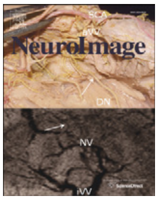
NeuroImage 61 (2012) 32–40

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg



Full Length Articles

The neural mechanisms of affect infusion in social economic decision-making: A mediating role of the anterior insula

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ARTICLE INFO

Article history:
Accepted 11 February 2012
Available online 21 February 2012

Keywords:
Anterior insula
fMRI
Mood
Decision-making

ABSTRACT

Though emotions have been shown to have sometimes dramatic effects on decision-making, the neural mechanisms mediating these biases are relatively unexplored. Here, we investigated how incidental affect (i.e. emotional states *unrelated* to the decision at hand) may influence decisions, and how these biases are implemented in the brain. Nineteen adult participants made decisions which involved accepting or rejecting monetary offers from others in an Ultimatum Game while undergoing functional magnetic resonance imaging (fMRI). Prior to each set of decisions, participants watched a short video clip aimed at inducing either a sad or neutral emotional state. Results demonstrated that, as expected, sad participants rejected more unfair offers than those in the neutral condition. Neuroimaging analyses revealed that receiving unfair offers while in a sad mood elicited activity in brain areas related to aversive emotional states and somatosensory integration (anterior insula) and to cognitive conflict (anterior cingulate cortex). Sad participants also showed a diminished sensitivity in neural regions associated with reward processing (ventral striatum). Importantly, insular activation uniquely mediated the relationship between sadness and decision bias. This study is the first to reveal how subtle mood states can be integrated at the neural level to influence decision-making.

Introduction

It is now well established that affective influences play an important role in decision-making, and indeed that emotional states can be useful and adaptive tools in informing decisions (Kahneman, 2003). To date, however, the majority of this research has focused on emotional states intrinsic to the decision process itself, that is, emotions directly related to the decision at hand (e.g. anxiety about the future returns on a prospective risky investment). In contrast, much less is known about how decision-making is impacted by incidental emotions, such as preexisting mood states, though it appears that these can be equally powerful in biasing simple decisions (Loewenstein and Lerner, 2003). While little is known about the neural mechanisms that underlie these influences, incidental affect can modulate individuals' goals, attitudes, and perception of their social environment by priming mood-congruent concepts or dispositions, which in turn can affect social judgment and decision-making (Zajonc, 2000). Such mood influences, however, have been shown to be situation dependent. Thus, according to the Affect Infusion Model (AIM), incidental emotion can bias decision-making by priming mood-congruent concepts and dispositions. For instance, relative to neutral or positive moods, negative emotion is associated with a more pessimistic framing, more focus on negative aspects of a situation and negative traits in others, and more negative attitudes in interpersonal situations. Importantly, the extent to which incidental affective information is integrated into decision-making is proportional to the level of complexity, novelty and required information processing of and constructive thinking about a particular decision. For instance, direct access to preexisting evaluations of identical situations is a low infusion strategy, whereas a novel situation requiring generative evaluative processes should entail more infusion of affect (Forgas, 1995, 2002). The AIM has been supported by several behavioral studies. In relation to social decision-making, individuals in a sad mood relative to a positive mood have been shown to evaluate others and themselves in a more negative light, and sad individuals were also found to behave in more mood-congruent characteristics (i.e. less friendly, less comfortable) when formulating a request toward someone else. Importantly, mood effects in these experiments were stronger when observed interpersonal behaviors were more complex, serious and more demanding, demonstrating a stronger infusion of affect for more elaborate interactions (Forgas, 1995). Based on the AIM framework, and since it involves more elaborative and interpretative processes, social decision-making may be particularly susceptible to affect infusion and related behavioral shifts. In addition, the neural processes supporting such affect infusion may follow

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doi:10.1016/j.neuroimage.2012.02.027

a similar interactional pattern, with situation-specific neural events reflecting greater engagement of certain brain regions when the decision occurs in the context of competing social and economic factors.

Recent behavioral research indeed suggests that task-irrelevant mood states may bias social economic decision-making. For instance, induced physical disgust, a negatively-valenced emotional state, has been shown to alter unrelated decisions that involve a social framework, including both purchase and selling price valuation (Lerner et al., 2004), ultimatum bargaining (Harlé and Sanfey, 2010; Moretti and di Pellegrino, 2010) and moral decisions (Inbar and Pizarro, 2009; Schnall et al., 2008; Wheatley and Haidt, 2005). Another particularly relevant mood state which may covertly influence social economic decision-making, is sadness. Sad affect is likely to be experienced in the face of pain, losses, and bereavement, and is a prominent component of clinical disorders such as depression and bipolar disorder. Exploring the impact of sad mood on decision-making in a social framework has therefore important relevance for informing cognitive models of everyday decision-making and how it may be impacted by mood. The use of this emotion is also particularly appropriate for studying carry-over effects of incidental emotion, as it more readily contrasts with other potentially confounding task-related emotions often encountered in social decision-making tasks such as disgust and anger.

Sad mood has been shown to impact social economic decisions, for instance reducing selling prices (Lerner et al., 2004), promoting more generous offers in the dictator game (Tan and Forgas, 2010), as well as greater risk-aversion (Yuen and Lee, 2003). We recently demonstrated that sad mood can bias simple economic decisions in the Ultimatum Game (UG; Guth et al., 1982), a task in which subjects have to accept or reject proposals from other players on how to divide a sum of money between the two. Although individuals in a presumably neutral mood tend to react negatively to, and reject, about half of "unfair" offers (i.e. less than 30% of the pot; Camerer, 2003; Van 't Wout et al., 2006), we found that sadness led to even lower acceptance rates coupled with a more negative emotional reaction. In contrast, sadness did not impact emotional response to, or acceptance of, "fair" offers (i.e. 40–50% of the pot; Harlé and Sanfey, 2007). Thus, sadness may selectively prompt mood-congruent framing of unfair offers (e.g. stronger attention to the negative aspects), and bias behavior accordingly. Despite these findings, however, it remains unclear what neural mechanisms may mediate such mood-driven biases. While the neural correlates of experienced sadness have been investigated and point to multiple networks from limbic to frontal areas (Damasio et al., 2000; George et al., 1995; Lane et al., 1997), these studies do not address how and where in the brain mood may interact with other cognitive processes to eventually bias behavior. To address this question, we used functional magnetic resonance imaging (fMRI) to examine brain areas where such affective influences may be implemented. To our knowledge, this is the first study investigating mood-driven decision-making biases at the neural level. Ultimately, such work may improve our understanding of the biological basis of how transient negative emotional states can adversely impact decision-making, which may in turn have relevance for neurocognitive models of more chronic mood disturbances, as observed in certain clinical populations (e.g., depression).

Based on the AIM and previous behavioral findings, we expected mood to interact with offer fairness at the neural level, consistent with a moderating role of sad mood. Specifically, we expected a stronger influence of mood (and associated neural responses) for low offers. Indeed, because they combine possible monetary gain with the negative experience of social norm violation, unfair offers are likely more complex decisions (i.e. requiring more information processing and more constructive, elaborative processes to make a choice between two valid alternatives, i.e., accept or reject) as compared to fair offers (which do not involve negative consequences and are therefore more readily acceptable). The AIM would thus predict a stronger infusion of affective influences for unfair offers, as they require greater processing.

One brain area which may be associated with such selective mood influence is the anterior insula. In addition to being associated with higher likelihood of rejecting unfair offers in the Ultimatum Game (Sanfey et al., 2003), this region has been consistently linked to the integration of emotional and somatosensory information. Indeed, converging evidence points to the central role of the anterior insula in integrating and encoding representations of the physiological state of the body. The anterior insula receives interoceptive input of physical sensations of the muscles and viscera (such as temperature, hunger, thirst, and pain) from the posterior insular cortex, information which originates from small-diameter primary afferents and is relayed through the lamina I spinothalamocortical pathway. Such cortical representation of ongoing homeostasis provides in turn the basis of self-awareness and feeling states (Craig, 2002; Damasio, 1994). The anterior insula has bidirectional connections to the amygdala, nucleus accumbens, and orbitofrontal cortex, enabling rapid integration of inputs regarding the emotional salience of environmental stimuli, and also contains projections to the anterior cingulate cortex, highlighting the important role of interoceptive information in the allocation of attention (Paulus and Stein, 2006). Consistent with this integrative role, several studies have shown that the anterior insula is involved in the experience and self-awareness of emotional states such sadness, pain, disgust and anger (Calder et al., 2007; Damasio et al., 2000; Denson et al., 2009; Ploghaus et al., 1999). There is also neural evidence of the key role of this region in providing anticipatory interoceptive signals in decision-making. For instance, activation of the anterior insula has been associated with anticipation of monetary loss when making risky decisions (Paulus et al., 2003), and when presented with excessive purchase prices for consumer goods (Knutson et al., 2007). It may also be involved in supporting avoidance of risky card decks in the Iowa Gambling Task (Li et al., 2010). Importantly, insular activations in such decision tasks have been shown to predict more risk-averse decisions (Kuhnen and Knutson, 2005; Paulus et al., 2003), suggesting that this region has an important role in facilitating decision biases relating to negative affective influences (i.e. risk, fear). Thus, in the present study, stronger activation in this region when rejecting unfair offers may therefore indicate an aversive response to unfairness (a negative social signal), which may be enhanced by an incidental negative mood. Indeed, according to the AIM, more integration of emotional/interoceptive information would be expected for more complex decisions (i.e. unfair offers) and we may therefore expect more engagement of the neural system supporting such integrative process for these types of offers. Thus we predicted that, relative to a neutral mood, sadness would lead to stronger activation in the anterior insula when presented with unfair offers.

Inequitable UG offers may also prompt greater cognitive conflict sensitivity in sad participants. Because of its demonstrated role in the tracking of error and conflict (Botvinick et al., 1999; Hester et al., 2004) and the engagement of cognitive control (Kerns et al., 2004), and given previous evidence of increased anterior cingulate cortex (ACC) activation to unfair UG offers (Sanfey et al., 2003), we expected that sad mood may impact activation of the ACC for these types of offers. Previous research suggests that sad mood may be associated with increase in cognitive conflict and related hyperactivation of this neural region. For example, the rostral ACC, linked to affective conflict, has been shown to be hyperactive at baseline in both sad healthy individuals and depressed patients (Mayberg et al., 1999). Also several studies point to increased error sensitivity and hyperactivation of the ACC in depressed individuals in processes such as inhibitory control (Harvey et al., 2005; Holmes and Pizzagalli, 2008a; Mitterschiffthaler et al., 2007; Wagner et al., 2008). Knutson et al. (2008) also found increased ACC activation in depressed individuals in a financial decision-making task during anticipation of uncertain monetary gains, which the authors attributed to increased affective conflict. Such findings suggest that sad affect may recruit compensatory activation of this neural area to achieve a similar level of cognitive control performance as in non-depressed individuals (though, hypoactivation of this network has also been observed in depressed individuals; Fales et al., 2008; Holmes and Pizzagalli, 2008b). Based on these findings and the hypothesized increased infusion of negative affect for unfair offers predicted by the AIM (as mentioned above), we predicted increased activation of the ACC for unfair offers in sad relative to neutral mood participants. That is, if unfair offers require more generative decision-making processes, the AIM would predict a stronger infusion of negative affect, which may in turn result in enhanced conflict/error sensitivity supported by ACC activation.

Finally, sad affect has been associated with selective attention to mood-congruent stimuli and with decreased sensitivity to reward. For instance, at the behavioral level, induced sad mood in healthy individuals has been associated with decreased persistence in monetary gambles (Hills et al., 2001), while depression has been linked to decreased reward sensitivity and failure to maximize potential monetary earnings (Henriques and Davidson, 2000; Pizzagalli et al., 2008). Thus, relative to neutral mood individuals, sad participants may be less sensitive to the monetary reward intrinsic to UG offers. Previous imaging studies have linked activation of the ventral striatum, particularly the nucleus accumbens (NAcc), to expectation of monetary (Knutson et al., 2007) and social (Tabibnia et al., 2008) reward. There is also neural evidence that depressed individuals show a reduced activation of the NAcc in response to positively valenced stimuli (Epstein et al., 2006). Based on this literature, we hypothesized that, relative to those in a neutral mood, sad participants would show a reduced differential ventral striatum activation to fair (i.e. more rewarding) versus unfair offers. According to the AIM, we would further expect stronger mood effects for unfair offers relative to fair offers, thus we predicted a greater striatal activation difference between neutral mood and sad participants for unfair offers.

Finally, an important goal of this study was to further assess the selectivity of these areas in directly predicting the decisions ultimately made by the players. While mood may alter various cognitive and neural processes for these types of decisions, most of these biases may not directly translate into behavior change. Based on the aforementioned research, we predicted that insular activation in particular might mediate the relationship between emotion and decision-making.

Materials and methods

Participants

A total of 19 participants (10 females, mean age 22.4) were recruited on the University of Arizona campus. Participants were screened for standard magnetic resonance safety criteria (i.e. to rule out presence of metal in the body). In addition, participants were excluded if they reported any current neurological or psychiatric condition, or the use of psychotropic medications. All participants gave written informed consent.

Experimental procedures

Prior to the scanning session, participants were invited to participate in a first introductory group session during which they were instructed about the task they would be performing inside the scanner (i.e. Ultimatum Game) and met other participants (in groups of 3–4). Their pictures were taken and they were told that their partners in the task would see their de-identified picture when making their offer. To enhance realism, participants also played the UG as the proposer on a computer, making offers to various partners. The deidentified pictures of these partners were participants from a previous study (Harlé and Sanfey, 2007). Participants were told that the offers they would receive in the scanner when playing as the responder were offers that were made to their picture by other study participants in the same fashion. Such procedure has been shown effective in maximizing participants' beliefs they are playing with real partners (Chang and Sanfey, in press), which was confirmed by debriefing. To further ensure that subjects were sufficiently motivated to make real decisions, they were told that they would be paid a proportion (i.e. 20%) of their earnings in the game in addition to their participation fee (i.e. about $30 altogether). Finally, participants completed a 12-item questionnaire measuring emotional susceptibility (Caprara et al., 1983), aimed at assessing any potential group difference in susceptibility to the mood induction procedure. Participants' individual scanning session was then scheduled, typically within one week of the introductory group session.

Decision task (Ultimatum Game)

At the beginning of the scanning session, participants were asked to report their expectations of what offer amounts they would receive in the game, and in what proportions. Inside the scanner, they played in the role of the responder, receiving 24 one-time monetary offers. Half of these offers were from human proposers, and half were randomly generated computer offers. These offers were presented into 2 separate blocks of 12 offers to ensure sustained attention and monitor participant's comfort. In fact, participants saw the same predetermined set of offers across each block. Each offer involved a $10 split and their order was randomized. The total set included equal numbers (i.e. 6) of $5, $3, $2, and $1 offers (see Supplementary methods).

Emotion induction

To induce mood, we used short movie clips of 3–5 minute durations, a method shown to reliably induce specific emotions (Gross and Levenson, 1995). The clips selected had been previously piloted and used in our previous behavioral sadness induction study (Harlé and Sanfey, 2007). For each emotion condition (i.e. sadness and neutral mood), two clips that previously had reliably and discriminately evoked the target affect were used (see Appendix A). One clip was shown to participants inside the scanner immediately prior to each block of UG offers, and the order of the two clips within each condition was counterbalanced. Participants were randomly assigned to each condition (sad or neutral clips). To maximize attention to the clip while minimizing demand characteristics, participants were told to simply pay attention to the clips which were purportedly part of a separate memory task to be completed at the end of the session. Further, based on a substantial behavioral literature suggesting that making one aware of an emotional state can in itself bias the extent to which such mood state may be incorporated into other cognitive processes (Pham, 1998; Schwarz, 2004), mood levels were not explicitly measured during the UG task but rather at the end. Upon exiting the scanner, participants completed a brief questionnaire to evaluate their emotional responses to the clips. For each clip, participants were asked to rate to what extent they felt each of 12 basic emotions on an 8-point Likert scale (from 0 “not at all” to 8 “most ever felt”).

Trial timeline

At the beginning of each trial, a jittered fixation cross was presented for an average of 6 s. Then, participants saw a still frame from the previously viewed emotion-inducing clip for 6 s. This stimulus was included as a way to boost mood induction across the whole set of offers. Next, a picture of the proposer for that trial was presented (i.e. human partner or a computer picture) for 4 s. Participants then saw the offer and had up to 10 s to either accept or reject the offer by way of a button press. Finally, the decision outcome was presented for 4 s (Fig. 1a).

fMRI acquisition

E-prime software was used to present the UG task on a computer interface, which was projected onto goggles worn by participants via a fiber-optic cable. Participant's responses were recorded using a fiber-optic 2-button-press response box. Each scanning session started with a 20 second 3-D localizer scan, followed by an 8 minute T1-weighted scan ($\text{TR}=2000$ ms, $\text{TE}=25$ ms, slice thickness $=1.5$ mm, gap $=0$ mm, 120 sagittal slices) to obtain high-quality structural images. Four T2*-weighted functional scans of about 6 min long were then conducted while participants played the Ultimatum Game. Functional scans used a 3-shot echo planar imaging (EPI) GRAPPA sequence (Newbould et al., 2007) and scanning parameters were selected to maximize signal in regions associated with high susceptibility artifact such as the orbitofrontal cortex (Weiskopf et al., 2006; $\text{TR}=2000$ ms, $\text{TE}=25$ ms, $\text{FOV}=24$ mm, slice thickness $=2.6$ mm, gap $=0.4$ mm, 42 axial slices).

fMRI analysis

Image pre-processing and analyses were conducted using Brain Voyager software (Version 1.10). The first three volumes of the functional runs (6 s total) were discarded to account for T1 equilibrium effects. Image preprocessing for functional images included 6-parameter 3D motion-correction, slice scan time correction using linear interpolation, spatial smoothing with a 4 mm full width at half minimum Gaussian kernel, voxel-wise linear detrending, and high pass filter of frequencies below 3 cycles per time course. Motion correction parameters were visually inspected to ensure that participants' head motion was lower than 3 mm in each spatial axis. One participant's functional run (in the sadness condition) was removed from data analyses for severe head motion. Spatial normalization was performed using the standard 9-parameter landmark method of Talairach and Tournoux (1988). All functional analyses were overlaid on a group average of participants' high resolution structural scans in Talairach (TA) space.

A two-level mixed-effect general linear model (GLM) was used to analyze functional data. The model included first-level fixed regressors defined for each subject and for each epoch of the time course. These regressors modeled the BOLD response to emotion prime, partner presentation, outcome, as well as 8 types of offers over the first 4 s of the offer/decision phase including: $1 Human Offer, $1 Computer Offer, $2 Human Offer, $2 Computer Offer, $3 Human Offer, $3 Computer Offer, $5 Human Offer, and $5 Computer Offer. Each regressor was convolved with a standard gamma model of the hemodynamic impulse-response function, and the resulting general linear model was corrected for temporal autocorrelations using a first-order autoregressive model. To create whole-brain statistical maps, voxel-wise BOLD response associated with predictors of interest was examined in a mixed ANOVA, with condition as a between-subject second-level predictor, and offers amount and partner type as within-subject factors. Second-level contrasts of interest, presented here, tested for any significant mood (sad vs neutral) by offer ($.33\times\$1+.33\times\$2+.33\times\$3-1\times\$5$) interactions for human and computer offers. Thus unfair offers (i.e., $1–$3) were grouped together for consistency with prior studies. Any significant interactions were further examined with t-tests, which were Bonferroni corrected for the total number of tests. To correct for multiple comparisons, all statistical maps were cluster thresholded using a Monte Carlo simulation-based estimator to protect against overall FWE rate of $p<.01$, with a cluster defining threshold of $p<0.005$ (Forman et al., 1995). Finally, to assess whether averaged brain activation extracted from the obtained regions may mediate the relationship between emotion condition and acceptance rates of unfair offers, we conducted mediation analyses using a standard hierarchical regression technique (Baron and Kenny, 1986).

Results

Emotion induction check

Post-task self-reported emotion ratings for the clips (on a 0–8 scale) were used to conduct an emotional manipulation check. Replicating our previous study, and consistent with emotion ratings for these clips collected immediately after viewing (Gross and Levenson, 1995; Harlé and Sanfey, 2007), we found a strong and discrete mood induction effect as self-reported sadness was significantly higher in the sadness condition ($M=3.82$, $SEM=0.70$) than in the neutral condition ($M=0.89$, $SEM=0.37$; $p<.001$). The sad clips were further successful at selectively inducing sadness and not other emotions, as demonstrated by the low ratings in both other negative emotions (e.g., anger, disgust, fear; ratings <1.3 on a 0–8

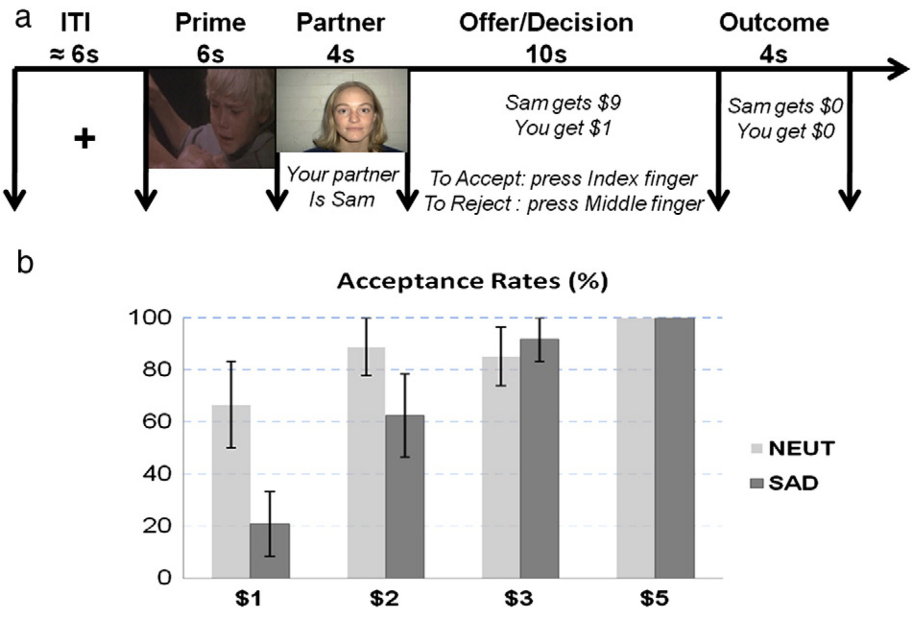

Fig. 1. a) Ultimatum Game (UG) trial timeline; b) aggregate acceptance rates of UG offers by offer amount (error bars: +/− 1 s.e.m.).

scale) as well as in positive emotions (e.g., happiness, amusement, contentment; ratings <1.6 on a 0–8 scale). Additionally, ratings obtained on a variety of discrete emotions in the neutral group were all consistently low (average ratings under 1.5). Further analyses indicated that participants' self-reported emotional susceptibility was moderately low ($M=1.67$, $SEM=0.22$). Importantly, participants' emotional susceptibly did not differ across conditions ($p>.05$). In addition, participants did not significantly differ in their pre-task expectations about what offers they may receive in the game ($p>.05$; weighted mean expected offer: \$4.30). Thus, any significant behavioral differences between emotion groups are thus unlikely to originate from a difference in susceptibilities to the mood induction procedure or in a-priori expectations about the UG.

Decision-making

A mixed effect logit model with random intercepts at the participant level was used to predict decision-making (i.e. acceptance or rejection) using offer amount and partner type (human vs computer) as within-subject predictors (nested within subjects) and emotion condition (neutral vs sad) as a between-subject predictor. A main effect of offer amount (Wald statistic $=20.99$, $p<.001$; odds ratio: 5.6) was found, with higher offer amounts more likely than lower amounts to prompt acceptances. Further, a main effect of emotion condition (Wald statistic $=3.88$, $p<.05$; odds ratio: 0.15) was significant, with a sad mood leading to fewer to acceptances as compared to a neutral mood. The offer amount × condition interaction was marginally significant ($p=0.06$). No main effect of partner type or any other interactions was observed (Fig. 1b).

Imaging results

Whole brain analyses (offer/decision)

Whole brain analyses revealed a significant condition × offer interaction in several areas including right anterior insula (TC: 39, 29, −8), left anterior insula (TC: −33, 11, −14), bilateral ACC (TC: 9, 38, 25), left ventrral striatum (TC: −18, 11, −8), right dorsolateral prefrontal cortex (DLPFC; TC: 42, 59, 19), right ventromedial prefrontal cortex (VmPFC; TC: 33, 59, 19), left orbitofrontal cortex (OFC; TC: −30, 45, 7), right cuneus (TC: 15, −73, 40), and right temporal pole (TC: 36, 5, −17; see Appendix B for full list for activation clusters). Two contrasts of interests were further examined to analyze this interaction. Specifically, receiving an unfair offer (\$1–\$3) from a human partner while in a sad versus neutral mood activated right and left anterior insula (Figs. 2a, b), left ventral striatum (Figs. 2a, c), and bilateral ACC (Fig. 3). A similar pattern was observed in right DLPFC, right VmPFC, left OFC, and right temporal pole. In contrast, receiving fair human offers (\$5) in a sad relative to neutral mood resulted in stronger activation in the right cuneus. Within-group contrasts further revealed a marginally significant double dissociation in the left ventral striatum. Specifically, participants in a neutral mood showed significantly stronger activation in this area in response to fair offers relative to unfair ($p<.05$, Bonferroni corrected) offers. Sad participants did not show such differential activation. In fact, a statistical trend was observed in the other direction, with sad participants exhibiting stronger activation to unfair relative to fair offers ($p=0.07$; Figs. 2a, c).

To assess how mood may interact with the social aspect of receiving UG offers, we further searched for brain areas that would reveal any significant condition × partner type or condition × partner type × offer amount interactions. No such interactions were observed, after correcting for multiple comparisons. Based on the above results for human offers, however, the same set of between group contrasts was conducted to assess for any mood condition differences in response to computer offers in the previously identified right and left anterior insula ROIs. In both areas, no significant difference in activation to unfair (\$1–3) computer offers was observed between sad and neutral participants ($p>.05$, Bonferroni corrected). Similarly, no mood condition effect was observed in response to fair (\$5) computer offers ($p>.05$).

Mediation analyses

Having identified several areas that tracked a moderational influence of mood on UG decisions (i.e. stronger activation to unfair offers

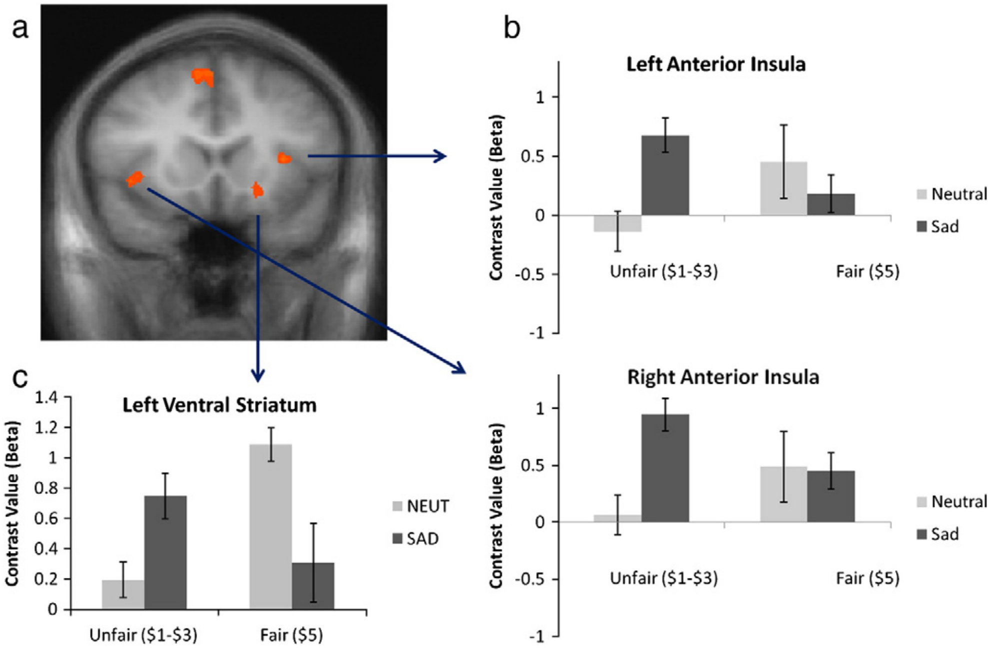

Fig. 2. a) Coronal view of BOLD response in right and left anterior insula and ventral striatum at offer presentation (initial 4 s) for human offers; activations represent significant mood condition (sad vs neutral) × offer amount (\$1–3 vs \$5) interactions (whole brain analysis, corrected for cluster-wise significance: $p<0.01$, minimum cluster size 270 mm^3); b) in both right and left anterior insula, stronger activation in the sad relative to neutral mood group was observed for unfair offers (\$1–\$3). No significant group differences in activation were observed for fair (\$5) offers; c) ventral striatum: significant group/condition differences were observed in average activation to both fair (\$5) and unfair (\$1–\$3) offers (error bars: +/− 1 s.e.m.).

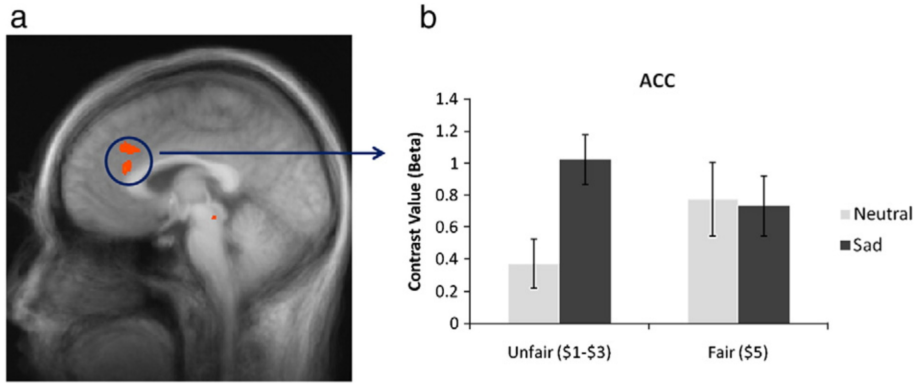

Fig. 3. a) Sagittal view of BOLD response in ACC at offer presentation (initial 4 s) for human offers; activations represent significant mood condition (sad vs neutral) × offer amount ($1–3 vs $5) interactions (whole brain analysis, corrected for cluster-wise significance: p<.01, minimum cluster size 270 mm^3). b) Activation to unfair offers ($1–$3) was significantly higher in sad relative to neutral mood participants. No group difference was observed for activation to fair ($5) offers (error bars: +/−1 s.e.m.).

in sad relative to neutral mood), an important next step was to assess whether any of these activations would directly predict the observed decision biases. We used a hierarchical regression method (Baron and Kenny, 1986) to examine the potential mediating role of the insula in explaining the relationship between mood and acceptance rates of human offers. A first model showed that right insular activation at offer onset significantly predicted acceptance rates in the expected direction (i.e. stronger activation associated with lower acceptance rates), F(1,17) = 8.4, p<.05 (beta = −.59). Another model showed that mood (i.e. sad or neutral condition) significantly predicted right insular activation, F(1,17) = 6.2, p<.05 (beta = .53). Mood was also related to acceptance rates of unfair offers, F(1,17) = 4.4, p = .05 (beta = −.45), with lower acceptance rates in the sad relative to neutral condition. Importantly, adding insular activation as a second predictor of acceptance rates removed the effect of mood (p = .55), leaving right insula activity as the only significant predictor of acceptance rates (beta = −51, t = −2.1, p<.05), consistent with a meditational role (Fig. 4a). A similar mediation pattern was observed with left insula activation (Fig. 4b). It is important to note that these results were specific to the insula, as we did not observe a similar meditational pattern for the ACC, ventral striatum, or any other region identified in the whole brain analyses.

In further support of these findings, we also found that the insula was associated with participant's self-reported sadness. That is, participants who reported greater levels of sadness from the mood primes were associated with strongest insula activation at offer onset (Fig. 4c).

Discussion

The goal of this research was to examine the neural underpinnings of how task-irrelevant negative moods can bias social economic decision-making. We were particularly interested in assessing what mood-specific neural events may mediate such decision-making biases, and show here that sad mood selectively biases acceptance decisions of the most unfair offers. Whole-brain analyses were conducted to examine these mood effects, and clearly revealed three areas we predicted a priori to be involved in such affective biases, which in turn led to three major findings.

Firstly, we showed that presentation of unfair offers was associated with higher bilateral anterior insula activations in participants who were in a sad as opposed to a neutral mood. In contrast, no group difference in activation emerged in response to fair offers. Importantly, we used mediation analysis to demonstrate that activation coefficients for the anterior insula actually predict rejection of unfair offers, and that the relationship observed between emotion condition and acceptance rates was mediated by these activations. This is consistent with research highlighting the key role of this region in integrating emotional and somatosensory information, including aversive physical states such as pain and disgust (Calder et al.,

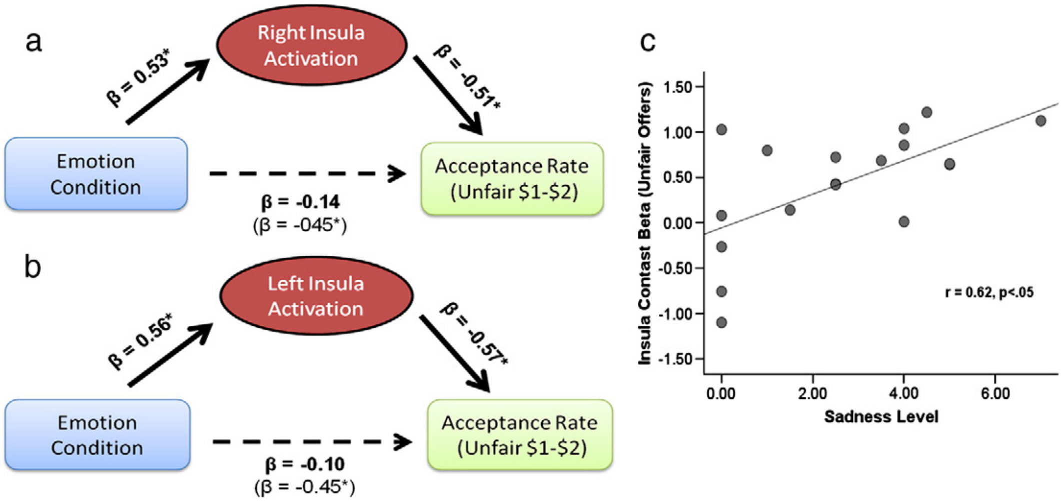

Fig. 4. Mediation models for a) right and b) left insular activations (averaged contrast beta value for unfair offers ($1–$2), *p ≤ .05; c) positive correlation (r = 0.62, p<.01) between right insula averaged contrast beta value ($1–$3 offers) and self-reported sadness from mood induction (across both conditions; 0–8 scale).

2007; Davis et al., 2002; Ploghaus et al., 1999). Interestingly, engagement of the anterior insula has also been linked to the experience and anticipation of aversive events such as negative economic outcomes (Knutson et al., 2007; Paulus et al., 2003). Activation in this area has even been shown to predict risk-averse purchase decisions to the point of overcompensating by risk-averse mistakes (Kuhnen and Knutson, 2005). These findings support a broader role of this region in processing not just basic emotional states related to primary punishers, such as aversive tastes or smells, but also more abstract forms of negative events such as monetary losses. Thus, our present results suggest that activation of the anterior insula may similarly support the integration of a carried-over negative mood state into the decision-making process, and as a result bias behavior. Activation in this region may signal individuals in a sad mood to avoid unfair offers to a greater extent than those in a neutral mood state. Importantly, while insular activation has been implicated in the experience of sadness (Damasio et al., 2000; Lane et al., 1997), here we show that the neural impact of mood is not merely a shift in the overall baseline activity in this region, but rather reflects a differential activation of this area which is context-specific and valence-congruent (i.e. receiving an “unfair” offer from a human partner).

A second finding was that receiving unfair offers in a sad versus neutral mood resulted in more activation in the ACC, a region linked to error and decision conflict monitoring (Botvinick et al., 1999; Hester et al., 2004). Thus, in line with previous studies of sad mood and depression (Knutson et al., 2008; Mayberg et al., 1999), sad affect may introduce an enhanced affective conflict. However, it should be noted that no difference in decision reaction times for unfair offers was observed between the two mood condition groups. A more plausible alternative therefore, may be how mood may affect individuals' perception of expectancy violations. Several fMRI, single cell recording, and ERP studies have linked activation of the ACC with error processing (Hester et al., 2004) and tracking of deviation from expectations (Chang and Sanfey, in press; Oliveira et al., 2007). Moreover, the dorsal part of the ACC (as found here) appears to be specifically related to expectancy violation (such as those of fairness and social inclusion) as opposed to emotional evaluation (Somerville et al., 2006). Thus, the increased ACC activation to unfair offers in sad individuals could be indicative of an enhanced perception of social norm violation for unfair offers, which indeed are typically expected less by players. This would be consistent with prior findings showing that sad individuals reported significantly more anger, disgust and surprise in response to unfair offers (Harlé and Sanfey, 2007). Importantly, however, such differential activation in the ACC did not predict or mediate behavioral biases in the present decision-making task. An unexpected result was that neutral mood participants' ACC activation to unfair offers was lower than their activation to fair offers, which is inconsistent with a previous UG study (Sanfey et al., 2003). We conjecture that this difference stems from a lower affective reaction to unfair offers (e.g. less expectancy violation) in this group (consistent with both lower ACC and insula engagement to these offers), which is supported by their generally higher acceptance rates of unfair offers. Such lower ACC activation to unfair offers may underlie relatively higher activation to fair offers.

Finally, and as predicted, we found a moderating effect of mood in the left ventral striatum, which has been consistently linked to reward processing and experience, with both primary reinforcers and social behavior (Knutson et al., 2007; Tabibnia et al., 2008). Specifically, we found that whereas individuals in a neutral mood showed stronger activation for fair offers (i.e. $5) relative to unfair offers (i.e. $1–$3) in these regions, sad individuals did not exhibit such differential activation. These results are consistent with decreased reward processing in sad individuals, which (speculatively) may be underlain by reduced sensitivity to rewarding social signals such as a peer's act of fairness. These findings also echo previous studies of clinical depression implicating decreased reward responsiveness and diminished striatal activation to rewarding stimuli (Epstein et al., 2006; Henriques and Davidson, 2000) and with the common depression symptom of anhedonia (American Psychiatric Association, 2000). It will be important to further investigate whether this pattern of results is also modulated by individuals' decisions to accept or reject unfair offers (i.e., whether rejecting or accepting an unfair offer in a sad mood is associated with more or less reward relative to a neutral mood). We do not report these analyses here as the present study was not designed and statistically powered to test such hypothesis. Nonetheless, activation in this area was not predictive of decision-making in the present study, which suggests such mood-related alterations in striatal activity may not play a key role in affect infusion during decision-making.

In conclusion, we compared behavioral and neural responses of individuals in both sad and neutral moods in a social economic decision task, and found interesting and important differences suggesting potential brain mechanisms underlying incidental affective influences on decision-making. Expanding on previous behavioral research (Harlé and Sanfey, 2007; Inbar and Pizarro, 2009; Schnall et al., 2008; Wheatley and Haidt, 2005), this study is the first to demonstrate how task-unrelated emotions, such as subtle mood states, can be integrated at the neural level in order to bias decision-making. Further, we highlight a specific mechanism whereby a low-arousal negative emotion can modulate behavior by engaging multiple neural systems, including the insular cortex, ACC, and ventral striatum. One limitation of this study is the lack of on-going, simultaneous, measure of mood during the decision task. We decided against this, as it would likely introduce demand characteristics and distort the availability of such affective information (Schwarz, 2004). However, the mood inducing clips used in this study have been shown to reliably and discretely induce mood (Gross and Levenson, 1995; Harlé and Sanfey, 2007, 2010) and the retrospective ratings used here were consistent with this previous research.

The increase in rejection rates of unfair offers, and the associated stronger recruitment of the anterior insula and ACC network that we observed in sad participants, echo and supplement previous work demonstrating the key role emotion regulation in supporting acceptance of unfair UG offers (Koenigs and Tranel, 2007; Van 't Wout et al., 2010). This pattern of results is consistent with prevalent interactional models of mood infusion in complex cognitive tasks such as decision-making. For instance, according to the Affect Infusion Model (AIM), the extent to which incidental affective information is integrated into decision-making depends on the level of complexity, novelty and required information processing of a particular decision (Forgas, 2002). Thus, as they combine negative (i.e. unfair social signal) and positive (i.e. monetary gain) prospects, inequitable monetary offers in the UG may be conceptualized as less obvious choices, entailing more detailed processing. As we find here, such offers should then prompt a deeper infusion of affect, with negative mood more likely to prompt mood-congruent framing of such offers (e.g. stronger attention to the negative aspects), and bias behavior accordingly.

The present findings are also consistent with complementary theoretical models of affective biases on decision-making. For instance, emotional states can be conceptualized not only in terms of valence congruent associations, but also in terms of specific appraisal tendencies congruent with the emotional state (e.g., certainty–uncertainty dimension; Lerner and Keltner, 2000). Such appraisal tendencies may in turn be integrated into decision-making as heuristics, providing information about how one feels about a given situation (Loewenstein et al., 2001; Schwarz and Clore, 1983). Thus, negative emotions such as fear and sadness can be associated with a sense of uncertainty and would be expected to prompt more cautious and risk-averse attitudes/responses to a given situation. Indeed, research has linked sad mood with overestimation of negative events and underestimation of positive events (Wright and Bower, 1992), as well as with greater risk aversion on a choice dilemma questionnaire (Yuen and Lee, 2003). When applied to *interactive* decision-making (as in the present study), sadness relative to neutral mood would be expected to promote a heightened sense of uncertainty. Thus, while there is no ambiguity about monetary outcomes when responding to UG offers, sad mood may still result in feeling more cautious, particularly toward unfair offers (e.g., uncertainty regarding proposers' motives), which may in turn prompt more avoidance (rejection) of these proposals, as was found here. Additionally, we find stronger insular activation in sad participants, activation of which has also been linked to intolerance for uncertainty (Simmons et al., 2008).

Overall, our findings confirm an interactional and context-specific model of affect infusion at the neural level. Importantly, they suggest a selective role of the anterior insula in mediating such mood influences on actual decision behavior. This, in turn, informs neurocognitive models of economic decision-making, and may have important implications for understanding how transient, and perhaps more chronic, affective states may impact decision-making.

Acknowledgments

This work was supported by funding from National Institute on Aging Grant R21 AG030768, and from a research grant from the University of Arizona Social and Behavioral Sciences Research Institute to Katia Harlé. We would like to thank Drs. John Allen, David Sbarra, and Lynn Nadel, as well as Filippo Rossi and Trevor Kvaran, for their helpful comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.neuroimage.2012.02.027.

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