.

2.2. Procedures

Overview. Experiment 1 consisted of three phases. In the first phase (pain titration), we measured each participant's pain threshold and determined the physical intensity (in mA) of the shocks in correspondence with the three levels of subjective pain experience. Moreover, participants made predictions of the co-players' helping rate in different conditions. In the second phase, the participants performed a social interactive task in the scanner, which was our main task. In the third phase, participants recalled each of the situations in the interactive task and rated their appraisals on the co-player's kind intention and feelings of gratitude. Several instructions and two additional behavioral experiments were included to exclude the potential confounding factors.

Pain titration. Upon arrival, each participant met three co-players (i.e., confederates). The participant was told that the three co-players and he/she would be randomly assigned to different roles according to their enrollment orders, and they would later play an interactive game together through intranet in separate rooms. Then the three co-players were led to another testing room. All the participants were told that pain stimulation would be carried out in the interactive task on all players, thus a calibration of pain level was performed prior to the task. An intra-epidermal needle electrode was attached to the back of the left hand of each participant for cutaneous electrical stimulation (Inui et al., 2002). The first pain stimulation was set as 8 repeated pulses, each of which was 0.2 mA and lasted 0.5-ms with a 10-ms interval in between. We gradually increased the intensity of each single pulse until the participant reported 9 on a 10-level pain scale (1 = not painful, 10 = intolerable, linearly increased). The participants reported that they could only experience the whole train of pulses as a single stimulation rather than as separate shocks. The 3 levels of pain stimulation used in the interactive task were calibrated to subjective pain ratings of "1," "5," and "9" (i.e., Level 1, 5, and 9 in the following procedures). All participants reported that the three levels of pain could be clearly distinguished from each other. Participants were told that these levels of pain would be used in the experiment, and the three levels of pain stimulation that each co-player would receive would be the ones that this co-player rated as "1, " "5," and "9" in pain intensity.

Social interactive task. After the calibration, each participant was instructed on the general rules of the following interactive task, which was designed based on previous studies on gratitude (Yu et al., 2017, 2018). Specifically, the participant was told that he or she was randomly assigned as the role to receive a pain stimulation of Level 9 in each round and was randomly paired to interact with one of the three co-players anonymously in the current round. This paired co-player could undertake an amount of pain stimulation in order to help the participant reduce the pain stimulation. No matter what cost the co-player would take, once being helped, the participant's pain stimulation would be reduced to Level 5; otherwise it would remain at Level 9. Each participant was informed that one of the three potential costs of help would be shown to the co-player, which was randomly chosen by the computer program: 1) the co-player would receive a pain stimulation of Level 5 for sure (Certain condition), 2) the co-player would receive a pain stimulation of either Level 1 or Level 9, each with 50% probability (Risky condition), and 3) the co-player would receive a pain stimulation of either Level 1 or Level 9, each with an unknown probability (Ambiguous condition). These three outcomes associated with the cost of help represented three levels of uncertainty and were set in accordance with the classic definition in neuroeconomic studies (Hsu et al., 2005). Moreover, each participant was informed that, in half of the rounds, the co-player could decide by him/herself whether to help the participant after being shown the cost of help (i.e., Human conditions). In the other half of rounds, the computer randomly decided whether the co-player would help the participant or not (i.e., Computer conditions). Importantly, however, unknown to the co-player but known to the participant, the actual pain stimulation that the co-player would receive in randomly chosen trials after the game was always at Level 5, regardless of the cost of help shown to the co-player. This manipulation was to ensure that the final costs of all co-players remained the same. Furthermore, since the participant was paired with only one co-player at one round, which might lead to the concern of unequal workload as the other two unpaired co-players would not be in a task state in the current round. Thus we told the participant that the unpaired co-players in each round would carry out tasks that were irrelevant to the interactive game during the un-pairing time.

In each round (Fig. 1), for each participant, after being paired with an anonymous co-player, he/she would see the cost of help (i.e., Certain, Risky, or Ambiguous pain stimulation) shown to the co-player along with the agent (i.e., the co-player or the computer) making the decision of whether to help (Decision period). After that, the decision on whether to help the participant, made by either the co-player or the computer, was revealed (Outcome period). At the end of each trial, the participant was asked to divide 20 points (1 point = 1 Yuan, 20 Yuan ~ 3 USD) between him/herself and the co-player paired in this trial (Allocation period). The money allocated to the co-player was treated as an index of gratitude-induced reciprocity. The participant was informed that his/her paired co-player was unaware of such allocation, eliminating the possibility that the co-player's decision to help was due to monetary concerns. The participant was informed that, after the experiment, five rounds paired with each co-player (15 rounds in total) would be randomly selected from all the rounds and realized to determine participant's and each co-player's final amounts of pain stimulation and monetary bonus. The participant's final pain stimulation depended on whether he/she was being helped in the selected trials. For each selected trial, once being helped, the participant's pain stimulation would be reduced to Level 5, regardless of the agent who made decisions or the Uncertainty level of the cost faced by the co-player; otherwise, it would remain at Level 9. The participants' final monetary bonuses were the average amount of endowment the participants allocated to themselves over the randomly selected trials. The pain stimulation and monetary bonus for each participant were realized at the end of the whole experiment.

There were 6 possible combinations of Agent and Uncertainty level of the cost faced by the co-player during the Help trials, forming a 2 (Agent: Human vs. Computer) × 3 (Uncertainty level of the cost faced by the co-player: Certain vs. Risky vs. Ambiguous amount of pain) within-subject design. Unbeknown to the participants, both the co-players' and the computer's decisions during the task were predetermined by a computer program with the helping rate of 50% of all the trials in each condition. The experiment consisted of 144 trials (12 trials for each of the above 6 Help conditions and 72 filler trials for Nohelp conditions). During the scanning, before and after the Decision period and the Outcome period, a fixation cross was presented for a variable interval ranging from 1 to 5 s for the purpose of fMRI signal deconvolution. The task was divided into 4 runs with equal number of trials for each condition in each run. Each run consisted of 36 trials in total and lasted for about 15 min. Trials within a run were pseudo-randomly mixed to ensure that no more than two consecutive trials were from the same condition. To avoid the influence of trial sequence, four sequences with pseudo-randomly order of trials were pre-determined and counterbalanced across participants.

Subjective ratings regarding the interactive task. Before the follow the displayed information. To avoid this situation, we did not execute pain stimulation online for each trial; instead, the participant was told that after the experiment was completed, five rounds of the game would be randomly selected and the amount of pain stimulation would be delivered as the one determined in the chosen trial. Consequently, participants were informed that the uncertainty of the cost that the co-players faced in Risky and Ambiguous trials remained the same throughout the task.

Further, to exclude the possibility that the prediction procedure before the interactive task might have influenced participants' performance during the task, we conducted an additional behavioral experiment (Experiment 2) in which the general procedure was the same as the one in Experiment 1 except that there was no prediction period before the task (See Supplementary Materials for details). Additionally, although participants could not learn the helping rate of each co-player, they might learn the actual helping rate of the whole co-player group; this learning might influence their performance. To rule out this possibility, we conducted another behavioral experiment (Experiment 3) in which participants predicted the possibility of being helped before the task and recalled the actual rate of being helped in each of the six Help conditions after the task (See Supplementary Materials for details).

In Computer conditions, the co-player was forced to accept the computer's decision with no clear voluntary intention to help. In contrast, in Human conditions, the co-player could take the uncertainty level of the cost into account and voluntarily decided whether to help the participant. Thus, we assumed that, in addition to the perceived co-player's cost at different levels of uncertainty, the inferred kind intention behind the co-player's decisions could be different for different levels of uncertainty in Human conditions; this difference might be driven by the difference in expected rate of being helped. Under such assumptions, in the following analyses, we treated Computer conditions as the control.

2.3. Neuroimaging data acquisition

Images were acquired through a 3.0 T MR scanner (GE MR750) with an eight-channel head coil. T2-weighted functional images were acquired in 40 axial slices parallel to the anterior commissural–posterior commissural line with no inter-slice gap, affording full-brain coverage. Images were acquired using an EPI pulse sequence (TR = 2000 ms; TE = 30 ms; flip angle = 90°; FOV = 192 mm × 192 mm; slice thickness = 3 mm). An ascending, interleaved slice acquisition order was used starting from the odd slices. A high-resolution, whole-brain structural scan (1 mm^3 isotropic voxel MPRAGE) was acquired after functional imaging.

2.4. Behavioral analyses

To examine whether the Uncertainty level of the cost faced by the co-player modulated participants' expected rate of being helped, perceived kind intention, gratitude feelings and subsequent reciprocal behaviors, we first fed participants' expected rate of being helped, perceived kind intention, ratings of gratitude and amount of monetary allocations into 2 (Agent: Human vs. Computer) × 3 (Uncertainty level of the cost faced by the co-player: Certain vs. Risky vs. Ambiguous pain stimulation) repeated-measures ANOVA and tested whether there were significant interactions between Agent and Uncertainty level on these variables, respectively.

Second, based on previous evidence (Ellsberg, 1961; Hogarth and Kunreuther, 1989; Hsu et al., 2005), we assumed that the level of uncertainty increased gradually along the Certain, Risky, and Ambiguous conditions. Thus, we coded these three conditions as parametric modulators (1, 2, and 3 for Certain, Risky and Ambiguous respectively) to test 1) whether the effect of Uncertainty level of the cost on participants' expected rate of being helped, perceived kind intention, ratings of gratitude and amount of monetary allocations exhibited linear trends in Human and Computer conditions; and 2) whether there were significant differences between such trends in these two conditions.

Third, to test whether the feeling of gratitude mediated the effect of Agent and the effect of Uncertainty level of the cost on subsequent reciprocity, we conducted a multivariate mediation model analysis using structural equation modeling through the 'lavaan' package in R software (Rosseel, 2012). In the model, Agent (Human defined as 1, and Computer defined as −1), Uncertainty level of the cost faced by the co-player (Certain, Risk, and Ambiguity defined as 1, 2, 3 respectively) and the interaction of the two factors were taken as independent variables, while ratings of gratitude and amounts of monetary allocation as the mediating variable and the dependent variable, respectively. To test whether perceived kind intention mediated the effect of Agent and the effect of Uncertainty level of the cost on gratitude, we conducted a multivariate mediation model analysis, taking experimental factors as independent variables, and taking ratings of perceived kind intention and gratitude as the mediating variable and the dependent variable, respectively. To test whether the expectation violation of being helped ("100% - expected rate of being helped" in Human conditions, and "50% - expected rate of being helped" in Computer conditions, as participants knew the rate of being helped is 50% when Computer made decisions) mediated the effect of Agent and Uncertainty level of the cost on perceived kind intention, similar multivariate mediation model analysis was conducted, with experimental factors as independent variables, expectation violation of being helped as the mediator and ratings of perceived kind intention as the dependent variable. All the variables of the multivariate mediation model were normalized within participant before the analyses. Coefficients for each path of the model were labeled on corresponding figures. For each path of the model, the values of c indicated the effect of the corresponding independent variable on dependent variable before controlling for the effect of mediator; the values of c' indicated the effect of the corresponding independent variable on dependent variable after controlling for the effect of mediator. A significant c' indicated a partial mediation while a non-significant c' indicated a complete mediation (James and Brett, 1984; Preacher and Hayes, 2008, 2004).

2.5. fMRI data preprocessing and analysis

Images were preprocessed and analyzed using the Statistical Parametric Mapping software SPM8 (Wellcome Trust Department of Cognitive Neurology, London, UK). Images were slice-time corrected (with the middle slice as the reference, i.e., the 39th slice), motion corrected, normalized to Montreal Neurological Institute space by affine transformation followed by nonlinear registration to an EPI template, spatially smoothed using an 8-mm full-width at half-maximum Gaussian filter, and temporally filtered using a high-pass filter with a 1/128 Hz cutoff. T1-based normalization was not applied as the field maps necessary to adjust geometric distortion of EPI relative to the T1 images were not obtained (Calhoun et al., 2017).

To investigate how participants evaluate co-players' altruistic decisions and generate gratitude, we performed whole-brain event-related fMRI analyses of participants' neural responses at the time when they viewed the co-player's or the computer's decisions that the co-player helped the participant (Outcome period). As participants were informed explicitly that the actual pain stimulation for both themselves and the co-players were the same in all Help conditions, the differences between conditions in this period should primarily result from the uncertainty of information known by the co-player and the agent who made the decision. Therefore, by comparing the differences between conditions in Outcome period, we were able to identify neural bases of how participants linked the consequence of decision ("help") with the level of uncertainty faced by the co-players and used this information to generate emotional responses and reciprocity. At whole-brain level, we conducted 1) parametric analysis to identify brain regions that were involved in participants' gratitude processing, and 2) conjunction analysis to further test whether there existed shared or differential neural substrates in processing others' altruistic decisions under risk and ambiguity. Results of whole-brain parametric and conjunction analyses were corrected for multiple comparisons with the threshold of peak-level $p < 0.001$ (uncorrected) and cluster-level $p < 0.05$ (FWE-corrected). Statistical neuroimaging maps are presented at this threshold unless otherwise noted.

Parametric analysis. To identify brain regions that were involved in participants' gratitude processing, in the first-level (participant-level) analysis, we built generalized linear model 1 (GLM1) employing parametric analysis. Specifically, we built a design matrix with separable run-specific partitions. The regressors in GLM1 for each run were defined as: Help condition (onsets of Outcome periods for all trials in the six Help conditions, spanning the 3 s duration of this event, R1), Nohelp condition (onsets of Outcome periods for Nohelp trials, duration 3 s, R2), Decision period (the period that the co-player or the computer was making decision, duration 2 s, R3), and Allocation period (the period for allocation, spanning from the start of this event to the time that the participants responded, i.e., reaction time, R4). Six movement parameters were included as regressors of no interest (R5-R10) for each run as well. Four regressors modeling the average activity in each run were included at the end of the design matrix. All regressors were convolved with a canonical hemodynamic response function (HRF). The gratitude ratings for the corresponding conditions were defined as a parametric modulator under Help conditions. For each participant, the beta map for this parametric modulator was fed into second-level (group-level) one-sample t tests. Positive and negative effects of this parametric modulator were defined to identify brain areas involved in gratitude-related processing in Help conditions.

Conjunction analysis. Although we have identified brain regions corresponding to gratitude processing, the activation pattern of each region might vary under different level of uncertainty. For example, when the co-player decided to help, compared with the one in Certain condition, the activity of area A might be significantly greater in both the Risky and the Ambiguous conditions (i.e., this region might be involved in the processing of general uncertainty), while area B might show significantly greater activation in the Ambiguous condition only (i.e., this region might be sensitive to the processing of ambiguity). Therefore, we conducted conjunction analyses to further test whether there existed shared or differential neural bases in processing others' altruistic decisions under risk and ambiguity. Specifically, we aimed to identify regions involved in general-uncertainty-related, ambiguity-sensitive, and risk-sensitive processing respectively when participants received co-players' voluntary help, and to test whether these processes were specific to Human conditions. We built a design matrix with separable run-specific partitions in GLM2. In the first-level analysis, for each run, we modeled Help trials with six separate regressors corresponding to the six conditions, spanning from the time the decision on whether to help was revealed to the end of this event (3 s): Human_Certain, Human_Risky, Human_Ambiguous, Computer_Certain, Computer_Risky, and Computer_Ambiguous (R1 to R6). Other included regressors were: Nohelp condition (six separate regressors corresponding to Help condition, onset of Outcome periods for Nohelp trials, R7-R12), Decision period (onset of Decision period, R13), and Allocation period (the period for allocation, R14). Six movement parameters were also included as regressors of no interest (R15-R20) for each run. Four regressors modeling the average activity in each run were included at the end of the design matrix. All regressors were convolved with a canonical hemodynamics response function (HRF).

We defined four contrasts corresponding to four simple effects in Human conditions when participants were presented that the co-player decided to help: Human_Ambiguous > Human_Certain, Human_Risky > Human_Certain, Human_Ambiguous > Human_Risky, and Human_Risky > Human_Ambiguous in Help conditions. Then, we conducted three conjunction analyses to identify the neural response of general-uncertainty-related, ambiguity-sensitive and risk-sensitive brain regions in Human conditions: (1) general-uncertainty-related: [Human_Ambiguous > Human_Certain] ∩ [Human_Risky > Human_Certain] (i.e., Human_Ambiguous > Human_Certain in conjunction with Human_Risky > Human_Certain), (2) ambiguity-sensitive: [Human_Ambiguous > Human_Risky] ∩ [Human_Ambiguous > Human_Certain], and (3) risk-sensitive: [Human_Risky > Human_Ambiguous] ∩ [Human_Risky > Human_Certain].

To test whether these processes were specific to Human conditions, the beta values in these six Help conditions for each brain region identified in conjunction analyses (i.e., the average beta value of 27 voxels around the peak coordinate of each region) were extracted and fed into 2 (Agent: Human vs. Computer) × 3 (Uncertainty level of the cost faced by the co-player: Certain vs. Risky vs. Ambiguous pain stimulation) repeated-measures ANOVA; the important issue here was whether there were significant interactions between Agent and Uncertainty level on these beta values. This method of identifying regions of interest (ROIs) in the analysis for crucial conditions and extracting beta values in ROIs to test their specificities has been widely used in social neuroimaging studies (e.g., Chung et al., 2015; de Berker et al., 2019; Gao et al., 2018; Lockwood et al., 2018). A same set of conjunction analyses were conducted for Computer conditions. Moreover, the same analyses were conducted for Nohelp conditions to test whether the brain activities observed in Help conditions were also activated in Nohelp conditions or were specific to Help conditions.

To test whether there existed other general-uncertainty-related, ambiguity-sensitive or risk-sensitive regions that failed to survive thresholding in conjunction analyses, we examined whether regions identified by the Human_Ambiguous > Human_Certain contrast were significant in the Human_Risky > Human_Certain contrast, and whether regions identified by the Human_Risky > Human_Certain contrast were significant in the Human_Ambiguous > Human_Certain contrast after performing small volume correction (SVC). For SVC, the small volumes were defined as spheres with 10 mm radius centered on the peak coordinate of each region, and were identified with the threshold of peak-level $p < 0.05$ (FWE-corrected).

Individual differences analysis. To further test whether the brain regions identified in the conjunction analysis were related with the processing of gratitude under both risk and ambiguity conditions, only under risk condition, or only under ambiguity condition, we conducted correlation analysis to test whether the differences in gratitude ratings between Human_Ambiguous and Human_Certain conditions, and between Human_Risky and Human_Certain conditions were correlated with the differences in brain activities across the corresponding conditions. To guard against spurious associations and to further validate our findings, we conducted a Monte Carlo permutation test for each correlation. This method is a widely accepted correction approach in statistical testing (Belmonte and Yurgelun-Todd, 2001; Camargo et al., 2008). By resampling the data of beta values with 10,000 permutations, we computed the regression coefficient in each shuffled sample and the probability of the estimated regression coefficients being greater than the observed regression coefficient (i.e., permutation p).

Neurosynth meta-analytical decoding. To investigate whether the neural responses in ambiguity-sensitive and general-uncertainty processing identified in conjunction were associated with differential psychological components, we employed the online platform Neurosynth Image Decoder (neurosynth.org; Yarkoni et al., 2011) to meta-analytically decode the unthresholded T maps of different contrasts. This analysis allowed us to quantitatively evaluate the level of similarity between any Nifti-format brain images and each selected meta-analytical image generated by the Neurosynth database, indicated by the effect of spatial correlation (r value) between the two maps. We decoded unthresholded contrast maps corresponding to [Human_Ambiguous > Human_Certain], [Human_Risky > Human_Certain] and [Human_Ambiguous > Human_Risky] using reverse inference meta-analytical maps to identify the shared and differential cognitive processes associated with ambiguity-sensitive and general-uncertainty-related brain activations. If a term of psychological component was general-uncertainty-related, the similarity between this term and contrasts [Human_Ambiguous > Human_Certain] as well as [Human_Risky > Human_Certain] would be higher than the similarity between this term and contrast [Human_Ambiguous >

Human_Risky]. Similarly, if a term of psychological component was related to ambiguity-sensitive processing, the similarity between this term and contrasts [Human_Ambiguous > Human_Certain] as well as [Human_Ambiguous > Human_Risky] would be higher than the similarity between this term and contrast [Human_Risky > Human_Certain]. Psychological terms were selected based on previous reviews on uncertainty processing, social cognition and basic cognition, including: 1) five terms related to uncertainty processing ("uncertain," "risky," "ambiguous," "fear," and "anxiety") (Grupe and Nitschke, 2013; Levy, 2017; Morriss et al., 2019; Rosen and Donley, 2006); 2) four terms related to social cognition ("mentalizing," "social," "imitation," and "empathy") (Adolphs, 2009); and 3) nine terms related to basic cognition ("memory," "monitoring," "conflict," "executive control," "inhibition," "attention," "imagine," "switching," and "salience network") (Barrett and Satpute, 2013).

3. Results

3.1. Effects of Agent and Uncertainty level on monetary allocation, gratitude and perceived kind intention

Two (Agent: Human vs. Computer) by three (Uncertainty level: Certain vs. Risky vs. Ambiguous) repeated measures analysis of variance (ANOVA) was conducted, respectively, for the monetary allocation when participants received help, and self-reported gratitude and perceived kind intention in the post-scan questionnaires, and the expected rate of being helped before the scan. Significant main effects of Agent were found for the amount of monetary allocation ($F_{1, 37} = 57.31$, $p < 0.001$, Fig. 2A; see Supplementary Materials and Fig. S1 for monetary allocation in Nohelp trials), self-reported gratitude ($F_{1, 37} = 68.08$, $p < 0.001$, Fig. 2B), and perceived kindSnm61.23770TD(68.08,)Tj/F13.94D(2p11472)]4TD015193.9464447.633Tm[(1,)-628.6(37)]TJ/F101Tf7.0w13.1653439.9369Tr

although marginally significant for kind intention: $t_{37} = 2.40$, $p = 0.065$). The expected rate of being helped was higher in Human_Certain condition than in Human_Risky condition ($t_{37} = 4.62$, $p < 0.001$) and Human_Ambiguous condition ($t_{37} = 5.73$, $p < 0.001$), yet there was no difference between the latter two conditions ($t_{37} = 2.18$, $p = 0.107$). In contrast, the effects of Uncertainty level were much weaker in Computer conditions (allocation: $F_{2, 74} = 3.86$, $p = 0.034$; gratitude: $F_{2, 74} = 6.68$, $p = 0.002$; kind intention: $F_{2, 74} = 2.79$, $p = 0.068$; expected rate of being helped: $F_{2, 74} = 1.00$, $p = 0.373$).

Linear trend analyses showed that, participants' amounts of monetary allocation, ratings of gratitude and perceived kind intention increased linearly from Human_Certain, Human_Risky to Human_Ambiguous conditions (allocation: $F_{1, 37} = 35.91$, $p < 0.001$; gratitude: $F_{1, 37} = 35.39$, $p < 0.001$; kind intention: $F_{1, 37} = 20.43$, $p < 0.001$; expected rate of being helped: $F_{1, 37} = 29.51$, $p < 0.001$). These linear trends were either absent or significantly reduced in Computer conditions (allocation: $F_{1, 37} = 5.61$, $p = 0.023$; gratitude: $F_{1, 37} = 12.86$, $p = 0.001$; kind intention: $F_{1, 37} = 2.79$, $p = 0.103$; expected rate of being helped: $F_{1, 37} = 1.00$, $p = 0.324$). Direct comparisons showed that the differences between Human and Computer conditions also exhibited a linearity effect over Uncertainty level (i.e., significant Agent by Uncertainty level interaction) on the amount of monetary allocation ($F_{1, 37} = 17.25$, $p < 0.001$), the rating of gratitude ($F_{1, 37} = 14.69$, $p < 0.001$), the rating of perceived kind intention ($F_{1, 37} = 13.73$, $p = 0.001$), and the expected rate of being helped ($F_{1, 37} = 28.60$, $p < 0.001$), indicating that the linearity effects over Uncertainty level were significantly larger in Human conditions than the ones in Computer conditions.

Multivariate mediation analyses were conducted to test whether the expectation violation of being helped contributed to the increase in participants' perceived kind intention of the co-players, and led to the increase in their feelings of gratitude and reciprocity. Firstly, results showed that the rating of gratitude significantly mediated the effect of experimental manipulations (Agent, Uncertainty level of the cost faced by the co-player and their interaction) on the amount of monetary allocation, with normalized coefficient of overall mediating effect = 0.278, $p < 0.001$, $c = 1.135$, $p < 0.001$, $c' = 0.857$, $p < 0.001$, partial mediation. The normalized coefficients of the mediating effect of rating of gratitude on Agent to the amount of monetary allocation, Uncertainty level of cost to the amount of monetary allocation, and Agent * Cost interaction to the amount of monetary allocation were 0.177, $p < 0.001$, $c' = 0.515$, $p < 0.001$, partial mediation; 0.072, $p = 0.001$, $c' = 0.221$, $p < 0.001$, partial mediation; 0.029, $p = 0.027$, $c' = 0.121$, $p = 0.005$, partial mediation, respectively (see Fig. 2E for the path coefficients). After controlling for the effects of Agent, Uncertainty level of the cost faced by the co-player and their interaction, the correlation between gratitude and monetary remained significant ($\beta = 0.133$, $t = 2.016$, $p = 0.045$). These findings support the hypothesis that the feeling of gratitude serves as a moral motive, which motivates behavioral changes when receiving help from benefactors who are faced with different uncertainty levels of cost.

Secondly, the multivariate mediation model analysis showed that the rating of perceived kind intention significantly mediated the effect of experimental manipulations on rating of gratitude, with normalized coefficient of overall mediating effect = 0.455, $p < 0.001$, $c = 1.157$, $p < 0.001$, $c' = 0.702$, $p < 0.001$, partial mediation. The normalized coefficients of the mediating effect of rating of perceived kind intention on Agent to gratitude rating, Uncertainty level of cost to gratitude rating, Agent * Cost interaction to gratitude rating were 0.327, $p < 0.001$, $c' = 0.391$, $p < 0.001$, partial mediation; 0.074, $p < 0.001$, $c' = 0.230$, $p < 0.001$, partial mediation; 0.054, $p = 0.003$, $c' = 0.081$, $p = 0.042$, partial mediation, respectively (see Fig. 2F for the path coefficients).

Thirdly, the expectation violation of being helped significantly mediated the effect of experimental manipulations on the rating of kind intention, with normalized coefficient of overall mediating effect = 0.411, $p = 0.002$, $c = 1.118$, $p < 0.001$, $c' = 0.708$, $p < 0.001$, partial mediation. The normalized coefficients of the mediating effect of expectation violation on Agent to kind intention rating, Uncertainty level of cost to kind intention rating, and Agent * Cost interaction to kind intention rating were 0.304, $p = 0.002$, $c' = 0.500$, $p < 0.001$, partial mediation; 0.053, $p = 0.004$, $c' = 0.130$, $p = 0.001$, partial mediation; 0.054, $p = 0.004$, $c' = 0.078$, $p = 0.055$, marginal complete mediation, respectively (see Fig. 2G for the path coefficients). These results support the hypothesis that as participants predicted that the co-players were less likely to help under uncertain cost, when co-players did decide to help in uncertain situations, the participants' perceived kind intention inferred from co-players increased as a result, leading to the increased feeling of gratitude.

To be noted, our behavioral results were replicated in the additional behavioral experiment (Experiment 2) in which participants did not predict the possibility of being helped before the interactive task. Significant interactions between Agent and Uncertainty level were observed for all of the three measures (allocation: $F_{2, 56} = 5.37$, $p = 0.012$, Fig. S2A; gratitude: $F_{2, 56} = 4.92$, $p = 0.011$, Fig. S2B; kind intention: $F_{2, 56} = 5.89$, $p = 0.009$, Fig. S2C). No significant Agent * Uncertainty level * Experiment (Experiment 1 vs. Experiment 2) interactions was observed when data of Experiments 1 and 2 were combined, allocation: $F_{2, 130} = 1.23$, $p = 0.291$; gratitude: $F_{2, 130} = 2.00$, $p = 0.139$; kind intention: $F_{2, 130} = 0.10$, $p = 0.886$, indicating that the prediction procedure in the fMRI experiment (Experiment 1) did not influence participants' performance during the task.

Moreover, in the third experiment (Experiment 3) in which participants made predictions before the task and recalled the actual rate of being helped later for each of the six Help conditions, no signi similar pattern was observed for gratitude ratings, although it did not reach statistical significance (Fig. S4B; $F_{2,\ 188} = 2.63$, $p = 0.074$). Moreover, although we did not find a significant Agent * Uncertainty level * gender interaction, we found a stronger main effect of Agent and a stronger main effect of Uncertainty level in intention ratings in females than in males (Fig. S4C; Agent * gender interaction: $F_{1,\ 93} = 4.80$, $p = 0.031$; Uncertainty level * gender interaction: $F_{2,\ 186} = 3.91$, $p = 0.022$). These results indicated that compared with male participants, female participants' reciprocity, gratitude and perceived kind intention from help were likely to be more sensitive to Agent and Uncertainty level.

3.2. Neural bases of the gratitude-related processing

At the neural level, we focused on participants' neural responses at the time when they viewed the co-player's decision to help, as in this period participants were able to link the consequence of decision ("help") with the level of uncertainty faced by the co-players and to use this information to generate emotional responses and reciprocity. Using gratitude ratings as a first-level parametric modulator, we first identified the voxels in which neural responses increased as the gratitude increased when participants receiving help. This contrast revealed activations in brain regions including middle cingulate cortex (MCC), vmPFC (extending to dmPFC), inferior temporal gyrus (ITG), bilateral lOFC (extending to aINS), ventral striatum (extending to amygdala), dlPFC, precuneus and inferior parietal gyrus (IPG) (Fig. 3, Table 1). We observed no region whose activation was negatively modulated by the rating of gratitude.

3.3. Brain regions underlying general-uncertainty-related and ambiguity-sensitive processing of others' altruistic decisions

We conducted conjunction analyses to further investigate whether the regions related to gratitude processing were involved in general-uncertainty-related, ambiguity-sensitive or risk-sensitive processing, and test whether these processes were specific to Human conditions. The conjunction analysis on Human_Ambiguous > Human_Certain contrast and Human_Risky > Human_Certain contrast revealed significant activations in right lateral OFC [lOFC: 33, 44, −5] extending to aINS, fusiform [-30, −73, −17], middle occipital gyrus [-30, −82, 4 and 33, -70, 13], and cerebellum [36, −43, −32] (Fig. 4A, Table 2). In contrast, no region survived the whole-brain threshold in the same conjunction analysis for Computer conditions. To further confirm that the activation of lOFC/aINS was only present in Human but not in Computer conditions, we extracted and plotted the beta estimates of lOFC/aINS. Two (Agent: Human vs. Computer) by three (Uncertainty level: Certain vs. Risky vs. Ambiguous) repeated measures ANOVA on lOFC betas revealed a significant interactions effect, $F_{2,\ 74} = 4.67$, $p = 0.012$. Specifically, significant differences were observed between the three levels of uncertainty in Human conditions ($F_{2,\ 74} = 6.66$, $p = 0.002$) but not in Computer conditions ($F_{2,\ 74} = 0.49$, $p = 0.612$). In Human conditions, compared with Human_Certain condition, lOFC was activated more strongly in Human_Ambiguous condition ($t_{37} = 3.61$, $p = 0.001$) and in Human_Risky condition ($t_{37} = 2.75$, $p = 0.009$). The difference between Human_Risky and Human_Ambiguous conditions was not significant ($t_{37} = 0.63$, $p = 0.530$) (Fig. 4B). Moreover, the differences in lOFC activations between Human_Ambiguous and Human_Certain conditions and between Human_Risky and Human_Certain conditions were positively correlated with the differences in gratitude ratings between the corresponding conditions (Fig. 4C), $r = 0.332$, $p = 0.042$, and $r = 0.330$, $p =$
5TD[(5])-323.7(extending)-318.6(to.9934J/F(10],eveF4co1.315940TDF101Tf11.2

Table 1
Results of whole-brain parametric analysis.

Cluster Number	Regions	Hemisphere	t value	Cluster size (voxels)	MNI coordinates		
					x	y	z
Brain regions sensitive to gratitude ratings.							
1	MCC	R	6.28	1769	3	−13	34
2	dmPFC	R	5.93	2543	6	44	46
	vmPFC	R	5.70		3	44	4
3	Inferior temporal gyrus	R	5.85	920	54	−31	−23
4	lOFC-aINS	R	5.52	412	42	26	−14
	Striatum/amygdala	R	4.32		12	17	−8
5	dlPFC	R	4.69	399	45	5	55
6	lOFC-aINS	L	4.51	352	−48	23	−14
7	Precuneus	R	4.35	147	3	−76	49
8	Inferior parietal gyrus	R	4.22	147	36	−52	55

Note: dmPFC, dorsal medial prefrontal cortex; vmPFC, ventral medial prefrontal cortex; lOFC, lateral orbitofrontal cortex; aINS, anterior insula; MCC, middle cingulate cortex; dlPFC, dorsal lateral prefrontal cortex.

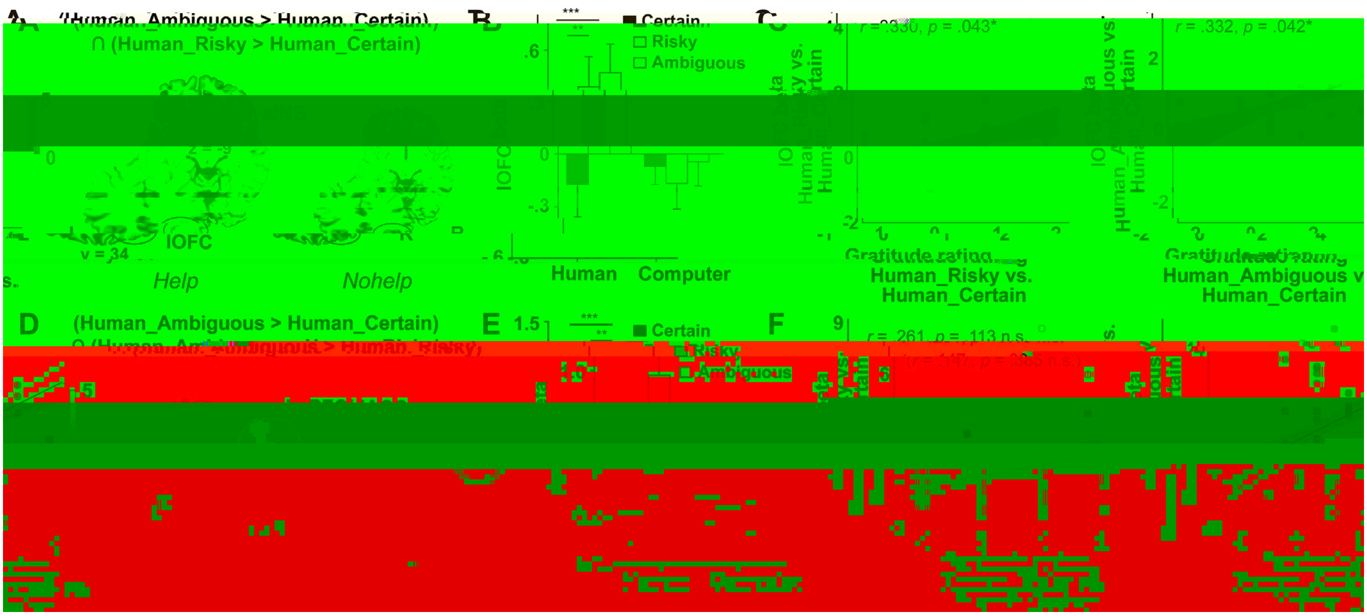

Fig. 4. Brain regions activated in the conjunction analysis. (A) Brain regions activated in [Human_Ambiguous > Human_Certain] ∩ [Human_Risky > Human_Certain], indicating the involvement of these regions in general-uncertainty-related processing. (B) Parameter estimates (β values) corresponding to six conditions were extracted from right lOFC. Error bars indicate standard error of means. (C) The differences in lOFC activities between Human_Ambiguous and Human_Certain conditions ($r = 0.332$, $p = 0.042$), and between Human_Risky and Human_Certain conditions ($r = 0.330$, $p = 0.043$) were positive correlated with the differences in gratitude ratings between corresponding conditions. (D) Brain regions activated in [Human_Ambiguous > Human_Certain] ∩ [Human_ Ambiguous > Human_ Risky], indicating the involvement of these regions in ambiguity-sensitive processing. (E) Parameter estimates (β values) corresponding to six conditions for dmPFC. (F) The differences in dmPFC activities between Human_Ambiguous and Human_Certain conditions ($r = 0.386$, $p = 0.017$), but not Human_Risky and Human_Certain ($r = 0.261$, $p = 0.113$, taking out 2 outliners: $r = 0.147$, $p = 0.385$) were positive correlated with the differences in gratitude ratings between corresponding conditions. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

lOFC (see Table S1 for detailed statistics).

No significant activation was found in conjunction analysis on the Human_Risky > Human_Ambiguous contrast and the Human_Risky > Human_Certain contrast (i.e. risk-sensitive processing). We also tested the possibility of subthreshold risk-sensitive effect by estimating the Human_Ambiguous > Human_Certain contrast with the group-level map of Human_Risky > Human_Certain contrast (using a liberal masking threshold $p < 0.05$) as exclusive mask. The activations of this contrast were similar to the results of the conjunction analysis on the Human_Ambiguous > Human_Certain contrast and the Human_Ambiguous > Human_Risky contrast, involving wide range of clusters (Fig. S5; including aINS, dlPFC, temporoparietal junction and calcarine). This analysis ruled out potential subthreshold risk-sensitive effects.

To further test whether there exist other general-uncertainty-related, ambiguity-sensitive or risk-sensitive regions that failed to survive thresholding in conjunction analyses, we examined whether any region identified by Human_Ambiguous > Human_Certain contrast could survive small volume correction (SVC) in Human_Risky > Human_Certain contrast, and whether any region identified by Human_Risky > Human_Certain contrast could survive SVC in Human_Ambiguous > Human_Certain contrast. Results of SVC were consistent with those of conjunction analyses, showing the involvement of lOFC/aINS in general-uncertainty-related processing and the involvement of dmPFC/dACC in ambiguity-sensitive processing. No specific risk-sensitive region was observed (see Supplementary Materials and Table S2 for details).

As a comparison, the same set of conjunction analyses conducted for NoHelp trials revealed no above-threshold activations (Fig. 4, A and D), indicating that the observed activations might be closely related to Help rather than Nohelp conditions. However, it was not sufficient to demonstrate that the neural processes observed in Help trials were specific to receiving help. One needs to show "separate modifiability" (e.g., Woo et al., 2014) of two constructs (e.g., Help vs. NoHelp) to

Table 2
Results of conjunction analysis.

Cluster number	Regions	Hemisphere	t value	Cluster size (voxels)	MNI coordinates		
					x	y	z
(Human_Ambiguous > Human_Certain) ∩ (Human_Risky > Human_Certain)							
1	Fusiform	L	4.94	233	−30	−73	−17
2	Middle occipital gyrus	L	4.92	261	−30	−82	4
3	Cerebellum	R	4.84	173	36	−43	−32
4	lOFC/aINS	R	4.56	134	33	44	−5
5	Middle occipital gyrus	R	4.56	339	33	−70	13
(Human_Ambiguous > Human_Certain) ∩ (Human_Ambiguous > Human_Risky)							
1	dACC	R	4.77	188	6	29	34
	dmPFC		3.57		0	29	55
2	Inferior temporal gyrus	R	4.72	135	57	−28	−23
3	Inferior temporal gyrus	L	4.46	123	−63	−28	−26
4	Thalamus		4.38	157	0	−52	10
5	Cerebellum	R	4.22	121	6	−82	−23

Note: lOFC, lateral orbitofrontal cortex; aINS, anterior insula; dmPFC, dorsal medial prefrontal cortex; dACC, dorsal anterior cingulate cortex.

demonstrate specificity, which is beyond the scope of the current study. Moreover, since the current study aimed to investigate how other's altruistic decisions under uncertainty influence individuals' gratitude, no post-hoc appraisals or emotion ratings were obtained for Nohelp conditions. Therefore, we were unable to build specific hypotheses for the neural analyses of Nohelp conditions based on behavioral observations. Given the potential relationship between negative prediction error and anger (Chang et al., 2015; Chang and Jolly, 2018), it is possible that in addition to the decrease of gratitude, co-players' decisions of no-help or help withdraw may induce individuals' other emotions, such as anger. Future studies specifically designed to evaluate no-help or help withdraw are needed.

Another possibility is that lOFC and dmPFC were also involved in the recognition and processing of uncertainty before being helped and were not specific to the gratitude-related uncertainty processing after being helped. To test this possibility, for the Decision period in which participants received the information of the condition but did not know the co-player's decision, we conducted the same set of conjunction analyses as we did for the Outcome period. We also conducted the same set of conjunction analyses for Allocation period as for Outcome period. A variable interval ranging from 1 to 5 s was inserted before and after Outcome period in each trial, which effectively avoided multicollinearity between regressors in Decision, Outcome and Allocation periods (Fig. S6). Results showed that no region survived the whole-brain threshold in any of the three conjunction analyses in Decision period or Allocation period. We also extracted beta values in lOFC and dmPFC for the six Help conditions in Decision period and Allocation period, based on coordinates obtained for the Outcome period. In contrast to Outcome period, neither the activity in lOFC (Decision: $F_{2,\,74} = 0.58$, $p = 0.563$; Allocation: $F_{2,\,74} = 0.63$, $p = 0.537$) nor the activity in dmPFC (Decision: $F_{2,\,74} = 0.43$, $p = 0.656$; Allocation: $F_{2,\,74} = 0.33$, $p = 0.718$) showed significant interactions between Agent and Uncertainty level in Decision period or Allocation period. These results highlighted the role of lOFC and dmPFC in gratitude-related uncertainty processing after being helped.

3.4. Differential psychological components associated with general-uncertainty-related and ambiguity-sensitive processing

To investigate whether the general-uncertainty-related processing and the ambiguity-sensitive processing of other's altruistic decisions were associated with differential psychological components, we employed the online platform Neurosynth Image Decoder (neurosynth.org; Yarkoni et al., 2011) to meta-analytically decode the unthresholded T map of different contrasts (see Neurosynth meta-analytical decoding). Although no firm conclusion linking each processing with one or more psychological components could be drawn specifically, this analysis could help us infer the psychological components associated with each contrast based on the meta-analytical maps, rather than making reverse-inference based on potentially biased selections of literature (Chang et al., 2013; Yarkoni et al., 2011). Results demonstrated that the general-uncertainty-related and ambiguity-sensitive processing might be associated with differential psychological components. Compared with the pattern of Human_Ambiguous > Human_Risky contrast, activation patterns of Human_Ambiguous > Human_Certain contrast and Human_Risky > Human_Certain contrast showed more association with meta-analytical patterns of "fear" and "anxiety" terms, indicating that compared with Certain condition, the processing in Risky and Ambiguous conditions (i.e., general-uncertainty-related processing) were more closely associated with fear- and anxiety-related processes (Fig. 5). Meanwhile, compared with the pattern of Human_Risky > Human_Certain contrast, the activation patterns of Human_Ambiguous > Human_Certain contrast and Human_Ambiguous > Human_Risky contrast were more closely associated with meta-analytical patterns of "mentalizing," "memory," "conflict," and "monitoring", suggesting that compared with Certain and Risky conditions, the processing in Ambiguous condition (i.e., ambiguity-sensitive processing) was more closely associated with mentalizing-, memory- and conflict-monitoring-related processes (Fig. 5).

To exclude the possibility that results of the whole-brain meta-analytical decoding were driven mainly by effects in posterior regions identified in conjunction analyses (i.e., fusiform, middle occipital gyrus, inferior temporal gyrus, thalamus, and cerebellum) rather than dmPFC/dACC and lOFC/aINS, we re-conducted meta-analytical decoding using a combined exclusive mask of the posterior regions defined by the Automated Anatomical Labeling (AAL; Tzourio-Mazoyer et al., 2002). The pattern of results remained the same after excluding activations in these regions (Fig. S7; correlation between results of the whole-brain analysis and the analysis with exclusive mask: $r = 0.984$, $p < 0.001$), indicating that the results of the whole-brain meta-analytical decoding were not simply driven by effects in the posterior regions. To be noted, this did not indicate that the identified psychological components were driven only by activities in dmPFC/dACC or lOFC/aINS, since the meta-analytical decoding is most effective at whole-brain level and reflects the whole-brain processing of each psychological component (Chang et al., 2013; Yarkoni et al., 2011). Therefore, the meta-analytical decoding provided further evidence suggesting how extensive regions in the brain responded together with the regions identified in the above analyses to support the evaluations on others' altruistic decisions under risk and ambiguity.

4. Discussion

When deciding whether to behave altruistically, individuals need to

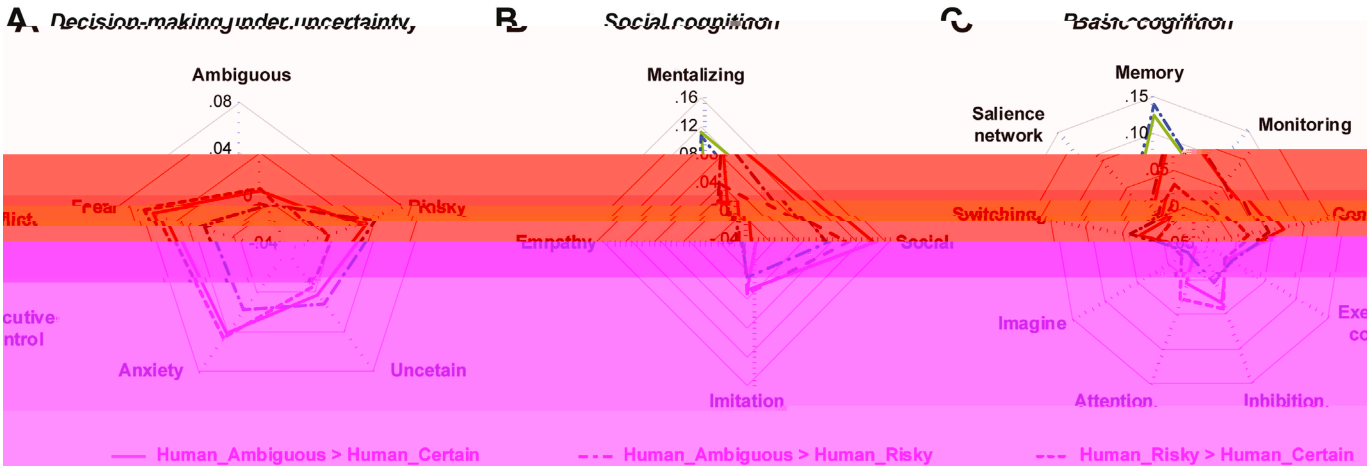

Fig. 5. Meta-analytical decoding results. The green solid, blue dot-dash, and red dash lines correspond to the similarities between the meta-analytical maps of terms of psychological components generated from Neurosynth database and Human_Ambiguous > Human_Certain, Human_Ambiguous > Human_Risky, and Human_Risky > Human_Certain contrasts, respectively. Compared with the one of Human_Ambiguous > Human_Risky contrast, activation patterns of Human_Ambiguous > Human_Certain contrast and Human_Risky > Human_Certain contrast showed more association with meta-analytical patterns of "fear" and "anxiety" terms (with both the green solid line and red dash line extending further than the blue dot-dash line at those dimensions). Compared with the one of Human_Risky > Human_Certain contrast, the activation patterns of Human_Ambiguous > Human_Certain contrast and Human_Ambiguous > Human_Risky contrast were associated more with meta-analytical patterns of "mentalizing," "memory," "conflict," and "monitoring" (with both the blue dot-dash line and green solid line extending further than the red dash line at those dimensions).

weigh the benefit of altruistic choice against the cost in various circumstances (Penner et al., 2004), in which the cost is usually uncertain. Although a number of studies have investigated how participants make altruistic decisions under uncertainty (e.g., Hu et al., 2017; Vives and Feldmanhall, 2018), it remains largely unknown as to how individuals perceive and respond to others' altruistic behaviors under different uncertain situations (e.g., ambiguity vs. risk). The current study contributes to the understanding of this issue by providing both behavioral and neuroimaging evidence in the context of interpersonal gratitude. Our results suggest that 1) perceived kind intention is a mediating factor for beneficiary's generation of gratitude when faced with other's help under uncertain cost; 2) there are both shared and differential neurocognitive processes of gratitude in response to benefactor's altruistic decisions in risky and ambiguous conditions.

4.1. Perceived kind intention as a mediating factor for the feeling of gratitude

Intention inference is crucial for social interactions (Falk et al., 2008; Falk and Fischbacher, 2006; Sanfey, 2007). According to theories of reciprocity (Fehr and Gächter, 1998; Fehr and Schmidt, 2006; Matthew Rabin, 1993), when an individual perceives the care and benevolence from another person, the utility of acting kindly towards this person increases. In studies of social psychology, individuals are more likely to trust and cooperate with those who engage in altruistic interactions under uncertainty than they do under certainty, as decisions under uncertainty are rarer than decisions under certainty (Hu et al., 2017; Vives and Feldmanhall, 2018) and reflect the concern about others' intention (Capraro and Kuilder, 2016; Jordan et al., 2016; Pérez-Escudero et al., 2016). Consistent with these studies, the current results provide novel evidence demonstrating that, the degree of beneficiary's gratitude varied as a function of the level of uncertainty in the cost faced by the benefactor, which was mediated by the perceived kind intention behind the help decision. In uncertain situations where the benefactor was thought to be less likely to help, the beneficiary perceived the benefactor to be kinder. In line with the find-remind-and-bind theory (Algoe, 2012; Algoe et al., 2013, 2008; Algoe and Stanton, 2012), our results demonstrate a crucial role of intention inference in generating gratitude, reflecting a significant social function of gratitude from the perspective of evolution. That is, the help stemming from sincere intention without calculating the cost of help, rather than from the precise calculation of the cost (and the outcome), functions to signal a high-quality, and perhaps long-term, cooperative relationship that should be responded with gratitude and reciprocity.

A number of studies have investigated how the three major antecedents (i.e., benefactor's intention, benefactor's cost, and the value of benefit) independently influence beneficiary's degree of gratitude (Tesser, 1968; McCullough et al., 2001; Tsang, 2007; Yu et al., 2017, 2018). Although the benefactor's actual cost was the same in the current study, our results indicated a close relationship between benefactor's kind intention and cost: information regarding the benefactor's cost contributed to the beneficiary's perception of the benefactor's intention, subsequently influencing beneficiary's gratitude. This is consistent with Algoe et al. (2008) which showed that perceived care mediated the effect of gift costs on gratitude rating in gift-giving contexts. However, most other studies either investigated how the three antecedents influenced gratitude independently or did not examine the relationships between the perceived intention and other antecedents directly. The question as to whether these three antecedents influence gratitude independently remains unclear. Moreover, here we found that the participants' gratitude and reciprocity also increased as a function of Uncertainty level in Computer conditions, in which the co-players' "help" decision was made by the computer (i.e., unintentional). This result indicated that, in this context of forced help, there might exist other factors influencing gratitude and reciprocity independently of the perceived kind intention, such as the perceived benefactor's psychological burden driven by uncertainty. Yet the psychological bases of gratitude in the context of forced help have rarely been investigated and deserve further research effort.

4.2. Shared neurocognitive processes responding to benefactor's altruistic decisions under risk and ambiguity

In the conjunction analysis, we found that lOFC extending to aINS was activated more in both the Risky and the Ambiguous conditions than in the Certain condition when the co-player decided to help, indicating the involvement of lOFC and aINS in general-uncertainty-related processing. These brain regions have been suggested to be associated with various emotional and cognitive functions involved in processing general uncertainty during one's own decision-making. For example, lOFC has been shown to be correlated with uncertainty processing and uncertainty aversion in both risky and ambiguous situations when individuals make decision under uncertainty (Christopoulos et al., 2009; Hsu et al., 2005 ;

decision making but they failed to survive the whole-brain threshold. On the other hand, we compared the neural processing pattern for other's risk and ambiguity in the current study with the meta-analytical maps for these terms in studies related to one's own uncertainty. Weak spatial similarities (near zero) were observed between the meta-analytical map of "ambiguous" term and the map of Human_Ambiguous > Human_Certain contrast, between the meta-analytical map of "risky" term and the map of Human_Risky > Human_Certain contrast, or between the meta-analytical map of "uncertain" term with the map of any contrasts in Human conditions. One possible explanation is that, although some brain regions (i.e., lOFC, aINS, and dmPFC) are commonly observed for processing one's own and others' decisions under uncertainty, the neural pattern for evaluating others' decisions under uncertainty might be different from the pattern related to one's own. However, given that the current study was not specifically designed to address theses questions, the differences in stimuli or contexts might also contribute to the results, calling for future research.

Previous studies have consistently demonstrated interpersonal gratitude as a moral emotion, which functions to recognize moral behaviors and motivate individuals to reciprocate these moral behaviors (Algoe et al., 2008; Bartlett and DeSteno, 2006; DeSteno et al., 2010; McCullough et al., 2001; Tsang, 2006; Yu et al., 2017). Therefore, in addition to emotional response, reciprocal behavior is a constitutive part of gratitude

Akitsuki, Y., Decety, J., 2009. Social context and perceived agency affects empathy for pain: an event-related fMRI investigation. Neuroimage 47, 722–734. https://doi.org/10.1016/j.neuroimage.2009.04.091.
Algoe, S.B., 2012. Find, remind, and bind: the functions of gratitude in everyday relationships. Soc. Personal. Psychol. Compass 6, 455–469. https://doi.org/10.1111/j.1751-9004.2012.00439.x.
Algoe, S.B., Stanton, A.L., 2012. Gratitude when it is needed most: social functions of gratitude in women with metastatic breast cancer. Emotion 12, 163–168. https://doi.org/10.1037/a0024024.
Algoe, S.B., Haidt, J., Gable, S.L., 2008. Beyond reciprocity: gratitude and relationships in everyday life. Emotion 8, 425–429. https://doi.org/10.1037/1528-3542.8.3.425.
Algoe, S.B., Fredrickson, B.L., Gable, S.L., 2013. The social functions of the emotion of gratitude via expression. Emotion 13, 605–609. https://doi.org/10.1037/a0032701.
Ames, D.R., Flynn, F.J., Weber, E.U., 2004. It's the thought that counts: on perceiving how helpers decide to lend a hand. Pers. Soc. Psychol. Bull. 30, 461–474. https://doi.org/10.1177/0146167203261890.
Barasch, A., Levine, E.E., Berman, J.Z., Small, D.A., 2014. Selfish or selfless? On the signal value of emotion in altruistic behavior. J. Pers. Soc. Psychol. 107, 393–413. https://doi.org/10.1037/a0037207.
Barrett, L.F., Satpute, A.B., 2013. Large-scale brain networks in affective and social neuroscience : towards an integrative functional architecture of the brain. Curr. Opin. Neurobiol. 1–12. https://doi.org/10.1016/j.conb.2012.12.012.
Bartlett, M.Y., DeSteno, D., 2006. Gratitude and prosocial behavior. Psychol. Sci. 17, 319–325. https://doi.org/10.1111/j.1467-9280.2006.01705.x.
Bartra, O., McGuire, J.T., Kable, J.W., 2013. The valuation system: a coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of subjective value. Neuroimage 76, 412–427. https://doi.org/10.1016/j.neuroimage.2013.02.063.
Belfi, A.M., Koscik, T.R., Tranel, D., 2015. Damage to the insula is associated with abnormal interpersonal trust. Neuropsychologia 71, 165–172. https://doi.org/10.1016/j.neuropsychologia.2015.04.003.
Bell, S.B., DeWall, N., 2018. Does transcranial direct current stimulation to the prefrontal

Jenkins, A.C., Mitchell, J.P., 2010. Mentalizing under uncertainty: dissociated neural responses to ambiguous and unambiguous mental state inferences. Cerebr. Cortex 20, 404–410. https://doi.org/10.1093/cercor/bhp109.
Jones, R.M., Somerville, L.H., Li, J., Ruberry, E.J., Libby, V., Glover, G., Voss, H.U., Ballon, D.J., Casey, B.J., 2011. Behavioral and neural properties of social reinforcement learning. J. Neurosci. 31, 13039–13045. https://doi.org/10.1523/JNEUROSCI.2972-11.2011.
Jordan, J.J., Hoffman, M., Nowak, M.A., Rand, D.G., 2016. Uncalculating cooperation is used to signal trustworthiness. Proc. Natl. Acad. Sci. Unit. States Am. 113, 8658–8663. https://doi.org/10.1073/pnas.1601280113.
Kable, J.W., Glimcher, P.W., 2009. The neurobiology of decision: consensus and controversy. Neuron 63, 733–745. https://doi.org/10.1016/j.neuron.2009.09.003.
Kappes, A., Nussberger, A.M., Faber, N.S., Kahane, G., Savulescu, J., Crockett, M.J., 2018. Uncertainty about the impact of social decisions increases prosocial behaviour. Nat. Hum. Behav. 2, 573–580. https://doi.org/10.1038/s41562-018-0372-x.
Karns, C.M., Moore, W.E., Mayr, U., 2017. The cultivation of pure altruism via gratitude: a functional MRI study of change with gratitude practice. Front. Hum. Neurosci. 11, 1–14. https://doi.org/10.3389/fnhum.2017.00599.
King-Casas, B., Tomlin, D., Anen, C., Camerer, C.F., Quartz, S.R., Montague, P.R., 2005. Getting to know you: reputation and trust in a two-person economic exchange. Science 308, 78–83. https://doi.org/10.1126/science.1108062.
Kini, P., Wong, J., McInnis, S., Gabana, N., Brown, J.W., 2016. The effects of gratitude expression on neural activity. Neuroimage 128, 1–10. https://doi.org/10.1016/j.neuroimage.2015.12.040.
Koster-Hale, J., Saxe, R., 2013. Theory of mind: a neural prediction problem. Neuron 79, 836–848. https://doi.org/10.1016/j.neuron.2013.08.020.
Krain, A.L., Wilson, A.M., Arbuckle, R., Castellanos, F.X., Milham, M.P., 2006. Distinct neural mechanisms of risk and ambiguity: a meta-analysis of decision-making. Neuroimage 32, 477–484. https://doi.org/10.1016/j.neuroimage.2006.02.047.
Lamm, C., Decety, J., Singer, T., 2011. Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. Neuroimage 54, 2492–2502. https://doi.org/10.1016/j.neuroimage.2010.10.014.
Larsen, R.J., Fredrickson, B.L., 1999. Measurement issues in emotion research. In: Well-being: the Foundations of Hedonic Psychology. Russell Sage Foundation, New York, NY, US, pp. 40–60.
Levy, I., 2017. Neuroanatomical substrates for risk behavior. Neuroscience 23, 275–286. https://doi.org/10.1177/1073858416672414.
Lo Gerfo, E., Gallucci, A., Morese, R., Vergallito, A., Ottone, S., Ponzano, F., Locatelli, G., Bosco, F., Romero Lauro, L.J., 2019. The role of ventromedial prefrontal cortex and temporo-parietal junction in third-party punishment behavior. Neuroimage 200, 501–510. https://doi.org/10.1016/j.neuroimage.2019.06.047.
Lockwood, P.L., Wittmann, M.K., Apps, M.A.J., Klein-Flügge, M.C., Crockett, M.J., Humphreys, G.W., Rushworth, M.F.S., 2018. Neural mechanisms for learning self and other ownership. Nat. Commun. 9, 4747. https://doi.org/10.1038/s41467-018-07231-9.
McCullough, M.E., Kilpatrick, S.D., Emmons, R. a, Larson, D.B., 2001. Is gratitude a moral affect? Psychol. Bull. 127, 249–266. https://doi.org/10.1037/0033-2909.127.2.249.
Molenberghs, P., Johnson, H., Henry, J.D., Mattingley, J.B., 2016. Understanding the minds of others: a neuroimaging meta-analysis. Neurosci. Biobehav. Rev. 65, 276–291. https://doi.org/10.1016/j.neubiorev.2016.03.020.
Morriss, J., Gell, M., van Reekum, C.M., 2019. The uncertain brain: a co-ordinate based meta-analysis of the neural signatures supporting uncertainty during different contexts. Neurosci. Biobehav. Rev. 96, 241–249. https://doi.org/10.1016/j.neubiorev.2018.12.013.
Nagel, R., Brovelli, A., Heinemann, F., Coricelli, G., 2018. Neural mechanisms mediating degrees of strategic uncertainty. Soc. Cognit. Affect Neurosci. 13, 52–62. https://doi.org/10.1093/scan/nsx131.
Nakagawa, S., 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. Behav. Ecol. 15 (6), 1044–1045. https://doi.org/10.1093/beheco/arh107.
Nisbett, R.E., Wilson, T.D., 1977. Telling more than we can know: verbal reports on mental processes. Psychol. Rev. 84 (3), 231. https://doi.org/10.1037/0033-295X.84.3.231.
Ondobaka, S., Kilner, J., Friston, K., 2017. The role of interoceptive inference in theory of mind. Brain Cognit. 112, 64–68. https://doi.org/10.1016/j.bandc.2015.08.002.
Penner, L.A., Dovidio, J.F., Piliavin, J.A., Schroeder, D.A., 2004. Prosocial behavior: multilevel perspectives. Annu. Rev. Psychol. 56, 365–392. https://doi.org/10.1146/annurev.psych.56.091103.070141.
Pérez-Escudero, A., Friedman, J., Gore, J., 2016. Preferential interactions promote blind cooperation and informed defection. Proc. Natl. Acad. Sci. Unit. States Am. 113, 13995–14000. https://doi.org/10.1073/pnas.1606456113.
Phan, K.L., Sripada, C.S., Angstadt, M., McCabe, K., 2010. Reputation for reciprocity engages the brain reward center. Proc. Natl. Acad. Sci. U.S.A. 107, 13099–13104. https://doi.org/10.1073/pnas.1008137107.
Platt, M.L., Huettel, S.A., 2008. Risky business: the neuroeconomics of decision making under uncertainty. Nat. Neurosci. 11, 398–403. https://doi.org/10.1038/nn2062.
Preacher, K.J., Hayes, A.F., 2004. SPSS and SAS procedures for estimating indirect effects in simple mediation models. Behav. Res. Methods Instrum. Comput. 36, 717–731. https://doi.org/10.3758/BF03206553.
Preacher, K.J., Hayes, A.F., 2008. Asymptotic and resampling strategies for assessing and comparing indirect effects in multiple mediator models. Behav. Res. Methods 40, 879–891. https://doi.org/10.3758/BRM.40.3.879.
Rabin, Matthew, 1993. Incorporating fairness into game theory and economics. Am. Econ. Rev. 83, 1281–1302. https://doi.org/10.2307/2117561.
Rangel, A., Camerer, C., Montague, P.R., 2008. A framework for studying the neurobiology of value-based decision making. Nat. Rev. Neurosci. 9, 545–556. https://doi.org/10.1038/nrn2357.
Rilling, J.K., Sanfey, A.G., 2011. The neuroscience of social decision-making. Annu. Rev. Psychol. 62, 23–48. https://doi.org/10.1146/annurev.psych.121208.131647.
Rilling, J.K., Goldsmith, D.R., Glenn, A.L., Jairam, M.R., Elfenbein, H.A., Dagenais, J.E., Murdock, C.D., Pagnoni, G., 2008. The neural correlates of the affective response to unreciprocated cooperation. Neuropsychologia 46, 1256–1266. https://doi.org/10.1016/j.neuropsychologia.2007.11.033.
Rizzolatti, G., Sinigaglia, C., 2016. The mirror mechanism: a basic principle of brain function. Nat. Rev. Neurosci. 17, 757–765. https://doi.org/10.1038/nrn.2016.135.
Rosen, J.B., Donley, M.P., 2006. Animal studies of amygdala function in fear and uncertainty: relevance to human research. Biol. Psychol. 73, 49–60. https://doi.org/10.1016/j.biopsycho.2006.01.007.
Rosseel, Y., 2012. lavaan: an R package for structural equation modeling. J. Stat. Software 48, 1–36. R package version 0.5-15. http://lavaan.org.
Ruff, C.C., Fehr, E., 2014. The neurobiology of rewards and values in social decision making. Nat. Rev. Neurosci. 15, 549–562. https://doi.org/10.1038/nrn3776.
Sanfey, A.G., 2007. Social decision-making: insights from game theory and neuroscience. Science 318, 598–602. https://doi.org/10.1126/science.1142996.
Sanfey, A.G., Civai, C., Vavra, P., 2015. Predicting the other in cooperative interactions. Trends Cognit. Sci. 19, 364–365. https://doi.org/10.1016/j.tics.2015.05.009.
Sarinopoulos, I., Grupe, D.W., Mackiewicz, K.L., Herrington, J.D., Lor, M., Steege, E.E., Nitschke, J.B., 2010. Uncertainty during anticipation modulates neural responses to aversion in human insula and amygdala. Cerebr. Cortex 20, 929–940. https://doi.org/10.1093/cercor/bhp155.
Seidel, E.M., Pfabigan, D.M., Hahn, A., Sladky, R., Grahl, A., Paul, K., Kraus, C., Küblböck, M., Kranz, G.S., Hummer, A., Lanzenberger, R., Windischberger, C., Lamm, C., 2015. Uncertainty during pain anticipation: the adaptive value of preparatory processes. Hum. Brain Mapp. 36, 744–755. https://doi.org/10.1002/hbm.22661.
Seo, H., Lee, D., 2012. Neural basis of learning and preference during social decision-making. Curr. Opin. Neurobiol. 22, 990–995. https://doi.org/10.1016/j.conb.2012.05.010.
Shackman, A.J., Salomons, T.V., Slagter, H.A., Fox, A.S., Winter, J.J., Davidson, R.J., 2011. The integration of negative affect, pain and cognitive control in the cingulate cortex. Nat. Rev. Neurosci. 12, 154–167. https://doi.org/10.1038/nrn2994.
Shankman, S.A., Gorka, S.M., Nelson, B.D., Fitzgerald, D.A., Phan, L., O'Daly, O., 2014. Anterior insula responds to temporally unpredictable aversiveness. Neuroreport 1. https://doi.org/10.1097/WNR.0000000000000144.
Sherry Jr., J.F., 1983. Gift giving in anthropological perspective. J. Consum. Res. 10, 157. https://doi.org/10.1086/208956.
Singer, T., Critchley, H.D., Preuschoff, K., 2009. A common role of insula in feelings, empathy and uncertainty. Trends Cognit. Sci. 13, 334–340. https://doi.org/10.1016/j.tics.2009.05.001.
Smith-Collins, A.P.R., Fiorentini, C., Kessler, E., Boyd, H., Roberts, F., Skuse, D.H., 2013. Specific neural correlates of successful learning and adaptation during social exchanges. Soc. Cognit. Affect Neurosci. 8, 887–897. https://doi.org/10.1093/scan/nss079.
Tanovic, E., Gee, D.G., Joormann, J., 2018. Intolerance of uncertainty: neural and psychophysiological correlates of the perception of uncertainty as threatening. Clin. Psychol. Rev. 60, 87–99. https://doi.org/10.1016/j.cpr.2018.01.001.
Tesser, A., 1968. Some determinants of gratitude. J. Pers. Soc. Psychol. 9, 233–236.
Tobler, P.N., O'Doherty, J.P., Dolan, R.J., Schultz, W., 2006. Reward value coding distinct from risk attitude-related uncertainty coding in human reward systems. J. Neurophysiol. 97, 1621–1632. https://doi.org/10.1152/jn.00745.2006.
Tsang, J.-A., 2006. BRIEF REPORT Gratitude and prosocial behaviour: an experimental test of gratitude. Cognit. Emot. 20, 138–148. https://doi.org/10.1080/02699930500172341.
Tsang, J.A., 2007. Gratitude for small and large favors: a behavioral test. J. Posit. Psychol. 2, 157–167. https://doi.org/10.1080/17439760701229019.
Tzieropoulos, H., 2013. The Trust Game in neuroscience: a short review. Soc. Neurosci. 8, 407–416. https://doi.org/10.1080/17470919.2013.832375.
Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., et al., 2002. Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. Neuroimage 15, 273–289. https://doi.org/10.1006/nimg.200.1.0978.
Van de Calseyde, P.P.F.M., Keren, G., Zeelenberg, M., 2014. Decision time as information in judgment and choice. Organ. Behav. Hum. Decis. Process. 125, 113–122. https://doi.org/10.1016/j.obhdp.2014.07.001.
Vanyukov, P.M., Hallquist, M.N., Delgado, M., Szanto, K., Dombrovski, A.Y., 2019. Neurocomputational mechanisms of adaptive learning in social exchanges. Cognit. Affect Behav. Neurosci. 19, 985–997. https://doi.org/10.3758/s13415-019-00697-0.
Vives, M.L., Feldmanhall, O., 2018. Tolerance to ambiguous uncertainty predicts prosocial behavior. Nat. Commun. 9, 25–27. https://doi.org/10.1038/s41467-018-04631-9.
Volz, K.G., Schubotz, R.I., Von Cramon, D.Y., 2004. Why am I unsure? Internal and external attributions of uncertainty dissociated by fMRI. Neuroimage 21, 848–857. https://doi.org/10.1016/j.neuroimage.2003.10.028.
Weller, J.A., Levin, I.P., Shiv, B., Bechara, A., 2009. The effects of insula damage on decision-making for risky gains and losses. Soc. Neurosci. 4, 347–358. https://doi.org/10.1080/17470910902934400.
Will, G.J., Rutledge, R.B., Moutoussis, M., Dolan, R.J., 2017. Neural and computational processes underlying dynamic changes in self-esteem. Elife 6, 1–22. https://doi.org/10.7554/eLife.28098.

Woo, C.W., Koban, L., Kross, E., Lindquist, M.A., Banich, M.T., Ruzic, L., Andrews-Hanna, J.R., Wager, T.D., 2014. Separate neural representations for physical pain and social rejection. Nat. Commun. 5, 1–12. https://doi.org/10.1038/ncomms6380.

Wood, W., Eagly, A.H., 2012. Biosocial construction of sex differences and similarities in behavior. In: Advances in Experimental Social Psychology. Elsevier Inc., pp. 55–123. https://doi.org/10.1016/B978-0-12-394281-4.00002-7

Wood, A.M., Maltby, J., Stewart, N., Linley, P.A., Joseph, S., 2008. A social-cognitive model of trait and state levels of gratitude. Emotion 8, 281–290. https://doi.org/10.1037/1528-3542.8.2.281.

Xiang, T., Lohrenz, T., Montague, P.R., 2013. Computational substrates of norms and their violations during social exchange. J. Neurosci. 33, 1099–1108. https://doi.org/10.1523/JNEUROSCI.1642-12.2013.

Yarkoni, T., Poldrack, R.A., Nichols, T.E., Van Essen, D.C., Wager, T.D., 2011. Large-scale automated synthesis of human functional neuroimaging data. Nat. Methods 8, 665–670. https://doi.org/10.1038/nmeth.1635.

Yu, H., Cai, Q., Shen, B., Gao, X., Zhou, X., 2017. Neural substrates and social consequences of interpersonal gratitude: intention matters. Emotion 17, 589–601. https://doi.org/10.1037/emo0000258.

Yu, H., Gao, X., Zhou, Y., Zhou, X., 2018. Decomposing gratitude: representation and integration of cognitive antecedents of gratitude in the brain. J. Neurosci. 38, 4886–4898. https://doi.org/10.1523/JNEUROSCI.2944-17.2018.

Zahn, R., Moll, J., Paiva, M., Garrido, G., Krueger, F., Huey, E.D., Grafman, J., 2009. The neural basis of human social values: evidence from functional MRI. Cerebr. Cortex 19, 276–283. https://doi.org/10.1093/cercor/bhn080.

Zhu, L., Mathewson, K.E., Hsu, M., 2012. Dissociable neural representations of reinforcement and belief prediction errors underlie strategic learning. Proc. Natl. Acad. Sci. U.S.A. 109, 1419–1424. https://doi.org/10.1073/pnas.1116783109.