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 re-
cent 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 so-
cial 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 de-
liberation—delayed, reflective processing. Some argue, for in-
stance, that humans' unique capacity for self-reflection (i.e. 
compared to other primates) provides a critical avenue to pro-
mote 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
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, we leverage neuro-psychological 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; Lebrun 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 (Koschik 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 = 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 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 = 30). All participants gave written informed consent. Across all groups, seven participants failed to meet our inclusion criteria (see Supplementary Table S1), 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 participant. Six (out of the eight) frontal patients had diffuse damage overlapping both vmPFC and dlPFC (r(6) = 0.26, 95% bootstrap 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,

\[ x^2(1) = 2.05, \quad P = 0.153 \]

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
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 $P$s > 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...
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 dPFC damage associated with reduced cooperation, and the patient with the greatest dPFC damage did not cooperate on a single trial. Considering recent associations between dPFC 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. dPFC 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 (Ferari 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/).

Acknowledgements
The authors would like to thank Augustus Baker for extensive assistance with data collection. The authors would also like to thank Elizabeth Phelps, Ph.D. for providing lab equipment and helpful comments on the manuscript as well as Oliver Vikbladh for technical assistance with the region of interest analysis and overlay maps. Furthermore, the authors would like to thank members of the NYU Social Perception and Evaluation Lab for insightful comments on this research and earlier drafts of this manuscript.

Supplementary data
Supplementary data are available at SCAN online.

Funding
The authors gratefully acknowledge the financial support of the National Science Foundation grant #1349089 awarded to Jay Van Bavel and the National Science Foundation Graduate Research Fellowship awarded to Julian Wills.

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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