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Dissociable contributions of the prefrontal cortex in group-based cooperation

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Abstract

The success of our political institutions, environmental stewardship and evolutionary fitness all hinge on our ability to prioritize collective-interest over self-interest. Despite considerable interest in the neuro-cognitive processes that underlie group cooperation, the evidence to date is inconsistent. Several papers support models of *prosocial restraint*, while more recent work supports models of *prosocial intuition*. We evaluate these competing models using a sample of lesion patients with damage to brain regions previously implicated in intuition and deliberation. Compared to matched control participants (brain damaged and healthy controls), we found that patients with dorsolateral prefrontal cortex (dlPFC) damage were *less* likely to cooperate in a modified public goods game, whereas patients with ventromedial prefrontal cortex (vmPFC) damage were *more* likely to cooperate. In contrast, we observed no association between cooperation and amygdala damage relative to controls. These findings suggest that the dlPFC, rather than the vmPFC or amygdala, plays a necessary role in group-based cooperation. These findings suggest cooperation does not solely rely on intuitive processes. Implications for models of group cooperation are discussed.

Key words: prosocial behavior; lesions; cooperation; public goods game

Introduction

Prioritizing collective-interest over self-interest is essential for adaptive group living and is critical for resolving numerous social problems, including voter turnout (Ostrom, 1990), climate change (Jacquet *et al.*, 2013), scientific integrity (Everett and Earp, 2015) and evolutionary fitness (Axelrod and Hamilton, 1981). For centuries, philosophers have debated whether prosocial tendencies are rooted in institutions that regulate our selfish impulses (Hobbes, 1650) or emerge through natural intuitions, only to be suppressed by civilized and calculated self-interest (Rousseau, 1754). This debate persists to this day.

This debate is often framed through the lens of dual-process theories that carve the mind into two core systems (Kahneman, 2011): *intuition*—immediate, reflexive mental processes—and *deliberation*—delayed, reflective processing. Some argue, for instance, that humans' unique capacity for self-reflection (i.e. compared to other primates) provides a critical avenue to promote prosocial behavior (Stevens and Hauser, 2004). There is additional evidence that depleting cognitive resources impairs helping behavior (DeWall *et al.*, 2008; Capraro and Cococcioni, 2016) and amplifies dishonesty (Mead *et al.*, 2009), supporting models of *prosocial restraint*, whereby cooperation stems from

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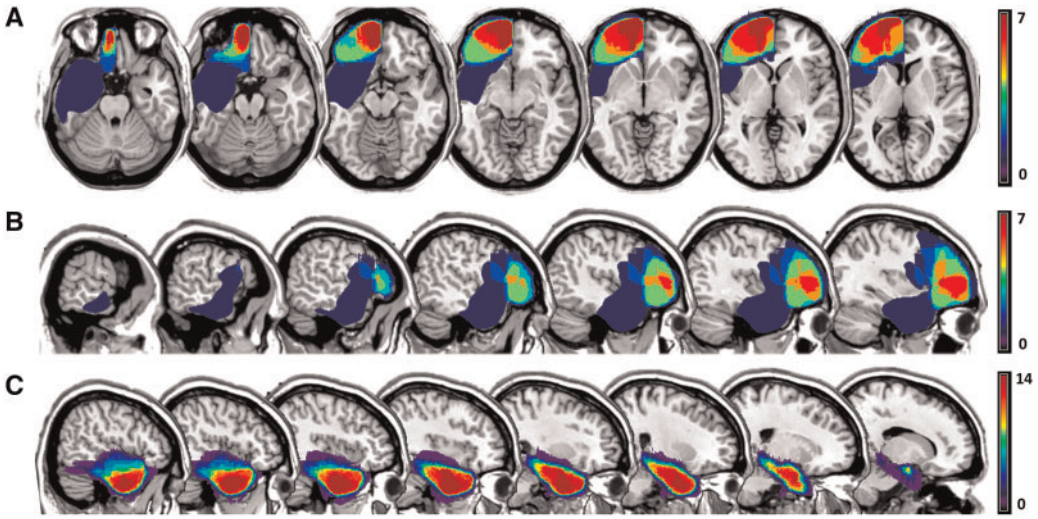

Fig. 1. Lesion overlap of patients. (A) Patients with vmPFC damage ($n = 7$) are shown in axial slices $Z = [-24, -19, -14, -9, -4, 1, 6]$. (B) Patients with dlPFC damage ($n = 7$) are shown in sagittal slices $X = [64, 59, 54, 49, 44, 39, 34]$. Both images include patients with combined vmPFC and dlPFC damage ($n = 6$). Patients with right hemisphere damage ($n = 2$) were flipped to generate the overlap lesion reconstruction. (C) ATL patients with amygdala damage ($n = 14$) are shown in sagittal slices $X = [44, 39, 34, 29, 24, 19, 14]$. For symmetric visualization purposes, lateralized damage has been reflected onto both hemispheres.

deliberate restraint of our selfish impulses (Martinsson *et al.*, 2012; Achtziger *et al.*, 2016; Lohse, 2016).

These models have been recently challenged by opposing models of *prosocial intuition* (Zaki and Mitchell, 2013), whereby intuitive cooperation is compromised by calculated self-interest (Rand *et al.*, 2014). Research supporting these models often involves experimental economic games that use real money to pit self-interest against collective-interest. In the public goods game (PGG), for instance, the group benefits when everyone contributes their money, even though it is in each individual's self-interest to keep their money (i.e. free-riding). Observations that people are relatively slower to free-ride in these games was initially interpreted as evidence for intuitive cooperation (Rand *et al.*, 2012). Follow-up investigations however suggest these slower reaction times more likely index decision conflict, rather than deliberation, *per se* (Evans *et al.*, 2015; Krajbich *et al.*, 2015). In addition, some recent meta-analyses and preregistered studies indicate that experimentally inducing intuition (e.g. manipulating time-pressure) tends to boost group contributions in these games (Rand, 2016; Everett *et al.*, 2017), whereas others have reported inconclusive or null results (Tinghög *et al.*, 2013; Bouwmeester *et al.*, 2017). Given this mixed evidence with behavioral measurements and manipulations, we leverage neuropsychological samples to help evaluate these conflicting models of prosocial restraint and prosocial intuition.

Despite extensive research devoted to promoting group-based cooperation (Van Lange, 1999), we still know relatively little about the neuro-cognitive processes that guide this adaptive behavior. Early work in social neuroscience attempted to map intuition and deliberation onto specific brain systems (Lieberman, 2007; see also Cunningham *et al.*, 2007). Evidence from functional magnetic resonance imaging (fMRI) suggests the ventromedial prefrontal cortex (vmPFC) is implicated in immediate, automatic evaluations (Satpute and Lieberman, 2006; Lebreton *et al.*, 2009), whereas the dorsolateral prefrontal cortex (dlPFC) is associated with delayed, controlled deliberation and self-restraint (Hare *et al.*, 2009; Hutcherson *et al.*, 2012). In addition, patients with vmPFC damage show blunted affective processing (Bechara *et al.*, 1996; but see Dunn *et al.*, 2006 for a review of alternate conclusions), while dlPFC damage appears to impair deliberative processes, such as working memory, reasoning and self-regulation (Barbey *et al.*, 2013; Zhu *et al.*, 2014). Evidence from fMRI, brain lesions and single-cell recordings further implicates subcortical structures like the amygdala in rapid, affective processing that precedes evaluations in the vmPFC (Phelps and LeDoux, 2005).

Thus, examining cooperative behavior among patients with damage to their dlPFC, vmPFC or amygdala can help arbitrate between prosocial restraint *vs* intuition models. Unlike the inherent correlational nature of fMRI, lesion approaches can effectively probe the causal contribution of these regions (Fellows *et al.*, 2005). Prior studies leveraging this method have suggested causal links between dlPFC damage and honesty (Zhu *et al.*, 2014), vmPFC damage and fairness (Koenigs and Tranel, 2007), as well as amygdala damage and trust (Koscik and Tranel, 2011). While these studies provide valuable insight into dyadic social decision-making, no study (to our knowledge) has examined how damage to these regions impacts cooperation in group contexts. We measure group cooperation using a PGG, pitting the *prosocial intuition hypothesis*—whereby patients with vmPFC or amygdala damage should contribute to the public goods less frequently than controls, against the *prosocial restraint hypothesis*—whereby patients with dlPFC damage should contribute to the public good less frequently. PGGs measure group cooperation by allowing players to make fiscal contributions to their group that are then multiplied and distributed equally (i.e. even to players who keep all their money for themselves). Even though it is in the group's collective-interest if all players contribute, it is in each individual's self-interest to contribute nothing and reap the benefits of other's generosity (i.e. free-riding).

Materials and methods

Participants

We report how we determined our sample size, all data exclusions, all manipulations and all measures in the study. Thirty-seven patients ($M_{Age} = 40.7$ years, $s.d._{Age} = 11.5$ years) with brain

lesions due to stroke, tumor, head injury and surgical resection of tumor, epileptogenic tissue, abscesses and cortical malformations were recruited from the New York University Patient Registry for the Study of Perception, Emotion and Cognition. Using lesion masks created by a clinical neuropsychologist prior to data collection (Supplementary Material Section S1), patients were classified into different groups reflecting the primary location of resection or tissue damage. This procedure resulted in 10 patients with frontal lobe damage extending into vmPFC or dlPFC, 16 patients with anterior temporal lobe (ATL) resections (involving the amygdala and hippocampus), and 11 brain-damaged comparison (BDC) patients with mixed lobar (frontal, parietal or temporal) lesions different than those resected/damaged in the frontal and ATL groups.

Among the 10 frontal patients, 2 had primarily vmPFC damage and 2 had primarily dlPFC damage. The remaining six frontal patients had substantive damage to both vmPFC and dlPFC and could not be cleanly categorized into either group (see Supplementary Table S1). Twenty-nine age-matched ($M = 36.1$ years, s.d. $= 10.9$ years) healthy comparison participants (HC) with no brain damage were recruited from the NYC community. Our target sample size for patients was to recruit *all* eligible volunteers within the registry. Given the limited ability to recruit eligible frontal patients ($n = 10$), we intentionally oversampled healthy controls by a factor of three ($n \sim 30$). All participants gave written informed consent. Across all groups, seven participants failed to meet our inclusion criteria (see Supplementary Material Section S2), leaving a final sample of 26 HC participants, 8 frontal patients (1 vmPFC, 1 dlPFC, 6 mixed), 14 Amygdala patients and 11 BDC patients (see Figure 1). Since most frontal patients had a mixture of vmPFC and dlPFC damage, our primary analysis treated degree of damage to each subregion as a continuous regressor (see Supplementary Material Section S4).

Neuroanatomical analysis

Each patient's lesion was manually reconstructed by a clinical neuropsychologist using MRIcron and FSL View software (Supplementary Material Section S1). ROIs were constructed with MarsBar toolbox by combining corresponding structures from the Harvard-Oxford Maximum Probability Atlases (Supplementary Material Section S1).

Stimuli and task

Participants played 20 one-shot PGGs. In each PGG, participants were given $8.00 that they could either keep for themselves or contribute to benefit the group (see Figure 2). Players interacted in groups of four; all contributions were doubled and split equally amongst all group members. There was no time limit for making decisions and reaction times were recorded. After each choice, participants were shown feedback about the other players' decisions and resulting payouts. To ensure all payouts were based on real economic interactions with other humans *without* deception, other players' decisions were based on real responses from publicly available data. These decisions were predetermined and presented in randomized order. On average, the other players gave 60% of the time with the following distribution: 0 givers (1 trial), 1 giver (6 trials), 2 givers (9 trials) and 3 givers (4 trials). Participants were informed that their decisions were anonymously recorded and could be used to influence the payment of future participants.

After reading through instructions with visualized examples of gameplay, participants completed a brief comprehension quiz. Participants were unable to begin the task until they correctly answered all quiz questions. The experimenter then walked through two example rounds illustrating how, no matter what the other players decided, it was always in the participant's self-interest to keep their money and always in the group's collective-interest to give their money. During debriefing, participants were again assessed as to (1) whether they understood the task and (2) whether they believed their decisions could actually influence others. Participants who misunderstood instructions or expressed suspicion about the prosocial nature of the task were excluded (see Supplementary Material Section S2). This intensive comprehension assessment helped alleviate concerns that cooperative behavior stemmed from misunderstanding or confusion (Burton-Chellew *et al.*, 2016). Participants received $10 for participating, and could earn up to $20 more based on one randomly selected trial. The procedure typically lasted 15 min but was nested within a longer, 90-min protocol with other measures which are being analyzed for a separate report (see Supplementary Section S3 for full protocol).

Data availability

All materials, analysis scripts and summary data will be made available to other scientists upon publication on the Open Science Framework (https://osf.io/r8gwx/).

Analysis strategy

Our primary analysis aimed to test the relationship between group cooperation and damage to vmPFC, dlPFC and amygdala. Cooperation was operationalized as a trial-by-trial binary outcome (0 = *keep*, 1 = *give*). Given the multilevel structure of the data, we used generalized estimating equations (GEE) to fit a multiple logistic regression with exchangeable correlation matrices clustered on each patient.[1] Six (out of the eight) frontal patients had diffuse damage overlapping both vmPFC and dlPFC ($r(6) = 0.26$, 95% bootstrapped CI [−0.23, 0.87], $P = 0.536$). To help assess the independent effects of each brain region, we simultaneously included vmPFC, dlPFC and amygdala damage as predictors of each participant's decision to give. This ROI analysis converged with the traditional group analysis.

Results

Behavioral results

Participants chose to cooperate on 38.5% of trials (s.d. = 48.6%), indicating they were more inclined to free-ride than give their money to the group. Participants spent an average of 1.85 s deciding (s.d. = 1.87). Although they were faster to keep ($M = 1.75$ s, s.d. = 1.48) than to give ($M = 2.02$ s, s.d. = 2.35), this difference was not significant ($P > 0.13$). Finally, although cooperation tended to decrease over the course of the 20 trials (see Supplementary Figure S1), this trend was not significant,[2] $\chi^2(1) = 2.05$, $P = 0.153$. Thus, we find insufficient evidence that decisions in our task change over time or differ in response time.

Primary analysis

The *prosocial intuition hypothesis* predicts reduced cooperation among vmPFC or amygdala patients, whereas the *prosocial*

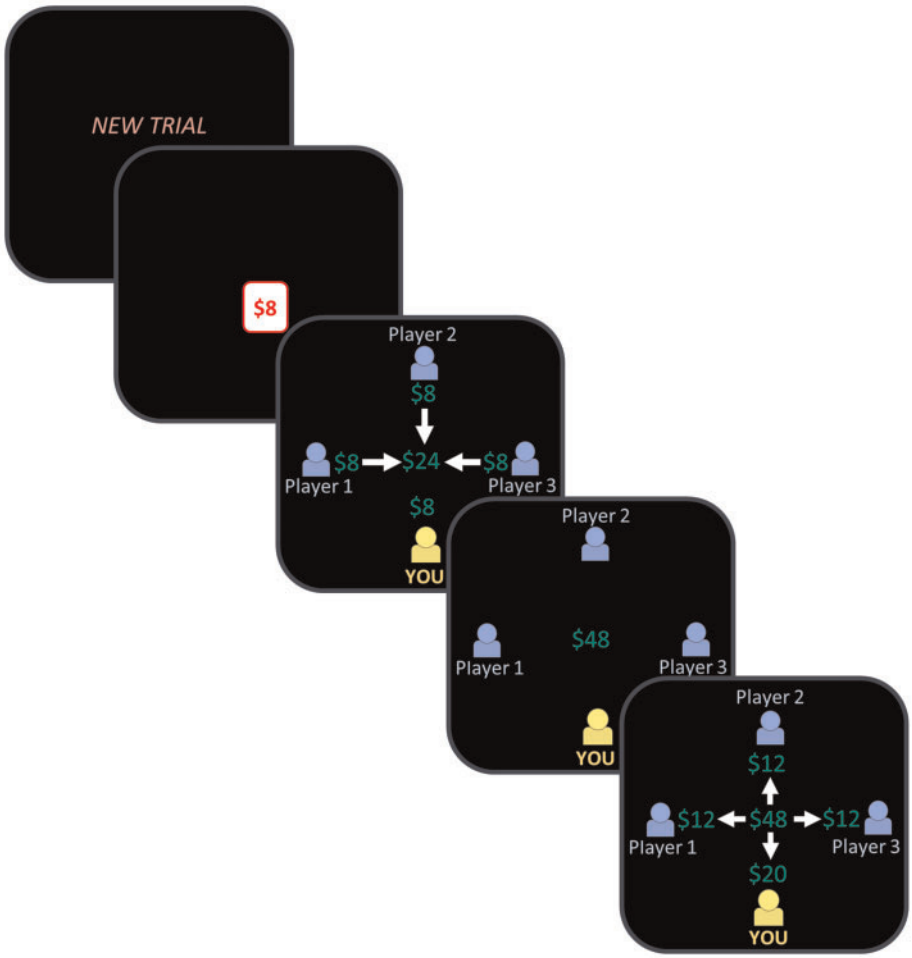

Fig. 2. The PGG. Each game began with a prompt indicating that a new round was about to begin. Participants decided whether to keep or give $8.00. Participants then saw three stages of guided feedback: (1) each player's contribution to the public good, (2) the total contribution multiplied by two, then (3) each player's resulting payout. Each feedback stage was presented for 5 s. The next trial began immediately afterwards, for a total of 20 games. Each game consisted of a separate one-shot interaction with three new players. In the example above, the participant decides to keep and then learns, in the feedback stage, that the other three players chose to give. Decisions to keep and give were depicted in yellow and blue, respectively. Not shown to scale.

restraint hypothesis predicts reduced cooperation among dlPFC patients. In contrast to the prosocial intuition hypothesis, vmPFC damage was associated with heightened cooperation [odds ratio (OR) = 1.55, 95% CI [1.06, 2.26], $\chi^2(1) = 5.09$, $P = 0.024$], such that the odds of cooperating were 1.55 times larger for each additional 10% of vmPFC damage. Consistent with the prosocial restraint hypothesis, dlPFC damage was associated with reduced cooperation (OR = 0.49, 95% CI [0.27, 0.90], $\chi^2(1) = 5.31$, $P = 0.021$), such that the odds of free-riding were 2.04 times larger for each additional 10% of dlPFC damage (Figure 3; see Supplementary Material Section S3 for analysis details). The degree of amygdala damage was not significantly associated with cooperative behavior (OR = 0.82, 95% CI [0.62, 1.06], $P = 0.133$). The overall results were consistent with models of prosocial restraint.

Secondary analyses

In addition to the ROI analysis using continuous regressors, we also tested whether overall cooperation rates differed between lesion groups (Figure 4; see Supplementary Material Section S5 for analysis details). The amygdala group (29.6% overall cooperation) cooperated at similar rates compared to the HC (41.0%) and BDC groups (43.8%), with no statistical difference between the HC and BDC participants (all $Ps > 0.15$). In contrast to the prosocial intuition hypothesis, the vmPFC patient cooperated more often (90%) than both the HC groups [OR = 13, $\chi^2(1) = 104.07$, $P < 0.001$] and BDC groups [OR = 10, $\chi^2(1) = 38.57$, $P < 0.001$]. Moreover, a bootstrapped 95% confidence interval indicated a lower bound of 15.36% cooperation among the amygdala group, suggesting neither amygdala nor vmPFC appear necessary for cooperation. Consistent with the prosocial restraint hypothesis, the patient with isolated dlPFC damage did not cooperate (0%) across the entire task, indicating the dlPFC may be necessary for cooperation. Although we are reluctant to draw general conclusions about task-specific effects of damage from single patients, this overall pattern of results (along with the primary ROI analysis) is consistent with the prosocial restraint hypothesis. A secondary analysis using voxel-based lesion symptom mapping produced convergent results consistent with models of prosocial restraint (Supplementary Material Section S6 and Supplementary Figure S4).

Several follow-up analyses were conducted in order to rule out alternative explanations. There is extensive evidence, for

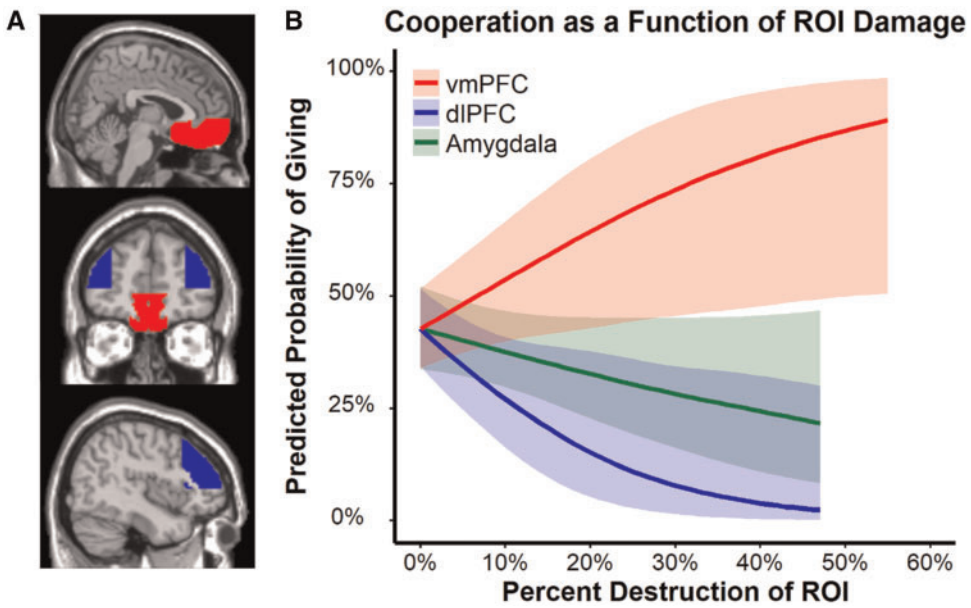

Fig. 3. Cooperation as a function of ROI damage. (A) vmPFC (red) and dlPFC (blue) ROIs are pictured at the following slices: Sagittal $X = 4$ (top), Coronal $Y = 40$ (middle), Sagittal $X = 44$ (bottom). (B) Predicted probabilities of giving are plotted against damage within each ROI, after adjusting for external ROI damage. Lines are interpolated through the range of the observed levels of predictors. Bands indicate 95% confidence intervals.

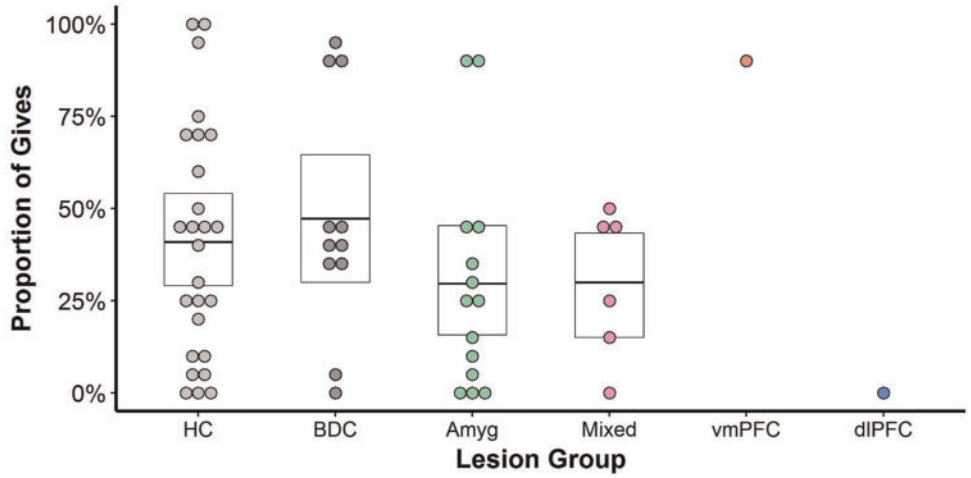

Fig. 4. Frequency of giving between isolated lesion groups. Proportions of 'give' decisions are shown for each participant group. Across all twenty trials, no differences were observed between healthy comparison (light grey), BDC (dark grey), and amygdala patients (green; all Ps >0.26). However, all three comparison groups differed significantly from the vmPFC and dlPFC patients. Results show that dlPFC damage is associated with reduced cooperation, and vmPFC damage is associated with greater cooperation. Violin plot width represents the density of the distribution for each frequency of giving (e.g. healthy comparison participants give 41% of the time more often than 100% of the time). Plot height is constrained to the range of the data for each group (e.g. amygdala patients never gave more than 90% of the time). Circles reflect mean for each lesion group. Vertical lines indicate ±1 SEM. Since the isolated vmPFC and dlPFC groups each consist of one patient, horizontal lines at the mean are used instead of error bars.

instance, that cooperation decays once participants learn that others are exploiting their generosity by free-riding (Frey and Meier, 2004). However, vmPFC patients may be particularly insensitive to trial-by-trial feedback, given fMRI work implicating this region in social norm learning (Behrens *et al.*, 2008). To address this possibility, we used the number of 'givers' (i.e. other players who cooperated on each trial) to compute two additional measures for each participant: (1) the number of givers on the trial preceding each decision and (2) the running average of givers across all trials that preceded each decision. Moreover, given evidence linking increased self-interest with slower decisions (Rand *et al.*, 2012) and experience (Rand *et al.*, 2014), we also entered reaction time and trial number into the model. Hierarchically entering these covariates into the analysis did not predict cooperation, nor did it qualitatively change the prior associations between ROI damage and cooperation (see Supplementary Table S2). Moreover, constraining the analysis to each participant's *first* decision (trial 1) revealed results consistent with the full data (Supplementary Figures S5 and S6). Prior PGG studies have occasionally revealed higher

contributions from women and younger participants (Rand *et al.*, 2012). However, our results did not significantly change when adjusting for participant age and gender (Supplementary Table S4). Overall, these follow-up analyses suggest the associations between ROI damage and cooperation are robust, even when adjusting for learning (see Supplementary Figures S10 and S11 for raw temporal data) and individual differences (see Supplementary Material Section S4 for further analyses).

Discussion

We investigated the necessity of several brain regions for group-based cooperation. A sample of lesion patients provided no evidence that the vmPFC or amygdala are necessary for cooperation in a PGG. This is particularly striking given prior fMRI investigations linking vmPFC (Rilling *et al.*, 2002) and amygdala (Fermin *et al.*, 2016) with cooperative decisions in two-player games. In contrast, the extent of dlPFC damage associated with reduced cooperation, and the patient with the greatest dlPFC damage did not cooperate on a single trial. Considering recent associations between dlPFC damage and greater dishonesty (Zhu *et al.*, 2014), this study adds to a growing body of literature showing that the lateral prefrontal cortex may be necessary for a broad range of prosocial behaviors.

Our findings have implications for competing models of prosocial behavior. The prosocial intuition hypothesis predicts that (1) impaired intuition (e.g. vmPFC or amygdala damage) will decrease cooperation, and (2) impaired deliberation (e.g. dlPFC damage) should increase (or at minimum preserve) cooperation. None of these predicted outcomes was observed, suggesting intuition did not guide cooperation in our sample. Instead, our behavioral and neuropsychological data were more consistent with prosocial restraint models.

We believe that there may still be contexts in which intuitive processes guide cooperative behavior (Rand, 2016). For instance, recent findings suggest that concerns over equity (i.e. fair allocations of resources) are intuitive whereas concerns over efficiency (i.e. maximizing collective resources, a likely component of our PGG) are deliberative (Capraro *et al.*, 2017). In addition, incentivizing cooperation (by manipulating the payoff contingencies) results in relatively faster and more frequent decisions to cooperate, whereas more costly cooperation produces the opposite pattern (Krajbich *et al.*, 2015). In our task, free-riding was the most common response among healthy controls. As a result, the neuropsychological associations we observed may reverse under conditions when cooperation is the modal response or involves efficiency tradeoffs.

The dual-process models of cooperation we tested have admittedly been largely silent to neuroscience. We hope that this investigation helps trigger the development of multi-level theories of cooperation and encourages future work leveraging the methods and samples from neuroscience to develop a more comprehensive understanding of human cooperation. For instance, there is growing evidence that models pitting intuition against deliberation may not capture the dynamic and widely distributed nature of evaluation and moral decision-making (Cunningham *et al.*, 2007; Van Bavel *et al.*, 2015). Thus, future investigations should examine broader neural substrates implicated in prosocial behavior, such as the ventral striatum (Fareri *et al.*, 2015), insular cortex (Lamm *et al.*, 2011), subgenual anterior cingulate cortex (FeldmanHall *et al.*, 2015) and temporal parietal junction (Hutcherson *et al.*, 2015). We also believe this approach will move theoretical debates beyond broad constructs, like intuition and deliberation, and focus on the underlying neural computations of value that guide cooperation.

One limitation of our primary analysis is that it assumes the ROIs we selected are fungible homogenous substrates (e.g. 10% damage to anterior vmPFC is equivalent to 10% damage to posterior vmPFC). Given evidence suggesting anterior vmPFC encodes more abstract, secondary reinforcers (Klein-Flügge *et al.*, 2013), future investigations should leverage larger samples that can fully capitalize on more spatially granular analyses, such as voxel-based lesion-symptom mapping (Rorden *et al.*, 2007). Nevertheless, while our sample size is smaller than typically seen in psychology papers, it is quite normal for lesion studies (e.g. Bechara *et al.*, 1996; Koenigs and Tranel, 2007; Spunt *et al.*, 2015). Indeed, lesion samples can provide critical insights into underlying cognitive processes. For instance, our models of human memory were revolutionized by a single participant (H.M.; Scoville and Milner, 1957).

Conclusion

The success of our political institutions, environmental stewardship, scientific progress and evolutionary fitness all hinge on our ability to prioritize collective-interest over self-interest. The present research illustrates how combining behavioral and neurological measures can help advance ancient philosophical debates about human benevolence. Understanding the neural systems involved helps clarify the underlying neuro-cognitive processes guiding cooperation and may ultimately inform interventions that push the limits of our cooperative potential.

Prior to this paper, JW presented these findings at various meetings and conferences. In addition, an earlier draft of the paper was posted as a preprint on PsyArXiv (https://osf.io/juhbx/).

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Supplementary data

Supplementary data are available at *SCAN* online.

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Conflict of interest. None declared. Competing financial interests: The authors declare no competing financial interests.

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Appendix

NYU PROSPEC Collaboration: The New York University Patient Registry for the Study of Perception, Emotion, and Cognition (NYU PROSPEC) includes the following group of clinical researchers and their affiliations.

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