



HOW DOES SAD MOOD AFFECT RESPONSES TO UNFAIRNESS IN SOCIAL ECONOMIC DECISIONS? A NEUROPHYSIOLOGICAL INVESTIGATION

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HOW DOES SAD MOOD AFFECT RESPONSES TO UNFAIRNESS IN SOCIAL
ECONOMIC DECISIONS? A NEUROPHYSIOLOGICAL INVESTIGATION

by

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As members of the Dissertation Committee, we certify that we have read the dissertation

prepared by Katia M. Harlé

entitled: How does sad mood affect responses to unfairness in social economic decisions?
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and recommend that it be accepted as fulfilling the dissertation requirement for the

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I hereby certify that I have read this dissertation prepared under my direction and
recommend that it be accepted as fulfilling the dissertation requirement.

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DEDICATION

To my parents, Kira Cheboldaeff and Henri L.J. Harlé,
for their untiring support and generosity.

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ABSTRACT

Empirical evidence suggests that complex cognitive processes such as decision-making can be influenced by incidental affect (i.e. emotional states *unrelated* to the decision), which may have importance implications for furthering our understanding and treatment of mood disorders. Following up on previous behavioral findings suggesting that sad mood leads to biases in social decision-making, the present research first investigated how such biases are implemented in the brain. Nineteen adult participants made decisions that involved accepting or rejecting monetary offers from others in an Ultimatum Game (a well known economic task), while undergoing functional magnetic resonance imaging (fMRI). Prior to each set of decisions, participants watched a short video clip aimed at inducing either sadness or a neutral emotional state. Results indicated that sad participants rejected more “unfair” offers than those in the neutral condition, thereby replicating our previous findings. 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, demonstrating how subtle mood states can be integrated at the neural level to bias decision-making.

In a second study, we assessed to what extent such affect infusion in decision-making may translate to clinical depression, a mood disorder involving chronic sad affect. Fifteen depressed and twenty-three nondepressed individuals made decisions to accept or reject monetary offers from other players in the Ultimatum Game. Like transiently sad, but healthy, individuals, depressed participants reported a more negative emotional reaction to unfair offers. However, unlike sad healthy individuals, they accepted significantly *more* of these offers than did controls. A positive relationship was observed in the depressed group, but not in controls, between acceptance rates of unfair offers and resting cardiac vagal tone, a physiological index of emotion regulation capacity. These findings suggest distinct biasing processes in depression, which may be related to higher reliance on regulating negative emotion.

INTRODUCTION

Context and Significance

Social interaction and the perception of various social signals are essential aspects of human decision-making. Yet they are largely underrepresented in economic and psychological models of decision-making, and are rarely studied empirically. However, within such interactional contexts, we often make decisions that defy our concept of “rationality” and seem to rely more on intuitive processes or “gut feelings”, whether the decision involves deciding to sell one’s possession to a stranger or to propose to one’s significant other. While the influence of emotional factors in decision-making has been increasingly recognized, a more specific understanding of the neural and motivational systems involved in such cognitive process is still lacking. For instance, one may ask what specific motivational processes are responsible for sad individuals turning down financial compensation that is deemed “unfair”, despite the obvious economic disadvantage. In addition, there is little empirical work investigating the similarities and differences between transient sad affect in healthy subjects and clinical depression. Contrasting such populations may shed light on whether depressives’ decision-making is impaired and whether it is necessarily less adaptive than sad healthy individuals’ in an ecologically valid context. Mood disturbances, such as those observed in depression, may indeed lead to decision biases in a social context. These types of decisions may have the greatest influence on the day-to-day lives of depressed individuals, thus such research

may contribute to practical efforts to improve these individuals' confidence, self-esteem, and social connectedness.

A neuro-economic approach may prove particularly useful to study the interaction of mood and decision-making. Indeed, recent advances in brain imaging techniques have prompted new research endeavors to identify what neural systems are engaged in supporting higher-order cognitive processes such as social economic decision-making. For instance, distinct neural subsystems have been shown to contribute to rule maintenance and implementation, on the one hand, and affective influences on the other hand (Sanfey et al., 2003). The present research used functional magnetic resonance imaging (fMRI), which combines high spatial and temporal resolution, to further assess how mood may bias neural processes in these various systems. Such endeavor may help refine our understanding of affect infusion in decision-making, which may in turn have important therapeutic implications. For instance, such data may be used for developing behavioral treatments that address specific cognitive processes, or neurofeedback interventions.

Research Goals

Following up on findings from the author's Masters thesis (Harlé & Sanfey, 2007), the present research aimed at investigating the emotional, motivational, and neural basis of how incidental sadness, a prominent symptom of clinical depression, may bias simple economic decisions. The primary decision paradigm was a well known economic

task, the Ultimatum Game, in which individuals had to decide on accepting or rejecting monetary offers from various partners. These offers were designed to range from fair (i.e. equitable) to unfair. While designed to enhance our understanding of the psychological and neuronal mechanisms involved in real-life interactive decision-making under sad affect, this study further sought to assess whether the more chronic sad mood involved in depression had similar behavioral and physiological effects on such decisions. The specific aims and research questions were as follows:

1) Examine the neural underpinnings of how sad mood may infuse and bias social economic decision-making.

1.a. The first experiment attempted to replicate our previous behavioral findings that, relative to a neutral mood, a transient sad affect induced in healthy participants leads to more rejections of unfair offers in the Ultimatum Game. The experiment was also designed to explore any within-subject mood effects on decision-making.

1.b. In this experiment, participants played the Ultimatum Game while undergoing fMRI in order to assess what neural systems may be engaged by, and possibly mediate, such biases. The main hypothesis was that induced sadness may “prime” the insular cortex, a region associated with aversive emotional experience and previously associated with more rejections of unfair offers in this task. Sad mood was also expected to prompt more activation in the dorsolateral and ventro-medial prefrontal cortex in the context of receiving unfair offers, as these areas are typically engaged in integrating and regulating

emotional information. Activations in these areas were particularly targeted as potential mediators of affect infusion in this decision-making framework.

2) Assess the behavioral, emotional and physiological impact of clinical depression in the same economic decisions, and compare such potential biases to those arising from transient sad affect in healthy participants.

2.a. The second experiment was aimed at assessing performance in the same decision task in unmedicated depressed individuals. Based on evidence of decreased reward responsiveness in depression and recent findings that sad mood (Harlé & Sanfey, 2007) and transient serotonin depletion (Crockett et al., 2008) in healthy participants results in lower acceptance rates in this task, we predicted that depressed individuals, relative to healthy controls, will also accept fewer unfair offers and exhibit a more negative emotional response to these offers. Alternatively, some evidence suggests that depressed individuals may be more realistic and less likely to overestimate the impact of their decisions, which may lead them to behave more “rationally” and accept more unfair offers than controls.

2.b. A second aim of this experiment was to assess the regulatory processes associated with acceptance or rejection of unfair offers, as emotion regulation is a well-known dysfunction in mood disorders such as depression. We investigated the relationship between decision-making and a physiological measure of emotion regulation capacity (cardiac vagal tone; Porges, 2007). Based on evidence that emotion regulation plays an important role in the presently used decision task, and that depression has been

associated with deficits in such regulatory processes, we hypothesized that, relative to healthy controls, depressed individuals would have on average lower indexes of cardiac vagal tone, reflecting lower capacity to regulate emotion, which would in turn predict a more negative emotional reaction to unfair monetary offers.

Background

A Dual-Process Framework of Decision-making

Until recently, standard economic models of decision-making have overlooked the contribution of emotional processes. However, people are often inconsistent and easily biased when making decisions. Notably, they may react very differently to the same situation depending on their emotional state (e.g., when deciding to purchase something, or to ask someone out). Recent behavioral and neuropsychological research has shown that certain neural structures that provide and incorporate information of an affective nature are in fact essential to effective decision-making (Damasio, 1994). Driven by this understanding, “dual process” models of decision-making have emerged, attempting to incorporate emotional influences in the decision process by positing the reciprocal modulation of an affective, intuitive system (“System 1”), and a logical, deliberative component (“System 2”; Stanovich & West, 2000; Sloman, 2002).

The Ultimatum Game

Empirical findings from a simple interactive game, known as the Ultimatum Game (UG, Guth et al., 1982), provide supporting evidence for the dual-system models.

This game is a well studied task incorporating an economic choice framework and important consequential aspects of decision making (e.g. involving an interactive context with human partners). The task involves a player assigned as a “proposer” making monetary offers to another player (the “responder”) concerning a given amount of money the two must split between them. The responder must then either accept or reject the offer. If the offer is accepted, the money is split as proposed. However, if the offer is rejected, neither player receives anything. While the standard economic solution to the game is for the responder to accept any offers, as any monetary amount is preferable to none, numerous UG studies have consistently shown that, irrespective of future interactions with proposers, unfair offers are rejected about 50% of the time. This robust experimental finding is particularly interesting as it shows that, under certain social circumstances, people are motivated to actively turn down monetary reward. Interestingly, responder’s physiological arousal, measured by skin conductance activity, appears to increase significantly when presented with unfair offers and has been associated with the rejection of unfair offers (Van 't Wout et al., 2006). In addition, responders frequently report feeling indignation, disgust, even anger, when they receive unfair offers (Camerer, 2003; Harlé & Sanfey, 2007).

At the neural level, specific brain regions associated with deliberative processes (dorsolateral prefrontal cortex, DLPFC), emotional processing (insula), as well as cognitive conflict (anterior cingulate cortex, ACC), have been associated with the decision-making process in the UG (Sanfey et al., 2003). Additionally, the magnitude of

such activations was significantly greater for offers coming from human partners compared to computer offers, showing that the social nature of the decision context and its relevance to the decision itself may be implemented at the neural level. Notably, this study showed that insular activation was significantly greater in response to unfair offers that were later rejected than to subsequently-accepted unfair offers. Additionally, a recent study has shown that the ventromedial prefrontal cortex (VMPFC) may sub-serve responders' ability to regulate emotion and accept unfair offers in the UG task (Koenigs & Tranel, 2007). Taken together, this research suggests that the Ultimatum Game embodies a dual-process paradigm of decision-making, combining a negative "emotional" response to unfairness and a more rational response to maximize one's economic gains despite an offensive proposal (i.e. rejecting or accepting an unfair offer, respectively). Such task therefore provides a good theoretical basis to explore the neural basis of additional affective biases in those types of decisions.

Incidental Emotion and decision-making

Loewenstein and Lerner (2003) have identified two categories of emotional influences: expected (i.e. task-driven) emotions and immediate emotions (such as incidental moods). The latter are particularly noteworthy, as they may be unconscious and unrelated to the decision at hand, but nonetheless have the potential to influence decision-making in important ways. The emotion and social psychology literatures in turn provide ample evidence that incidental emotional states can influence people's goals, plans, attitudes and ultimately their behaviors in realistic social interactions (Zajonc,

2000, Forgas, 2003). Emotional states can affect risk perceptions and choice in more constructive processing (Fedorikhin & Cole, 2004) and can also foster stronger memory for mood-congruent details when making judgments on people (Forgas & Bower, 1987, 2001). In comparison to neutral and negative moods, a positive affect is typically associated with more confidence about the encounter, higher expectations about success, more optimistic framing, more cooperation and leniency (Forgas, Bower, & Moylan, 1990), and higher willingness to use integrative strategies and make/reciprocate deals (Forgas, 1998c). Positive emotional states are also associated with more global processing (Gasper, 2004), more favorable ratings and higher task satisfaction (Isen & Shalker, 1982), and tend to give access to a wider range of material from memory and to a more complex cognitive context in which to interpret material (Isen & Daubman, 1984). This can lead to more inclusive categorizations, greater creativity and more divergent thinking (Clapham, 2001). In contrast, negative mood states, such as sadness, are usually associated with lower confidence and more risk-averse behaviors. Negative affect seems to trigger a more effortful, analytic, and vigilant processing style (Clark & Isen, 1982; Isen, 1984). However, it should be noted that distinct mood carry-over effects on decision-making have been identified within the same valence modality. For instance, induced disgust and sadness, two negatively valenced emotions, were found to respectively eliminate or reverse the endowment effect in economic decisions, whereby selling prices tend to exceed buying prices for the same object (Lerner, Small, & Loewenstein 2004).

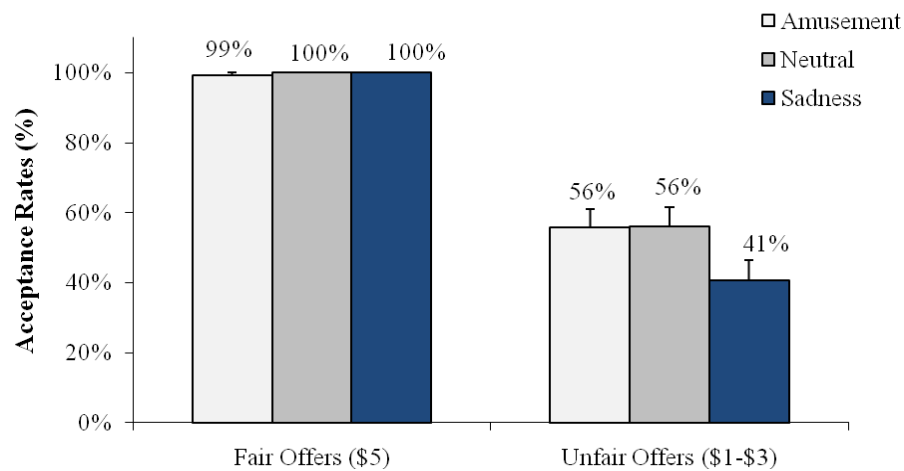
Previous Work by the Author

Sadness biases acceptance rates in the Ultimatum Game

In an effort to explore how mood may influence decisions, we previously compared the effect of induced sadness, induced amusement, and a neutral state on decision-making in a computerized version of the Ultimatum Game (Harlé and Sanfey, 2007). This was the basis of the author's Master's thesis. To induce specific mood states, we used short movie clips (mostly selected from commercial movies), an effective and empirically tested method (Gross & Levenson, 1995). All clips were piloted in a sample of undergraduate students at the University of Arizona, prior to the UG experiment. A total of 119 undergraduate played the UG as responders and received a total a 24 offers, which varied in their degree of unfairness and the type of partner (human partners or computer). To enhance realism, subjects were paid upon completion of the task, based on a proportion of their actual accumulated earnings. Decision-making performance was operationalized by subjects' average acceptance rates for different types of offers (fair vs unfair). Induced sadness resulted in significantly lower acceptance rates of unfair offers ($M=40.7\%$) in comparison to the neutral and happiness conditions ($M= 55\%$, $p<.05$; see Figure 1). Acceptance rates in the neutral condition were similar to typically observed acceptance rates of unfair offers in this task (with no emotional manipulation) based on previous UG studies (50-60%; Camerer, 2003). Thus, this study showed that a task-unrelated negative mood state can bias decision-making. Importantly, such mood effect was context specific, that is behavioral differences were only observed for unfair offers.

Such type of mood task interaction is in line with prevalent models of affect infusion (Affect Infusion Model; Forgas, 2002), which predicts that incidental affect is more likely to be incorporated into other cognitive processes such as decision-making when the task is more ambiguous and complex, thereby requiring more information processing.

Figure 1. Acceptance Rates for Human Offers



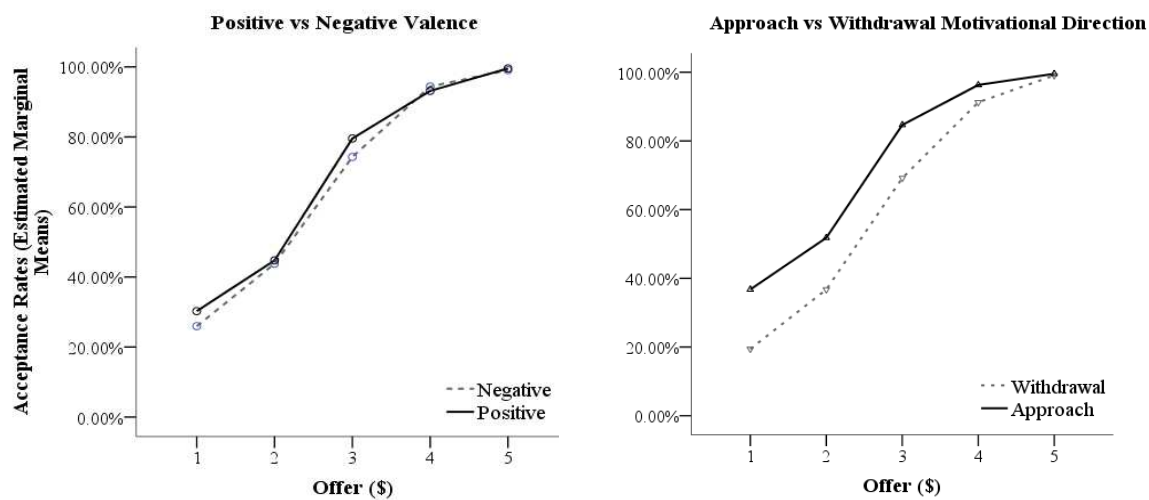
Avoidant motivation may account for such affective biases

The above mentioned results suggest that a transient emotional state, sadness, may affect economic decisions in the context of social interaction. This result, however, raises new questions: how is such negative emotional state affecting decision-making in this context, and what dimensional framework of emotion can best account for this effect. For instance, do other negatively valenced emotions similarly bias such decisions or can another emotional dimension of sadness account for this effect. To address this question,

we jointly explored the role of emotional valence (i.e. positive vs negative) and motivational tendency (i.e. approach vs avoidance) on performance in the Ultimatum Game (Harlé & Sanfey, 2010). A total of 204 undergraduate psychology students (76% female) were recruited and each randomly assigned to one of five emotion conditions. After removal of participants who reported confounded emotion induction, the total sample included 179 participants (neutral, $n=38$; amusement, $n=37$; anger, $n=35$; serenity, $n=33$; disgust, $n=36$). As in our previous study, they were paid a small percentage of their actual earnings in the UG task. We used previously piloted short movie clips to induce the respective emotion in each condition. Participants received 24 offers from virtual partners, and each time had to either accept or reject the offer (\$10 split). Offers varied in their degree of unfairness as in the sadness experiment. A repeated-measure analysis of variance (ANOVA) was conducted using this offer acceptance rate as the dependent variable, the offer amount as the within-subject factor (\$1, \$2, \$3, \$4, \$5), and two statistically orthogonal contrast variables (negative-positive valence, withdrawal-approach motivation). The valence contrast compared anger and disgust (negative) with amusement and serenity (positive). The motivation contrast compared amusement and anger (approach) with serenity and disgust (withdrawal). In addition to a significant main effect of offer amount, $F(4, 171) = 125.00, p < .001$, a significant main effect of the motivational direction contrast (withdrawal vs approach), $F(1, 174) = 8.67, p < .005$, was observed, with acceptance rates for withdrawal emotions (disgust, serenity) being consistently lower than acceptance rates for approach emotions

(amusement, anger), after Bonferroni corrections ($p < .05$; see Figure 2). The valence contrast itself was not statistically significant ($p = .59$). Both induced disgust and serenity prompted greater rejection of unfair offers, relative to a neutral state.

Figure 2. Acceptance Rates by Valence and Motivational Tendency



The fact that sadness, disgust, and serenity lead to similar decision patterns regarding unfair offers lends credence to the hypothesis that a withdrawal motivational tendency, more than negative valence per se, plays an important role in biasing decisions in the UG. These results may have implications for the neural investigation for such affective biases, as one broader explanation for these data is that particular types of emotions (i.e. in the present case, those with a withdrawal motivational tendency) may ‘prime’ specific cognitive, and even neural, processes that are involved in the decision-

making process. One obvious candidate, related to emotional processing, is the anterior insula, which has been associated with rejection of unfair offers in the UG (Sanfey et al., 2003). Thus, results from these preliminary studies suggest that negative withdrawal-based emotional states, such as sadness, may further modulate these neural processes, which may translate into increased signaling of potentially aversive outcomes and thus prompt an avoidant response (i.e. withdrawal from the social exchange and punishment of the transgressor). In addition, although insular activation has been associated with a broad range of negative emotions in a variety of settings (e.g. pain, distress, disgust; Ploghaus et al., 1999; Davis et al., 2002; Calder et al., 2007), studies with both humans (Paulus & Stein, 2006) and animals (Weizkrantz & Wilson, 1958) suggest that the anterior insular region is consistently involved in the anticipation of aversive stimuli and indeed is necessary to implement harm withdrawal. Thus, our findings are consistent with the account that task-unrelated avoidant emotion may prime the insular region, resulting in heightened anticipation of aversive outcomes and hence more withdrawal responses, which was investigated in the first experiment of this dissertation (see Appendix A).

Format Choice

The above work, which was primarily designed and conducted by the author, led to specific research questions that were explored in the present dissertation (see Research Goals section). Drs Alan Sanfey and John Allen co-supervised statistical analysis for this research. These studies in turn produced publishable results. The first drafts of these

research articles were entirely drafted by the author. Some sections were edited by the author's primary advisors (Dr. Alan Sanfey), as well as Dr. John Allen for Study B. Thus the present papers are an accurate reflection of the author's research work in the course of her graduate tenure, and they were approved for the basis of the author's dissertation.

PRESENT STUDY

Neural Mechanisms of Affect Infusion in Social Economic Decision-making: a Mediating Role of the Anterior Insula.

The methods, results, and conclusions of this study are presented in the paper appended to this dissertation/thesis (see Appendix A). The following is a summary of the most important findings in this document.

Summary

Nineteen adult participants made decisions which involved accepting or rejecting monetary offers from human and non-human (computer) partners 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 sadness or a neutral emotional state. Participants in the sadness condition rejected more “unfair” (i.e. \$1-\$3) offers than those in the neutral condition, replicating our previous behavioral findings. Neuroimaging analyses revealed that receiving unfair offers while in a sad mood elicited activity in brain areas related to aversive emotional states (insula) and cognitive conflict (anterior cingulate cortex). In contrast, no neural correlates of sadness were observed during phases preceding offer proposal or when participants received “fair” offers (\$5). Importantly, this study also showed that the anterior insula uniquely mediated mood infusion in the present decisions, while other neural correlates of sad mood in the presence of unfairness did not directly predict behavior.

Clinical Depression and Social Economic Decision-Making

The methods, results, and conclusions of this study are presented in the paper appended to this dissertation/thesis (see Appendix B). The following is a summary of the most important findings in this document.

Summary

Fifteen depressed and twenty healthy individuals completed the decision task, in which they had to accept or reject monetary offers from human partners proposing to split an amount of money. Emotional experience to unfair offers was measured. Cardiac vagal control (CVC) was assessed during a resting baseline to obtain a physiological measure of emotion regulation capacity. Relationships between CVC and behavioral measures of decision-making were explored. Although depressed individuals reported a more negative emotional reaction when receiving unfair offers (i.e. < \$3 out of \$10), they accepted on average 20% more of these offers than healthy controls. A positive relationship between CVC and acceptance rates of unfair offers was observed in the depressed group, but not in healthy controls. This study shows a discrepancy between depressed individuals' emotional reactions to unfair offers and their decisions to accept more of these offers. Such decision patterns are inconsistent with recent findings that a sad mood or induced serotonin deficiency in healthy individuals lead to less acceptance of unfair offers, suggesting distinct biasing processes in clinical depression. Heightened need to regulate negative emotion may underlie such biases in depressed individuals.

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APPENDIX A: THE NEURAL MECHANISMS OF AFFECT INFUSION IN SOCIAL
ECONOMIC DECISION-MAKING: A MEDIATING ROLD OF THE ANTERIOR
INSULA

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The Neural Mechanisms of Affect Infusion in Social Economic Decision-Making:
a Mediating Role of the Anterior Insula

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Abstract

The neural mechanisms mediating the impact of emotion on decision-making remain relatively unexplored. Empirical evidence, however, suggests that decision-making can be influenced by incidental affect (i.e. emotional states *unrelated* to the decision). Here, we investigated how such 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 sadness or a neutral emotional state. Results indicated that 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 bias decision-making.

Introduction

Although the role of emotion in decision-making is well recognized (Kahneman, 2003), research has focused on the effect of task-related affect, such as transient mood states, rather than incidental emotion (Lerner and Loewenstein, 2004). We recently demonstrated that sad mood can bias economic decisions in the Ultimatum Game (UG; Guth et al., 1982), a task in which players must accept or reject proposals from others on how to divide a sum of money between the two. Although individuals in a neutral mood tend to reject about half of “unfair” offers (i.e. less than 30% of the pot; Camerer, 2003), sadness led to even lower acceptance rates coupled with a more defensive emotional reaction. In contrast, sadness did not impact acceptance of “fair” offers (i.e. 40-50% of the pot; Harlé and Sanfey, 2007). Based on these findings, however, it remains unclear what neural mechanisms mediate mood-driven biases. While the neural correlates of experienced sadness have been well-investigated and point to multiple networks from limbic to frontal areas (Lane et al., 1997; George et al., 1995), these studies do not address how mood interacts to bias behavior in other cognitive tasks. To address this question, we used functional magnetic resonance imaging (fMRI) to examine brain areas where these affective influences are implemented.

Based on previous behavioral work, we expected mood to interact with offer amount at the neural level, consistent with a moderating role of sad mood (i.e. stronger influence of mood for lower offers). One brain area that may be associated with such selective mood influence is the anterior insula. In addition, correlating with a higher

likelihood of rejecting unfair UG offers (Sanfey et al., 2003), this region has been consistently linked to the integration of emotional and somatosensory information, including the experience of disgust and anger (Calder et al., 2007; Denson, 2009) and anticipation of aversive (monetary) events (Paulus et al., 2003; Kohnen and Knutson, 2005). Stronger activation in this region when receiving unfair offers may therefore indicate an aversive response to unfairness (a negative social signal), enhanced by an incidental negative mood. Thus we predicted that, relative to neutral mood, sadness would lead to stronger anterior insula activation when presented with unfair offers, and that this activation would specifically mediate the relationship between mood and decision behavior.

Inequitable UG offers may also prompt greater cognitive conflict in sad participants. Because of its demonstrated role in the tracking of error and conflict (Hester et al., 2004; Botvinick et al., 1999), we predicted stronger anterior cingulate cortex (ACC) activation in sad mood states. Finally, sad mood has been associated with selective attention to mood-congruent stimuli and decreased sensitivity to reward (Hills et al., 2001; Epstein et al., 2006). Based on work linking activation of the Nucleus Accumbens (NAcc) to expectation of monetary (Knutson et al., 2007) and social (Tabibnia et al., 2008) reward, we hypothesized that while neutral mood participants would show increased NAcc activation for fair relative to unfair offers, sad participants would not show such differential NAcc activation.

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 typical 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. Their pictures were taken and they were told their partners in the task would see their de-identified picture when making their offer. To ensure that subjects were sufficiently motivated to make real decisions, they were told they would be paid a proportion 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, 1983), aimed at assessing any potential group difference in susceptibility to the mood induction procedure.

Decision Task (Ultimatum Game)

At the beginning of the individual 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 one-time monetary offers from 24 different partners as well as 24 randomly generated computer offers. The 48 offers were presented into 4 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. 12) of \$5, \$3, \$2, and \$1 offers. The pictures that participants saw were selected from a pool of actual UG players' photographs from previous studies (Harlé & Sanfey, 2007).

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 & 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. One clip was shown to participants inside the scanner immediately prior to each block of UG offers. All four clips were shown to participants in counterbalanced order (half saw the two sadness clips first, and the other half saw the two neutral clips

first¹). Participants were randomly assigned to each clip sequence (neutral first or sadness first). To maximize attention to the clip while minimizing demand characteristics, participants were told these clips were part of a separate memory task and that they would be asked questions about the clips at the end of the session. 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 screen shot from the previously watched emotion inducing clip for 6 s. Such stimulus was included as a way to boost mood induction over the whole set of offers based on a prior behavioral pilot. Next, a picture of the proposer for that trial was presented (i.e. human partner or a computer picture) for 4s. Participants then saw the offer and had up to 10s to either accept or reject the offer by way of a button press. Finally, the decision outcome was presented for 4 s (Figure 1).

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 minutes T1-weighted scan (TR=2000ms, TE=25ms, 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 minutes long were then conducted while participants played the Ultimatum Game. Functional scans used a 3-shot echo planar imaging (EPI) sequence to maximize signal in regions associated with high susceptibility artifact such as the orbitofrontal cortex (Weiskopf et al., 2006; TR = 2000 ms, TE = 25 ms, 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 (6s 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 4s 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 offer amount and partner type as within-subject factors. Contrasts of interest for any significant factor interactions were further examined with t-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). In addition to whole-brain analyses, we conducted region of interest (ROI) analyses to tease apart any significant condition by offer interactions in our three hypothesized ROIs. Averaged brain activation was extracted from these ROIs, including four functionally

defined areas in right and left anterior insula ACC, and left ventral striatum, as well as two anatomically defined spherical regions of 216 mm^3 for right and left NAcc (centered on TA coordinates: $\pm 10, 16, 0$). NAcc ROIs were identified based on previous studies implicating this region in reward processing (Knutson et al., 2007). Bonferroni corrections for multiple comparisons were applied to specific contrasts of interests in these ROIs correcting for the total number of tests. Finally, to assess whether averaged brain activation extracted from various ROIs 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, we found a strong and discrete mood induction effect as self-reported sadness was significantly higher in the sadness condition ($M = 3.82$) than in the neutral condition ($M = 0.89$; $t(18) = 6.59, p < .001$). Additionally, ratings obtained on a variety of discrete emotions in the neutral group were all consistently low (average ratings under 1.5, on a 0-8 scale). Further analyses indicated that participants' self-reported emotional susceptibility was moderately low ($M = 1.67, SEM = 0.22$). Importantly, participants' emotional susceptibility 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: \$4.3). 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 effects logit model with random intercepts at the subject level was used to predict decision-making (i.e. acceptance or rejection) using offer amount and partner type 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 sad mood less likely to lead to acceptances relative to a neutral mood. The offer amount X condition interaction was marginally significant ($p = 0.06$; Figure. 1b). No main effect of partner type or any other interactions were observed.

Imaging Results

Whole Brain Analyses (Offer/Decision)

Whole brain analyses revealed a significant condition x offer interaction in several areas including right and left anterior insula, bilateral ACC, right dorsolateral prefrontal cortex (DLPFC), right ventromedial prefrontal cortex (VmPFC), left orbitofrontal cortex (OFC), left ventral striatum, right cuneus, and bilateral temporal poles (Table 1). 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 (Figure 2a, 2b), bilateral ACC (Figure 3). A similar pattern was observed in right DLPFC, right VmPFC, left OFC, and bilateral temporal poles. In contrast, receiving fair human offers (\$5) in a sad relative to neutral mood resulted in stronger activation in the right cuneus, but not in the other regions.

Between-group contrasts also revealed a double dissociation in a functionally identified ROI in the left ventral striatum. Specifically, relative to those in a neutral mood, sad participants showed a significantly lower activation to fair offers (i.e. \$5) and a significantly higher activation to unfair offers (i.e. \$1-\$3). Based on our hypotheses, within group comparisons were also conducted to contrast activation to unfair offers and fair offers. 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 ($p = 0.07$; Figure 2a, 2c).

Supplemental Region of Interest Analyses (NAcc):

Based on our hypotheses, the same set of within group contrasts was examined for two anatomically defined ROIs in the right and left NAcc. A significant mood by offer amount interaction was observed. For neutral mood participants, average activation to fair (i.e. \$5) offers was significantly higher than activation to unfair (i.e. \$1-\$3) offers in both right and left ROIs ($p < .05$; Bonferroni corrected). No such activation differences between unfair and fair offers were observed in the sad condition ($p > .05$; Figure 4).

Prediction Analyses

Having identified several areas that tracked a moderational influence of mood on UG decisions (i.e. stronger activation to unfair offers 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. Based on behavioral results revealing a strongest effect of mood on acceptance of \$1 and \$2 offers (the most “unfair” offers), we used a hierarchical regression method (27) to examine the potential mediating effect of insular activation to

unfair offers in explaining the relationship between mood and acceptance rates. 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 condition significantly predicted right insular activation, $F(1,17)=6.2$, $p<.05$ ($\beta=.53$), consistent with previously reported imaging results. Condition was 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 (i.e. in addition to condition) removed the effect of condition ($p=.55$), leaving right insular activation as the only significant predictor of acceptance rates ($\beta=-.51$, $t=-2.1$, $p<.05$), consistent with a meditational role (Figure. 5a). A similar mediation pattern was observed with left insula activation (Figure. 5b).

In addition, individual contrast coefficients of insular activation at onset of offer were significantly correlated with the level of sadness participants reported from the primes, consistent with the significant condition effect (Figure. 5c). Similar mediation analyses were conducted for NAcc and ACC activations to unfair offers. NAcc activation did not significantly predict acceptance rates. Although emotion condition was significantly related to ACC activation, such activation was not a significant predictor of acceptance rates.

Discussion

The goal of this research was to examine the neural underpinnings of how a transient negative mood 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. Interestingly, 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, in line with this cognitive model, and because 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 conflict and involved processing. 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.

Whole-brain analyses were conducted to provide a comprehensive examination of these mood effects, and revealed three areas we a priori predicted 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 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. Notably, engagement of the anterior insula has been linked to the experience and anticipation of aversive events such as negative economic outcomes (Paulus et al., 2003, Knutson et al., 2007). Activation in this area has even been shown to predict risk-averse purchase decisions to the point of overcompensating by risk-averse mistakes (Kuhnen & Knutson, 2005). Thus, the present study is the first to show that incidental and task-unrelated emotional states can be similarly integrated into the neural processes underlying decision-making 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.

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 (Hester et al., 2004; Botvinick et al., 1999). Thus, in line with previous studies of sad mood and depression (Mayberg et al., 1999; Knutson et al., 2008), sad affect may introduce an enhanced affective conflict. Alternatively, 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, 2009). Moreover, the dorsal part of 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.

A final set of findings involved the ventral striatum, including the Nucleus Accumbens (NAcc), 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 suggest sadness may not necessarily result in overall decreased reward processing, but rather in a decreased sensitivity to different levels of monetary reward. These findings echo previous studies of clinical depression implicating decreased reward responsiveness and diminished NAcc activation to rewarding stimuli (Henriques and Davidson, 2000; Epstein et al., 2006) and with the common depression symptom of anhedonia (American

Psychiatric Association, 1994). Thus, the present study may have important implications to refine neuro-cognitive models of decision-making in affective disorders involving recurrent sad mood such as depression. Nonetheless, differences in how transient sadness in healthy individuals, on the one hand, and depression on the other hand, may affect economic decision-making have been observed both behaviorally (Harlé et al., 2010) and neurally (Mayberg et al., 1999). Future studies should therefore seek to disentangle how these two conditions may similarly and distinctly impact reward circuitry and economic decision-making, while considering other symptoms of depression and potential differences in regulatory processes.

In conclusion, we compared behavioral and neural responses of individuals in both sad and neutral moods in a social economic decision task. This study is the first to demonstrate how task-unrelated emotions, such as subtle mood states, can be integrated at the neural level to bias decision-making. Further, we highlight the mechanism whereby a low-arousal negative emotion can modulate behavior by engaging multiple neural systems, including the insular cortex, ACC, and ventral striatum. Importantly, results suggest a selective role of the anterior insula in mediating mood influences on actual decision behavior. Consistent with an important behavioral literature, these findings also confirm an interactional, context-specific, model of mood-driven decision biases at the neural level, which in turn informs neuro-cognitive models of economic decision-making and has important implications for cognitive models of mood disorders such as clinical depression.

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Footnote

¹ Based on examination of computed acceptance rates for each type of offer and clip/emotion condition, and as expected based on likely carry-over effect of mood and training effect, no within-subject effect of emotion condition was observed (i.e. across all 4 blocks). Thus we decided to limit data analyses to the first half of trials only (i.e. with emotion as a between subject factor), whereby keeping the same mixed design used in our previous behavioral study (Harlé and Sanfey, 2007).

Table and Figure Legend

Table 1. BOLD Activation Foci for Mood Condition (Sad-Neutral) X Offer Type (Unfair-Fair) Interaction; offer onset period (human offers); whole brain random effect analysis; corrected for cluster-wise significance: $p < .01$, minimum cluster size 10 voxels/270 mm³).

Figure 1. a) Ultimatum Game (UG) trial timeline; b) Acceptance rates of UG offers by offer amount.

Figure 2. a) Coronal view of BOLD response in right and left anterior insula and ventral striatum at offer presentation (initial 4s) for human offers (whole brain analysis, corrected for cluster-wise significance: $p < .01$, minimum cluster size 270 mm³); 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).

Figure 3. a) Sagittal view of BOLD response in ACC at offer presentation (initial 4s) for human offers (whole brain analysis, corrected for cluster-wise significance: $p < .01$, minimum cluster size 270mm³). 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).

Figure 4. Average activations to fair and unfair offers by condition in both right and left NuAcc. (Error bars: ± 1 s.e.m).

Figure 5. Mediation models for a) right and b) left insular activations (averaged contrast beta value for unfair offers (\$1-\$2), $*p \leq .05$; 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 (0-8 scale).

Tables and Figures

Table 1

Region	Talairach coordinates (x y z)			F	p	Cluster Size (voxels)
R Anterior Insula / Orbitofrontal Cortex	39	29	-8	9.24	0.000055	111
R Dorsolateral Prefrontal Cortex	42	17	34	6.10	0.00126	14
R Precentral Gyrus	36	5	46	5.90	0.001555	23
R Superior Temporal Pole	36	5	-17	6.61	0.000738	12
R Ventromedial Prefrontal Cortex	33	53	19	5.45	0.002493	31
R Lateral Prefrontal Cortex	27	50	31	6.04	0.001336	17
R Putamen	27	8	-5	6.31	0.001004	15
R Supplemental Motor Area (SMA)	6	23	49	7.77	0.000227	86
R Parahippocampal Area	21	-22	-14	8.88	0.000078	12
R Cuneus / Precuneus	15	-73	40	8.07	0.00017	20
Bilateral Anterior Cingulate Cortex	9	38	25	7.87	0.000208	102
R Cerebellum	18	-34	-23	6.56	0.000775	14
L Supplemental Motor Area (SMA)	-9	11	49		0.000007	42
L Cerebellum	-12	-34	-20	8.09	0.000167	17
L Temporal Pole / Anterior Insula / Putamen	-33	11	-14	7.70	0.000246	72
L Orbitofrontal Cortex	-30	47	7	5.97	0.001438	25
L Inferior Parietal Gyrus	-45	-43	40	8.22	0.000146	27

Figure 1

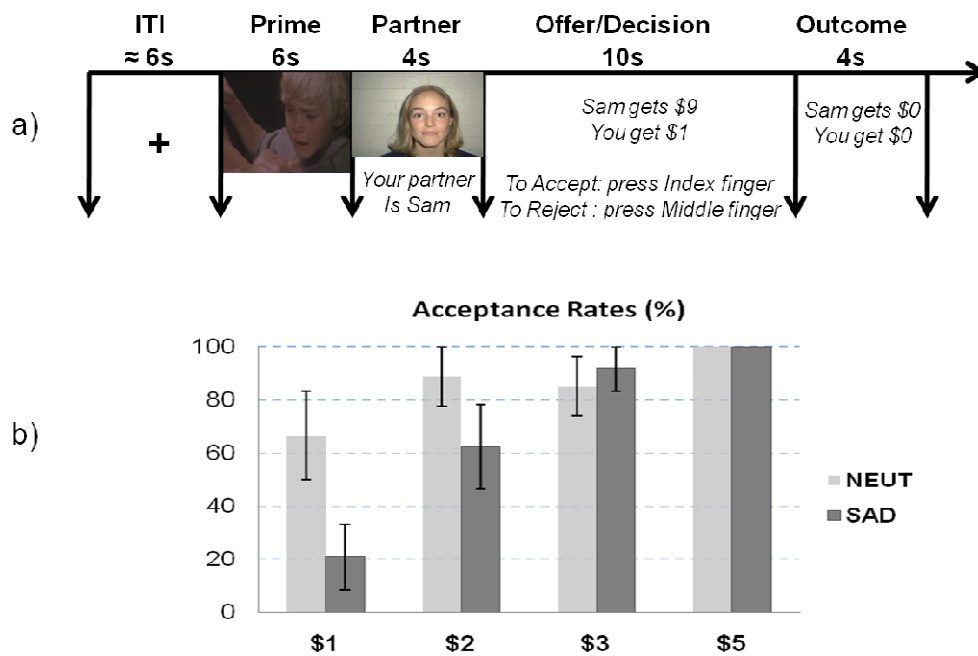


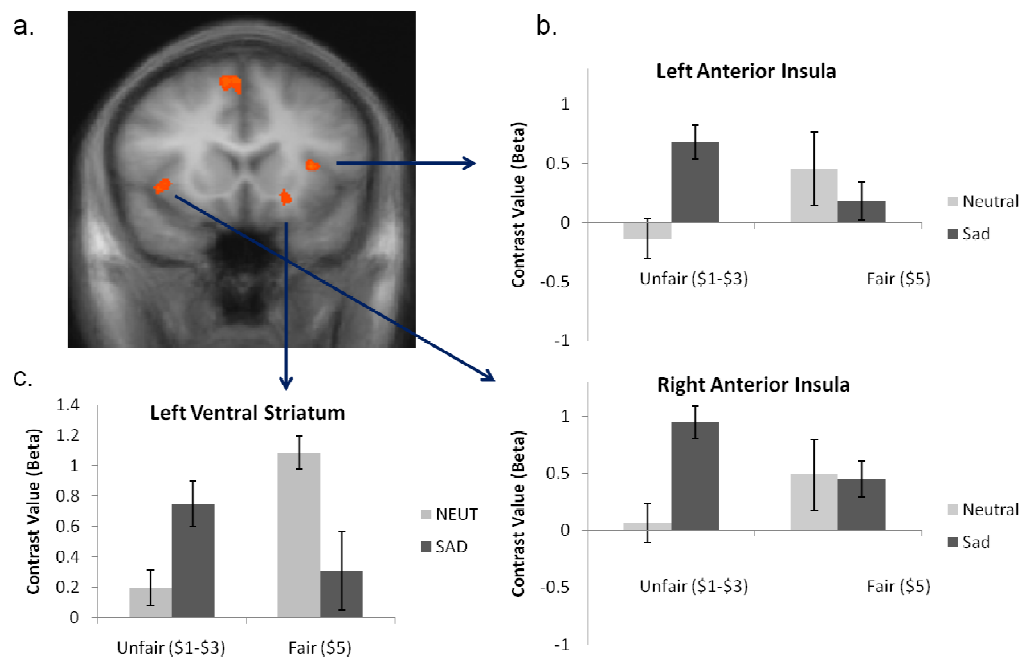
Figure 2

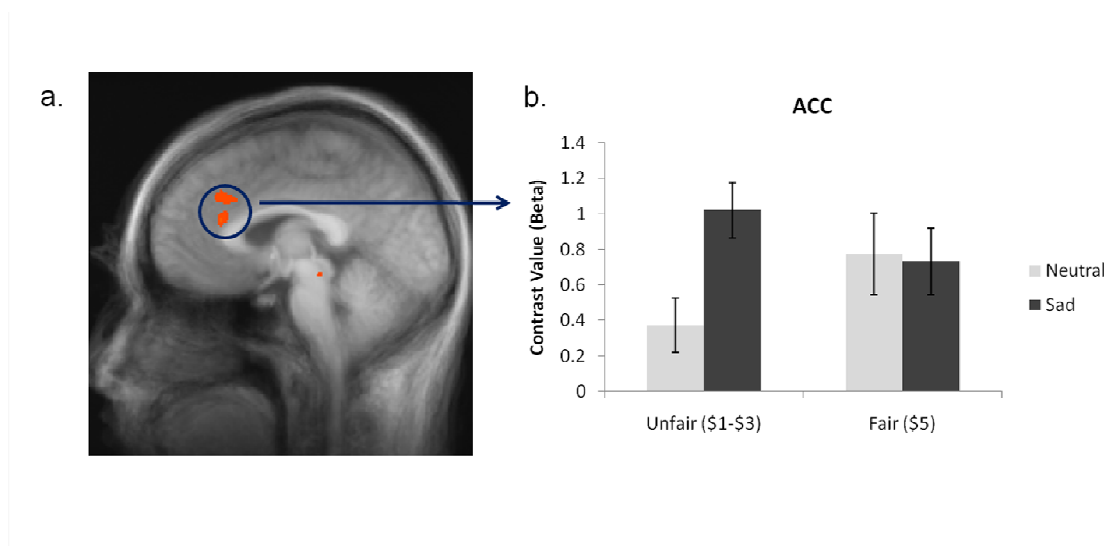
Figure 3

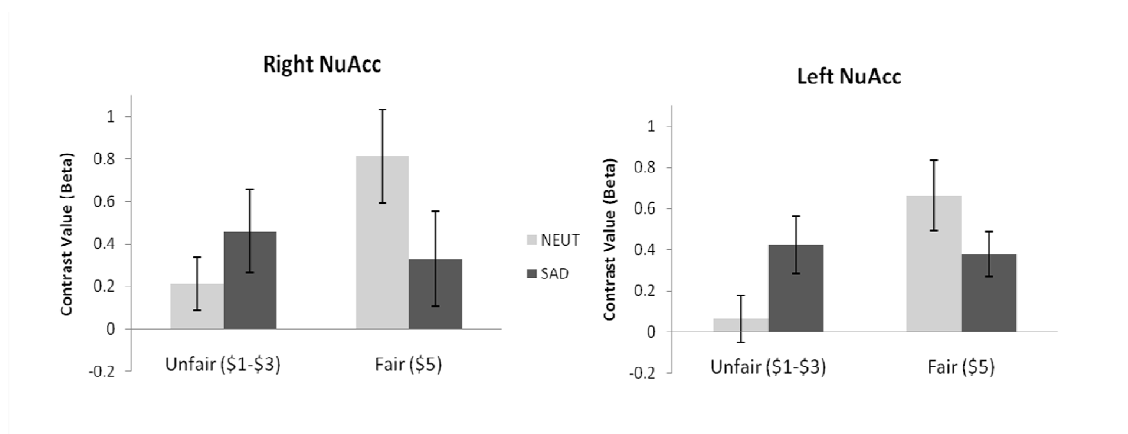
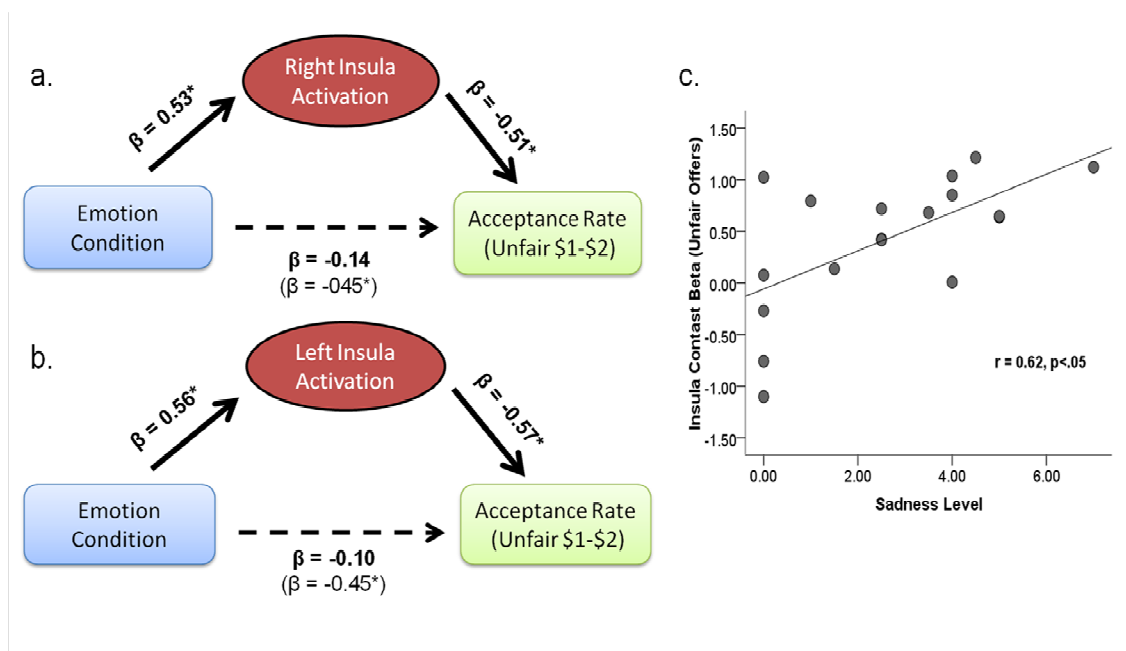
Figure 4

Figure 5



APPENDIX B: THE IMPACT OF DEPRESSION ON SOCIAL ECONOMIC
DECISION-MAKING

The Impact of Depression on Social Economic Decision-making

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Abstract

Although the role of emotion in social economic decision-making has been increasingly recognized, the impact of mood disorders, such as depression, on such decisions has been surprisingly neglected. To address this gap, fifteen depressed and twenty-three nondepressed individuals completed a well-known economic task, in which they had to accept or reject monetary offers from other players. Although depressed individuals reported a more negative emotional reaction to unfair offers, they accepted significantly more of these offers than did controls. A positive relationship was observed in the depressed group, but not in controls, between acceptance rates of unfair offers and resting cardiac vagal control, a physiological index of emotion regulation capacity. The discrepancy between depressed individuals' increased emotional reactions to unfair offers and their decisions to accept more of these offers contrasts with recent findings that negative mood in nondepressed individuals can lead to lower acceptance rates. This suggests distinct biasing processes in depression, which may be related to higher reliance on regulating negative emotion.

Key Words: decision-making, depression, cardiac vagal control

Introduction

Cognitive biases or distortions are well-documented in depression (Beck, 2008) and are often the focus of therapeutic intervention with cognitive behavioral therapy (Whisman, Miller, Norman, & Keitner, 1991). Much of the empirical literature focuses on alteration in attributions, but comparatively little research has examined how such cognitive alterations in depression influence decision-making. Outside of treatment decisions, very few studies have actually examined the degree to which decision-making is altered in depression, and whether any such disturbances lead to sub-optimal outcomes. As the role of both task-related and incidental emotion in decision-making is increasingly incorporated in general economic models of decision-making (Loewenstein & Lerner, 2003), *social* decision-making (i.e. involving interactions of two or more individuals) has been shown to engage an ensemble of neural systems relevant to emotion, reward valuation, and planning (Sanfey, 2007). Therefore, mood disturbances, such as those observed in depression, may well lead to decision biases in a social context (Strack & Coyne, 1983). These types of decisions may in fact have the greatest influence on the day-to-day lives of patients, and thus such research may contribute to practical efforts to improve depressed individuals' confidence, self-esteem, and social connectedness.

Reward in depression

The limited decision-making research with unmedicated patients suggests that depression is associated with decreased approach-related behavior and reduced sensitivity

to reward, which appears to underlie a failure to maximize potential monetary earnings (Henriques & Davidson, 2000; Pizzagali, Iosifescu, Hallett, Ratner, & Fava, 2008). These findings are consistent with both anhedonia and the tendency to neglect pleasurable stimuli often found in depression, as well as with research showing that sad affect may focus attention more on threatening cues (Forgas, 2003) than on opportunities to profit (Lerner, Small, & Lowenstein, 2004). Recent neuroimaging research further suggests that depressed individuals' decreased sensitivity to reward may stem more from a relative increase in affective conflict and monitoring efforts than failure to engage dopaminergic reward systems (Holmes & Pizzagali, 2008; Knutson, Bhanji, Cooney, Atlas, & Gotlib, 2008). Although these investigations do not directly touch on social contexts, they do provide evidence of distinct patterns of decision-making in depression.

Social decision-making

In order to examine the impact of depression on social decision-making, we employed a well-known economic task, the Ultimatum Game (UG; Guth et al., 1982), in which one player (the “proposer”) makes an offer to another player (the “responder”) regarding how to split an amount of money between them. The responder can either accept the offer, in which case the money is split as proposed, or reject the offer, in which case neither player receives anything. Whereas standard economic models would predict that responders should accept any non-zero offers (still preferable to no gain at all), individuals typically accept about 50% of unfair offers (defined as 30% or less of the pot; Camerer, 2003), and experience a negative emotional response and increased arousal

when receiving unfair offers (Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003; Van 't Wout, Kahn, Sanfey, & Aleman, 2006). Although social decision-making has been extensively studied, the use of this task in clinical populations is still in its infancy (Agay, Kron, Carmel, Mendlovic, & Levkovitz, 2008). Two recent studies, however, suggest that characteristics associated with depression, sad affect and serotonin depletion, may lead to more aggressiveness and retaliation in the UG. Our group recently reported that induced sad mood resulted in lower acceptance rates of unfair UG offers, with sad participants also reporting significantly more anger than neutral participants when receiving unfair offers (Harlé & Sanfey, 2007). Another study (Crockett, Clark, Tabibnia, Lieberman, & Robbins, 2008) found that nondepressed subjects undergoing tryptophan depletion, which leads to decreased brain serotonin and has been associated with more social aggressiveness, exhibited lower acceptance rates of unfair offers as compared to a placebo control group. Because sadness and disruption of serotonergic neurotransmission have been implicated in clinical depression (Porter, Mulder, Joyce, Miller, Kennedy, 2008), one hypothesis is that depressed individuals may process unfair offers as more offensive and thus might be more sensitive and aggressive towards negative social signals. Compared to controls, the depressed group might then on average accept fewer unfair offers and report a more negative emotional reaction when receiving these offers.

Alternatively, some research has shown that depressed individuals are more accurate than nondepressed in estimating contingencies between behavior and external events, and that such estimation is not affected by the valence of such prediction

outcomes (e.g. reward vs. loss). Thus depressed individuals may be more realistic about their degree of control over certain transaction outcomes (Alloy & Abramson, 1979). If depressed individuals are indeed more realistic in assessing unfair offers, they may be less likely than controls to think that their decisions will affect either their partners or the subsequent offers they will receive, and thus may expect lower offers in the first place (i.e. being more realistic regarding the opportunistic nature of proposers). Therefore, an alternative hypothesis is that depressed individuals may exhibit higher acceptance rates of unfair offers compared to controls. These higher rates may be independent of their emotional reaction to unfair offers (e.g. they may still react more negatively to unfairness), particularly if they more realistically assess the lack of impact of their decisions.

Emotion Regulation

In addition to assessing behavioral performance and emotion, the present study examined the role of physiologically-driven emotion regulation processes in such decisions, as research suggests that brain regions subserving one's ability to regulate emotion are involved in responders' ability to accept unfair UG offers (Koenigs & Tranel, 2007). Numerous studies have suggested that parasympathetically-driven cardiac vagal control (CVC; i.e. respiratory-linked changes in heart rate), may index one's ability to regulate emotion and respond adaptively to various stressors, with higher CVC reflecting a stronger ability to self-regulate (Porges, 2007; Thayer & Lane, 2000). Moreover, there is evidence that, compared to nondepressed individuals, depressed

individuals' CVC may be reduced (Booij et al., 2006), suggesting emotion regulation may be impaired in depression, although others have failed to show such group differences (Lehofer et al., 1997). Thus, it is of interest to examine whether individual differences in CVC are related to UG decisions, potentially due to CVC's putative influence on emotion regulation.

Methods

Participants

Participants were recruited from among students who participated in a 4-session study of psychophysiological indicators of risk for depression, and which examined individuals with a wide range of depression, ranging from nondepressed to clinical severity. A total of 38 participants (15 depressed; 23 controls) aged 18-24 consented to complete the UG at the conclusion of the fourth session. We derived two groups based on participants' scores on the Beck Depression Inventory (BDI-II, Beck, Steer, & Garbin, 1988) on the day of the UG task. The 'depressed' group was defined as those with BDI scores greater than 16 and included 11 meeting DSM-IV criteria for MDD and 4 having subthreshold MDD, defined as meeting at least 4 out of 5 DSM-IV symptoms for MDD or scoring >30 on the BDI on the UG day. The 'control' group was defined as those with no current or past MDD diagnosis and a BDI score below 5. MDD diagnostics were based on intake interviews with the Structured Clinical Interview (SCID) for the DSM-IV (First, Spitzer, Gibbon, & Williams, 1994) conducted by Masters- or Ph.D.-level clinical psychology graduate students ($Kappa=.81$) about two weeks prior the UG

session. Exclusion criteria for the study included: any other current Axis I diagnosis as assessed by the SCID, any current psychotropic pharmacological treatment (e.g. antidepressant medication), history of psychosis or mania, substance abuse/dependence within the past 4 months, any medical disorder or CNS history that could affect emotional function¹. All procedures were approved by the Human Subjects Protection Program at the University of Arizona.

Experimental Procedures

In addition to the SCID and BDI measures, participants were administered the Hamilton Rating Scale for Depression (HRSD, Hamilton, 1967), to obtain a clinician-based measure of depression, and completed the State-Trait Anxiety Inventory (STAI, Spielberger, Vagg, Barker, Donham, & Westberry, 1995) at the intake session, in order to assess the relationship between anxiety and CVC. In addition, the Positive and Negative Affect Scale (PANAS, Watson, Clark, & Tellegen, 1988) was administered at the start of the fourth experimental session to assess the potential mediating role of negative affect in participants' emotional reaction to unfair offers.

Cardiac Activity

Resting electrocardiographic (ECG) activity was recorded for two 8-minute periods before participants played the UG. ECG was recorded using silver-silver chloride electrodes placed on the left clavicle and digitized at 2000 Hz. Participants were instructed to rest quietly. Interbeat interval (IBI) series were derived from the ECG and

were hand-corrected for artifacts and ectopic beats. In addition to heart rate, Respiratory Sinus Arrhythmia (RSA), a vagal-based measure of heart rate variability in the high frequency band (0.12–0.4 Hz), was extracted using CMetX software (Allen, Chambers, & Towers, 2007). This program converts the IBI series to a timeseries sampled at 10 Hz, filters the series using a 0.12-0.4 Hz finite impulse response filter, and then takes the natural log of the variance of this filtered waveform as the estimate of RSA.

Decision-making

Participants first filled out a short instructional handout about the UG summarizing the basic rules (mentioned above) and asking them about their expectations in the game (e.g. range of offers expected, etc). They were told they would play as responders and receive one-time offers from various proposers. After completing two practice trials and indicating that they fully understood the game, participants played the UG, receiving 24 different offers presented in a randomized order. Each offer involved a \$10 split, and participants were informed they would be playing for real money and would be paid in cash based on a percentage of their earnings in the game. A computerized version of the UG was used, and participants were told that they would be playing the game over a computer network with partners located at other universities. The pictures that participants saw were selected from a pool of actual UG players' photographs with equal proportion of males and females, and with emotionally neutral expressions (Harlé & Sanfey, 2007; Sanfey et al., 2003). On each trial, participants saw a

picture of their proposer partner for 4 seconds. They then saw the proposer's offer, at which point they were instructed to choose from two options (Accept or Reject) by way of a button press. They had a maximum of 10 seconds to decide to either accept or reject this offer. After the decision, the outcome (e.g. how much each player received) was presented for 4 seconds. Based on the assumption that proposers would behave sensibly (i.e. not offer more than half of the pot), proposer offers ranged from 50 cents to \$5 and included 6 fair offers (3x\$5, 3x\$4), 6 slightly unfair offers (3x\$3, 3x\$2.50), 6 moderately unfair offers (3x\$2, 3x\$1.50), and 6 highly unfair offers (3x\$1 and 3x\$0.50). At the end of the task, participants completed a brief questionnaire asking them to rate the extent to which they felt each of twelve basic emotions "when receiving unfair offers (e.g. \$1 or \$2 out of \$10)", each rated using an 8-point Likert scale from (Harlé & Sanfey, 2007).

Results

Clinical Profile

The depressed group (mean BDI=27.8) included 11 (73%) individuals diagnosed with current MDD. The depressed group had higher HRSD scores ($M=14.5$) than the control group ($M=1.6$, $t=5.3$, $p<.001$). Depressed participants also reported higher state ($M=56.4$, $t=9.2$, $p<.001$) and trait ($M=56.1$, $t=9.1$, $p<.001$) anxiety than controls ($M=29.6$ and $M=32.0$, respectively), as measured by the STAI. Groups did not differ in age ($M=19.0$, $t=.98$, ns). No significant gender group difference was observed ($\chi^2=2.5$, ns), although the depressed group had more females (78%) than did the control group (52%).

However, gender did not relate to the dependent variables in the present study and did not affect the main analyses results when added as a predictor or moderator. Data analyses of cardiac vagal control (RSA) were conducted after removing three subjects with ectopic cardiac patterns (2 controls and 1 depressed), as well as one (depressed) outlier based on Cook's distance. RSA in the control group ($M=6.83$) did *not* differ significantly from RSA in the depressed group ($M=6.76$, $t=.26$, ns). Nonetheless, within the depressed sample, BDI scores were negatively related to RSA ($r=-.56$, $p<.05$). This relationship, however, was mediated by trait anxiety ($R^2=.78$; using the hierarchical regression method advocated by Baron and Kenny (1986). After accounting for anxiety scores ($\beta=-.66$, $t=-3.56$, $p<.05$), depression severity (measured by BDI scores) no a longer significantly predicted RSA ($\beta=-.33$, $t=-2.15$, ns), consistent with partial mediation.

Decision-Making

The primary metric of interest in the UG was the proportion of offers accepted for each offer amount. Two aggregate acceptance rates were also computed for “fair” (i.e. \$4-\$5) and “unfair” (i.e. \$0.50-\$3) offers respectively. These categories were based on questionnaire data confirming that \$4 and \$5 offers were consistently considered fair by most participants, as in previous UG studies (Camerer, 2003; Harlé & Sanfey, 2007). Depressed and control participants did not differ in their pre-task perceived cutoff between unfair and fair offers ($M=\$4.10$, $SD=\$0.80$), or in the offer they would typically

make as a proposer ($M=\$4.20$, $SD=\$1.10$). Based on debriefing results, no participants indicated any suspicion of deception with regards to the use of virtual partners.

After mean-centering all independent variables, a linear mixed model (LMM; West, Welch, & Galecki, 2007) was fit to the data using offer acceptance rate as the dependent variable, offer amount as a within-subject (level 1) factor, and clinical status as a between-subject factor (level 2). Subject was modeled as a random factor and a diagonal matrix structure was specified to model residual variance across offer amounts (allowing the model to fit a different variance component at each level). Significant main effects of offer amount ($F(1,104)=393.0, p<.001$) and clinical status ($F(1,53)=4.3, p<.05$), as well as a significant offer by clinical status interaction ($F(1,104)=13.6, p<.001$) were obtained. More specifically, the depressed group accepted significantly more \$0.5, \$1.0, \$1.5, \$2.0 and \$2.5 offers than the nondepressed group ($p<.05$ with Bonferroni corrections), whereas groups did not differ in accepting \$3.0, \$4.0, and \$5.0 offers.

In terms of aggregate acceptance rates, and thus consistent with our alternative hypothesis, groups did not differ in their acceptance rates of fair offers (average acceptance rate = 99%, $SEM= 0.8\%$), but depressed participants accepted significantly more unfair offers (61%, $SEM= 7.1\%$) than controls (41%, $SEM=5.7\%$; $t=2.2, p<.05$; Cohen $d=0.74$, see Figure 1. Total earnings in the game were \$50.30 for the depressed group and \$43.02 for the control group ($t=2.4, p<.05$; $d=.87$).

Emotional Reaction to Unfair Offers

Following the UG, participants rated their subjective emotional state for unfair offers. Twelve basic emotions, including both positive and negative emotions, were rated using an 8-point Likert scale: anger, arousal, amusement, confusion, contentment, disgust, fear, happiness, pain, sadness, surprise, and tension. Compared with the controls, depressed participants reported significantly higher levels of disgust ($t=-2.33, p<.05, d=.78$), as well as surprise ($t=-2.58, p<.05, d=.71$). Depressed participants also showed a trend in reporting greater levels of anger ($p=.07, d=.59$). No group differences emerged regarding the other emotions.

Regression analyses were further conducted to assess whether the clinical status had still an impact on these emotion ratings above and beyond the generally more negative affect observed in depressed individuals. Clinical status significantly predicted disgust ($F=6.6, p<.05$; adjusted $R^2=.14$) and surprise ($F=10.4, p<.05$ adjusted $R^2=.21$) in response to unfair offers, with depressed status resulting in higher level of these negative emotions. Clinical status remained a statistically significant predictor in models that included participants' negative reported affect (from the PANAS) as an additional continuous independent variable. Squared semi-partial correlations for clinical status were 0.12 and 0.11 when predicting disgust and surprise, respectively, while simultaneously accounting for negative affect.

Cardiac Vagal Control (RSA) & Acceptance Rates

Using regression analysis, cardiac vagal control, indexed by RSA, was examined as a predictor of acceptance rates of unfair UG offers, with clinical status as a potential moderator. A moderated regression model was statistically significant ($F=3.13$, $p<.05$, adjusted $R^2=.17$), with a significant effect of clinical status ($\beta=.38$, $t=2.37$, $p<.05$) and a marginally significant clinical status X RSA interaction ($\beta=.43$, $p=.05$). More specifically, a statistically significant positive relationship was observed between RSA and acceptance rates of unfair offers in the depressed group ($r=.59$, $p<.05$), but was not evident in the control group ($r=.01$, ns; see Figure 2).

Discussion

This sample of depressed, un-medicated participants demonstrated significantly altered social decision-making patterns compared to controls, accepting more unfair monetary offers than control participants in a well-studied social decision-making task. Interestingly, such increased acceptance rates in depressed individuals would appear more “rational” from a standard economic standpoint (i.e. maximizing financial gain), and indeed this group made more money in the task. However, despite higher acceptance rates, the depressed group actually reported higher levels of disgust, anger, and surprise upon receiving unfair offers.

The finding of greater disgust, surprise, and anger in the depressed group upon receiving the offers appears consistent with recent empirical findings showing that both

transient sad mood manipulations (Harlé & Sanfey, 2007) and acute tryptophan depletion (Crockett et al., 2008) prompt a similar emotional reaction to unfairness using the same task. Such findings raise the possibility that the same reaction of anger in both the depressed group and the transiently sad nondepressed group (Harlé & Sanfey, 2007) may involve similar neural systems. One hypothesis is that a depressed state or a sad mood may engage the anterior insula, a neural region associated with the processing of bodily emotions, and also previously implicated when responders receive unfair UG offers (Sanfey et al., 2003). Thus, depression, like sad mood, may result in an increased negative perception of the social signal underlying unfair offers, mediated by increased activity in anterior insula. In addition, serotonergic reserves may be lower in depressed individuals than in nondepressed adults (Porter et al., 2008), which may contribute to a more aggressive emotional reaction to unfairness (Crockett et al. 2008).

Despite this, we observed higher acceptance rates of unfair offers among the depressed participants, which contrast with the findings of the aforementioned studies. Thus, while the depth of emotional reactivity may be similar across depressed and sad but nondepressed groups, it appears that in clinical depression distinct processes may intervene prior to the decision itself. One possibility for such behavioral discrepancy is that the increased acceptance of unfair offers observed in depressed individuals reflects more realistic expectations in the UG task (Alloy & Abramson, 1979). Though depressed participants did not differ from controls in terms of their expectations of offers and fairness in the task, they may still have been more realistic (perhaps resulting from a

more analytic processing style or negative cognitive bias) about the impact their decisions have on their partners.

Another more plausible potential explanation for the higher acceptance rates observed in the depressed group relates to emotion regulation processes, with psychophysiological data indicating a possible relationship between cardiac vagal control and the ability to manage one's emotional reaction to unfair offers in order to maximize one's economic gain. Although the depressed and control groups did not differ in terms of average RSA, a positive relationship between RSA and acceptance rates was observed in the depressed group, but not in the control group. These findings, suggest that depressed individuals' larger negative emotional responses to unfair offers may prompt a stronger reliance on regulating these emotions, as compared with nondepressed participants (who are not as indignant about lower offers). Thus, independent of trait or baseline capacity to regulate emotion, depressed individuals may be more likely to use emotion regulation processes when making these social interactive decisions, which may in fact help them in managing emotional reactions, and in turn lead to more acceptances. Additionally, nondepressed individuals may have various strategies available to regulate their emotional responses to unfairness besides RSA driven mechanisms (e.g. more global, optimistic framing), whereas such alternative processes may be impaired or insufficient in depressed individuals, leaving vagal control as a primary option to self-regulate. Nonetheless, caution is warranted in interpreting these results, as the present

study did not measure phasic changes in RSA during the task itself. Future research should assess for group differences in RSA suppression in response to unfair UG offers.

The similar resting levels of cardiac vagal control (RSA) between depressed and control participants may appear inconsistent with research reporting lower heart rate variability in depressed groups (Booij et al, 2006). Other work, however, has shown no difference in vagal control between depressed and control groups (Lehofer et al. 1997). Some have also shown that anxiety symptoms, and not depression severity, are typically more strongly associated with lower cardiac vagal control (Friedman, 2007), which is further consistent with the presently observed negative relationship between RSA and trait anxiety in the depressed group. Moreover, to control for confounding variables of a clinical nature, participants in the present study were excluded on the basis of clinical conditions other than unipolar depression, including anxiety disorders. Thus, the range of state and trait anxiety measures within the present sample may be more constrained and lower than in other depressed groups described in the literature, and thus less inclusive of high anxiety/low cardiac vagal control individuals. This may in turn explain why the depressed sample did not have lower average RSA than the control group.

The present study has some limitations, including a small sample size (particularly for depressed individuals), stringent exclusion criteria, the use of recalled post-task emotion ratings, and the use of an undergraduate student sample, limiting the generalizability of our results. This study also used BDI scores to establish depression status as opposed to MDD diagnosis based DSM-IV criteria to maximize sample size and

favor depression severity on the day of the decision-making task, which limits generalizability to a pure MDD population. However, most individuals in the depressed sample (73%) had a current diagnosis of MDD and effect sizes were similar when including only those with current MDD in the analyses. In addition, internal validity is increased by the use of a non-medicated sample.

In conclusion, the present study revealed a nuanced emotional and behavioral pattern in unmedicated depressed individuals when they make simple interactive financial decisions. These results suggest that the impact of clinical depression on social decision-making may be more complex than the impact of sad mood or even serotonin deficiency in nondepressed individuals. In fact, despite a well-documented pattern of negative cognitive framing in depression, depressed individuals actually ended the task monetarily better off than nondepressed controls. Thus the present study emphasizes the importance of studying decision-making within a realistic and ecologically valid context, for instance using socially interactive tasks with real financial contingencies. These findings underscore the need to refine our understanding of higher-order cognitive processes in depression.

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Footnotes

¹ 44 (54%) were excluded during the recruitment period; UG and excluded participants did not differ in average BDI ($t=.64, ns$), in proportion of individuals with current MDD ($\chi^2=.89, ns$) and in gender distribution ($\chi^2=3.1, ns$).

² Data analyses were redone defining the depressed group to include only MDD. The LMM offer X group interaction remained statistically significant ($p<.005$), with similar effect sizes for group mean differences in acceptance rates of unfair offers ($p=.06, d=.74$), reported disgust ($p<.05, d=.84$), surprise ($p=.07, d=.71$) and anger ($p<.05, d=.91$) when receiving unfair offers, and in the correlation between RSA and acceptance rates of unfair offers ($r=.53, p=.11$)

Figure Captions

Figure 1. Acceptance rates by offer amount. Depressed Total includes participants with and without a current DSM-IV diagnosis of MDD, whereas Depressed with MDD includes only those with a DSM-IV diagnosis of MDD.

Figure 2. Acceptance rates of unfair offers as a function of respiratory sinus arrhythmia (RSA) by clinical group.

Figures

Figure 1.

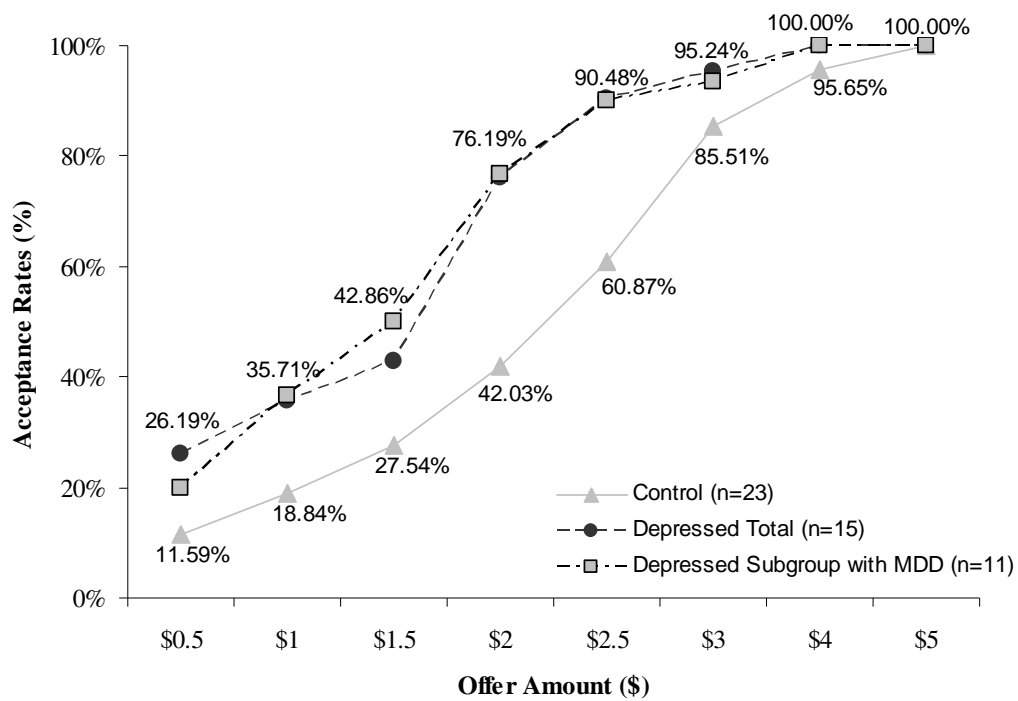


Figure 2.

