Neural and cognitive characteristics of extraordinary altruists

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Altruistic behavior improves the welfare of another individual while reducing the altruist's welfare. Humans' tendency to engage in altruistic behaviors is unevenly distributed across the population, and individual variation in altruistic tendencies may be genetically mediated. Although neural endophenotypes of heightened or extreme antisocial behavior tendencies have been identified in, for example, studies of psychopaths, little is known about the neural mechanisms that support heightened or extreme prosocial or altruistic tendencies. In this study, we used structural and functional magnetic resonance imaging to assess a population of extraordinary altruists: altruistic kidney donors who volunteered to donate a kidney to a stranger. Such donations meet the most stringent definitions of altruism in that they represent an intentional behavior that incurs significant costs to the donor to benefit an anonymous, nonkin other. Functional imaging and behavioral tasks included face-emotion processing paradigms that reliably distinguish psychopathic individuals from controls. Here we show that extraordinary altruists can be distinguished from controls by their enhanced volume in right amygdala and enhanced responsiveness of this structure to fearful facial expressions, an effect that predicts superior perceptual sensitivity to these expressions. These results mirror the reduced amygdala volume and reduced responsiveness to fearful facial expressions observed in psychopathic individuals. Our results support the possibility of a neural basis for extraordinary altruism. We anticipate that these findings will expand the scope of research on biological mechanisms that promote altruistic behaviors to include neural mechanisms that support affective and social responsiveness.

psychopathy | organ donation | prosocial behavior

Altruistic behaviors reduce the immediate fitness of the altruist to improve the fitness of another individual (1). As such, altruism has long been seen to pose singular problems for evolutionary theory (2). This is particularly true in the case of rare and extraordinary instances of altruistic behavior such as altruistic organ donation, in which an altruistic donor incurs significant costs to benefit a genetically unrelated, anonymous stranger; this is a behavior that dominant biological models of altruism such as reciprocity and inclusive fitness cannot obviously explain (3). However, even extraordinary acts of altruism may have a biological basis: At the level of the gene, strong evidence supports polygenic mediation of altruistic behavior as well as specific genetic variants that may support increased altruism in humans (4–7).

At the level of the organism, neural endophenotypes that may support extraordinary altruism have not been identified, although possible mechanisms can be inferred from studies of highly antisocial individuals, such as psychopaths. Psychopathy is a heritable developmental disorder characterized by an uncaring nature, antisocial and aggressive behavior, and deficient prosocial emotions such as empathy, guilt, and remorse (8). Psychopaths exhibit consistent patterns of neuroanatomical and functional impairments, such as reductions in the volume of the amygdala and in the responsiveness of this structure to fear-relevant stimuli (9–13). These deficits may underlie the perceptual insensitivity to fearful facial expressions and other fear-relevant stimuli observed in this population (14, 15). Given emerging consensus that psychopathy is a continuously distributed variable within the general population (16) and that psychopaths represent one extreme end of a caring continuum, we hypothesized that extraordinary altruism may represent the opposite end of this continuum and be supported by neural and cognitive mechanisms that represent the inverse of psychopathy; in particular, increased amygdala volume and responsiveness to fearful facial expressions. We focused on responses to fearful facial expressions because abundant empirical evidence supports the relationship between individual differences in neural and behavioral responsiveness to fearful expressions and both psychopathy and altruism (10, 11, 14, 15, 17). In contrast, the evidence that individual differences in responses to other expressions, such as sadness, predict these outcomes is relatively weak (14, 15, 17). We tested this hypothesis in a rare population of extraordinary altruists (altruistic kidney donors) and matched controls (Table 1), using structural and functional magnetic resonance imaging (fMRI) to identify whether individuals who engage in costly acts of extraordinary, life-saving altruism can be distinguished from typical individuals by specific anatomical or functional neural features.

We conducted a face-emotion neuroimaging paradigm directly replicating one that has identified amygdala hypoactivation in psychopathy (9, 18). During fMRI scanning, altruists and controls viewed fearful, angry, and neutral facial expressions drawn from

Significance

Altruism, and particularly costly altruism toward strangers, such as altruistic kidney donation, represents a puzzling phenomenon for many fields of science, including evolutionary biology, psychology, and economics. How can such behavior be explained? The propensity to engage in costly altruism varies widely and may be genetically mediated, but little is known about the neural mechanisms that support it. We used structural and functional brain imaging to compare extraordinary altruists, specifically altruistic kidney donors, and controls. Altruists exhibited variations in neural anatomy and functioning that represent the inverse of patterns previously observed in psychopaths, who are unusually callous and antisocial. These findings suggest extraordinary altruism represents one end of a caring continuum and is supported by neural mechanisms that underlie social and emotional responsiveness.

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Table 1. Participant characteristics

Variable	Altruists (n = 19), n (%)	Controls (n = 20), n (%)	P
Sex			
Women	7 (37)	11 (55)	0.26
Men	12 (63)	9 (45)	
Handedness			
Right	18 (95)	19 (95)	0.99
Left	1 (5)	1 (5)	
Race			
White	18 (95)	17 (85)	0.32
Black	—	2 (10)	
Asian	1 (5)	—	
Other	—	1 (5)	
Education level			
≥4-y degree	12 (63)	16 (80)	0.24
Household income*			
>$60,000	13 (68)	8 (40)	0.27
IQ, mean (SD)	115.7 (11.1)	112.0 (13.1)	0.34
Age, y, mean (SD)	46.3 (8.7)	44.8 (6.4)	0.52

*Four controls did not report their household income.

the Pictures of Facial Affect series (19), presented in randomized order, in the context of an implicit emotion processing task (9, 20). After fMRI scanning, participants underwent anatomical MRI scanning and neurocognitive testing that included a measure of face-emotion recognition in which participants viewed the same emotional expressions presented during scanning, in addition to disgust, happiness, sadness, and surprise expressions, and indicated the expressed emotion in each. Finally, all participants completed a personality assessment of psychopathy (21) as well as assessments of empathy (22) and mentalizing (23) (see *Materials and Methods*).

To analyze neuroimaging data, we conducted a region-of-interest analysis and applied a double contrast (fearful > neutral expressions, altruists > controls) to activation in right and left amygdalae. In right amygdala [xyz = 31, 1, −23; $P < 0.05$ $_{\text{small volume corrected (SVC)}}$], altruists exhibited increased blood oxygen level-dependent (BOLD) signal in response to fearful facial expressions compared with controls, as hypothesized (Fig. 1*A*). No similar cluster was identified in the left amygdala. We next extracted parameter estimates of BOLD signal from the functionally defined right amygdala cluster to compare amygdala responsiveness with accurate emotion recognition. Across the sample, amygdala responsiveness to fearful expressions predicted recognition accuracy for these expressions [r (33) = 0.49; $P < 0.005$] (Fig. 1*B*); this was the only expression for which the correlation with extracted signal value survived Bonferroni correction for multiple comparisons. Results of a whole-brain analysis (fear > neutral, altruists > controls) for responses to fearful expressions yielded only a single other region in which altruists exhibited increased BOLD signal in comparison with controls: right lateral prefrontal cortex ($P < 0.001_{\text{uncorrected}}$; xyz = 59, 36, 9, Brodmann area 46). No clusters were identified in which controls exhibited increased BOLD signal relative to altruists. Region-of-interest analyses examining BOLD responses to anger (anger > neutral expressions, altruists > controls) in right and left amygdalae yielded no comparable group differences, parallel to previous investigations of psychopathy (9). Instead, two clusters in the left amygdala were identified in which controls exhibited an increased BOLD signal relative to altruists in response to anger ($P < 0.05$ $_{\text{SVC}}$; xyz = −20, −7, −22; −27, −4, −29). The results of a repeated-measures ANOVA identified a pattern of emotion recognition in the behavioral task that paralleled imaging results. A group (altruists, controls) × emotion (anger, fear) interaction [$F(1, 33) = 5.71$; $P < 0.05$] was observed, whereby altruists recognized fear (mean = 0.48; SD = 0.20) relatively better than controls (fear mean = 0.40; SD = 0.19), whereas the same was not true for anger [altruists mean = 0.45 (SD = 0.11); controls mean = 0.52 (SD = 0.15)] (Fig. 1*C*). (Pairwise comparisons did not reveal significant group differences in recognition of these expressions, however; Ps > 0.05).

Structural brain images were acquired using a high-resolution T1-weighted image, and then segmented using the FreeSurfer image analysis suite. We exported observer-independent volume estimates of segmented brain regions from FreeSurfer and then performed a multiple regression analysis using the volumes of left and right amygdalae while controlling for total intracranial volume to account for observed group differences; altruists' mean intracranial volume exceeded that of controls by 9.1% (mean difference = 129,396 mm^3; $P < 0.05$). Results showed group differences in right amygdala volume ($t = 2.04$; $P < 0.05$), but not left amygdala volume ($t = 1.64$; $P > 0.10$). Mean right amygdala volume of altruists was 1,782 mm^3 (SD = 137) compared with 1,648 mm^3 (SD = 152) for controls, corresponding to a volume difference of 8.1% (Fig. 2 *A* and *B*). No comparable differences were observed in adjacent subcortical structures, including right ($t = 1.52$; $P > 0.10$) and left ($t = 0.66$; $P > 0.10$) hippocampus or right ($t = -0.25$; $P > 0.10$) and left ($t = -0.71$; $P > 0.10$) caudate. No correlation between amygdala volume and emotion recognition was identified.

We next tested the hypothesis that altruists were not merely particularly unlikely to obtain low scores in amygdala reactivity to fearful expressions, amygdala volume, and recognition of fearful expressions but, rather, were unusually likely to obtain scores in the high end of the distribution on these variables. This hypothesis would suggest that altruists in fact represent a distinct subset of the population at the opposite end of the distribution from psychopathic individuals, rather than simply reflecting the normal population minus those relatively more psychopathic individuals. To do this, we first calculated normalized (Z) scores for all participants based on the mean and SD scores for these three variables in the control group, which were then averaged. The resulting composite Z scores thus enabled a determination of how altruists' scores were distributed compared with the distribution expected in a population of typical adults. Compared with controls, whose average Z score was 0, 18/19 altruists (95%) scored above 0, indicating that nearly all altruists' scores on the constituent measures are in the top half of the distribution of typical adults. Using a more stringent cutoff of $Z = 0.50$, a cutoff exceeded by only 4/20 (20%) controls, we found that 14 altruists (74%) exceeded this threshold, representing a significant difference at the upper end of the distribution [χ^2 (1) = 11.30; $P < 0.001$]. This is consistent with altruists being overrepresented at the high end of the distribution, rather than only being underrepresented at the low end. Next, we conducted a Levene's test for equality of variance on altruists' and controls' composite scores and assessed skewness in the distribution of both samples. If altruists simply represented the upper half of the distribution of controls, we would predict reduced variance in their scores relative to controls' scores, as well as increased skewness. Results of the Levene's test suggest similar variance across samples [$F(1, 37) = 0.16$; $P = 0.70$]. Similarly low estimates of skewness were obtained in controls (skewness = 0.24) and altruists (skewness = 0.22). Together, these results support the conclusion that our sample of altruists represents a distinct subset of individuals.

We further assessed group differences in personality indices of psychopathy, empathy, and mentalizing. No group differences in self-reported total psychopathy scores were observed [t (37) = 1.52; $P > 0.10$]. Considering the major component scores separately, altruists scored lower in Self-Centered Impulsivity (mean = 118.5; SD = 15.5) than controls [mean = 133.4; SD = 22.1; t (37) = 2.43; $P < 0.05$], whereas no group difference was observed for Fearless Dominance [t (37) = 0.07; $P > 0.10$]. This pattern is consistent with prior findings that Self-Centered Impulsivity more reliably predicts behavioral outcomes. Differences in this

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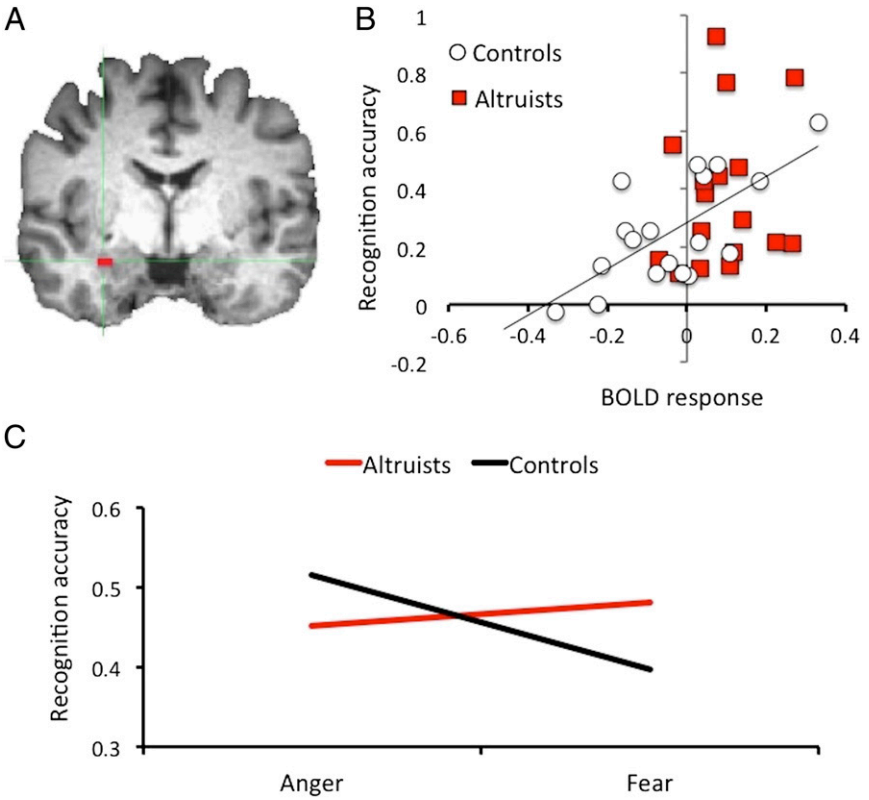

Fig. 1. Group differences in right amygdala BOLD signal and recognition accuracy in response to fearful emotion facial expressions. (*A*) Altruists show increased BOLD signal in right amygdala (radiological orientation) compared with controls while viewing fearful facial expressions. (*B*) Parameter estimates from right amygdala BOLD signal were extracted and compared with fear recognition accuracy from the face-emotion recognition paradigm. Scatterplot shows the relationship [r (33) = 0.49; $P < 0.005$] between strength of BOLD signal and fear recognition accuracy. (*C*) Relative to controls, altruists demonstrate superior recognition accuracy for fear, but not anger [$F(1, 33) = 5.71$; $P < 0.05$].

component were primarily accounted for by differences in the Blame Externalization [t (37) = 2.53; $P < 0.05$] and Machiavellian Egocentricity [t (37) = 2.08; $P < 0.05$] subscales of Self-Centered Impulsivity. Consistent with the results of previous laboratory studies of altruistic behavior (17), no group differences were observed in self-reported empathy [t (37) = 0.01; $P > 0.05$] or mentalizing [t (36) = 0.06; $P > 0.05$].

In sum, our findings suggest that individuals who have performed an act of extraordinary altruism can be distinguished from healthy controls by increased right amygdala volume, as well as heightened responsiveness in right amygdala to fearful facial expressions, which may support enhanced recognition of these expressions. These patterns are consistent with previous suggestions of a biological basis for individual differences in altruistic behavior (6, 7) and with previous findings that sensitivity to fearful facial expressions predicts increased altruism in the laboratory (17). Nonverbal distress cues such as facial expressions of fear are strong elicitors of compassion and altruism (24, 25), supporting the interpretation that individuals who are highly sensitive to these cues may be unusually motivated to respond altruistically to others' distress. It should be emphasized, however, that the mechanisms we have identified are unlikely to represent a complete explanation for altruistic kidney donation, given the extreme rarity of this phenomenon, and given the overlapping distributions we observed for the variables we measured. Acts of extraordinary altruism are likely to reflect a combination of the neurocognitive characteristics identified here, along with other individual- or community-level variables (26).

Our findings also support our hypothesis that extraordinary altruists may represent the antithesis of highly psychopathic

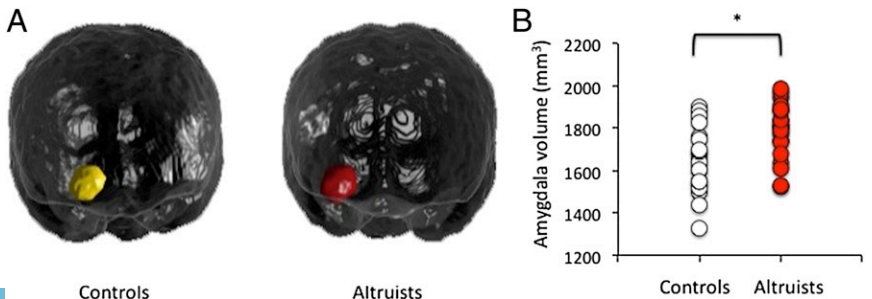

Fig. 2. Group differences in right amygdala volume, controlling for total intracranial volume. Images presented in radiological orientation (right = left).

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individuals, in whom reduced amygdala responsiveness to, and impaired behavioral recognition of, fearful facial expressions has previously been observed (9, 14, 15, 20), as has reduced amygdala volume (12, 13). As a result, our data reveal support for the possibility of a continuum of caring anchored at the low end by highly psychopathic individuals and at the high end by highly altruistic individuals.

This study focused on how participants respond to others' fear because extensive empirical evidence links responses to fearful expressions with both psychopathy and altruism (10, 11, 14, 15, 17). These expressions also appear particularly likely to elicit caring responses in perceivers, perhaps because fear is a relatively intense expression associated with urgent need and because fearful expressions possess infantile appearance characteristics such as wide eyes and high brows that eliciting caring responses from perceivers (24, 27). However, future research might explore the relationship between altruism and neural and behavioral responses to a wider array of cues, such as pain or sadness expressions, body postures, or vocalizations. In theory, responses to sadness cues may also be linked to altruism (28).

Our findings reinforce the importance of considering the distinct etiological pathways that can result in antisocial behavior. In particular, it is important to distinguish between antisociality that results from psychopathy, which is specifically associated with reduced empathy and concern for others, as well as with reduced sensitivity to others' fear and distress (9, 14, 15, 20), and antisociality that results from any of a variety of other factors, such as impulsivity or trauma exposure, that are not closely related to empathy. Two previous studies, including a large twin study (29) and a study of risk-takers (30), reported that altruistic and antisocial tendencies were largely unrelated. In the twin study, altruism and antisociality were uncorrelated, and in the study of risk-takers, antisocial and prosocial risk-takers were characterized by distinct discriminant functions. However, both studies focused on general antisociality. Since these studies were conducted, clear evidence has emerged for the importance of distinguishing antisocial individuals with psychopathic traits from those whose antisociality reflects distinct mechanisms (8). Our findings suggest that highly altruistic individuals may represent the inverse of psychopathic individuals, but the patterns we observed may be unrelated to the patterns one would observe in other antisocial populations. The contrast may even be more specific, as emerging evidence suggests psychopathy itself may be a multidimensional rather than a unidimensional construct (16). Extraordinary altruism may represent the inverse of only some components of psychopathy, but not other components such as social dominance or impulsivity. Interestingly, the subscales within the Self-Centered Impulsivity component that best distinguished between altruists and controls (Machiavellian Egocentricity and Blame Externalization) have also been found to strongly predict lifetime antisocial behavior (31).

In addition, our findings may support suggestions that demand characteristics may render self-report measures of altruism and empathy less sensitive to individual differences in these constructs than physiological or surreptitious measures (25). Unlike the Psychopathic Personality Inventory-Revised (PPI-R), which was explicitly developed to circumvent problems with self-report scales such as social desirability biases (21), the Interpersonal Reactivity Index (IRI) and other self-report empathy scales are relatively transparent measures that may be prone to biased responding, which may help explain why they are not always reliable predictors of individual differences in altruistic or antisocial behavior (17, 32).

Altruistic kidney donation is an exceedingly rare phenomenon, and the neurocognitive basis of this or any other form of extraordinary altruism has not previously been assessed. Because dominant self-serving explanations for altruism, including kin selection, reciprocity, or adherence to social norms, do not explain costly unreciprocated altruism toward anonymous nonkin in a straightforward way (33), altruistic donors' actions have been variously described as pathological or even superhuman (34). The present findings suggest, instead, that extraordinary altruism emerges via mechanisms that are consistent with existing biological and psychological theories. In particular, extraordinary altruism in humans may be associated with variations in established neurocognitive phenomena that support social responsiveness and caring for others' welfare, especially enhanced sensitivity to others' fear. Because fearful facial expressions convey both vulnerability and infantile qualities (27), this conclusion is consistent with theories that the capacity for altruistic responding is rooted in the ancient mammalian neural architecture designed to promote the care of vulnerable offspring (35). These theories, and the present findings, are not incompatible with established theories regarding the evolution of altruistic behavior such as kin selection and reciprocity but, rather, widen the range of available explanations for the biological basis of altruism.

Materials and Methods

Participants. Thirty-nine healthy adults between 23 and 56 y old (mean age = 45.51 y; SD = 7.54) took part in this study for monetary payment (see Table 1 for all demographic characteristics). They included 19 altruistic kidney donors (7 women) recruited nationally using mailings and electronic advertisements through local and national transplant organizations. Altruists residing more than a 2-h drive from the university were provided with airfare and up to 2 nights' lodging. All altruists had donated a kidney to a stranger (an individual unknown to them personally at the time of donation). Sixteen altruistic donors were nondirected donors for whom the recipient was anonymous at the time of donation. The remaining three directed their donations to a specific individual who was known to them at the time of donation but whose need for a kidney they had learned about through, for example, a flier or Internet posting. All donations were verified through independent sources, including hospital or transplant center records or local or national media reports. Using data obtained from the Organ Procurement and Transplantation Network, which is administered by the United Network of Organ Sharing under contract with the US Department of Health and Human Services, we confirmed that altruists recruited for this study were representative of the national population of altruistic donors in terms of sex and race (exact ages are not available for the national sample). In addition, 20 healthy volunteers (11 women) were recruited from the local community using fliers, online advertisements, and electronic participant databases. Exclusion criteria for all participants included current use of psychotropic medication, history of head injury or neurological illness, IQ < 80 (as assessed using the Kaufman Brief Intelligence Test-Second Edition) (36), and pregnancy or other contraindications to safe MRI scanning, including metal fragments or implants. Controls were excluded if they reported having ever volunteered to donate an organ to any individual (not including consenting to become a deceased organ donor). All study procedures and tasks were approved by the Internal Review Board at Georgetown University in Washington, DC, and all participants provided written informed consent before testing.

Procedures. All interested volunteers initially completed a 90-min online screening measure assessing stated exclusion and inclusion criteria and demographic variables. After preliminary screening, eligible volunteers were then screened by telephone to confirm their eligibility as altruists or controls. Researchers then coordinated altruists' travel to and lodging at the Georgetown University campus to enable them to complete all behavioral, neurocognitive, and MRI testing on-site. To ensure groups were matched for basic demographic criteria, eligible controls completed additional laboratory screening including IQ, income, education, psychological history, medication use, and MRI compatibility before MRI scanning (groups did not significantly differ in terms of these variables; $P > 0.05$ for all measures; see Table 1). After final confirmation of eligibility, controls then completed neurocognitive tasks and MRI scanning in a final visit.

Neuroimaging Task and Acquisition. We acquired MR images with a 3T Siemens Tim Trio scanner (Siemens Medical Solutions) and a 12-channel phased-array head coil. Functional data were collected using a T2*-weighted echo-planar imaging sequence (56 3.0-mm transversal slices; 64 × 64 matrix; repetition time, 3,000 ms; echo time, 30 ms; field of view, 192 mm; 3.0 × 3.0 × 3.0-mm voxels). The first four repetition times (TRs) of each functional run were excluded from analysis to account for magnet stabilization. High-resolution

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T1-weighted anatomical images were also acquired (3D Magnetization Prepared Rapid Acquisition Gradient Echo; 176 1.0-mm axial slices; field of view, 250 mm; repetition time, 1,900 ms; echo time, 2.52 ms; 246 × 256 matrix).

During functional scanning, participants completed an implicit face-emotion processing task used in previous studies of children with conduct problems and psychopathic traits (9). Stimulus images included 10 male and female adults from the Pictures of Facial Affect series (19), who were shown displaying fearful, angry, or positive-neutral expressions. Fearful and angry expressions included full-intensity expressions and morphed expressions of 50% and 150% intensity levels. Positive-neutral stimuli were morphs of neutral and happy expressions (25% happiness). Neck, ears, and hair for all faces were masked, and faces appeared against a black background. Faces were presented in randomized order for 2,000 ms, followed by a 1,000-ms fixation cross. During the task, participants categorized the sex of each face, using a button-box response, such that the emotional component of the task remained implicit (9, 20). The four 5.5-min consecutive runs of the task each included 80 face trials and 20 jittered interstimulus interval trials.

Behavioral Tasks. After completing the neuroimaging task, participants were given a short (1–2 h) break, after which they completed a facial emotion recognition task. The emotion recognition task was adapted from paradigms used in similar populations (19). The task featured individual presentations of static faces from the Pictures of Facial Affect set expressing six basic emotions (anger, disgust, fear, happiness, sadness, and surprise) (19). Both full-intensity and 50% intensity versions of each expression were included. Participants therefore viewed 120 expressions total (6 expressions × 10 exemplars × 2 intensity levels), presented in randomized order. Each expression appeared for 2,000 ms and was followed by a screen that instructed participants to make a forced choice among responses corresponding to the 6 possible emotions. Responses were self-paced. Both response selections and latencies were recorded.

After the emotion recognition task, participants completed self-report based measures of psychopathy and empathy and a computerized mentalizing task. Psychopathy was measured using the PPI-R (21). The PPI-R is a 154-item self-report measure that assesses psychopathic traits dimensionally (16) and that demonstrates good criterion validity with file review-based clinical assessments of psychopathy (37). The PPI-R's primary subscales are Fearless Dominance and Self-Centered Impulsivity. Empathy was assessed using the IRI (22). The IRI is a self-report measure of empathy composed of four subscales: Perspective Taking, Fantasy, Empathic Concern, and Personal Distress. To assess mentalizing, participants completed the Reading the Mind in the Eyes Test (23). This test evaluates emotion perception accuracy via 36 presentations of eyes of actors. For each, participants choose the best-fitting affective description of the eyes from four preselected options.

Analysis of Neuroimaging Data. Functional data were preprocessed and analyzed according to the general linear model, using Analysis of Functional NeuroImages (38). The four runs of the task were concatenated, despiked, motion-corrected, and spatially smoothed using a 6.0-mm full-width half-maximum Gaussian filter. Functional data were aligned to the anatomical grid, transformed to the Talairach and Tournoux Atlas (39), and masked with an extents mask to account for motion artifacts and to exclude voxels without valid data at every TR for every run, helping to control for false activations. Eight regressors were created to model task events: fearful and angry expressions at each intensity (6 regressors), neutral expressions, and an error regressor of no interest for incorrect or invalid participant responses, as needed. Fixation trials were modeled implicitly; baseline was modeled by a first-order function, and motion artifacts were modeled using the six estimated rigid-body motion parameters. The train of stimulus events was then convolved with a gamma-variate hemodynamic response function. This resulted in normalized time series such that amplitude and regression coefficients represent a percentage signal change from the mean, producing our beta-coefficients and associated *t*-statistics for each voxel and regressor. Data were then analyzed according to our a priori hypotheses. With neutral faces modeling baseline, we performed two region-of-interest double-contrast analyses within right and left amygdalae, using Analysis of Functional NeuroImages to compare responses to 100% intensity emotions (fear > neutral, altruists > controls; anger > neutral, altruists > controls). Regions were anatomically defined based on the Talairach and Tournoux Atlas (39), using the Analysis of Functional NeuroImages draw-dataset plug-in. Parameter estimates were extracted from significant clusters of interest and compared with behavioral measures using SPSS.

Structural data were analyzed using the FreeSurfer image analysis suite (http://surfer.nmr.mgh.harvard.edu/). Individual subject data were segmented into white matter, gray matter, and cerebral spinal fluid, resulting in 70 cortical (35 per hemisphere) and 42 subcortical (17 per hemisphere plus eight midline structures) parcellations per subject. Volume estimations were extracted via FreeSurfer and exported into Excel. Using FreeSurfer's estimation of total intracranial volume, which takes into account the scaling required per subject for the transformation of data to the Talairach and Tournoux Atlas (39), we calculated left and right amygdala volumes. We used SPSS to conduct regressions modeling the proportional volumes, with Group as the outcome variable, to identify group differences in the volume of, respectively, right and left amygdala and comparison regions.

Analysis of Behavioral Data. Response accuracy and response times were measured during the neuroimaging task to identify any group differences in attention during the task. A repeated-measures ANOVA was performed to assess group differences in responding to fearful versus angry expressions, which were the expressions assessed during the neuroimaging task.

Emotion recognition accuracy in the behavioral task was assessed using an unbiased hit rate analysis calculated across expression intensity levels (17). This procedure determines accuracy by assessing both raw accuracy, or how frequently a stimulus is identified compared with how often it appears (hits divided by the number of stimuli of that type), and differential accuracy, or how frequently a response category is used correctly compared with how often it is used (hits divided by the total number of uses of that type of response). Then the difference between the resulting value and the accuracy that would be expected by chance is then computed, such that final scores represent above-chance accuracy, and the resulting value is arcsine transformed. The relationship between recognition of individual emotions and the results of our functional and structural imaging analyses were then assessed using Pearson's correlation analyses. Responses to the PPI-R, IRI, and Reading the Mind in the Eyes Test were scored according to standard requirements of each task to derive total score and subscale scores for each instrument. The threshold for all statistical tests was set at $P < 0.05$, two-tailed.

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