Why humans deviate from rational choice

JOHANNES HEWIG,[a,d] NORA KRETSCHMER,[a] RALF H. TRIPPE,[a] HOLGER HECHT,[a]
MICHAEL G. H. COLES,[b] CLAY B. HOLROYD,[c] AND WOLFGANG H. R. MILTNER[a]

[a]Department of Biological and Clinical Psychology, Friedrich–Schiller–University, Jena, Germany
[b]Donders Centre for Cognitive Neuroimaging, Nijmegen, The Netherlands
[c]Department of Psychology, University of Victoria, Victoria, British Columbia, Canada
[d]Department of Psychology I, Julius–Maximilians–University Würzburg, Würzburg, Germany

Abstract

Rational choice theory predicts that humans always optimize the expected utility of options when making decisions. However, in decision-making games, humans often punish their opponents even when doing so reduces their own reward. We used the Ultimatum and Dictator games to examine the affective correlates of decision-making. We show that the feedback negativity, an event-related brain potential that originates in the anterior cingulate cortex that has been related to reinforcement learning, predicts the decision to reject unfair offers in the Ultimatum game. Furthermore, the decision to reject is positively related to more negative emotional reactions and to increased autonomic nervous system activity. These findings support the idea that subjective emotional markers guide decision-making and that the anterior cingulate cortex integrates instances of reinforcement and punishment to provide such affective markers.

Descriptors: Decision-making, Microeconomics, Feedback negativity, Somatic markers, Ultimatum game

In the Ultimatum and Dictator games, a "proposer" and a "responder" play against each other. In each case, the proposer is instructed to divide 12 cents into 2 shares, the proportion of which can range between 6:6 and 11:1. In the Ultimatum game, the responder is required to decide whether or not to accept the proposer's offer. If the responder accepts the partitioning, then each player receives the money offered by the proposer. If the responder rejects the offer, then neither player receives any money. Accordingly, this provides an opportunity for the receiver to punish the proposer for unfair offers. In the Dictator game, the proposer's role is the same but the responder cannot reject the offer. Thus the responder has no option to reject unfair offers and the money is always apportioned between the proposer and the responder as the proposer dictates. In repeated games, one and the same "proposer" and "responder" interact several times whereas, in one-shot interactions, each responder is confronted with a certain proposer only once.

In the one-shot Ultimatum game, economic rationality of utility as derived from classical game theory (von Neumann & Morgenstern, 1953) predicts that the responder should accept all offers since receiving at least some money is always preferable to receiving no money. However, empirical evidence shows that humans often deviate from rational choice to varying degrees in such experiments (Camerer, 2003; Güth, Schmittberger, & Schwarze, 1982). While some participants act rationally and accept all offers, other participants reject offers that deviate even slightly from an equal distribution. The latter might be motivated by negative affective responses to unfairness (Nowak, Page, & Sigmund, 2000; van 't Wout, Kahn, Sanfey, & Aleman, 2006).

Indeed, previous research indicates the importance of affective processes in Ultimatum decisions. For example, in a study by Pillutla and Murnighan (1996), participants who reported more anger rejected more offers. More recently, Harle and Sanfey (2007) showed that participants in the Ultimatum game who were exposed to a sadness induction before playing rejected relatively more fair offers, demonstrating that decision-making can be influenced by negative emotions that are unrelated to the task at hand. Furthermore, in another study, the skin conductance response to unfair offers, an autonomic measure of affect, also predicted rejection of unfair offers in the Ultimatum game (van 't Wout et al., 2006). Skin conductance responses have been repeatedly associated with the reaction to aversive stimuli (e.g., Hajcak, McDonald, & Simons, 2004; Meriau, Wartenburger, Kazzer, Prehn, Villringer, et al., 2009). Furthermore, electrodermal activity is believed to be related to physiological arousal elicited by the behavioral inhibition system (Fowles, 1980), which, in turn, is supposed to be the biological basis of punishment and negative affect (Gray, 1982, 1994). In addition, unfair offers in the Ultimatum game activate brain regions that are associated with negative emotional reactions, such as the insula (Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003; Tabibnia,

Satpute, & Lieberman, 2008). Moreover, the fMRI data from Sanfey and colleagues show that anterior cingulate cortex is activated by unfair offers, which is consistent with the very recent report of an increased negativity in the event-related potential (ERP) between 240 and 320 ms in response to unfair Ultimatum offers for receivers in a repeated Ultimatum Game against one and the same proposer (Polezzi, Daum, Rubaltelli, Lotto, Civai, et al., 2008). This negativity may be classified as a feedback negativity because of its topography and timing (Holroyd & Coles, 2002; Miltner, Braun, & Coles, 1997). Most importantly, we suggest that participants will generate expectations in each trial about the offer to be made by the other person. The presentation of the actual offer represents feedback as to whether the monetary outcome is equal to, or better or worse than, the participants' expectation.

The feedback negativity (FN, also known as the feedback error-related negativity/feedback ERN) is a negative deflection in the ERP, the maximum amplitude of which is recorded at the scalp over frontal brain regions at about 250–300 ms following negative as compared to positive performance feedback (Holroyd & Coles, 2002; Miltner et al., 1997) or losses as compared to wins in gambling situations (Hewig, Trippe, Hecht, Coles, Holroyd & Miltner, 2007; Nieuwenhuis, Yeung, Holroyd, Schurger, & Cohen, 2004; Yeung & Sanfey, 2004). Holroyd and Coles (2002) have suggested that the process manifested by the FN is involved in reinforcement learning. In terms of reinforcement learning theory, more negative amplitudes to losses are related to punishment when events are worse than expected. Punishment leads to negative affective responses and is linked with the concept of habitual or trait-like differences in negative affect (Gray, 1982, 1994). Thus, greater FN amplitudes indicating punishment should evoke stronger negative affect. In contrast, more positive amplitudes are thought to be related to a reinforcement response when upcoming events are better than expected (Holroyd, Pakzad-Vaezi, & Krigolson, 2008). Amplified FN amplitudes in response to aversive events have been found for participants who are sensitive to aversive stimuli or negative affect, such as those high in neuroticism, in trait negative affect, or behavioral inhibition (Boksem, Tops, Wester, Meijman, & Lorist, 2006; Hajcak et al., 2003; Hajcak, McDonald, & Simons, 2004; Luu, Collins, & Tucker, 2000; Pailing & Segalowitz, 2004). In the context of the Ultimatum game, greater FN amplitudes to unfair offers should reflect more negative responses and should lead to an increased likelihood of remedial action in terms of rejection of these unfair offers.

In the present study, we adopted a multilevel approach to examine both basic mechanisms and individual differences in decision-making in the one-shot Ultimatum and Dictator Games. We collected data on behavior, subjective affect, and central and autonomic nervous system activity to reveal the contribution or influence of multiple levels of affective processing to decision-making in these games. Specifically, we expected that greater negative affective valence, larger skin conductance responses, and larger FN amplitudes—all indicating negative affective processing—would predict larger deviations from rational choice. This finding would provide direct evidence that individual differences in affective processing contribute to differences in economic decision-making. It would further allow us to analyze the relative contribution of, and the relationship among, different aspects of affective processing that have been shown to contribute significantly to decision-making in the Ultimatum Game (Polezzi et al., 2008; van 't Wout et al., 2006).

Methods

Participants

Thirteen participants were recruited from the student population of the Friedrich Schiller University. The data of one participant were excluded because he/she did not believe in the cover story of the experiment and suspected that he/she had played the games against a computer instead of a real human player. All others denied having any such suspicion when asked at debriefing. The remaining 12 participants (8 females and 4 males; mean age: 21.6 years, $SD = \pm 1.5$ years, range 20–25 years) were paid €6 per hour plus an extra bonus that varied between €10.01 and €12.87 (Mean = 11.81; $SD = \pm 0.98$) according to their decisions in the games. After receiving verbal instructions about the experiment, participants gave written consent for participation.

Task and Procedure

Each participant played both the Ultimatum and the Dictator games repeatedly in a series of one-shot trials as a proposer and as a receiver. In each trial, a proposer is instructed to divide a fixed amount of money (here 12 cents) into two shares: one for him- or herself and the other for the responder. In the Ultimatum game, the responder is prompted to decide whether or not he or she accepts the offer of the proposer. If the responder accepts the offer, then each player receives the money assigned by the proposer. If the responder rejects the offer, then no money is given to either player. In the Dictator game, the responder cannot reject the offer and the money is always assigned to both players as dictated by the proposer. First, the participants acted in the role of the proposer in both games. Then they switched roles and became responders.

In the role of the proposer, participants made 40 Ultimatum and 10 Dictator proposals by typing in their proposals via a PC. They were told that their proposals would be stored and used for future participants and that they would receive only one offer from a particular proposer when they later played the role of responder. In addition, a photograph was taken of each participant, which was used to enhance the plausibility of the cover story. This picture and that of the virtual proposer were presented following the feedback in the responder games. Figure 1 shows a single trial in the responder condition of the Ultimatum game.

After playing the game as proposers, the participants were prepared for recording of electroencephalogram (EEG) and skin conductance (see section on EEG and skin conductance responses (SCR) recording and quantification). Then, participants played the games in the role of the responder and received a randomized series of 240 Ultimatum game offers (40 for each of 6 conditions: 6:6, 5:7, 4:8, 3:9, 2:10, 1:11). Each trial started with the presentation of a fixation cross (750 ms). This was followed by a divided color bar (Figure 1) that indicated the amount of the offer. The length of the blue portion indicated the amount offered by the proposer, while the red portion indicated the amount retained by the proposer. Four hundred milliseconds later, a tone (100 ms duration, 800 Hz) prompted the participants to respond and to either accept or reject the offer within 2 s. Immediately after their button press response, the amount of money that the participant would receive on that trial was presented for 600 ms. Finally, a photo of the participant and the pseudo-proposer on that trial were presented for 1 s together with the amount of money received by each one of them and the cumulative amount of the participant's winnings. On each trial, a different proposer was presented, chosen randomly from a set of photographs either
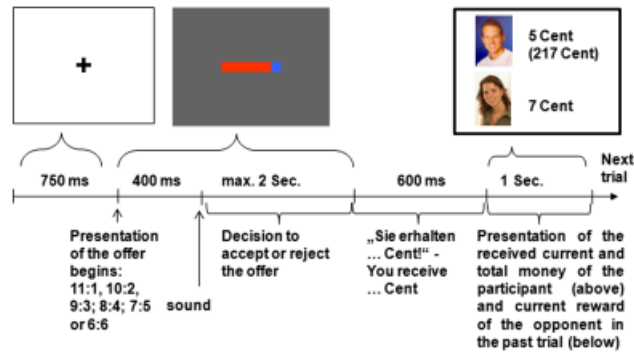
Figure 1. Timeline of a single trial in the Ultimatum game.

taken from preceding participants or from an archive of face images. No proposer's image was presented more than once throughout the entire experiment. The picture was shown after each trial in order to avoid confounding influences of the gender of the opponent on decision-making (Solnick & Schweitzer, 1999). The Ultimatum game was followed by 60 trials of the Dictator game with 10 trials for each of the 6 conditions. The timing of each trial was the same as in the Ultimatum game. In addition, after the participants finished all trials of each game, they completed a subjective rating of the emotional valence (from 1/negative to 9/positive) that they had experienced in each condition (6:6 through 11:1) while playing the role of responder.

EEG and Skin Conductance Recording and Quantification

EEG and SCRs were measured when participants were in the role of the responder. Participants were seated individually in an electrically shielded, dimly lit, and temperature controlled EEG cabin, and Ag/AgCl electrodes were applied for the measurement of electro-oculogram (EOG) and EEG. The EEG montage of electrodes was realized by the Brain-Cap MR 128-channel electrode system (EasyCap, Munich Germany) and included all electrodes according to the extended 10–20 system (128 electrode sites) referenced to vertex (Cz). Additionally, vertical EOG activity was recorded from an electrode fixed under the left eye. All electrode sites were cleaned with alcohol and gently abraided prior to electrode application to keep the impedances of electrodes below 5 kΩ, and the differences of impedance between homologous sites below 1 kΩ. EEG and EOG were amplified with four 32-channel DC BrainAmp MR plus amplifiers (Brain Products, Munich, Germany; input impedance: 10 MΩ). Band-pass filter was set to 0.015–250 Hz; the signals were digitized online at 500 Hz and stored on hard disk for later off-line analyses. After data acquisition, EOG and EEG recordings were subjected to off-line ocular correction, and automatic artifact correction procedures were performed using the Vision Analyzer software (BrainProducts). Trials with response times greater than 2000 ms were discarded from all analyses (mean: 3.75, SD: 5.72). Data for each electrode were filtered (high cut-off: 20 Hz), epoched from -150 ms to $+400$ ms following stimulus onset (presentation of the color bar), and baseline corrected using the average activity of the 100 ms preceding the offer onset. Finally, EEG waveforms were averaged separately for each participant, each experimental condition, and each electrode.

The peak amplitude of the FN to the presentation of the offer was defined as the average between 280 and 320 ms at electrode Fz and was determined for each participant and each exper-

imental condition. Additionally, difference waves between fair (6:6) and unfair (11:1) offers were calculated as the mean of the difference in the time window of 280 to 320 ms. In addition, P3 amplitude was defined as the average amplitude between 350 and 450 at electrode Pz (Coles & Rugg, 1995). The analysis of variance (ANOVA) of EEG data (FN amplitudes) associated with offer presentation included the factors Fairness (6 levels: 6:6 to 11:1) and Game (Ultimatum versus Dictator). Additionally, two factors for the topography of brain electrical activity were used (Anterior—5 levels: frontal, frontocentral, central, centroparietal, parietal; and Laterality—5 levels: lateral left, left, midline, right, lateral right), which included the following 25 channels: F3, F1, Fz, F2, F4, FC3, FC1, FCz, FC2, FC4, C3, C1, Cz, C2, C4, CP3, CP1, CPz, CP2, CP4, P3, P1, Pz, P2, and P4, all referenced to linked mastoids. For topographical analyses, all electrodes were used. Huynh-Feldt correction was applied as appropriate to protect against violations of sphericity.

Skin conductance was recorded from the sole of the left foot with Ag/AgCl electrodes (6 mm diameter and 0.28 cm² recording area) during application of a constant voltage of 0.5 Volt using a VARIOPORT-C skin conductance amplifier (Becker Meditech, Karlsruhe, Germany). The measurement range was set to 50 μS with a resolution of 0.002 μS. The data were high-pass filtered (0.1 Hz). The single trial data were baseline corrected (-1 to 0 s pre-stimulus). The maximum of the skin conductance response was detected automatically between 1.5 and 7.5 s after the presentation of the offers. Only positive values were accepted as valid changes of electrodermal activity (EDA). A Fairness (6 levels; 6:6 to 11:1) × Game (Ultimatum versus Dictator) ANOVA was performed on the skin conductance responses.

Results

Behavior
We first examined the general effect of the fairness of offers by the proposer on the responders' behavior in the Ultimatum game. Fairness was defined in terms of the proportional offer by the proposer with 11:1 being most unfair and 6:6 being most fair. An ANOVA revealed a main effect of Fairness ($F(5,55) = 31.37$, $p < .001$, $\eta^2 = .74$). Figure 2A indicates that the probability of the responder accepting an offer in the Ultimatum game decreased as a function of unfairness. Offers of 9:3 were accepted significantly more often ($p = .005$) and offers of 11:1 were rejected more often ($p = .004$) than offers of 10:2. Offers of 10:2 were accepted by responders on about 50% of trials and were associated with the highest variance across participants, in accordance with previous results (Camerer, 2003).

Affect
Participants provided ratings of valence (on a Likert Scale, from very negative 1 to very positive 9) to the monetary offers in both games. The inclusion of the Dictator Game made it possible to examine whether the absence (Dictator) or presence (Ultimatum) of the response choice influenced the dependent variables. An ANOVA with the factors Game (2 levels; Ultimatum versus Dictator) and Fairness (6 levels; 6:6 to 11:1) on these ratings revealed a significant effect of Fairness on the valence ratings ($F(5,55) = 82.92$, $p < .001$, $\eta^2 = .88$) and no significant main effect of game or interactions with game (Ultimatum versus Dictator, all values of $p > .282$). Accordingly, when confronted with increasingly unfair offers in both games, participants reported more negative emotional reactions (Figure 2B).
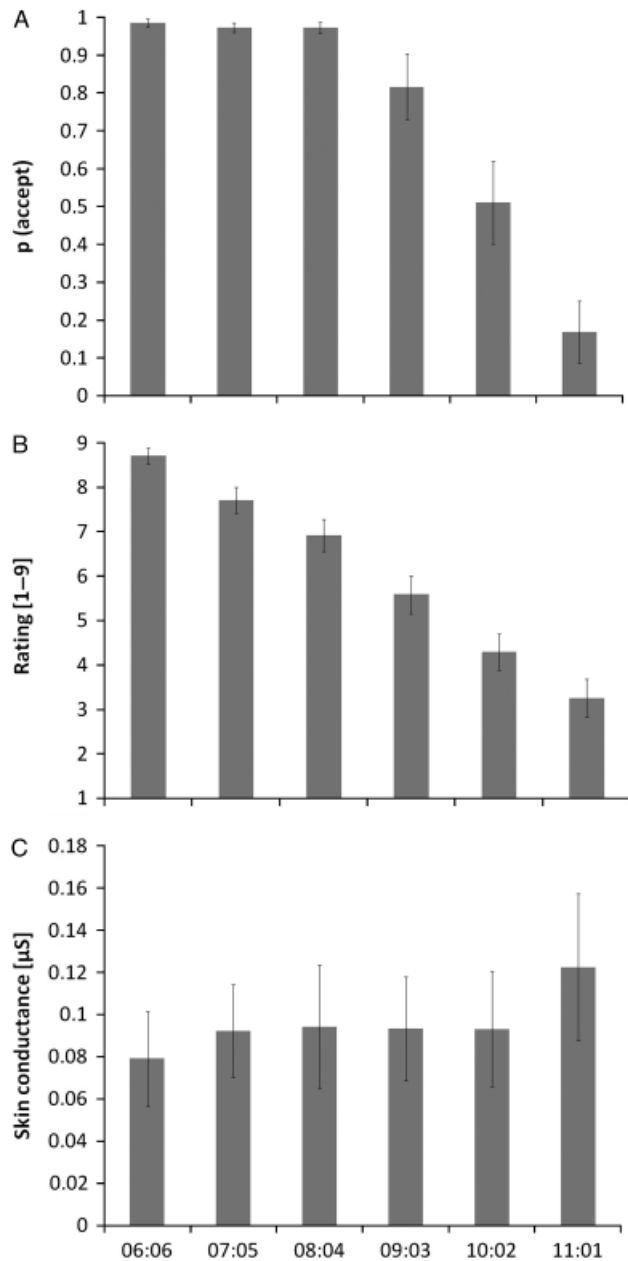
Figure 2. Unfairness is related to rejections of offers, negative emotions, and the amplitude of the skin conductance response. (A) Mean probabilities of "accept" decisions across all participants and for all decisions in the Ultimatum game show a decrease in acceptance with increasing unfairness. (B) Subjective ratings of emotional valence for each level of fairness across Ultimatum and Dictator games show more negative emotional responses with increasing unfairness (1 extremely negative to 9 extremely positive). (C) Skin conductance responses for each level of fairness across Ultimatum and Dictator games show an increase in the response with increasing unfairness.

Electrodermal Responses

An analysis of the skin conductance responses revealed a marginally significant main effect of fairness ($F(5,55) = 2.65$, $p = .072$, $\eta^2 = .19$) and a significant linear contrast effect of fairness ($F(1,11) = 5.24$, $p = .043$, $\eta^2 = .32$), indicating greater skin conductance responses as a function of increasing unfairness (see Figure 2C). In particular, extremely unfair offers (11:1) elicited higher skin conductance responses as compared to extremely fair (6:6) offers ($p = .015$). Data were collapsed across games because of an absence of significant main or interaction effects involving Game (all values of $p > .131$).

Electrophysiology

An ANOVA on FN amplitudes elicited by the offer with the factors Fairness, Game, and Electrode Position revealed a significant interaction between Fairness and Electrode Position (Fairness × Anterior: $F(20,220) = 3.04$, $p = .011$, $\eta^2 = .22$). Post-hoc tests of this interaction showed a linear trend with more negative amplitudes for increasingly unfair offers at more anterior sites indicating stronger FN amplitudes for unfair as compared to fair offers ($F(1,11) = 6.20$, $p = .030$, $\eta^2 = .36$). Data were collapsed across games because of an absence of significant main or interaction effects involving Game (all values of $p > .2$). Figure 3A depicts the ERP waveforms for extremely unfair (11:1) versus fair (6:6) offers, averaged across games. The associated difference wave between unfair and fair offers, illustrated in Figure 3A, reflects the pure effect of fairness on FN and, consistent with classical definitions of FN, exhibits a frontocentral topographical distribution over the scalp as shown in Figure 3B. An ANOVA on the P3 data revealed a main effect of Fairness ($F(5,55) = 3.36$, $p = .011$, $\eta^2 = .23$) and a quadratic trend in post-hoc contrasts ($F(1,11) = 5.38$, $p = .041$, $\eta^2 = .33$). The P3 was largest for extremely unfair offers (11:1; $M = 5.04$ μV), and declined with fairness showing a minimum for 9:3 offers ($M = 2.26$ μV) and then increased again with increasing fairness (for 6:6; $M = 3.01$ μV). Thus, P3 showed a different effect pattern as compared to FN. There were no other significant main or interaction effects of Game or Fairness for the P3 data (all values of $p > .062$).

Individual Difference Analyses

The previous analyses showed that rejection rates, negative emotional reactions, FN amplitudes, and skin conductance responses were all inversely related to the fairness of the offers. Subsequent correlation analyses investigated the factors associated with individual differences in the responders' choice behavior in the Ultimatum game. Hypotheses about correlations with other measures were tested with one-tailed tests. Because the between-participant variability in the decision to accept the 10:2 offers was largest, it most clearly reflects individual differences in decision-making. According to rational choice theory, the more likely a person rejects these offers the greater is the deviation from rationality. The data associated with this condition were evaluated in subsequent individual difference analyses. In these analyses, for each participant, we averaged the ratings of subjective valence across the Fairness and Game conditions to provide an overall measure of each individual's affective response to outcomes in general, since the ratings in different conditions were highly correlated. The reliability of the aggregated measure was .91 (Cronbach's alpha). Because skin conductance responses in each condition were also highly correlated across the Ultimatum and Dictator games, we also used an aggregated measure for subsequent correlation analyses (Cronbach's alpha: .97). This aggregated measure reflected the responsiveness of the autonomic nervous system of each participant. We further utilized individual differences in FN to examine its relationship with decision-making and affect. For the analysis of the FN, the FN was measured at its maximum at channel Fz by evaluating the ERPs elicited by fair (6:6) and unfair offers (11:1) as well as their difference in the
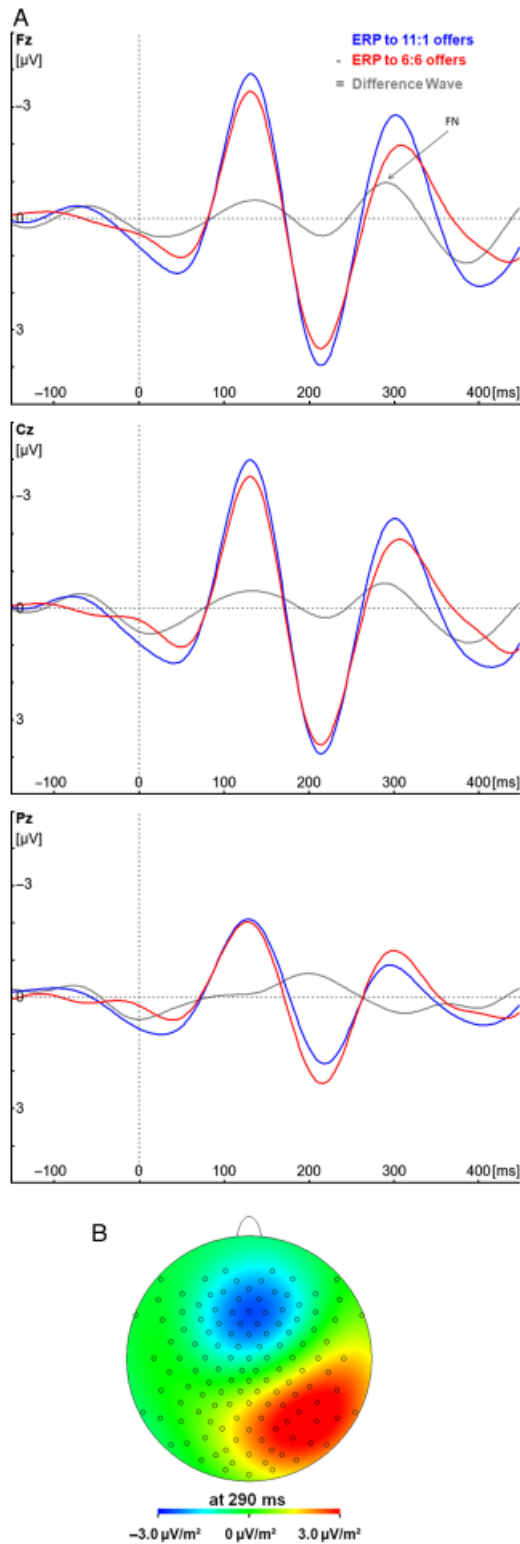
Figure 3. The effect of fairness on event-related potentials and their topography after the presentation of fair versus unfair offers across games. (A) ERPs for 11:1 and 6:6 offers and the difference waveform. Data for frontal (Fz), central (Cz), and parietal (Pz) electrodes are presented. A greater negativity at frontal sites is present for unfair as compared to fair offers at 290 ms. (B) The topographic current source density map of the peak of the difference waveform shows the distribution of the feedback negativity over the cortex. The data were band-pass filtered to exclusively show FN related theta activity for the figure only (3–8 Hz).
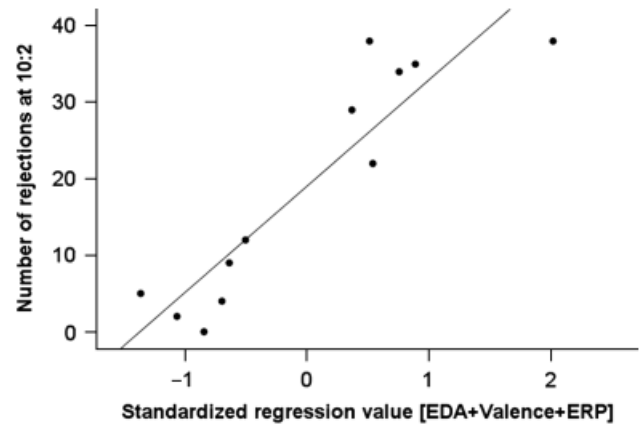

Figure 4. Results of a multiple regression in which the number of rejections of the 10:2 offer is predicted by ERP amplitudes to fair offers, subjective emotional ratings (Valence), and skin conductance responses (EDA). These variables together explain 84% of the variance in number of rejections (for more details, see Table 1).

Ultimatum Game. Recent evidence (Holroyd et al., 2008) shows that the main effect in ERP analyses of FN amplitudes is due to the reduction of FN after good outcomes (fair offers in the present study) rather than increased FN to bad outcomes (here unfair). Thus, we examined the separate contribution of FN responses to extremely fair (6:6) and unfair (11:1) offers in subsequent analyses in addition to the difference amplitudes.

The correlation analyses addressed the question of the relationship between subjective emotional responses, FN amplitudes, and skin conductance responses, on the one hand, and the degree of participant rationality, as defined in terms of their responses to the 10:2 offers. Results show that the responders who more frequently rejected the 10:2 offer rated the proposers' offers as emotionally more negative in general ($r = -.61$, $p = .017$). Larger skin conductance responses also predicted higher rejection rates ($r = .56$, $p = .028$). Those who tended to reject the 10:2 offer also tended to show larger FN amplitudes to unfair (11:1) versus fair (6:6) offers in the Ultimatum game ($r = -.44$, $p = .078$). While FN amplitudes to 11:1 offers were not related to rejection rate ($r = -.04$), reduced FN amplitudes to 6:6 offers in the Ultimatum Game were significantly related to the rejection rate, with high rejection rates being associated with smaller FN amplitudes ($r = .58$, $p = .023$). For FN amplitudes to offers of 10:2, 9:3, 8:4, and 7:5, there was no significant correlation with rejections (all values of $p > .17$). Accordingly, in subsequent multiple regression analyses the FN amplitude to fair offers was used. As shown in Figure 4, a multiple regression analysis on individual differences in 10:2 rejection rates revealed that FN amplitudes to fair offers, SCR amplitude, and emotional valence ratings together accounted for a large proportion of variance of the behavioral data ($R^2 = .84$, $F(3,8) = 13.7$, $p = .002$). The stepwise introduction of each of these three predictors revealed that each predictor explained a substantial independent amount of variance (see Table 1). Emotional ratings and skin conductance responses explained 38% and 35% of variance, respectively. FN introduced as the third predictor further explained a marginally significant but substantial amount of additional variance (11%). In order to further verify these results, we used a Jackknife method repeating the multiple regression analysis 12 times, omitting a different participant in each analysis (Tukey, 1958). The

Table 1. *Results of the Multiple Regression Analysis*

Model	R	R^2	corrR^2	SE	ΔR^2	ΔF	$df1$	$df2$	p of ΔF
a	.614	.377	.315	12.56	.377	6.05	1	10	.034
b	.855	.731	.672	8.69	.354	11.87	1	9	.007
c	.915	.837	.776	7.18	.106	5.21	1	8	.052

Notes. Model a. Variables: (constant), Valence. Model b. Variables: (constant), Valence, EDA. Model c. Variables: (constant), Valence, EDA, ERP at Fz for 6:6 in Ultimatum. Dependent variable: Rejections at 10:2 offers. R and R^2 multiple correlation and explained variance (corrR^2 = corrected); SE = standard error, ΔR^2 = change in R^2 specific for this variable, ΔF = change in F, df = degrees of freedom (nominator and denominator), p of ΔF = significance of change in ΔF.

standardized beta weights were consistent for all analyses. The weights varied between $-.52$ and $-.74$ for the influence of the subjective emotional ratings, between .37 and .66 for the SCR scores, and between .13 and .45 for the ERP amplitudes (see Table 2).

Exploratory analyses of the relationship between P3 amplitudes and variables discussed in this section failed to reveal any significant effects. Further, analysis of the behavior of the participant when acting as proposer failed to reveal any significant relations with their behavior as responder or any of the variables mentioned above (all values of $p > .5$).

Discussion

We have shown that unfair offers in the one-shot Ultimatum game were rejected more frequently, evoked more negative subjective emotional ratings, led to greater SCRs, and elicited larger FNs, than fair offers. Moreover, individual differences in the number of rejected 10:2 offers in the Ultimatum Game could be explained to a large extent by a combination of subjective emotional ratings, SCRs, and reduced FN amplitudes to fair offers. Our results are consistent with previous work that has reported finding similar relationships between emotional responses and rejection rate (Pillutla & Murnighan, 1996), between SCRs and rejection rate (van 't Wout et al., 2006), and between FN amplitudes and rejection rate in a repeated Ultimatum game (Polezzi et al., 2008). In particular, by measuring these three different correlates of rejection rates within the same experimental context,

Table 2. *Correlation Between Variables and beta Weights in the Multiple Regression*

Correlations	EDA	FN	Rej10:2	Multiple Regression			
				beta	T	p–value	beta range
Valence	.050	$-.054$	$-.614$	$-.616$	-4.303	.003	$-.522$ to $-.742$
EDA		.427	.564	.440	2.785	.024	.371 to .661
FN			.582	.361	2.282	.052	.133 to .456

Notes. Valence = emotional ratings; EDA = electrodermal activity/skin conductance responses; ERP at Fz for 6:6 in Ultimatum = FN, Rej10:2 = number of rejections for 10:2 offers. Beta = standardized beta weight in the multiple regression analysis; T and p-values of the standardized beta weight, beta range = range of beta values in the 12 Jackknife regression analyses.

we have shown that smaller FNs to fair offers, more negative emotional ratings, and larger SCRs predicted more rejections, that is, larger deviations from rational choice. The multiple regression analysis indicated that each of these three indicators of affective processing contributed an independent additional portion of variance (see Table 1). The physiological variables were uncorrelated with the subjective emotional responses (see Table 2), indicating that conscious emotional experience can be independent from physiological responses.[1]

On the level of the physiological variables, the regression analysis might suggest that two systems involved in affective processing contribute independently to influence irrational decision-making. First, the autonomic nervous system as reflected by SCRs has been associated with activation of the amygdala (e.g., Davis, 1992; Furmark, Fischer, Wik, Larsson, & Fredrikson, 1997; Phelps & LeDoux, 2005). The amygdala is—among other structures—said to control SCRs through the regulation of the sympathetic nervous system. For example, Furmark et al. (1997) found a significant relation between regional cerebral blood flow in the amygdala and electrodermal fluctuations. It has to be noted that SCRs and feedback negativity were correlated (see Table 2). This is in line with findings that anterior cingulate is also involved in electrodermal control (Fredrikson, Furmark, Olsson, Fischer, Andersson, & Langstrom, 1998). However, the regression analyses revealed that the FN explained an additional independent amount of variance. This suggests that the activities of a reinforcement learning system, as reflected in the FN and associated with the midbrain dopamine system and the anterior cingulate cortex, contributes independently to the explanation of variability in decision-making (Hewig, Straube, Trippe, Hecht, Kretschmer, et al., 2009; Hewig et al., 2007; Holroyd & Coles, 2002; Holroyd, Nieuwenhuis, Yeung, Nystrom, Mars, et al., 2004; Jocham & Ullsperger, 2009; Ullsperger & von Cramon, 2003). Mathematical models of reinforcement learning (Sutton & Barto, 1998) suggest that individuals learn from the detection of differences between the expected and actual reinforcement. Thus, any outcome of a decision or a behavioral act can be either better or worse than expected, and the size and valence of the discrepancy is proposed to be reflected in the amplitude of the FN. In line with this proposal, FN amplitude is smaller when an outcome is better than expected and larger when the outcome is worse than expected, (e.g., Hewig et al., 2007; Holroyd & Krigolson, 2007). Conversely, outcomes that are better than expected lead to an increase in the activity of the midbrain dopamine system, inhibition of the apical dendrites of motor neurons in the ACC, and production of small amplitude FNs or of an outcome positivity (OP) or a feedback-related positivity (Holroyd et al., 2008). Within this theoretical framework, anterior cingulate cortex is thought to integrate reinforcement history to guide voluntary behavior (Holroyd & Coles, 2008). It has further

---

[1]It might be argued that using several dependent variables increases the number of statistical tests and thus may lead to a type I error inflation. However, for the present study most of the effects for each single variable had been found previously and were clearly predicted by directed hypotheses. Thus, they are conceptual replications, which is one of the most important tools to oppose type I error problems. Moreover, a type I error correction does increase the probability of a type II error—the probability not to detect an effect that is present in the population. Accordingly, replicating previous results is hindered significantly if type II error probability is increased because the chance of a successful replication is reduced. Hence, we decided to avoid an increase in type II error and did not use a type I error correction.

been suggested that FN amplitude may reflect somatic markers of reinforcement and punishment (Holroyd, Nieuwenhuis, Yeung, & Cohen, 2003). The somatic marker hypothesis (e.g., Bechara & Damasio, 2005; Bechara, Damasio, & Damasio, 2000) holds that somatic markers, which are autonomic signals that indicate the positive and negative consequences of experienced stimuli, guide decision-making. Positive somatic markers associated with an action increase the likelihood of its selection, whereas negative somatic markers of an action decrease the likelihood of its selection. Accordingly, the present findings suggest that affective somatic markers may contribute to rejections in the Ultimatum Game. Such markers may also be an important source of motivation for altruistic punishment against other players who defect, do not cooperate, or show egoistic behavior (Fehr & Camerer, 2007; Fehr & Gachter, 2002). The proposed neuroanatomical basis for the somatic marker is the ventromedial prefrontal cortex (VMPFC), which includes the orbitofrontal, the medial frontal, and parts of the anterior cingulate cortex. Taken together, these findings suggest that a reinforcement learning mechanism involving anterior cingulate cortex and VMPFC uses affective markers to guide behavior in complex decision-making situations.

We hypothesized that increased FN would be related to heightened rejection rate. However, the present data indicate that the number of rejections was related to more positive amplitudes to fair offers rather than to more negative amplitudes to unfair offers. The present data cannot provide an explanation for this finding. On the one hand, it may be argued that lower FN amplitudes to fair offers would indicate that participants expect proposers to make unfair offers and hence are positively surprised when the offers are fair. In line with this reasoning, negative views of others and negative expectations concerning others' intentions might at the same time lead to more rejections of unfair offers. On the other hand, the fact that participants showed increased positivity towards fair offers might suggest that the participants were particularly sensitive to reward. For example, pathological gamblers show more positive amplitudes to reinforcing events (Hewig, Kretschmer, Trippe, Hecht, Coles, et al., 2010). According to this idea, more reward-sensitive participants might be disappointed by unfair offers and reject them more often. Future research will be necessary to shed more light on this result.

The statistical analyses revealed no significant effects of Game in the sense that there were no differences in the EEG, EDA, or subjective responses between offers in the Ultimatum as compared to the Dictator game. Accordingly, our findings indicate that the processes we have identified are related primarily to an evaluation of unfairness and the motivation to oppose unfairness, rather than the preparation or initiation of remedial action against unfairness. Thus, the data also indicate that FN might not primarily reflect direct behavioral reinforcement learning here but rather a more general form of reinforcement learning—the learning of action values or the learning of the motivational value of a situation (e.g., Holroyd & Coles, 2002, 2008; Kennerley, Walton, Behrens, Buckley, & Rushworth, 2006; Walton, Croxson, Behrens, Kennerley, & Rushworth, 2007). In accordance with this suggestion, previous studies have shown that a FN is present in the absence of response choice (Yeung, Holroyd, & Cohen, 2005), which is in line with the observed FN in the Dictator game in the present study. In addition, it may be noted that, in the Dictator game and in the Ultimatum game (accepted offer trials), the presentation of the offers indicates the exact monetary feedback that can be expected. Moreover, for all low offers in the Ultimatum game, the presentation of the offer already signals the low outcome of the current trial (either being 1 or 2 cents upon accept and 0 cents upon reject). Since FN seems to migrate back to the earliest indicator of reinforcement, as shown by Dunning and Hajcak (2007), the offer—in terms of reinforcement learning—already implies the likely decision and thus the final outcome. Thus, the presentation of the offer conveys very similar information about outcome in both games. Taken together, this might explain the absence of differences between the Ultimatum and Dictator games.

In summary, our data corroborate previous findings indicating the importance of emotional processes in decision-making. Our data further reveal the presence of several independent sources of variance that each contribute to human decision-making in the Ultimatum game.

REFERENCES

Bechara, A., & Damasio, A. R. (2005). The somatic marker hypothesis: A neural theory of economic decision. *Games and Economic Behavior, 52*, 336–372.

Bechara, A., Damasio, H., & Damasio, A. R. (2000). Emotion, decision making and the orbitofrontal cortex. *Cerebral Cortex, 10*, 295–307.

Boksem, M. A., Tops, M., Wester, A. E., Meijman, T. F., & Lorist, M. M. (2006). Error-related ERP components and individual differences in punishment and reward sensitivity. *Brain Research, 1101*, 92–101.

Camerer, C. F. (2003). *Behavioral game theory: Experiments in strategic interaction.* New York, NY: Russell Sage Foundation.

Coles, M. G. H., & Rugg, M. D. (1995). Event-related brain potentials: An introduction. In M. D. Rugg & M. G. H. Coles (Eds.), *Electrophysiology of mind: Event-related brain potentials and cognition.* Oxford: Oxford University Press.

Davis, M. (1992). The role of the amygdala in fear and anxiety. *Annual Review of Neuroscience, 15*, 353–375.

Dunning, J. P., & Hajcak, G. (2007). Error-related negativities elicited by monetary loss and cues that predict loss. *NeuroReport, 18*, 1875–1878.

Fehr, E., & Camerer, C. F. (2007). Social neuroeconomics: The neural circuitry of social preferences. *Trends in Cognitive Sciences, 11*, 419–427.

Fehr, E., & Gachter, S. (2002). Altruistic punishment in humans. *Nature, 415*, 137–140.

Fowles, D. C. (1980). The three arousal model: Implications of Gray's two-factor learning theory for heart rate, electrodermal activity and psychopathy. *Psychophysiology, 17*, 87–104.

Fredrikson, M., Furmark, T., Olsson, M. T., Fischer, H., Andersson, J., & Langstrom, B. (1998). Functional neuroanatomical correlates of electrodermal activity: A positron emission tomographic study. *Psychophysiology, 35*, 179–185.

Furmark, T., Fischer, H., Wik, G., Larsson, M., & Fredrikson, M. (1997). The amygdala and individual differences in human fear conditioning. *NeuroReport, 8*, 3957–3960.

Gray, J. A. (1982). *The neuropsychology of anxiety: An enquiry into the functions of the septo-hippocampal system.* Oxford: Oxford University Press.

Gray, J. A. (1994). Personality dimensions and emotion systems. In P. Ekman & R. J. Davidson (Eds.), *The nature of emotion.* New York: Oxford University Press.

Güth, W., Schmittberger, R., & Schwarze, B. (1982). An experimental analysis of ultimatum bargaining. *Journal of Economic Behaviour and Organization, 3*, 367–388.

Hajcak, G., McDonald, N., & Simons, R. F. (2003). Anxiety and error-related brain activity. *Biological Psychology, 64*, 77–90.

Hajcak, G., McDonald, N., & Simons, R. F. (2004). Error-related psychophysiology and negative affect. *Brain & Cognition, 56*, 189–197.

Harle, K. M., & Sanfey, A. G. (2007). Incidental sadness biases social economic decisions in the Ultimatum Game. *Emotion, 7,* 876–881.

Hewig, J., Kretschmer, N., Trippe, R. H., Hecht, H., Coles, M. G., Holroyd, C. B., & Miltner, W. H. (2010). Hypersensitivity to reward in problem gamblers. *Biological Psychiatry, 67,* 781–783.

Hewig, J., Straube, T., Trippe, R. H., Hecht, H., Kretschmer, N., Coles, M. G. H., & Miltner, W. H. R. (2009). Decision-making under risk: An fMRI study. *Journal of Cognitive Neuroscience, 21,* 1642–1652.

Hewig, J., Trippe, R. H., Hecht, H., Coles, M. G. H., Holroyd, C. B., & Miltner, W. H. R. (2007). Decision-making in Blackjack: An electrophysiological analysis. *Cerebral Cortex, 17,* 865–877.

Holroyd, C. B., & Coles, M. G. (2008). Dorsal anterior cingulate cortex integrates reinforcement history to guide voluntary behavior. *Cortex, 44,* 548–559.

Holroyd, C. B., & Coles, M. G. H. (2002). The neural basis of human error processing: Reinforcement learning, dopamine, and the error-related negativity. *Psychological Review, 109,* 679–709.

Holroyd, C. B., & Krigolson, O. E. (2007). Reward prediction error signals associated with a modified time estimation task. *Psychophysiology, 44,* 913–917.

Holroyd, C. B., Nieuwenhuis, S., Yeung, N., & Cohen, J. D. (2003). Errors in reward prediction are reflected in the event-related brain potential. *NeuroReport, 14,* 2481–2484.

Holroyd, C. B., Nieuwenhuis, S., Yeung, N., Nystrom, L., Mars, R. B., Coles, M. G., & Cohen, J. D. (2004). Dorsal anterior cingulate cortex shows fMRI response to internal and external error signals. *Nature Neuroscience, 7,* 497–498.

Holroyd, C. B., Pakzad-Vaezi, K. L., & Krigolson, O. E. (2008). The feedback correct-related positivity: Sensitivity of the event-related brain potential to unexpected positive feedback. *Psychophysiology, 45,* 688–697.

Jocham, G., & Ullsperger, M. (2009). Neuropharmacology of performance monitoring. *Neuroscience & Biobehavioral Reviews, 33,* 48–60.

Kennerley, S. W., Walton, M. E., Behrens, T. E., Buckley, M. J., & Rushworth, M. F. (2006). Optimal decision making and the anterior cingulate cortex. *Nature Neuroscience, 9,* 940–947.

Luu, P., Collins, P., & Tucker, D. M. (2000). Mood, personality, and self-monitoring: Negative affect and emotionality in relation to frontal lobe mechanisms of error monitoring. *Journal of Experimental Psychology: General, 129,* 43–60.

Meriau, K., Wartenburger, I., Kazzer, P., Prehn, K., Villringer, A., van der Meer, E., & Heekeren, H. R. (2009). Insular activity during passive viewing of aversive stimuli reflects individual differences in state negative affect. *Brain and Cognition, 69,* 73–80.

Miltner, W. H. R., Braun, C. H., & Coles, M. G. H. (1997). Event-related brain potentials following incorrect feedback in a time-estimation task: Evidence for a "generic" neural system for error detection. *Journal of Cognitive Neuroscience, 9,* 788–798.

Nieuwenhuis, S., Yeung, N., Holroyd, C., Schurger, A., & Cohen, J. D. (2004). Sensitivity of electrophysiological activity from medial frontal cortex to utilitarian and performance feedback. *Cerebral Cortex, 14,* 741–747.

Nowak, M. A., Page, K. M., & Sigmund, K. (2000). Fairness versus reason in the ultimatum game. *Science, 289,* 1773–1775.

Pailing, P. E., & Segalowitz, S. J. (2004). The error-related negativity as a state and trait measure: Motivation, personality, and ERPs in response to errors. *Psychophysiology, 41,* 84–95.

Phelps, E. A., & LeDoux, J. E. (2005). Contributions of the amygdala to emotion processing: From animal models to human behavior. *Neuron, 48,* 175–187.

Pillutla, M. M., & Murnighan, J. K. (1996). Unfairness, anger, and spite: Emotional rejections of ultimatum offers. *Organizational Behavior and Human Decision Processes, 68,* 208–224.

Polezzi, D., Daum, I., Rubaltelli, E., Lotto, L., Civai, C., Sartori, G., & Rumiati, R. (2008). Mentalizing in economic decision-making. *Behavioural Brain Research, 190,* 218–223.

Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2003). The neural basis of economic decision-making in the Ultimatum Game. *Science, 300,* 1755–1758.

Solnick, S. J., & Schweitzer, M. E. (1999). The influence of physical attractiveness and gender on ultimatum game decisions. *Organizational Behavior and Human Decision Processes, 79,* 199–215.

Sutton, R. S., & Barto, A. G. (1998). *Reinforcement learning: An introduction.* Cambridge, MA: MIT Press.

Tabibnia, G., Satpute, A. B., & Lieberman, M. D. (2008). The sunny side of fairness: Preference for fairness activates reward circuitry (and disregarding unfairness activates self-control circuitry). *Psychological Science, 19,* 339–347.

Tukey, J. W. (1958). Bias and confidence in not-quite large samples. *Annals of Mathematical Statistics, 29,* 614–614.

Ullsperger, M., & von Cramon, D. Y. (2003). Error monitoring using external feedback: Specific roles of the habenular complex, the reward system, and the cingulate motor area revealed by functional magnetic resonance imaging. *Journal of Neuroscience, 23,* 4308–4314.

van 't Wout, M., Kahn, R. S., Sanfey, A. G., & Aleman, A. (2006). Affective state and decision-making in the Ultimatum Game. *Experimental Brain Research, 169,* 564–568.

von Neumann, J., & Morgenstern, O. (1953). *Theory of Games and Economic Behavior.* Princeton: Princeton University Press.

Walton, M. E., Croxson, P. L., Behrens, T. E., Kennerley, S. W., & Rushworth, M. F. (2007). Adaptive decision making and value in the anterior cingulate cortex. *NeuroImage, 36*(Suppl 2), T142–154.

Yeung, N., Holroyd, C. B., & Cohen, J. D. (2005). ERP correlates of feedback and reward processing in the presence and absence of response choice. *Cerebral Cortex, 15,* 535–544.

Yeung, N., & Sanfey, A. G. (2004). Independent coding of reward magnitude and valence in the human brain. *Journal of Neuroscience, 24,* 6258–6264.