Neural Correlates of Social Cooperation and Non-Cooperation as a Function of Psychopathy

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Background: Psychopathy is a disorder involving a failure to experience many emotions that are necessary for appropriate social behavior. In this study, we probed the behavioral, emotional, and neural correlates of psychopathic traits within the context of a dyadic social interaction.

Methods: Thirty subjects were imaged with functional magnetic resonance imaging while playing an iterated Prisoner's Dilemma game with human confederates who were outside the scanner. Subjects also completed two self-report psychopathy questionnaires.

Results: Subjects scoring higher on psychopathy, particularly males, defected more often and were less likely to continue cooperating after establishing mutual cooperation with a partner. Further, they experienced more outcomes in which their cooperation was not reciprocated (cooperate–defect outcome). After such outcomes, subjects scoring high in psychopathy showed less amygdala activation, suggesting weaker aversive conditioning to those outcomes. Compared with low-psychopathy subjects, subjects higher in psychopathy also showed weaker activation within orbitofrontal cortex when choosing to cooperate and showed weaker activation within dorsolateral prefrontal and rostral anterior cingulate cortex when choosing to defect.

Conclusions: These findings suggest that whereas subjects scoring low on psychopathy have emotional biases toward cooperation that can only be overcome with effortful cognitive control, subjects scoring high on psychopathy have an opposing bias toward defection that likewise can only be overcome with cognitive effort.

Key Words: Cooperation, decision-making, emotion, fMRI, psychopathy, social cognition

Psychopathy is a disorder involving a failure to experience many emotions that are necessary for appropriate social behavior. It has been defined as "a socially devastating disorder defined by a constellation of affective, interpersonal, and behavioral characteristics, including egocentricity; impulsivity; irresponsibility; shallow emotions; lack of empathy, guilt, or remorse; pathological lying; manipulativeness; and the persistent violation of social norms and expectations" (Hare 1998). Psychopaths often are described as emotionally detached and as demonstrating selfish and manipulative behavior. They also are typically shallow, callous, and incapable of or unwilling to form long-lasting bonds (Hare 1978).

Many studies have examined physiological responses of psychopaths to aversive social stimuli such as pictures of angry or sad faces and have found diminished reactions compared with nonpsychopathic controls (Levenston *et al.* 2000; Patrick 1994; Patrick *et al.* 1993). Other studies have attempted to identify the neural bases of psychopathic behavior. Some researchers argue that psychopathic behavior is mainly the result of amygdala dysfunction (Blair 2003, 2005). The amygdala is critically involved in aversive conditioning (Davis 1997; Ledoux 1998), in which psychopaths are deficient (Angrilli *et al.* 1996; Bechara *et al.* 1995; Flor *et al.* 2002; Hare and Quinn 1971; Levenston *et al.* 2000; Lykken 1957; Patrick *et al.* 1993). Moreover, psychopathy is associated with reduced amygdala volume (Tiihonen, unpublished data, 2000) and decreased amygdala activation on emotional tasks in fMRI paradigms (Gordon *et al.* 2004; Kiehl *et al.* 2001; Veit *et al.* 2002). Others argue that deficiencies in frontolimbic circuitry are the primary contributor to psychopathic behavior. For example, results from two recent fMRI studies of fear conditioning suggest that psychopathy is associated with orbitofrontal hypoactivity (Birbaumer *et al.* 2005; Veit *et al.* 2002). Moreover, patients with lesions to orbitofrontal cortex (OFC) often develop personality characteristics similar to psychopathy and even have been said to develop "acquired sociopathy" (Tranel 2002). In addition to hypotheses concerning insufficient functioning of certain brain systems, some investigators have proposed that psychopaths compensate for deficiencies in the prefrontal–limbic circuit by recruiting dorsolateral prefrontal cortex (DLPFC) to process emotional stimuli in a primarily cognitive way (Gordon *et al.* 2004; Kiehl *et al.* 2001; Muller *et al.* 2003).

Previous functional imaging studies of psychopathy have involved basic emotional stimuli such as words and pictures. Yet the true nature of the disorder lies not only in an abnormality in emotional processing but in how this deficiency leads to disturbances in social behavior. The present study aimed to examine neural correlates of emotions experienced during social interactions by scanning subjects as they were engaged in an interaction with nonscanned social partners outside the scanner in the context of an iterated Prisoner's Dilemma (PD) game (Figure 1).

The iterated PD game models relationships that are based on reciprocal altruism, or the reciprocal exchange of favors. In the game, two players simultaneously and independently choose to either cooperate with each other or not. The matrix in Figure 1 specifies four possible outcomes of a round and their associated payoffs for both players: player A and player B cooperate (C; thus, this is a CC outcome), player A cooperates and player B defects (D; thus, this is a CD outcome), player A defects and player B cooperates (DC), or player A and player B defect (DD).

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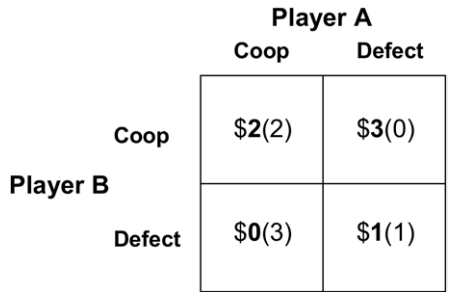

Figure 1. Payoff matrix for the four outcomes in the Prisoner's Dilemma game. Scanned subject's choices (cooperate [Coop] or Defect; player A) are listed atop columns, and nonscanned subject's choices (cooperate [Coop] or Defect; player B) are listed aside rows. Dollar amounts in bold are awarded to player A. Amounts in parentheses are awarded to player B.

Each cell of the payoff matrix corresponds to a different outcome of the social interaction and typically elicits a different set of social emotions. Mutual cooperation often is associated with friendship, love, trust, or obligation; mutual defection with feelings of rejection and hatred; and cooperation by one and defection by the other typically results in the cooperator feeling anger or indignation and in the defector feeling anxiety, guilt, or elation from successfully exploiting the partner to their own advantage.

The optimal strategy in the iterated PD game depends on the partner's strategy. However, one strategy that is effective against a wide range of partner strategies is tit for tat, which begins an interaction by cooperating and then simply reciprocates the partner's move from the previous round. Tit for tat is a successful strategy because it is good at getting other players to cooperate with it (Axelrod 1984). The success of tit for tat demonstrates that establishing and maintaining mutual cooperation is often the best long-term strategy. The PD game is a unique decision-making task insofar as optimal decisions can arise from either emotional or cognitive motivations. That is, some people may play tit for tat because it feels appropriate to them to reciprocate cooperation and to retaliate for defection, whereas others may play tit for tat on the basis of strategic calculations, aimed at maximizing overall earnings.

Of the three regions discussed four paragraphs prior as being implicated in psychopathy (amygdala, OFC, DLPFC), one has been activated in previous fMRI studies of the PD game. OFC is activated when one decides to cooperate, presumably reflecting the region's role in emotionally guided decision making (Bechara *et al.* 2000; Tranel 2002). OFC also is activated when processing mutually cooperative outcomes (CC), presumably because these outcomes are rewarding and OFC is part of the brain's reward system (Rilling *et al.* 2002, 2004). Amygdala activation has not been reported in the PD game but might reasonably be expected in response to CD outcomes, which may be construed as a social threat.

Our study also differs from most referenced five paragraphs prior in that we do not include diagnosed psychopaths but instead explore the full variation in psychopathy scores among a group of unselected individuals drawn from a university community. This selection approach is justified by recent statistical analyses demonstrating that scores on psychopathy measures are underpinned by a latent dimension (continuum) rather than by a latent taxon (natural category; Edens *et al.* 2006; Marcus *et al.* 2004) and by evidence that psychopathic and nonpsychopathic individuals in nonpsychiatric populations exhibit differences in brain activity as measured by fMRI (Gordon *et al.* 2004). Moreover, in contrast to institutionalized (e.g., prison) samples, nonclinical individuals are relatively free of potentially confounding variables (e.g., severe substance use, physical abuse history) that can often complicate interpretation of brain-imaging deficits (Lilienfeld and Andrews 1996). Finally, research elsewhere indicates that several widely used self-report measures of psychopathy, including those used in the present study, exhibit good psychometric properties (e.g., reliability and construct validity) in undergraduate samples. For example, several of these measures correlate moderately to highly with interview and observer measures of psychopathy as well as with laboratory indices of deficits that ostensibly are relevant to psychopathy (e.g., poor passive-avoidance learning) in college students (Lilienfeld and Fowler 2006 has a review).

Results from previous psychopathy neuroimaging studies, in combination with results from previous PD fMRI studies, led us to the following five hypotheses regarding the behavioral, emotional, and neural correlates of psychopathy within the context of the PD game. Compared with individuals scoring low on psychopathy, individuals scoring high on psychopathy will show the following: (1) less cooperative behavior, (2) lower self-reported emotional responses to the various game outcomes, (3) decreased activation of OFC when deciding to cooperate, (4) decreased activation in amygdala in response to aversive CD outcomes, and (5) increased activation in DLPFC when processing outcomes that typically are emotionally arousing.

Methods and Materials

Subjects

Thirty participants (15 females) from the Emory University community were studied. Mean age was 21.2 years (SD = 2.9 y). All subjects gave written informed consent, and the study was approved by the Emory University Institutional Review Board.

Behavioral Procedures

In addition to evaluating the relation of psychopathy to game-playing behavior, emotional reactions, and brain activity, this experiment also was designed to investigate the relation between gender (male vs. female) and ingroup versus outgroup affiliation (to be published in a separate article). The ingroup–outgroup manipulation involved the following procedure. Before the day of the fMRI scan, subjects were asked to take a bogus personality test in which they estimated the frequency of various events. When subjects arrived on the day of the experiment, they were assigned to either the red group or the black group, allegedly on the basis of the answers they gave on the test, and were asked to wear a wristband of the respective color. Before entering the scanner, subjects met two confederates, one of whom was wearing a wristband of the same color and another who was wearing a wristband of a different color. Subjects were told that they would play 20 rounds of an iterated PD game with each of the two partners.

Before meeting the confederates, subjects completed a 10-min computer tutorial that explained the PD game and were given a two-question multiple-choice quiz to evaluate their understanding. If either question was answered incorrectly, study personnel explained to participants why that answer was wrong and why another answer was correct. If necessary, subjects repeated the tutorial. Study personnel continued with the experiment only after they were convinced that the subject fully comprehended the task. Before entering the scanner,

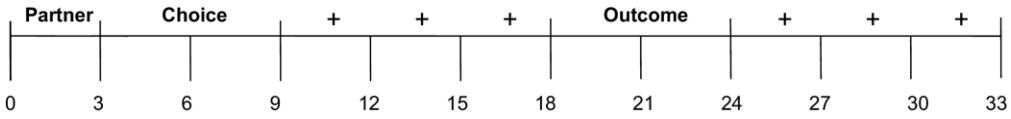

Figure 2. Timeline of a single Prisoner's Dilemma round in sec.

subjects also completed two practice rounds of the game by using the response box that they would be holding while in the scanner. The practice trials familiarized subjects with the feel of the game and the operation of the response box. After meeting the confederates, subjects were placed in the scanner.

Before the start of each game, the visual display inside the scanner indicated with which partner the subject was about to play the game, as well as the group status of that partner (i.e., ingroup or outgroup). While being imaged with fMRI, subjects played 20 rounds of an iterated PD game in each of two sessions. Subjects were told that they were playing with the each of the two human partners whom they had met previously. However, in actuality, partner choices were administered by a computer algorithm that played a so-called forgiving tit for tat strategy. This strategy cooperates in round 1, always reciprocates partner cooperation from the previous round, and reciprocates partner defection from the previous round 67% of the time. The forgiving aspect of the strategy helps to prevent long runs of mutual defection.

E-prime software (Psychology Software Tools, Pittsburgh, Pennsylvania) was used for stimulus presentation. Stimuli were projected onto a screen that subjects could view through a mirror mounted on the head coil of the scanner. Subject responses were recorded by using a response box. A timeline for a single PD trial is depicted in Figure 2. The name of the partner, along with his or her group affiliation (i.e., red or black), appeared at the beginning of each trial for 3 sec. Subjects then had 6 sec to choose to cooperate or defect. Afterward, subjects viewed a fixation cross for 9 sec before the partner's choice (i.e., trial outcome) was revealed and displayed for 6 sec. An additional 9-second rest period separated the outcome from the beginning of the next round.

After each of the two games, while still in the scanner, subjects rated their emotional reaction to the four PD game outcomes (CC, CD, DC, and DD). Seven-point Likert scales were used to rate the following emotions or feelings: afraid, envious, angry, sad, happy, ashamed, irritated, contemptuous, jealous, guilty, camaraderie, trust, betrayed, indignant, disappointed, and relieved.

Subjects then were removed from the scanner and completed two widely used paper-and-pencil self-report psychopathy questionnaires, both of which have been extensively validated in studies of both institutionalized (e.g., prison) and noninstitutionalized (e.g., student) samples (see Lilienfeld 1998 and Lilienfeld and Fowler 2006 for reviews). Both of these measures minimize the risk of impression management and defensiveness by using items that are phrased so as to appear socially desirable (Lilienfeld and Widows 2005). The first psychopathy questionnaire was the Psychopathic Personality Inventory (PPI) Short Form, a measure designed for noncriminal populations that contains 56 items to be rated on a four-point Likert-type scale (Lilienfeld and Andrews 1996). This questionnaire yields a total score representing global psychopathy and scores on eight-factor, analytically derived subscales: Machiavellian Egocentricity, Social Potency, Fearlessness, Coldheartedness, Impulsive Nonconformity, Blame Externalization, Carefree Nonplanfulness, and Stress Immunity. Seven of these subscales (excluding Coldheartedness, which does not load highly on either factor) can be grouped to form two factors of the PPI that roughly parallel factor 1 and factor 2 of the Psychopathy Checklist–Revised (PCL-R), the most commonly used measure for assessing psychopathy in institutionalized populations (Hare *et al.* 1990). The first grouping, similar to the PCL-R factor 1, is the Emotional–Interpersonal dimension, which includes Social Potency, Stress Immunity, and Fearlessness. This factor is higher in individuals with low levels of anxiety, empathy, remorse, emotional arousal, and responsivity and high levels of superficial charm, manipulativeness, and lying. Factor 2 is the Social Deviance dimension and includes Carefree Nonplanfulness, Blame Externalization, Machiavellian Egocentricity, and Impulsive Nonconformity. This factor reflects antisocial behavior, stimulation seeking, aggressiveness, irresponsibility, and low impulse control (Benning *et al.* 2003).

The second psychopathy questionnaire was the Levenson Primary and Secondary Psychopathy Scales, developed by Levenson, Kiehl, and Fitzpatrick (Levenson *et al.* 1995). Like the PPI, this measure is designed for noninstitutionalized populations. It contains 26 items and is in a similar four-point Likert scale format. This measure is divided into factor analytically–derived primary and secondary psychopathy subscores, which also roughly parallel factor 1 and factor 2 of the PCL-R, respectively.

fMRI Image Acquisition

Subjects lay motionless in a supine position in the scanner. Functional images were acquired on a Siemens 3T Trio scanner by using an echo planar imaging (EPI) sequence with the following parameters: repetition time (TR) = 2000 ms, echo time (TE) = 22 ms, matrix = 64 × 64, field of view (FOV) = 192 mm, slice thickness = 3 mm, gap = 1 mm, 32 axial slices. The duration of each of the two EPI scans was 11 min. These were followed by a 7-min T1-weighted magnetization prepared rapid gradient echo (MPRAGE) scan (TR = 11 ms, TE = 4 ms, matrix = 256 × 256, slice thickness = 1.33 mm, gap = 0 mm).

fMRI Image Analysis

Image preprocessing was conducted by using Brain Voyager QX (version 1.3.8) software (Brain Innovation, Maastricht, The Netherlands). Preprocessing involved image realignment by six-parameter 3-D motion correction, slice scan time correction using linear interpolation, spatial smoothing with a 10-mm full width at half maximum (FWHM) Gaussian kernel, and temporal smoothing by using voxel-wise linear detrending and high-pass filtering of frequencies below three cycles per run length. Images subsequently were normalized into Talairach space (Talairach and Tournoux 1988). A separate general linear model (GLM) was defined for each subject that examined the neural response to both the epoch in which the choice was made as well as to the epoch in which the game outcome was revealed. We defined six regressors: choice C, choice D, CC outcomes, CD outcomes, DC outcomes, and DD outcomes. Each regressor was convolved with a standardized model of the hemodynamic response. The resulting GLM swas corrected for temporal autocorrelation by using a first-order autoregressive model. For each

subject, contrasts of parameter estimates for specified predictors (e.g., choice C – choice D) were computed at every voxel of the brain.

A one-sample *t* test was used to identify voxels in which the average contrast for the whole group ($n = 30$ subjects) differed significantly from 0 (i.e., a random-effect analysis). The resulting map of the *t* statistic was thresholded at $p < .001$, with a spatial extent threshold of 10 contiguous voxels. Activated regions then were explored in correlation analyses. Each subject's average contrast value within that region of interest (ROI) was correlated with each subject's scores on the PPI and the Levenson measure, including the factor 1 and 2 subscales of both instruments. The random-effects analysis identifies activations that are found in most subjects. However, because we were interested in exploring individual variability, we also conducted fixed-effects analyses, which identify areas that may show strong activation in only a subset of the sample. In the fixed-effects analysis, we maintained the same thresholds of $p < .001$ and 10 contiguous voxels. Here, we restricted our correlational analyses to activations that fell within our a priori ROIs (amygdala, OFC, DLPFC). Again, average contrast values within activated regions were correlated with psychopathy scores to determine whether activation in that area varied as a function of psychopathy.

In addition to functionally defined ROIs, we also defined anatomically based ROIs (amygdala, OFC, and DLPFC) that were relevant to our primary hypotheses that were articulated in the last paragraph of this article's introductory section. ROIs were drawn on one subject's Talairach-transformed anatomical scan, with the aid of a reference brain atlas (Duvernoy 1999). The average contrast value in the ROI was calculated for each subject, and these were correlated with subject psychopathy scores.

Finally, in an exploratory descriptive analysis, we entered psychopathy scores as a covariate in the GLM and tested for correlations between subject contrast values and psychopathy scores on a voxel-by-voxel basis. Maps of the correlation coefficient were thresholded at $r > .50$, with a 10-voxel spatial-extent threshold. For this analysis, it was possible only to include those subjects who had experienced all four of the PD game outcomes because of software limitations, leaving a sample size of 22 subjects.

Results

Self-report and Behavioral Data

As predicted, total scores and factor 1 scores on the PPI and the Levenson measure were positively correlated. However, the correlation between the factor 2 scores did not reach significance (Table 1). Factor 1 of the PPI correlated more highly with factor 2 of the Levenson measure than with Levenson factor 1.

Table 1. Correlations between the PPI and Levenson Scores ($N = 30$)

Group	PPI Total	Factor 1	Factor 2	Levenson Total	Factor 1	Factor 2
PPI Total						
PPI Factor 1	.629[b]					
PPI Factor 2	.744[b]	.063				
Levenson Total	.477[b]	.609[b]	.125			
Levenson Factor 1	.355[b]	.458[a]	.090	.916[b]		
Levenson Factor 2	.532[b]	.631[b]	.136	.785[b]	.471[b]	

PPI, Psychopathic Personality Inventory.
[a] $p < .05$.
[b] $p < .01$.

Table 2. Correlations Between Psychopathy Scores and Behavior

Outcome	PPI Total	Factor 1	Factor 2	Levenson Total	Factor 1	Factor 2
C choices						
All	−.06	.01	−.11	−.28	−.27	−.18
Males	.13	.11	−.12	−.58[a]	−.60[a]	−.30
Females	−.28	−.16	−.14	−.13	−.10	−.15
P (C/CC)						
All	−.21	−.03	−.23	−.34	−.34	−.24
Males	−.02	−.02	−.15	−.64[b]	−.64[a]	−.37
Females	−.46	−.19	−.37	−.22	−.19	−.19
CC						
All	−.100	−.031	−.123	−.321	−.298	−.246
Males	.061	.047	−.125	−.616[a]	−.601[a]	−.372
Females	−.307	−.195	−.171	−.180	−.130	−.200
CD						
All	.224	.179	.173	.371[a]	.271	.398[a]
Males	.231	.166	.161	.515[a]	.393	.494
Females	.273	.254	.211	.299	.202	.350
DC						
All	.057	.003	.091	.336	.313	.225
Males	−.074	.018	.033	.598[a]	.556[a]	.409
Females	.259	.092	.209	.204	.178	.183
DD						
All	.057	−.013	.093	.190	.204	.102
Males	−.175	−.212	.172	.517[a]	.590[a]	.171
Females	.255	.187	.076	.065	.029	.097

C, cooperate; D, defect; PPI, Psychopathic Personality Inventory.
[a] $p < .05$.
[b] $p < .01$.

Overall, there was no significant correlation between psychopathy scores and the number of times that subjects chose to cooperate in the two games. However, conducting the analysis separately for male and female subjects revealed significant negative correlations with Levenson total and factor 1 scores in males but not in females (Table 2).

We also were interested in whether psychopathy scores were related to the tendency of subjects to disrupt a mutually cooperative interaction. Here again, we found significant correlations for men but not women. In men, there was a significant negative correlation between the probability that the subject would choose to cooperate after a CC outcome in the previous round and their total and factor 1 scores on the Levenson measure (Table 2).

The total number of times that each subject experienced each of the four outcomes during the two games was tabulated and correlated with psychopathy scores. For the combined sample of male and female subjects, significant positive correlations were found between both Levenson total and factor 2 scores and the total number of CD outcomes that the subject experienced (Table 2). Although these were the only significant correlations, there was a clear trend for subjects higher in psychopathy to also experience more DC outcomes (all positive correlations), as well as fewer CC outcomes (all negative correlations; Table 2). As discussed in the previous paragraphs, significant correlations were observed in male but not female subjects. In particular, males showed significant negative correlations between Levenson scores and number of CC outcomes, as well as significant positive correlations with number of CD, DC, and DD outcomes. For CC, DC, and DD, correlations were significant for factor 1 but not factor 2 scores.

The various PD outcomes were associated with predicted social emotions (Figure 3). For CC outcomes, subjects reported

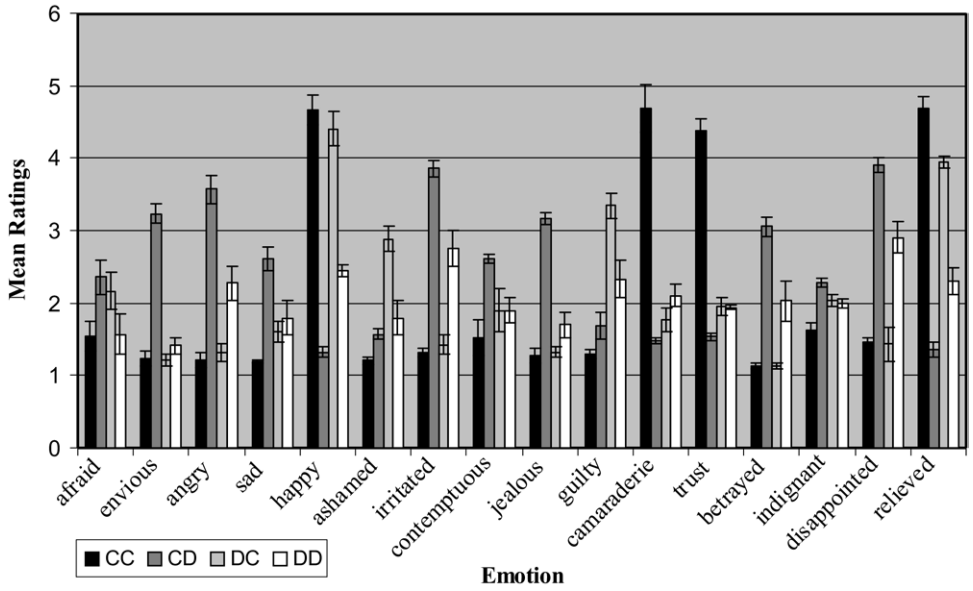

Figure 3. Mean emotion ratings across subjects ($n = 30$) for each outcome of the Prisoner's Dilemma game. C, cooperate; D, defect.

high levels of happiness, camaraderie, trust, and relief. For CD outcomes, they reported high levels of anger, irritation, and disappointment. During DC outcomes, subjects reported high levels of happiness, guilt, and relief. Finally, for DD outcomes, ratings were low and quite evenly distributed across the different emotions.

Although the PD game was effective in eliciting the predicted emotions across the group as a whole, no significant correlations were found between psychopathy scores and emotion ratings of interest for any of the game outcomes (all $p > .05$). Analyses were restricted to emotions that were predicted to distinguish between those scoring high and low on psychopathy. For CC outcomes, we tested for correlations between psychopathy and happiness ($r = -.05$ for PPI; $r = -.08$ for Levenson), trust ($r = -.11$ for PPI; $r = -.05$ for Levenson) and camaraderie ($r = -.05$ for PPI; $r = -.12$ for Levenson). For CD outcomes, we examined anger ($r = .02$ for PPI; $r = .19$ for Levenson), fear ($r = -.11$ for PPI; $r = .04$ for Levenson), and irritation ($r = -.08$ for PPI; $r = -.11$ for Levenson). For DC outcomes, we examined happiness ($r = -.16$ for PPI; $r = -.16$ for Levenson) and guilt ($r = -.12$ for PPI; $r = -.12$ for Levenson).

Analyzing the data separately by gender revealed a lone significant correlation between trust ratings for CC outcomes and Levenson psychopathy scores ($r = -.55$, $p < .05$) in female subjects.

Imaging Results

Choice Epoch. To examine the neural correlates of decision making in the PD game, we analyzed the epoch in which the subject chooses to cooperate or defect (sec 3–9; Figure 2). Activations during cooperation were contrasted with activations during defection (choice C – choice D). A random-effects analysis revealed a lone significant deactivation within rostral anterior cingulate cortex (ACC). Within this ROI, males but not females showed a significant positive correlation between contrast values for choice C – choice D and PPI Total and Factor 2 scores (Table 3; Figure 4A).

A follow-up fixed-effects analysis revealed deactivation in one of our a priori ROIs, the DLPFC. Within DLPFC, subjects with higher Levenson psychopathy scores, particularly factor 2, showed greater activation for this contrast (Table 4; Figure 4B). This effect was present in both males and females.

Given its involvement with emotions and decision making, OFC also was an a priori ROI for this contrast. OFC was not activated in either the fixed or random-effects analyses. However, for an anatomical ROI encompassing Brodmann's area 11, there was a significant negative correlation between Levenson total and factor 2 psychopathy scores and activation for the contrast of choice C – choice D (Table 5). In other words, subjects scoring higher on psychopathy had less activation in OFC for the contrast of choice C – choice D. However, this effect only was present when playing with ingroup partners.

Given that DLPFC activity was positively correlated with psychopathy scores and OFC activity was negatively correlated with psychopathy scores when playing with ingroup partners, we tested for and found an inverse relationship between activity in these two regions ($r = -.58$, $p < .01$; Figure 5). Thus, when choosing to cooperate, subjects with strong DLPFC activation showed weak OFC activation and vice versa.

Outcome Epoch. To test predictions regarding specific outcomes, activation during that outcome was contrasted with the average activation during the other three outcomes.

CC Outcomes. For the random-effects analysis of CC outcomes, significant deactivations were observed in insula and middle frontal gyrus bilaterally, as well as in right cuneus (Supplement 1).

Table 3. Correlation Coefficients Between Anterior Cingulate Deactivation and Psychopathy Scores for the Contrast of Choice C − Choice D

	PPI			Levenson		
Group	Total	Factor 1	Factor 2	Total	Factor 1	Factor 2
All	.463[a]	.263	.306	.069	−.025	.194
Males	.553[a]	−.359	.597[a]	−.367	−.497	.020
Females	.359	.426	.104	.162	.093	.215

PPI, Psychopathic Personality Inventory.
[a] $p < .05$.

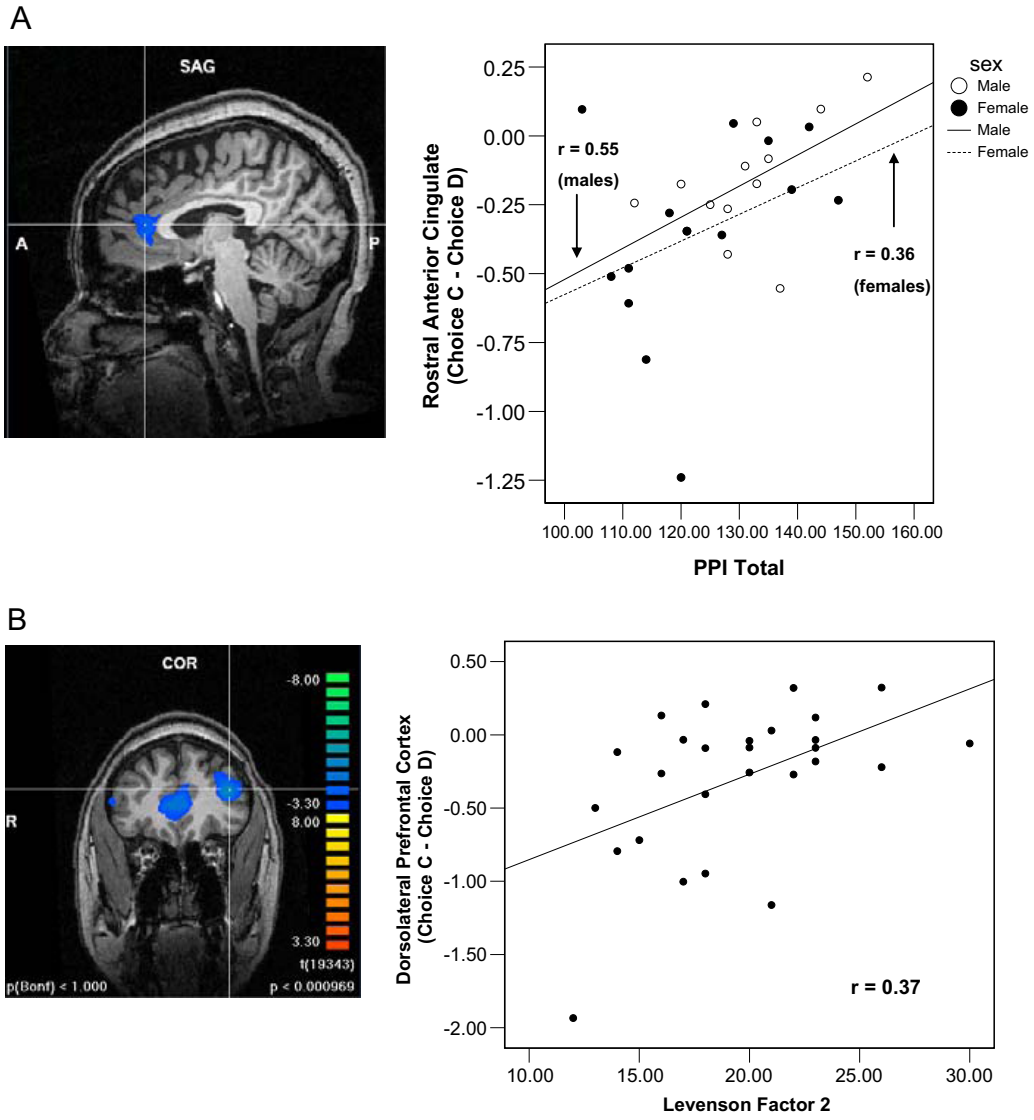

Figure 4. Deactivations for the contrast of choice C – choice D within (**A**) rostral anterior cingulate cortex, in which contrast values are positively correlated with PPI Total scores in male subjects and (**B**) dorsolateral prefrontal cortex, in which contrast values are positively correlated with Levenson Factor 2 scores.

Of these regions, a relationship with psychopathy measures was present only for the right cuneus, in which activation was negatively correlated with psychopathy scores for female but not male subjects (Table 6).

In addition to this whole-brain voxel-by-voxel analysis, an anatomical ROI was defined in OFC (Brodmann's area 11), and the average activation for the ROI was calculated in each subject. No significant correlations between brain activation and psychopathy scores were found within OFC.

Table 4. Correlation Coefficients Between DLPFC Activation and Psychopathy Scores for the Contrast of Choice C − Choice D

	PPI			Levenson		
Group	Total	Factor 1	Factor 2	Total	Factor 1	Factor 2
All	.289	.257	.153	.369[a]	.210	.495[b]
Males	.188	.297	.217	.445	.296	.503[a]
Females	.249	.143	.063	.273	.083	.466[a]

DLPFC, dorsolateral prefrontal cortex; PPI, Psychopathic Personality Inventory.
[a] $p < .05$ (1-tailed).
[b] $p < .01$ (1-tailed).

Table 5. Correlation Coefficients Between OFC Activation (BA 11) and Psychopathy Scores for the Contrast of Choice C − Choice D

	PPI			Levenson		
Group	Total	Factor 1	Factor 2	Total	Factor 1	Factor 2
Ingroup	−.290	−.218	−.173	−.428[a]	−.271	−.525[b]
Males	−.314	−.322	−.203	−.165	−.066	−.483
Females	−.221	−.100	−.122	−.476	−.352	−.517
Outgroup	−.199	.018	−.221	−.099	−.037	−.163
Males	−.525	−.108	−.369	−.152	−.042	−.273
Females	.151	.275	.010	.053	.089	−.013

OFC, orbitofrontal cortex; PPI, Psychopathic Personality Inventory.
[a] $p < .05$.
[b] $p < .01$.

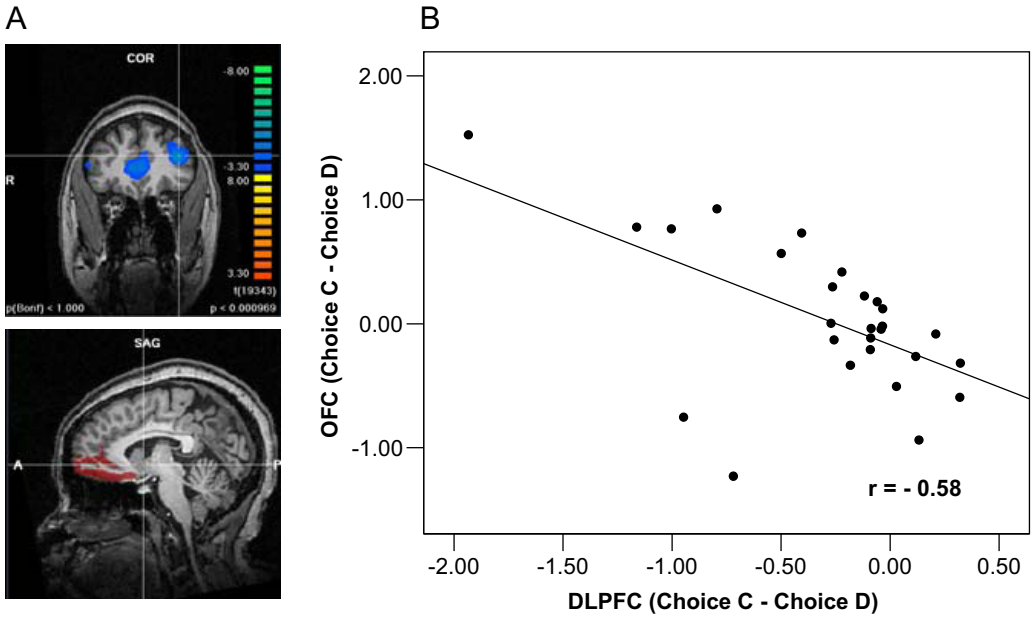

Figure 5. (**A**) Inverse relationship between dorsolateral prefrontal cortex (DLPFC) and orbitofrontal cortex (OFC) activity during decision making. (**B**) Location of DLPFC (top) and OFC (bottom) regions of interest used in the scatterplot and correlation that are presented.

CD Outcomes. CD outcomes were associated with activation in right thalamus (ventral lateral nucleus) and left parahippocampal gyrus (Supplement 2). However, in neither of these ROIs was activation significantly correlated with psychopathy measures. A fixed-effects analysis revealed activation within one of our a priori ROIs: DLPFC. However, there was no significant correlation between activation in this ROI and psychopathy measures.

Another a priori ROI for this contrast was the amygdala. For an anatomically defined ROI in the right amygdala, subjects with higher total scores of psychopathy on the Levenson measure showed reduced activation in response to CD outcomes (Table 7), but only when playing with outgroup partners. No significant correlations were found between brain activity in left amygdala and psychopathy scores.

DC Outcomes. For DC outcomes, no areas were activated in the random effects analysis, nor were any a priori ROIs activated in the fixed-effects analysis.

DD Outcomes. For DD outcomes, the right superior frontal gyrus (DLPFC) was activated for the random-effects analysis, but there were no significant correlations between psychopathy and activation within this ROI after DD outcomes.

Exploratory Analysis. In addition to conducting analyses on a priori ROIs, it also is important to explore the possible involvement of other neural systems in psychopathic behavior. In a whole-brain voxel-by-voxel analysis, we tested for correlations between contrast values for individual subjects and their total scores on the Levenson scale. The Levenson scale was used because it generated more significant results than did the PPI in the ROI analyses. The following contrasts were examined: CC versus others, CD versus others, DC versus others, DD versus others, main effect of partner choice, main effect of player choice, and choice C – choice D during decision making. Regions with a correlation coefficient of greater than .5 and consisting of 10 or more contiguous voxels are reported in Table 8. Of particular note is the negative correlation between psychopathy and CD versus others within right amygdala (Figure 6), a result that is consistent with the amygdala ROI analysis discussed in the CD Outcomes section.

Also consistent with the ROI analyses is a negative correlation between psychopathy and choice C – choice D in two regions of OFC (Figure 7).

Table 6. Correlation Coefficients Between Right Cuneus Activation After CC Outcomes and Psychopathy Scores (*r* values)

	PPI			Levenson		
Group	Total	Factor 1	Factor 2	Total	Factor 1	Factor 2
All	−.365[a]	−.402[a]	−.216	−.313	−.211	−.362[a]
Males	−.100	.001	−.125	.079	.158	−.087
Females	−.493	−.660[b]	−.272	−.537*	−.441	−.517[a]

CC, mutual cooperation; PPI, Psychopathic Personality Inventory.
[a] $p < .05$.
[b] $p < .01$.

Discussion

In this sample of subjects drawn from a university community, scores on the Levenson psychopathy instrument explained significant individual variation in social behavior occurring in the context of an iterated PD game. Particularly in male subjects, Levenson psychopathy scores were significantly positively correlated with both the number of times a player defected as well

Table 7. Correlation Coefficients Between Right Amygdala Activation After CD Outcomes and Psychopathy Scores (*r* values), with Ingroup and Outgroup Partners

	PPI			Levenson		
Group	Total	Factor 1	Factor 2	Total	Factor 1	Factor 2
Outgroup	−.146	−.331	−.017	−.380[a]	−.363	−.277
Ingroup	−.074	−.015	.092	−.046	−.049	−.027

C, cooperate; D, defect; PPI, Psychopathic Personality Inventory.
[a] $p < .05$.

Table 8. Brain Regions Showing Correlations with Total Score on the Levenson Psychopathy Measure

Brain Region	Brodmann's Area	X	Y	Z	Voxels	Peak *r*
CC vs. others						
Medial Frontal Gyrus	R 10	4	56	−4	11	.59
R Caudate		20	23	9	36	−.63
Insula	L 13	−33	13	18	36	−.64
Cingulate Gyrus	L 23	−8	−7	29	10	−.59
Superior Temporal Gyrus	L 22	−60	−7	6	24	.61
Superior Temporal Gyrus	L 22	−63	−32	13	52	.66
Middle Temporal Gyrus	R 19	41	−78	21	14	−.61
CD vs. others						
Parahippocampal Gyrus and Amygdala	R 34	14	0	−12	62	−.63
R Thalamus		1	−18	0	25	.59
DC vs. others						
Middle Frontal Gyrus	R 47	38	37	−5	23	.56
L Caudate		−13	21	8	21	−.59
Cingulate Gyrus	L 24	−4	−2	26	13	−.57
L Thalamus		−10	−32	14	37	−.65
Parahippocampal Gyrus	R 19	34	−41	−3	30	−.61
Inferior Temporal Gyrus	R 37	48	−66	2	30	−.64
Cuneus	R 17	14	−80	11	49	−.63
Calcarine Sulcus	L 17	−20	−70	7	32	−.59
Cuneus	R 18	11	−85	12	75	−.63
DD vs. others						
Middle Temporal Gyrus	L 21	−56	−29	−13	16	.55
Supramarginal Gyrus	R 40	51	−52	21	10	.55
Middle Temporal Gyrus	L 39	−50	−71	9	28	.59
Lingual Gyrus	R 18	16	−75	−12	37	.61
Cuneus	R 17	16	−94	0	22	.62
Partner C − D						
L Caudate		−17	22	8	70	−.61
Superior Temporal Gyrus	L 22	−59	−6	4	24	.60
Posterior Cingulate	L 30	−3	−58	8	120	−.66
Fusiform Gyrus	R 19	24	−68	−10	65	−.64
Precuneus	R 19	24	−74	34	24	−.57
Middle Occipital Gyrus Rilling	R 18	13	−91	18	13	−.61
Choice C − Choice D						
Anterior Cingulate	R 32	6	43	−4	13	−.55
Middle Frontal Gyrus	R 11	34	38	−10	45	−.70
Precentral Gyrus	L 4	−41	−11	57	11	.58
Middle Temporal Gyrus	R 21	63	−31	−6	47	−.71
Cerebellum		42	−65	−23	57	−.69
Cuneus	R 17	11	−95	7	69	−.67

Clusters are listed that include five or more voxels and have a correlation coefficient of .5 or higher.
C, cooperate; D, defect; L, left; R, right.

as with the probability of defection after a mutually cooperative interaction in the previous round of the game. Choosing to defect after mutual cooperation in the previous round often reflects an attempt to arrange a DC outcome in which the subject benefits in the short term at the partner's expense. Indeed, DC outcome frequency also was positively correlated with Levenson psychopathy scores in male subjects. Despite the immediate payoff of a DC outcome, this may be a poor long-term strategy insofar as it often will lead to partner retaliation. Indeed, male subjects scoring higher in psychopathy experienced more CD and DD outcomes, as well (Table 2). Subsequent analysis reveals that the correlation for CD outcomes only is significant for CD outcomes that follow DC outcomes ($r = .38$ for the combined male and female samples, $p < .05$), but not for CD outcomes after any other outcome.

Thus, it appears that subjects scoring higher in psychopathy experience more CD outcomes specifically in response to having provoked the partner by earlier defecting out of mutual cooperation. Most people find CD outcomes aversive and try to avoid them by defecting if they suspect that the partner will defect. However, in light of known deficits in aversive conditioning among psychopaths (Angrilli *et al.* 1996; Bechara *et al.* 1995; Flor *et al.* 2002; Hare and Quinn 1971; Levenston *et al.* 2000; Lykken 1957; Patrick *et al.* 1993), high-psychopathy subjects may not find CD outcomes as aversive and may not learn to avoid them as readily as those low in psychopathy.

If high-psychopathy subjects do indeed find CD outcomes less aversive than do low-psychopathy subjects, then they are expected to show attenuated amygdala activation in response to CD outcomes. Both ROI and whole-brain analyses support this prediction for the right amygdala (Figure 6), with the whole-brain analysis identifying a sizeable ROI within the right amygdala. For the anatomical ROI analysis, the relationship only held when playing with outgroup partners. If amygdala activation is involved in aversive conditioning to the CD outcome, then

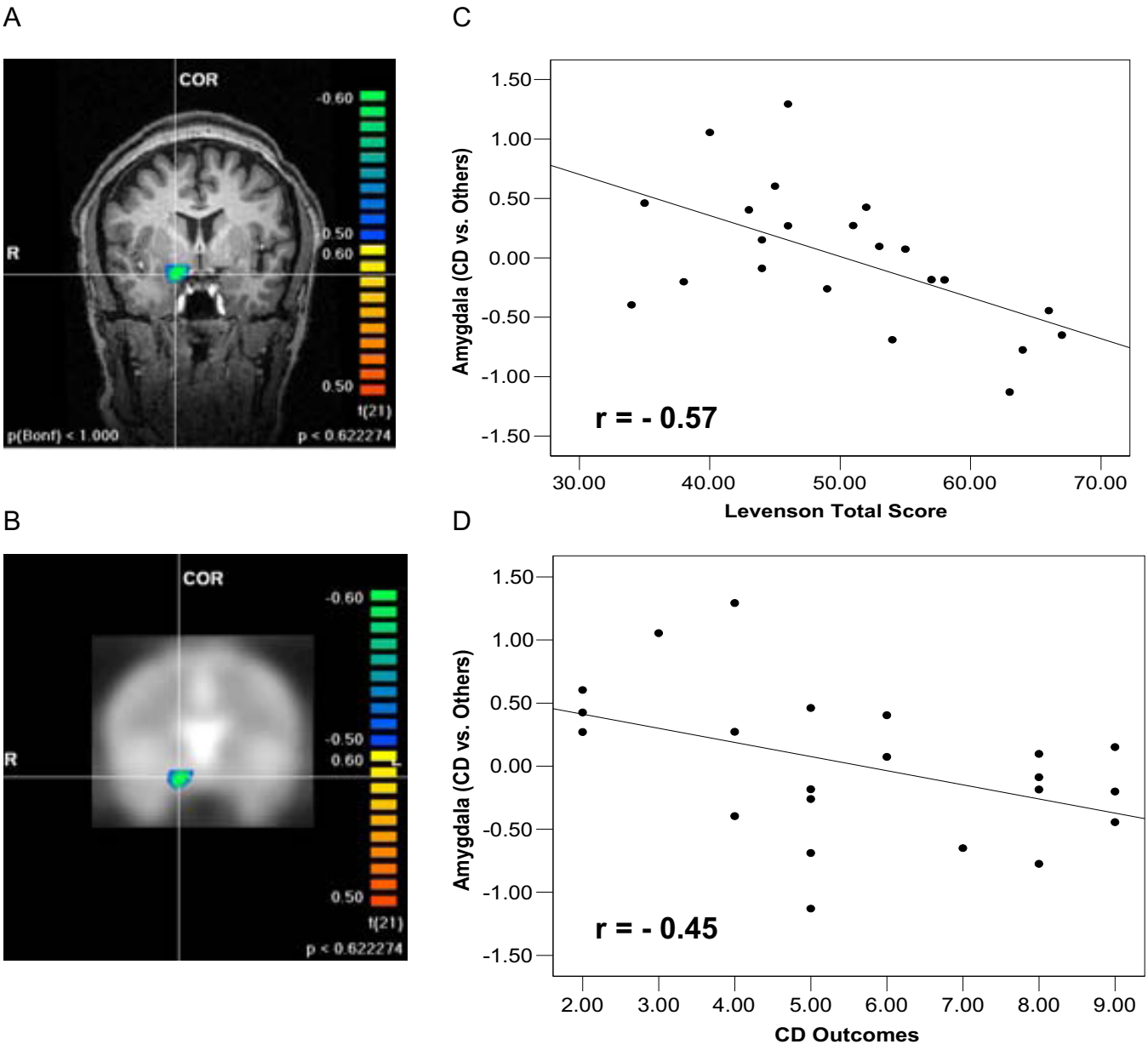

Figure 6. Negative correlation between Levenson Total psychopathy scores and activation for the contrast CD versus others within right amygdala. (**A**) Activation displayed on a single-subject, Talairach-transformed T1-weighted anatomical image. (**B**) Activation displayed on a single-subject, Talairach-transformed echo planar image. (**C**) Scatterplot of the correlation between Levenson total psychopathy score and activation strength for the contrast of CD vs. others. (**D**) Scatterplot of correlation between number of CD outcomes and activation strength for the contrast CD vs. others within right amygdala ROI. C, cooperate; D, defect.

subjects who show stronger amygdala activation to CD outcomes should be more motivated to avoid future CD outcomes. Indeed, within the right amygdala ROI identified in the whole-brain analysis, there was a significant negative correlation between activation strength and number of CD outcomes that a subject experienced ($r = -.45$, $p < .05$; Figure 6). A similar trend was found for the anatomically defined amygdala ROI ($r = -.23$, $p > .05$). This finding of reduced amygdala activation in response to the emotionally arousing CD outcome in high-psychopathy subjects is consistent with findings from previous imaging studies showing a blunted amygdala response on emotion tasks in psychopathic individuals (Blair 2003; Gordon *et al.* 2004; Kiehl *et al.* 2001; Veit *et al.* 2002).

For the decision-making epoch of the task, the contrast of choice C – choice D revealed deactivation within rostral ACC and DLPFC. In other words, choosing to defect was associated with stronger activation in rostral ACC and DLPFC compared with choosing to cooperate. Rostral ACC has been implicated in response conflict caused by salient emotional stimuli (Bishop *et al.* 2004). DLPFC, however, is implicated in exertion of cognitive effort to overcome prepotent response tendencies (Miller and Cohen 2001). For example, in one recent study, subjects who received unfair offers in an ultimatum game activated both DLPFC as well as the anterior insula, a region that is responsive to aversive stimuli. Those who subsequently accepted those unfair offers and who presumably were able to override a prepotent emotional impulse to reject the offer showed stronger activation in DLPFC relative to anterior insula (Sanfey *et al.* 2003).

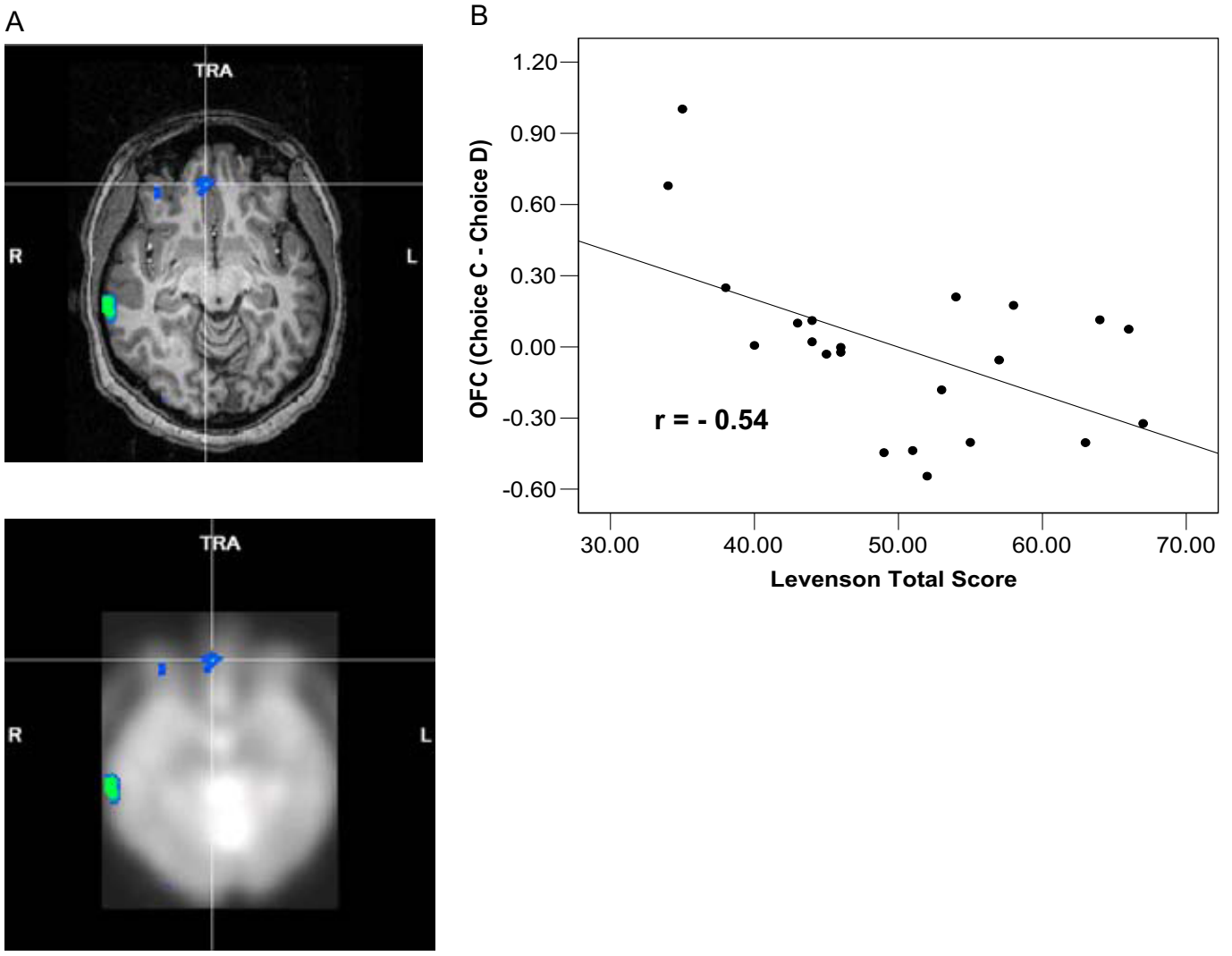

Figure 7. Correlations with psychopathy scores during the choice epoch. (**A**) Negative correlation within orbitofrontal cortex displayed on both a structural and an echo planar image. (**B**) Accompanying scatterplot.

Another study showed that DLPFC and ACC are involved in difficult personal moral decisions, particularly when those decisions involve violating the rights of others (Greene *et al.* 2004). According to the model of Greene *et al.* (2004), these decisions involve conflict between an evolutionarily older socioemotional system that drives people to disapprove of personal moral violations and a newer, countervailing system involved in abstract reasoning and cognitive control that can serve to override the socioemotional system in some cases. In this model, ACC activation is a neural correlate for the conflict inherent in the decision, and DLPFC is involved in the abstract reasoning and cognitive control processes. Our data can be interpreted usefully within this framework. Our subjects activate DLPFC and ACC when choosing to defect, suggesting that cooperation may be their prepotent emotionally biased response, which they can override with effortful cognitive control. Further, the observed correlations with psychopathy within these regions suggest that subjects scoring higher in psychopathy are less conflicted when defecting and require less cognitive control to do so.

Analysis of activation within OFC during decision making provides further evidence that cooperation is the prepotent emotional response of subjects who score low in psychopathy. OFC is proposed to activate the emotional states that are necessary for normal decision making. Patients with lesions in OFC have difficulty making appropriate decisions (Bechara 2004) and often develop some personality characteristics similar to those of psychopathy, such as dampening of emotional experience and reactions, disturbances in goal-directed and social behavior, and lack of insight into the inappropriateness of their behavior (Tranel 2002). In our study, only low-psychopathy subjects showed stronger activation within OFC when choosing to cooperate versus choosing to defect, suggesting that cooperation is the prepotent emotionally biased response for low- but not high-psychopathy subjects. It is important to note that the negative correlation between OFC and DLPFC activity (Figure 5) further suggests that stronger emotional biases toward cooperation (in OFC) require greater engagement of cognitive control (in DLPFC) to overcome this bias when choosing defection. This case describes low-psychopathy subjects, whereas high-psychopathy subjects who lack emotional biases toward cooperation (in OFC) would not require cognitive control (in DLPFC) to defect.

If OFC drives cooperation in low-psychopathy subjects, what neural systems might drive cooperation in high-psychopathy subjects? Our data are consistent with the possibility that in contrast to low-psychopathy subjects, high-psychopathy subjects have a weak emotional bias toward defection (stronger OFC activation for choice D versus choice C) that they can overcome through effortful cognitive control (DLPFC activation for choice C ≥ choice D).

If the emotional biases that motivate cooperation in low-psychopathy subjects are absent in high-psychopathy subjects, what is the specific rationale for cooperation among the latter? Analogous to the moral-reasoning study of Greene et al, one possibility is that high-psychopathy subjects exert effortful cognitive control (in DLPFC) to opt for a morally appropriate action, placing collective above individual interests by cooperating. An alternative possibility is that they reason their way to the conclusion that cooperation is in their best long-term self-interest. In this regard, the findings of McClure *et al.* (2004) are of particular interest. Those investigators showed that the relative balance between DLPFC and limbic activation, including OFC, predicted whether subjects would choose an immediate monetary reward or a larger reward to be delivered at a later time (McClure *et al.* 2004). In particular, greater DLPFC to limbic activity was associated with delayed gratification. Our subjects who score higher on psychopathy fit this pattern in that they show stronger DLPFC than OFC activation when opting for cooperation, a choice that involves trading off immediate for delayed benefits. Although psychopaths generally have been found to exhibit difficulties with delaying gratification in laboratory paradigms, it is important to remember that our high-psychopathy subjects, who were recruited from a university community, presumably are high functioning. As a consequence, it may not be surprising that they manage to cooperate and delay gratification. Our data suggest that when they do so, they exhibit stronger activation in DLPFC relative to OFC. However, our low-psychopathy subjects manage to make the same decision with the opposite pattern of activation, namely relatively stronger OFC than DLPFC activation. According to the model proposed by McClure et al, this would mean that cooperating has an immediate reward for low-psychopathy subjects, independent of the monetary payoff that it yields in the long-term. In other words, because of our tendency to prefer immediate over delayed rewards and an imperfect ability to override this tendency in the interest of delayed gratification, evolution has endowed human beings with the capacity to experience cooperation, in and of itself, as rewarding in the here and now (Rilling *et al.* 2002).

These findings are consistent with the notion that doing someone a favor or more specifically, cooperating in the PD game, can be based on either emotional (OFC) or strategic (DLPFC) considerations. That is, one can reason one's way to the conclusion that cooperating is the best long-term strategy, or one can rely on social emotions to guide adaptive decision making (Frank 1988; Trivers 1971). That these emotions are necessary for adaptive decision making, above and beyond strategic calculations is suggested by the fact that high-psychopathy subjects frequently defect out of mutually cooperative social interactions which, although beneficial in the short term, will in most cases run counter to long-term self-interest. Thus, subjects scoring higher on psychopathy may base their decision to cooperate on cognitive or strategic considerations that involve DLPFC activation during decision making, whereas subjects scoring lower on psychopathy tend to use emotionally guided decision making that is mediated by OFC.

Finally, we found only one significant correlation between self-reported emotional responses to various game outcomes and psychopathy scores. This was a significant negative association between Levenson total psychopathy scores and ratings of trust in response to CC outcomes for female subjects. A possible explanation for the lack of additional significant correlations is that individuals scoring high in psychopathy within this sample have a concept of which emotions they should be feeling during certain outcomes, so they tend to provide the socially correct answer when asked to report their emotions. Consistent with this possibility, Cleckley (1976) described the psychopath as one who does not understand matters of emotional significance, yet "can repeat the words and say glibly that he understands." Others have questioned the accuracy of self-report data on emotions in general (Ericcson and Simon 1980).

In summary, we observed several neural and behavioral correlates of psychopathy in the context of an iterated PD-game social interaction. Subjects reporting higher levels of psychopathy, particularly males, more often chose to defect and also were more likely to defect out of mutually cooperative social interactions in the PD game, effectively opting for an immediate payoff that entailed a long-term cost. This finding is of interest in light of psychopaths' reported weak impulse control and frequent failure to form long-lasting social bonds. High-psychopathy subjects also experienced more CD outcomes and showed less amygdala activation in response to such outcomes, implying deficits in aversive conditioning that manifested as a failure to learn to avoid these outcomes. Analyses of the decision-making epoch suggests that low-psychopathy subjects are characterized by emotional biases toward cooperation, represented in OFC, that only can be overcome with cognitive effort, which is represented in DLPFC, resulting in emotionally based conflict, represented in rostral ACC. In contrast, high-psychopathy subjects are characterized by weak emotional biases toward defection, represented in OFC, that must be overcome with cognitive effort, represented in DLPFC, to cooperate.

These results largely are consistent with a recent model of psychopathy proposed by Blair (2005; integrated emotion systems [IES] model), in which amygdala dysfunction causes conditioning deficits that lead to both impaired stimulus–punishment associations, which manifests as an increased frequency of CD outcomes, and the absence of prepotent biases toward minimizing the distress of others, which manifests as a lack of orbitofrontal activation when choosing cooperate. These results also are consistent with the observation that in contrast to other primates, many human beings are predisposed toward cooperation with nonrelatives, but observed patterns of human cooperation depend upon the interaction of both altruistic and selfish individuals (Fehr and Fischbacher 2003).

The extent to which the findings reported here can be generalized to more severely affected samples that presumably are characterized by higher levels of psychopathy (e.g., prisoners, severe substance abusers) is unclear. Although some of the laboratory-based deficits observed in prison psychopaths, such as poor passive-avoidance learning, also have been observed in noninstitutionalized (e.g., undergraduate) samples (e.g., Lynam *et al.* 1999), further investigation is needed to determine whether the present results apply to clinical samples. Moreover, the gender differences in correlations that were observed here should be interpreted with caution pending replication in independent samples. Finally, it also is unclear why behavioral correlations were observed only for one of two psychopathy measures (the Levenson psychopathy measure), especially in

light of evidence that the PPI possesses solid construct validity in undergraduate samples (Lilienfeld and Andrews 1996; Lilienfeld and Fowler 2006). Further research using multiple operationalizations of psychopathy will be needed to clarify potential differences in the behavioral and neuroimaging correlates of these measures.

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