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Altruistic decisions following penetrating traumatic brain injury

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The cerebral correlates of altruistic decisions have increasingly attracted the interest of neuroscientists. To date, investigations on the neural underpinnings of altruistic decisions have primarily been conducted in healthy adults undergoing functional neuroimaging as they engaged in decisions to punish third parties. The chief purpose of the present study was to investigate altruistic decisions following focal brain damage with a novel altruistic decision task. In contrast to studies that have focused either on altruistic punishment or donation, the Altruistic Decision Task allows players to anonymously punish or donate to 30 charitable organizations involved with salient societal issues such as abortion, nuclear energy and civil rights. Ninety-four Vietnam War veterans with variable patterns of penetrating traumatic brain injury and 28 healthy veterans who also served in combat participated in the study as normal controls. Participants were asked to invest \$1 to punish or reward real societal organizations, or keep the money for themselves. Associations between lesion distribution and performance on the task were analysed with multivariate support vector regression, which enables the assessment of the joint contribution of multiple regions in the determination of a given behaviour of interest. Our main findings were: (i) bilateral dorsomedial prefrontal lesions increased altruistic punishment, whereas lesions of the right perisylvian region and left temporo-insular cortex decreased punishment; (ii) altruistic donations were increased by bilateral lesions of the dorsomedial parietal cortex, whereas lesions of the right posterior superior temporal sulcus and middle temporal gyri decreased donations; (iii) altruistic punishment and donation were only weakly correlated, emphasizing their dissociable neuroanatomical associations; and (iv) altruistic decisions were not related to post-traumatic personality changes. These findings indicate that altruistic punishment and donation are determined by largely non-overlapping cerebral regions, which have previously been implicated in social cognition and moral experience such as evaluations of intentionality and intuitions of justice and morality.

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Abbreviation: TBI = traumatic brain injury

Introduction

Altruistic, or costly, punishment and helping lie at the core of interpersonal cooperation in all human societies (Henrich *et al.*, 2006), and, by extension, of legal codes and norms (Green and Groff, 2003). Altruistic punishment and helping entail costs to punish norm violators and support to norm enforcers, even under anonymity in which no reputation gains are at stake (Hoffman, 2014). The development of new experimental paradigms, which are usually designed as economic games (Fehr and Camerer, 2007) and hypothetical crime scenarios (Robinson and Kurzban, 2007), has greatly advanced the experimental investigation of altruistic decisions in their own right (Krueger and Hoffmann, 2016).

Moral motivations lie at the roots of altruistic behaviour (de Oliveira-Souza *et al.*, 2016). Studies using non-invasive virtual lesion methods, particularly transcranial direct-current stimulation and transcranial magnetic stimulation as well as lesion mapping, have provided important clues on the brain regions that are necessary for moral choices (Tassy *et al.*, 2012). Transcranial direct-current stimulation or transcranial magnetic stimulation using two-person economic games have shown that the right dorsolateral prefrontal cortex is necessary for making choices that maximize one's reputation (Knoch *et al.*, 2009) and for social norm compliance under the threat of punishment (Ruff *et al.*, 2013). These findings are consistent with the role of the right dorsolateral prefrontal cortex in reducing subjective values associated with the pursuit of immediate self-interests (Hare *et al.*, 2009). Decisions to uphold social norms in these experiments do not necessarily rely on moral motivation, because these decisions could also be driven by self-regarding motivations such as avoidance of punishment, preserving one's social reputation, and anger elicited by challenges to self-interests. By contrast, interference with medial frontopolar cortex function reduces guilt and increases deceitful behaviours, such as lying in mock crime interrogations (Karim *et al.*, 2010). In patients with frontotemporal dementia, degeneration of the frontopolar cortex and septal region led to impairments of guilt and compassion on an experimental moral sentiment task; impairment of 'other-critical' feelings (anger/indignation and disgust), in contrast, resulted from degeneration of the amygdala and posterior dorsomedial prefrontal cortex (Moll *et al.*, 2011). A recent study Zhu *et al.* (2014) showed that damage to the (mostly left) dorsolateral prefrontal cortex, but not to the orbitofrontal cortex, impaired honesty concerns. The economic decision task used in that study enabled the separation of honesty concerns from altruistic preferences *per se*: whereas all groups were equally altruistic in sharing money with anonymous participants in a dictator game, dorsolateral prefrontal cortex patients were less concerned about honesty and more indulgent in sending 'false messages'. These results highlight the distinct roles of the dorsolateral and medial prefrontal cortex in a specific moral motivation—abiding to honesty—and their interplay in self-control (Hare *et al.*, 2009; Hayashi *et al.*, 2013) and value computations (Prévost *et al.*, 2010). Taken together, these studies point to the importance of different sectors of the dorsolateral and medial prefrontal cortices for prosocial motivations and for honesty, self-reputation concerns and third party punishment (Coricelli *et al.*, 2005; Delgado *et al.*, 2005).

The neurological underpinnings of altruistic decisions have mostly been studied in normal volunteers, few studies having been conducted in brain-damaged patients (Haushofer and Fehr, 2008; Glass *et al.*, 2016). Notably, none of them has investigated anonymous third party punishment and reward towards societal causes. Patient studies can uniquely contribute causal information on the underpinnings of altruistic decisions and, by extension, to intuitions of justice (Rorden and Karnath, 2004). In this study, we investigated the performance of a large cohort of Vietnam War veterans with focal frontal, temporal and parietal injuries on a simple altruistic decision task. We hypothesized that anonymous costly punishments and donations toward organizations that back up salient societal causes such as women's rights, euthanasia, and the use of nuclear energy, would be altered by damage to different cerebral regions that have previously been implicated in social cognition and, more particularly, in intuitions of morality and justice.

Materials and methods

Participants

Participants were male combat veterans recruited from the WF Caveness Vietnam Head Injury Study Registry during phase 4, conducted between 2009 and 2012 at the National Institute of Neurological Disorders and Stroke at the National Institutes of Health in Bethesda, Maryland (Raymont *et al.*, 2011). Given its sample size and wealth of pre-injury and post-injury data, the Vietnam Head Injury Study provides a unique opportunity to investigate brain–behaviour relationships with lesion-mapping methods. Our sample consisted of 94 veterans with penetrating traumatic brain injury (TBI) and 28 controls who also served in combat in Vietnam but had no history of brain injury or other neurological disorders. All penetrating TBI and controls were recruited from the Vietnam Head Injury Study. The groups were matched on key demographic variables including age, sex, education, and war experience. Few participants in either group reported a diagnosis of substance abuse of cannabis, anxiolytics, stimulants, opioids, cocaine, phencyclidine, or other substances. All penetrating TBI participants were retired after their tour of duty ended or if injury mandated it; controls spent time in Vietnam but almost all retired shortly afterward. At phase 4, patients with penetrating TBI were evaluated ~40 years after injury, so it can be assumed that their lesions were stable because most of the compensatory mechanisms observed after penetrating TBI had likely occurred within the 3 years that follow the injury. Their screening at the time of phase 4 did not reveal any neurodegenerative diseases or additional lesions. Table 1 reports penetrating TBI and controls demographics and results from selected descriptive neuropsychological tests that were administered over a 5-day testing period. The Institutional Review Board at the National Institute of Neurological Disorders and Stroke in Bethesda approved all procedures and participants and caregivers provided written consent before inclusion in the study.

Table 1 Results of controls and patients

	Penetrating TBI	Controls
Number of participants	94	28
Age (years)	63.0 ± 2.4	63.0 ± 4.1
Education (years)	14.7 ± 2.1	15.1 ± 2.3
Handedness (L/RL/R)	16/2/76	2/3/23
Altruistic Decision Task		
Savings	40 ± 9	41 ± 8
Donations	13 ± 6	14 ± 7
Punishments	07 ± 5	06 ± 5
Neuropsychological results		
Global Cognitive Status and Intelligence		
Mini-Mental State Examination (current)	**28.7 ± 1.8**	**29.5 ± 0.6**
Wechsler Abbreviated Intelligence Scale		
Full Scale	110 ± 21	114 ± 11
Verbal	**106 ± 13**	**113 ± 11**
Performance	105 ± 13	111 ± 12
National Adult Reading Test	**103 ± 12**	**98 ± 12**
Executive Function		
Delis-Kaplan Sorting Test		
Total Free		
Sorting	**09 ± 2**	**10 ± 2**
Explanation	**34 ± 10**	**39 ± 9**
Total Recognition	**30 ± 11**	**35 ± 11**
Delis-Kaplan Verbal Fluency		
Letter	**32 ± 12**	**38 ± 11**
Category	**35 ± 8**	**40 ± 10**
Category Switching	11 ± 3	12 ± 4
Neuropsychiatric results		
NEO Personality Inventory		
Neuroticism	47 ± 11	51 ± 15
Extroversion	49 ± 12	44 ± 11
Openness	46 ± 10	47 ± 11
Agreeableness	51 ± 10	49 ± 12
Conscientiousness	50 ± 11	50 ± 12
Barratt Impulsiveness Scale	61 ± 10	63 ± 12

Results expressed as means ± 1 standard deviation. Significant differences in highlighted in bold (Mann-Whitney: $P < 0.05$, two-tailed).
L = left-handed; RL = ambidextrous; R = right-handed.

Imaging acquisition and lesion identification

Axial CT scans without contrast were acquired at the Bethesda Naval Hospital on a GE Medical Systems Light Speed Plus CT scanner in helical mode during phase 3. Structural neuroimaging data were reconstructed with an in-plane voxel size of 0.4×0.4 mm, an overlapping slice thickness of 2.5 mm, and a 1 mm slice interval. Lesion location and volume were documented from CT images with the Analysis of Brain Lesion software (Makale *et al.*, 2002; Solomon *et al.*, 2007) implemented in MEDx v.3.44 (Medical Numeric) with enhancements to include the Automated Anatomical Labeling Atlas (Tzourio-Mazoyer *et al.*, 2002). The CT image of each brain was normalized to a CT template in MNI space using an automated image registration algorithm with 12-parameter affine fit (Woods *et al.*, 1993). Both the subject's brain and the MNI template were skull-stripped to maximize the efficacy of the image registration from native space to MNI space; voxels inside the traced lesion were not included in the spatial normalization procedure (Tzourio-Mazoyer *et al.*, 2002). Similar to other lesion studies (Heberlein *et al.*, 2004), lesions were traced manually on each slice in native space by a neuropsychiatrist with experience in reading CT scans, and subsequently reviewed by the principal investigator of the Vietnam Head Injury Study (Krueger *et al.*, 2009). Both judges were blind to the results of the clinical evaluation. The clinical interpretation of scans acquired during phase 4 was consistent with that of phase 3 on which we had quantifiable information. A map of the lesion overlap is shown in Fig. 1.

Neurobehavioural protocol and background neuropsychological testing

Altruistic Decision Task

The Altruistic Decision Task was modified from a task formerly used in a functional MRI investigation of altruistic donations in normal adult volunteers (Moll *et al.*, 2006). The main goal of the Altruistic Decision Task is to assess preferences for real societal causes based on moral beliefs. Participants were invited to take part in a study on the psychology of judgements about societal causes such as euthanasia and gun control. After a brief practice session, they were presented with the names of 30 real societal organizations and a short description of their respective missions followed by a prompt to (i) punish (removing money from) or reward (donating money to) each organization; or (ii) save the

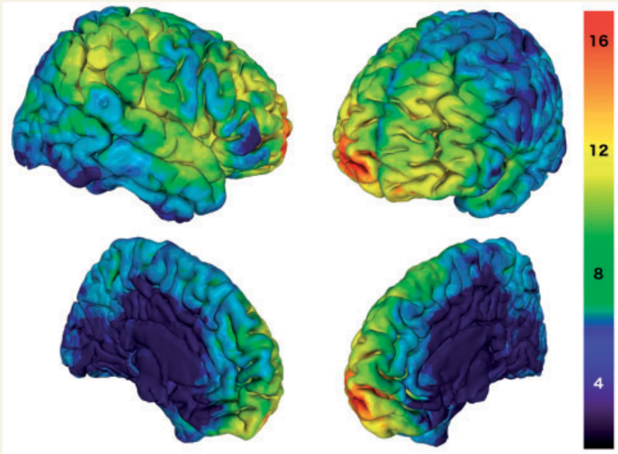

Figure 1 Lesion map illustrating the number of lesion overlap at each voxel across the whole penetrating TBI population (*n* = 94). The colour bar indicates the number of overlapping lesions at each voxel. Red in the scale indicates a higher number of subjects, and blue indicates a lower number. The maximum overlap occurred in the right rostrolateral prefrontal lobe.

money for themselves (the Supplementary material provides a list of the organizations and the instructions for the Altruistic Decision Task). Each decision to punish or donate cost \$1, while refraining from either incurred no costs, leading to savings. From the outset, participants received a sum of \$60 to spend on either rewarding or punishing the organizations. It was emphasized that they would deal with real money that they could keep for themselves (heretofore called 'savings'), or spend on donating to, or punishing, each organization as they wished. If the participant chose to donate funds to the organization, he should select 'yes' in the 'donate' situation and \$1 was deducted from his account and transferred to the organization; if he chose to punish the organization, he should select 'yes' in the 'punish' situation and \$1 was deducted from his and from the organization's account. (This was made possible by deducting from the donations of other participants to the same organization.) If the participant chose to neither donate nor punish, he was instructed to select 'no' and no money was added or subtracted from his account. Since each one of the 30 organizations was presented twice, each participant had the opportunity to keep a maximum of \$60, donate a maximum of \$30, or spend a maximum of \$30 in punishments. Therefore, all donations and punishments involved sacrificing one's own money and were, by definition, altruistic. The amounts saved or spent on punishing or donating were used for scoring the task. At the end of the session, the participant received the money that he did not spend on punishments and rewards.

For the purposes of the present study, we assumed that a participant's willingness to reward or punish a given organization reflected his moral attitudes towards the mission of the organization. We also assumed that decisions to punish or donate reflected moralistic punishment and generous response inclinations. Inferences like these have proved fruitful in lesion studies using economic games as surrogates of moral emotions like guilt and envy (Krajbich *et al.*, 2009).

Background neuropsychological tasks

Participants initially underwent a brief cognitive screening (Mini-Mental State Examination) followed by an extensive neuropsychological assessment, which included handedness (Oldfield Inventory) and intelligence (Wechsler Abbreviated Scale of Intelligence). Given the decisive influence of executive function in altruistic decisions (Glass *et al.*, 2016), we empirically controlled the executive performance of patients with penetrating TBI using their Delis-Kaplan raw scores on the Sorting and the Letter and Category Fluency tasks (Delis *et al.*, 2001). The Delis-Kaplan Executive Function Sorting Test measures fundamental component processes of executive functions by having participants to sort six cards along two columns into several possible categories (Free Sorting) and verbally explain how they reasoned to make the sorts the way they did (Free Sorting Explanation); this was followed by the participant's recognition of the concepts underlying the arrangement of the cards previously sorted by the examiner (Sorting Recognition). The Delis-Kaplan Executive Function Verbal Fluency subtests require verbal response generation within a 1-min time limit: Letter Fluency contains three trials that require generation of words starting with a specific letter (F, A, S); Category Fluency includes two trials that require generation of words that belong to a specific semantic category (animals and boys names); and Category Switching includes a single trial that requires the examinee to continuously alternate between two semantic categories (fruits and furniture). Personality and impulsivity were assessed with the NEO Personality Inventory (Costa and McCrae, 1985) and the Barratt scale (Patton *et al.*, 1995), respectively.

Lesions underlying decisions on the Altruistic Decision Task

Associations between lesion distribution and performance on the Altruistic Decision Task were assessed with support vector regression multivariate pattern analysis (Smith *et al.*, 2013). Multivariate pattern analysis was used in the estimation of the strength of associations between (i) lesion sites; and (ii) the number of punishments and donations. Unlike univariate analyses, this statistical technique does not assume independent contributions of different voxels, but rather the joint contribution of multiple voxels in the determination of the behaviour(s) of interest, in this case, the raw scores on the Altruistic Decision Task (Zhang *et al.*, 2014). This analysis provided independent q-maps for punishment and donation, each with a positive or a negative sign (i.e. the variable of interest is positively or negatively correlated with the presence of a brain lesion at a specific location. The steps used here followed the guidelines provided by Zhang *et al.* (2014): (i) a mask containing only the voxels that are lesioned in at least three individuals is applied to the whole brain; (ii) a β-map is generated from the raw data through a support vector regression model; (iii) the P-maps are obtained through a non-parametric bootstrap analysis with 5000 permutations of the Altruistic Decision Task raw scores; (iv) the P-maps thus generated are then corrected for multiple comparisons by applying a false discovery rate (FDR) using $P < 0.05$; and (v) clusters with less than 10 voxels are filtered from the FDR-corrected P-maps. The filtered FDR-corrected P-maps are the q-maps, which can be coded as positive or negative depending on the sign of the β-value of each voxel. For display purposes, colour-coded maps were generated by overlaying multivariate β-maps on high-resolution brain surface templates using Pycortex (Gao *et al.*, 2015). These maps were thresholded according to the procedures described above. It should be noted that whereas support vector regression computes the associations between lesion localization and performance on the Altruistic Decision Task across all patients, it does not provide information about subgroups of individuals. This is because decisions to punish or donate by a single individual may be modulated by lesions in different locations; furthermore, some lesions may not affect decisions on the Altruistic Decision Task. We thus moved on to perform further supporting analyses. Participants with penetrating TBI were then regrouped according to the patterns of lesion distribution, which were contingent on the associations between performance on the Altruistic Decision Task and lesion sites. These supporting analyses were performed for the punishment and donation *q*-maps and resulted in the following subgroups: for the punishment *q*-maps, there were (i) an indifferent lesion subgroup, i.e. a subgroup in which lesions did not influence decisions to punish; (ii) a lesion subgroup showing increase in punishments; (iii) a lesion subgroup showing a decrease in punishments; and (iv) a lesion subgroup harbouring lesions that modulated punishment non-specifically, either increasing or decreasing it. An equivalent categorization was derived for the multivariate donation *q*-maps. Controls composed the comparison group.

Statistical analyses

The statistical significance of differences among the five behavioural subgroups was assessed separately for punishments and donations with one-way analyses of variance followed up by pairwise comparisons with Tukey's test. The strength of the correlations between variables of interest was assessed with Pearson's coefficient (r). The significance threshold (α) for all statistical tests was set at 0.05, two-tailed. Statistical power and effect sizes (η^2) were estimated according to Cohen's guidelines for analysis of variance (Cohen, 1992) as small (0.10), medium (0.25) and large (0.40).

Results

There were no statistical differences between patients (all penetrating TBI cases pooled together) and controls on age, education, global intelligence, handedness, or impulsivity. Verbal intelligence and executive performance were slightly, but significantly, lower in the penetrating TBI group, whereas premorbid intelligence was slightly higher in the penetrating TBI group (Table 1). However, given the small size effect of these differences (all $\eta^2 \leqslant 0.11$) and their lack of significant correlation with Altruistic Decision Task scores, we did not enter them as covariates in the statistical model.

Both penetrating TBI and controls retained roughly two-thirds of the total amount of money they could dispose of. The remaining third was spent more in donations than in punishments ($F > 20$, df = 1, $P < 0.0001$; all pairwise comparisons: $P < 0.001$). The groups did not significantly differ in the amount saved and spent on either donations or punishments ($F < 32$, df = 1, $P > 0.23$). Although there was an expected inverse relationship between savings (not punishing plus not donating) and punishing (all r's $\leqslant -0.49$) or donating (all r's $\leqslant -0.53$) in both controls and all penetrating TBI pooled together, punishments and donations were not significantly related. The results of the multivariate analyses are detailed below.

Punishment

Lesions that increased punishments were found (i) bilaterally in the dorsomedial prefrontal cortex; and (ii) in the right rostrolateral frontal lobe (middle and inferior frontal gyri) (Fig. 2). The dorsomedial prefrontal damage was more extensive in the left hemisphere, where it additionally involved the depth of the anterior division of the paracingulate sulcus and the pregenual cingulate cortex. Lesions that decreased punishment (Fig. 2) were distributed in the left ventromedial temporal lobe, where they destroyed the anterior two-thirds of the uncus and the rostral-most tip of the parahippocampal gyrus. Injuries at this location deprive the amygdala of a major set of connections from prefrontal and parieto-temporo-occipital cortices (Stefanacci *et al.*, 1996). In the right hemisphere, the lesions leading to decreased punishment followed a perisylvian distribution which encompassed the lower third of the precentral, post-central and supramarginal gyri (frontal and parietal opercula), the insula, the posterior third of the middle temporal gyrus, and the posterior half of the superior temporal sulcus and superior temporal gyrus. The angular gyrus and temporoparietal junction (Decety and Lamm, 2007) were spared. Lesions extended into the subcortical white matter to varying degrees, where they injured the middle branch of the right superior longitudinal and the left uncinate fasciculi (less punishment), and the upper division of the left superior longitudinal fasciculus (more punishment).

Despite no overall differences were noted between penetrating TBI and controls for punishing and donating, all punishment subgroups spent more on punishing than on donating, as expected (all P's < 0.0001). Only in the subgroup that punished more was lesion volume correlated with the amount retained ($r = -0.37$, $P < 0.03$) and spent on punishments ($r = 0.42$, $P < 0.01$). Moreover, there were no statistical differences between controls and the indifferent subgroup on any variable of interest, particularly on the three main outcome variables of the Altruistic Decision Task. In other words, the absence of lesions (controls) had exactly the same effect on the Altruistic Decision Task as the lesions outside the regions that modulated the decisions to punish. The largest lesion volume was found in the subgroup of lesions that led to both punishing and donating. The total lesion volume of this subgroup was statistically larger than that of the indifferent subgroup only. The fact the lesion volume of the subgroup that punished more did not differ from the other subgroups suggests that lesion volume alone was not a determinant of performance on the Altruistic Decision Task. Thus, lesion location, rather than lesion size, was the primary determinant of

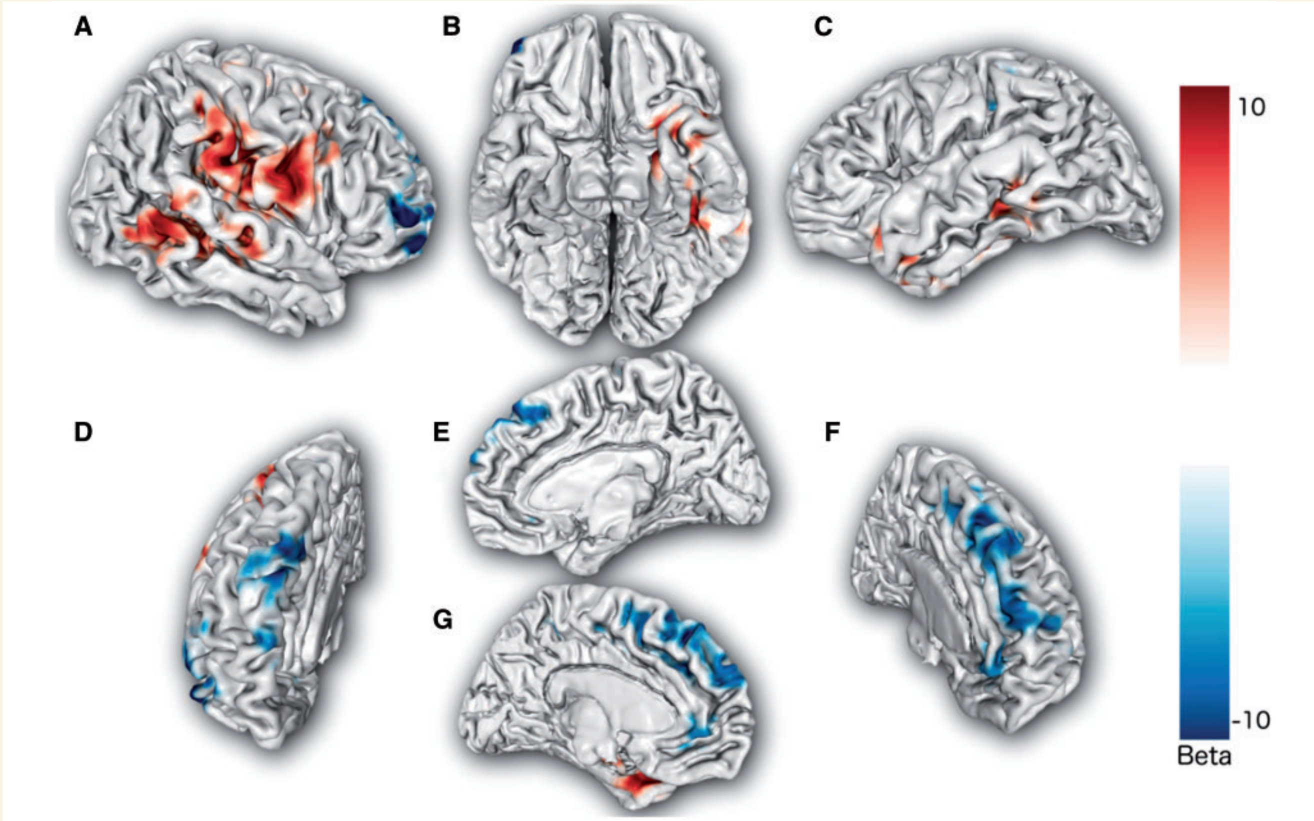

Figure 2 Statistical β-maps of lesions that decreased (red) or increased (blue) punishment on the Altruistic Decision Task. (**A**–**C**) Right rostrolateral prefrontal and perisylvian cortices, including the inferior parietal lobule, posterior middle temporal and superior temporal gyri. (**D**–**G**) Medial views of the dorsomedial prefrontal cortex and left medial temporal pole.

performance on the Altruistic Decision Task. This conclusion was strengthened by the absence of qualitative changes in the results after controlling for lesion volume in the support vector regression model.

Donation

Lesions that led to increased donations were restricted to the paracentral lobule and precuneus, as well as to small areas in the right dorsomedial prefrontal cortex (Fig. 3). Injuries leading to a decrease in donations were restricted to small sectors of the right ventrolateral occipital cortex and posterior middle temporal gyrus (Fig. 3). A decrease in donations was also related to a large subcortical lesion in the white matter beneath the right inferior and middle frontal gyri. This lesion, which was barely seen on the cortical surface, probably destroyed the middle branch of the superior longitudinal fasciculus (Supplementary Fig. 1).

Additional findings

The expected inverse correlations between punishments and savings (controls $r = -0.78$, penetrating TBI $r = -0.64$) and between donations and savings (controls $r = -0.66$, penetrating TBI $r = -0.60$), but not between punishments and donations ($r < 0.26$, $P > 0.13$), were confirmed, indicating that the money spent in punishments and donations came from the savings fund, a further indication of genuine costly altruism. There were no statistical differences in personality or impulsivity among groups in any condition; the statistical differences observed on a few intelligence and executive tests were of small magnitude (all $\eta^2 \leqslant 0.11$) and unrelated to Altruistic Decision Task performance. The ancillary results provided in Table 2 and in Supplementary Tables 1 and 2 describe the behaviour patterns of the Altruistic Decision Task in lesion subgroups and provide details on their neuropsychological performance. Total brain tissue volume loss exerted no overall effect on punishments or donations. The lesion volume of the subgroup that punished both more and less was statistically larger than that of the indifferent lesion subgroup, however. To rule out the possibility that results on the Altruistic Decision Task were biased by spurious associations between lesions and behaviour arising from small numbers, the total number of participants contributing to the observed statistical effects was computed. These results show that our statistical associations emerged from contributions of at least six and, more typically, between 10 and 25 penetrating TBI participants per brain lesion location (Table 3).

There was a significant rightward asymmetry of total lesion volume loss in relation to performance on the

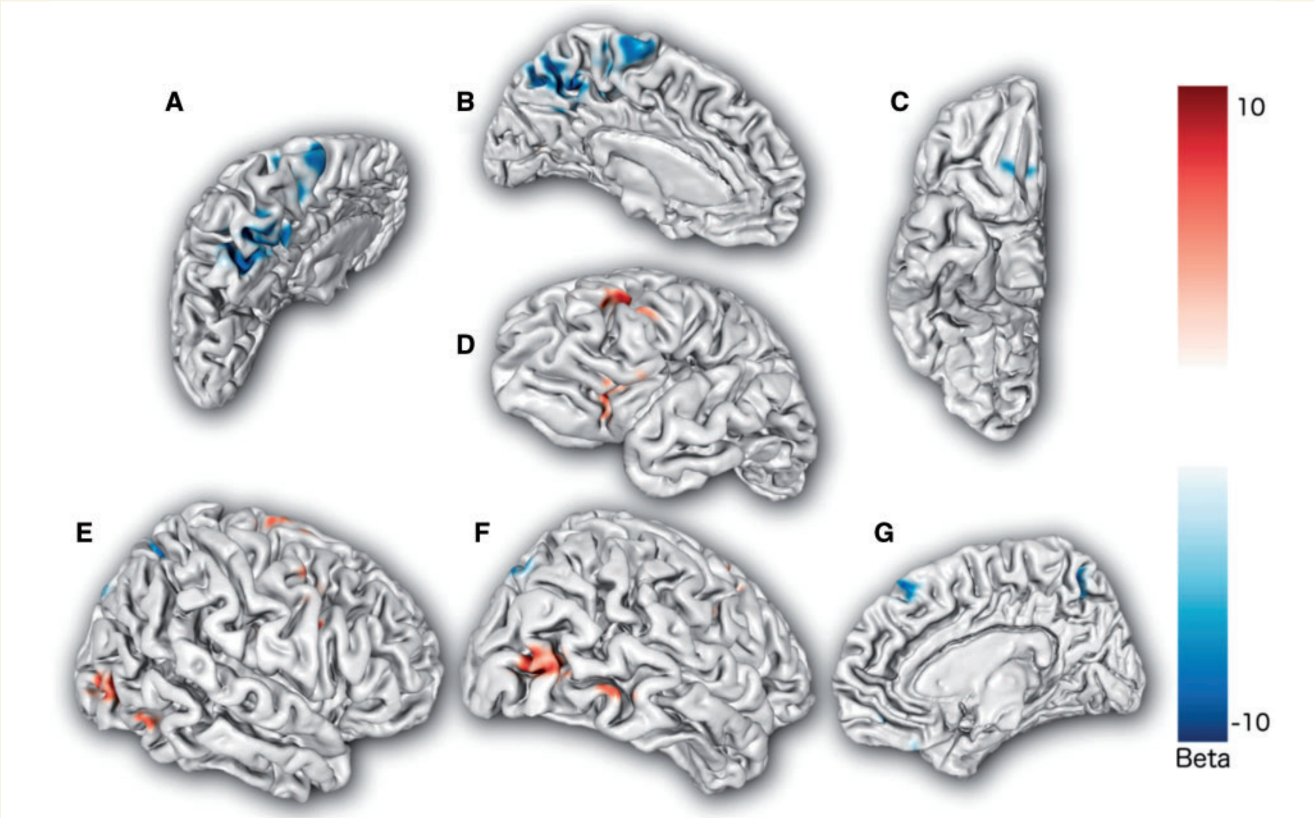

Figure 3 Statistical β-maps of lesions that decreased (red) or increased (blue) donations on the Altruistic Decision Task. (**A**) Precuneus, cingulate gyrus, superior parietal lobule, and postcentral gyrus. (**B**) Precuneus and dorsomedial frontal cortex. (**C**) Posterior orbitofrontal cortex (gyrus rectus and medial orbitofrontal cortex). (**D**) Ventrolateral orbital and precentral gyri, and precentral sulcus. (**E**–**G**) Dorsolateral occipital lobe/posterior middle temporal gyrus, superior parietal lobule (angular and supramarginal gyri), and posterior superior frontal gyrus.

Altruistic Donation Task (Wilcoxon test: $P < 0.02$, two-tailed). Finally, results from a voxel-based lesion mapping univariate analyses provided qualitatively similar results to the multivariate support vector regression method, though statistically less robust (Supplementary Fig. 2).

Discussion

To date, this has been the only lesion study tackling the causal neural underpinnings of altruistic decisions towards real societal organizations. Its main findings may be thus summarized: (i) bilateral dorsomedial prefrontal lesions increased altruistic (costly) punishment, whereas lesions of the right perisylvian region and left temporoinsular cortex decreased it; (ii) altruistic (costly) donations were increased by bilateral lesions of the dorsomedial parietal cortex, whereas lesions of the right posterior superior temporal sulcus and middle temporal gyri had the opposite effect; and (iii) neither altruistic nor selfish decisions were related to changes in personality. These aspects will be discussed in turn. First, the relationships between focal brain lesions and altruistic decisions using support vector regression-based multivariate pattern analysis; second, our study was designed to test the possibility that players may not only punish, but may also donate to third parties, or refrain from either donating or punishing, keeping their funds instead; third, our experimental design allowed us to assess the extent of overlap and segregation of the neural networks concerned with punishing and rewarding.

The Altruistic Decision Task

The Altruistic Decision Task has some features that distinguish it from other tasks designed to evoke altruistic decisions. For the most part, such tasks have concentrated on the neural substrates of decisions to punish, little attention being paid to decisions to donate (e.g. Krueger *et al.*, 2014). First, besides adding the alternative of donating, the Altruistic Decision Task allows the grading of more or less punishments or donations. Second, it grants real monetary incentives in real contexts. Third, the Altruistic Decision Task provides no clues on when the intent (the mission) of the organization (the moral agent) will be accomplished, or, for that matter, if it will ever be; therefore, the Altruistic Decision Task emphasizes established beliefs and attitudes towards the organizations and their missions at the expense of observable outcomes. This reasoning is in

Table 2 Descriptive statistics of performance on the Altruistic Decision Task according to the location of lesions that influenced punishments, donations, and savings (lesion subgroup analysis)

	Punishments				
	P^0	P^+	P^-	$P^\pm$	Controls
Number of participants per lesion subgroup	18	34	22	20	28
$ Donations	13.2 ± 9.2	16.1 ± 5.8	13.5 ± 6.4	14.1 ± 5.7	12.9 ± 5.9
$ Punishments	3.8 ± 5.3	6.6 ± 4.9	2.6 ± 3.4	4.0 ± 3.9	5.8 ± 4.9
$ Savings	42.9 ± 10.2	37.3 ± 8.4	39.4 ± 11.7	41.8 ± 7.2	41.2 ± 7.9
	Donations				
	D^0	D^+	D^-	$D^\pm$	Controls
Number of participants	43	23	28	0	28
$ Donations	14.7 ± 7.3	20.0 ± 2.6	9.7 ± 4.0	–	12.9 ± 5.9
$ Punishments	4.6 ± 4.6	4.7 ± 3.6	4.5 ± 5.7	–	5.83 ± 4.9
$ Savings	40 ± 9.4	35.2 ± 4.0	43.8 ± 11.2	–	41.2 ± 7.9
	Savings				
	S^0	S^+	S^-	$S^\pm$	Controls
Number of participants	32	25	32	5	28
$ Donations	14.3 ± 6.9	11.4 ± 5.0	17.9 ± 5.3	14.2 ± 7.6	12.9 ± 5.9
$ Punishments	4.4 ± 5.0	2.6 ± 2.8	6.7 ± 4.9	2.4 ± 4.2	5.8 ± 4.9
$ Savings	41 ± 8.5	45 ± 7.9	35 ± 6.7	43.4 ± 9.6	41.2 ± 7.9

0 = Lesions that exerted no influence on Altruistic Donation Task performance.
+ = Lesions that increased the rate of punishments (P), donations (D), or savings (S).
− = Lesions that decreased the rate of punishments (P), donations (D), or savings (S).
± = Lesions that either increased or decreased the rate of punishments (P), donations (D), or savings (S).

line with a recent study that parsed the ordered processes that end up in a decision to punish crimes of varying severity (Ginther *et al.*, 2016). Although we did not assess the subjective justifications behind the participants' decisions, we assumed that they reflected harmful, benevolent, or self-serving (saving) intentions. Not surprisingly, there was a consistent overlap of the lesions in our cases and the regions implicated in empathy and mental attribution both to individuals (Bzdok *et al.*, 2013) and corporations (Jenkins *et al.*, 2014). Further support for this interpretation is provided by clinicoanatomical correlations in patients with the behavioural variant of frontotemporal dementia, in whom the injury of subregions of the dorsomedial prefrontal and paracingulate cortices produce alterations of morality (Moll *et al.*, 2011; Schroeter *et al.*, 2015).

Support vector regression multivariate pattern analysis

Support vector regression multivariate pattern analysis allows a shift of emphasis from individuals to lesion location. This makes the interpretation of the results more realistic because it takes into account the fact that normal people and patients donate, punish, or save when they are left free to decide (Moll *et al.*, 2006). Support vector regression multivariate analysis circumvents the need to force individuals into somewhat artificial categories, like 'punishers' or 'donators'. It uses instead the location of lesions leading to specific decisions to settle a relationship of the type: lesion in area X increases decisions to punish, lesions in area Y reduce decisions to donate, and so forth. Therefore, it is the location of lesions that predicts decisions on the Altruistic Decision Task, not the particularities of the participants. Furthermore, this procedure takes into account lesion associations; for example, lesions in different locations leading to an increase or a decrease of punishments in different trials but in the same participant. Following this lead, two broad patterns of lesion location differentially accounted for punishments and donations. In all instances, the lesions were either grossly symmetric or asymmetric in favour of the right hemisphere; i.e. the right hemisphere was more influential than the left regarding the critical outcome variables. A corollary of this finding is that performance on the Altruistic Decision Task depends less on the integrity of the left than on the integrity of the right hemisphere. Indeed, a rightward asymmetry has been the rule in studies of empathy, moral cognition, and political inclinations both in normal individuals and in patients with brain damage (Driscoll *et al.*, 2012; Mendez, 2017).

Brain regions implicated in punishment

Many regions related to punishment decisions in the present study have previously been implicated in altruistic punishment. A functional MRI study in which normal adults assigned responsibility (a categorical variable) and graded

Table 3 Cerebral regions and corresponding Brodmann areas that were damaged, based on multivariate regression maps for punishments and donations

Anatomical region	Side	Brodmann area	Number of subjects (R/L)
Punishments			
Supramarginal/angular gyrus	R/L	40/39	11/15
Superior temporal gyrus	R	22	18
Middle temporal gyrus (posterior third)	R/L	37	9/6
Rostrolateral (lateral frontopolar) cortex	R/L	10	21/10
Dorsomedial prefrontal cortex	R/L	8m, 9m	32/18
Pregenual/ventral cingulate cortex	R/L	24/32/33	11/16
Temporal pole (rostromedial and dorsolateral)	L	28, 34, 38	15
Lateral/ventral temporal cortex	R/L	20/21	22/15
Limen insula		J ant	21/16
Donations			
Middle temporal sulcus (posterior half)	R	37	6
Dorsomedial parietal cortex (precuneus)	R/L	5/7m	12/11
Medial orbitofrontal/gyrus rectus	R/L	11	6/7
Inferior frontal gyrus	L	45/46/47	17

L = left; m = medial; R = right.

penalties (a dimensional variable) to different patterns of crimes showed that the right dorsolateral prefrontal cortex and intraparietal sulci were engaged by deciding between responsible and not responsible. Another set of regions were parametrically engaged by the assignment of degrees of punishment to different crimes, most notably the right amygdala, the dorsomedial and ventromedial prefrontal cortices, the temporal pole, and the posterior cingulate (Buckholtz *et al.*, 2008). Glass *et al.* (2016) reached essentially the same conclusions, and proposed that at least two domain-general networks operate in altruistic punishment, namely: (i) a mentalizing network for attribution of responsibility; and (ii) an executive network for determining how much punishment should be applied to specific cases or situations. Like us, they also found that punishment was modulated by lesions of the left dorsomedial prefrontal cortex and lateral prefrontal cortex, right dorsolateral prefrontal cortex extending into the supplementary motor area, and right inferior parietal lobule. However, neither the possible associations between the direction (more or less) of punishment (Buckholtz *et al.*, 2008) nor between lesion location and donations (Glass *et al.*, 2016) had so far been explored. Moreover, whereas there is agreement that punishments fit the severity of crimes (Buckholtz and Marois, 2012), the present study is the first lesion study to use altruistic decisions towards real societal organizations, and to explore the effects of brain lesions on altruistic giving.

Our findings concur with those of the aforementioned authors, further indicating that two interacting systems modulate altruistic punishment, one related to (i) the right perisylvian cortex, and the left anterior temporal lobe and insula; and the other related to (ii) the dorsomedial and rostrolateral prefrontal cortices.

Lesions that decreased punishment were primarily located in parts of the right perisylvian cortex. A number of imaging studies have implicated the temporoparietal junction and posterior fourth of the superior temporal sulcus in extracting moral salience from perceptual stimuli (Moll *et al.*, 2005*b*; Young *et al.*, 2010). This region only partially overlaps the supramarginal gyrus and the temporoparietal junction, which have been identified by functional MRI (Chakroff *et al.*, 2015) and transcranial magnetic stimulation (Baumgartner *et al.*, 2014) studies as being relevant to complex social cues and to individual differences of generosity (Morishima *et al.*, 2012). These functional-anatomic differences may be explained by damage to the right superior longitudinal fasciculus (Supplementary Fig. 1), which disrupted the connections among these regions (Mars *et al.*, 2012). Decreased punishment might also be explained by a decrease of moral disgust (indignation) resulting from the left temporo-insular damage (Moll *et al.*, 2005*a*). Overall, our findings suggest that the disposition to punish third parties is reduced by damage to the right posterior perisylvian and the left temporo-insular cortices.

The converse was true for injuries located in the prefrontal cortices. More specifically, bilateral dorsomedial prefrontal lesions and their ventral extension, and right rostrolateral prefrontal lesions increased the rate of punishments, a finding that concurs with a growing body of evidence showing that these regions exert a regulatory effect on the perisylvian and temporo-insular regions in judgments of moral responsibility. From the perspective of the viewer (or witness), the dorsomedial prefrontal cortex integrates representations of intent with the agent's actual behaviour (completed harm versus no harm at all) to come up with a final condemning or exculpating judgement (Young and Saxe, 2008). This tendency may be enhanced by the decrease of prosocial emotions that have been shown to follow dorsomedial prefrontal cortex damage (Moll *et al.*, 2011). We might speculate that the injury of the dorsomedial prefrontal cortex has released the social attribution processes carried out by the posterior temporoparietal and anterior temporal cortices (Zahn *et al.*, 2007; Young and Saxe, 2008), thus favouring the willingness to punish. Whatever the ultimate explanation for this finding might be, the net result of these interactions is consistent with the complementary role of these regions in altruistic punishment (Ruff *et al.*, 2013) as well as with Krajbich *et al.*'s (2009) interpretation of their own findings, as mentioned before.

Brain regions implicated in donations

A second advantage afforded by the Altruistic Decision Task and the multivariate support vector regression analysis was the possibility of delving into the cerebral correlates of altruistic donations. As it turned out, these were related to a different ensemble of cerebral regions. Damage to the left medial parietal lobe decreased donations, whereas damage to the right middle temporal gyrus increased donations. It was somewhat surprising that these regions were thus implicated in our patients because they have to date not been implicated in altruistic reward (Gluth and Fontanesi, 2016). The few associations between altruistic decisions and either activation or damage to the posteromedial hemispheric surface have pointed to the posterior cingulate in self-referential processes; however, the supracingulate cortex, which was related to performance on the Altruistic Decision Task, was not noted in those studies. Overall, our findings suggest that the superomedial parietal cortex is somehow involved in the facilitation of donations, whereas the ventrolateral occipitotemporal cortex is necessary for decisions that reduce the probability of donating.

Interpretation of our findings in the light of current knowledge

Although our study was not designed to tap the temporal dynamics of the cerebral regions engaged by the Altruistic Decision Task, taken together with the findings of other researchers, our results support the view that altruistic decisions emerge from a subtle interplay of neurocognitive modules that are called forth into action when a moral decision is demanded by a challenging context, such as when one is asked to decide for or against euthanasia (Moll *et al.*, 2002). Some of these regions underpin the attribution of mental states to third parties and the experience of the corresponding moral sentiments (e.g. witnessing a good deed evokes the moral sentiment of admiration), judgements of good and bad, and a final decision to punish, donate or save. Experiments in normal volunteers and brain-damaged patients have shown that these relatively independent processes (Ginther *et al.*, 2016) are to a great extent reliant on the integrity of the right cerebral hemisphere (Miller *et al.*, 2010).

It has long been known that the integrity of the ventromedial prefrontal cortex and neighbouring regions is critical for the enactment of altruistic behaviours, most notably when self-serving interests conflict with the interests of others (Moll *et al.*, 2016). Damage to this region enhances the enactment of selfish decisions at the expense of the well-being of others (Koenigs and Tranel, 2006; Moretto *et al.*, 2009). However, the ventromedial prefrontal cortex, which was injured in a few cases of the present series, did not bear a robust relationship to performance on the Altruistic Decision Task. Together with the lack of acquired changes in personality in the penetrating TBI group, this observation supports the claim that cerebral regions beyond the ventromedial prefrontal cortex must be critical for the regulation of altruistic punishment and donation (Morishima *et al.*, 2012). The present investigation provides further details on the workings and interactions among these brain regions.

Current limitations and opportunities for further research

The role of the dorsomedial prefrontal cortex in social cognition has increasingly lured researchers (Bzdok *et al.*, 2013). There is evidence that this region is functionally heterogeneous in humans. For example, damage to the septal nuclei and the anterior dorsomedial prefrontal cortex was implicated in a decrease of prosocial sentiments, while a decrease in anger and disgust followed damage to the posterior dorsomedial prefrontal cortex (Moll *et al.*, 2011). Thus, dorsomedial prefrontal injuries may enhance altruistic or selfish choices in economic games depending on their location and extent. Analogous reasoning may apply to the observation that damage to the posterior superior temporal sulcus and neighbouring regions that resulted in a diminished capacity for emotional empathy (Driscoll *et al.*, 2012). Further studies are needed to probe the differential role of these regions and their subcortical connections in specific domains of altruistic decisions.

The role of specific white matter pathways in higher-order social impairments has also attracted the attention of researchers (Philippi *et al.*, 2009). That they may have played a part in some of our cases was indicated by the subcortical extension of lesions that were related to the conditions of interest (Supplementary Fig. 1). How they might extend our findings is the subject of further lesion studies currently underway (Cristofori *et al.*, 2015).

It might be surprising that changes in personality were not observed in the 12 patients who sustained uni- or bilateral damage to the frontotemporo-insular region; in fact, statistically significant personality changes were not observed in any lesion subgroup, nor were significant differences in the core dimensions of personality found between controls and patients. The absence of personality changes may have been due to the small number of cases with lesions in the ventromedial prefrontal cortex and other appropriate locations. How acquired sociopathy might have influenced performance on the Altruistic Decision Task remains a topic for future studies.

Finally, because of the older and exclusive male composition of our groups, little can be said about how our findings could possibly apply to female or younger adults. In view of the well-known interactions between sex and hemispheric symmetries (Kimura, 1992), the cerebral underpinnings of female decisions on the Altruistic Decision Task and kindred altruistic decision tasks may differ in critical aspects (Harenski *et al.*, 2008). These differences are also an important topic for future studies.

To summarize, anonymous decisions to punish or donate to societal causes are grounded in non-overlapping cerebral regions that have also been implicated in the attribution of intentionality, morality, and justice both to individuals and social groups. Further refinement of the model should clarify the details of the neural organization of the many forms of altruism through experimental manipulations of context, amount and types of investment, diagnosis, and specific populations. In addition, the measurement and experimental study of altruism should consider (i) individual dispositions for altruism; (ii) altruistic actions towards organizations and the societal causes they support; (iii) attitudes towards individuals; and (iv) the patterns of brain organization that underpin (i–iii). Our study provides a step forward in this direction by showing that different brain regions are causally implicated in the anonymous sacrifice of one's own resources to punish or benefit genuine societal causes.

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Supplementary material

Supplementary material is available at *Brain* online.

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