Neural Mechanisms of Intergroup Exclusion and Retaliatory Aggression

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Abstract

Aggression occurs frequently and severely between rival groups. Although there has been much study into the psychological and socio-ecological determinants of intergroup aggression, the neuroscience of this phenomenon remains incomplete. To examine the neural correlates of aggression directed at outgroup (versus ingroup) targets, we recruited 35 healthy young male participants who were current or former students of the same university. While undergoing functional MRI, participants completed an aggression task against both an ingroup and an outgroup opponent in which their opponents repeatedly provoked them at varying levels and then participants could retaliate. Participants were then socially included and then excluded by two outgroup members and then completed the same aggression task against the same two opponents. Both before and after outgroup exclusion, aggression towards outgroup members was positively associated with activity in the ventral striatum during decisions about how aggressive to be towards their outgroup opponent. Aggression towards outgroup members was also linked to greater post-exclusion activity in the rostral and dorsal medial prefrontal cortex during provocation from their outgroup opponent. These altered patterns of brain activity suggest that frontostriatal mechanisms may play a significant role in motivating aggression towards outgroup members.

Keywords: aggression, intergroup aggression, exclusion, fMRI, reward

Introduction

Humans readily categorize people into ingroup and outgroups. This impulse has many consequences — chief of which is the promotion of intergroup conflict and hostility. Indeed, human aggression is often at its most severe against perceived outgroup members (Böhm et al., 2016; Brewer & Kramer, 1985; Cikara et al., 2011; Haslam, 2006; Jackson, 1993; Lickel et al., 2006). Decades of investigation have laid bare many of the psychological processes underlying aggression directed at outgroups, yet the neural mechanisms that subserve such intergroup aggression remain incompletely understood (for a review see Lantos & Molenberghs, 2021). To add to our understanding, we conducted a functional neuroimaging experiment in which participants were given the opportunity to physically harm (fictitious) ingroup and outgroup targets while we recorded their brain activity. Given the ability of perceived social exclusion to aggravate intergroup hostility (Hales & Williams, 2018), participants were also excluded by outgroup members and then given the opportunity to retaliate against one of them. Together, these procedures sought to simulate an antagonistic intergroup interaction, allowing us to peer into the neural mechanisms that promote hostility towards outgroup members.

Intergroup Aggression and its Psychological Bases

Aggression refers to any deliberate attempt to harm other people against their will (Allen & Anderson, 2017). Although aggression can and often does occur to all sorts of victims, it is often preferentially inflicted upon people that humans perceive to be members of disliked outgroups (Böhm et al., 2016; Brewer & Kramer, 1985; Cikara et al., 2011; Haslam, 2006; Jackson, 1993; Lickel et al., 2006). The psychological

mechanisms that underlying such outgroup-directed aggression are myriad. Aggressors against outgroup members are often motivated by the desire to defend their ingroup (Böhm et al., 2016), to avenge perceived harms done against their ingroup members (Lickel et al., 2006), to compete for resources (Jackson, 1993), as a consequences of dehumanizing them (Haslam, 2006), and due to failures of empathy (Cikara et al., 2011) — *inter alia*. Yet before any of these motivators can promote aggression against an outgroup, people must first undergo the cognitive process of forming an ingroup (i.e., an 'us') and then form contrastive and excluded outgroups (i.e., a 'them'; Reicher et al., 2008). Another key finding from the literature on intergroup aggression is that outgroup schadenfreude — the pleasure experience when perceiving the suffering of outgroup members — is a key driver behind the motivation to harm outgroup members (Cikara, 2015). Taken together, it is clear that intergroup aggression largely relies on (A) differentiating familiar ingroup members from dissimilar outgroup members (i.e., 'us' from 'them') and (B) transmuting pain into one's own pleasure.

The Neuroscience of Intergroup Hostility

Neuroscientific studies of intergroup conflict support the key role of 'us' and 'them' differentiation (Cikara & Van Bavel, 2014). This tendency toward group categorization is linked to functioning in multiple brain regions, including the anterior insula (Cikara et al., 2017; Lau et al., 2020). Another brain region that has particularly robust empirical links to group categorization is the medial prefrontal cortex (MPFC; Molenberghs & Morrison, 2014). The MPFC is involved in a host of psychological functions, but one of its most crucial is differentiating among the self, familiar others, and unfamiliar others (Denny et al., 2012; Lieberman et al., 2019). Meta-analytic

evidence supports the unique role of the dorsal MPFC in differentiating ingroup from outgroup members (Merritt et al., 2021). In combination with studies demonstrating the crucial role of the dorsal MPFC in promoting aggressive responses to provocation (e.g., Denson et al., 2009; Repple et al., 2017), the dorsal MPFC is a likely candidate underlying aggression against outgroup members.

Outgroup schadenfreude also has a clear neural basis that contributes to intergroup hostility — the ventral striatum. The ventral striatum is a subcortical region that includes the nucleus accumbens and olfactory tubercle, and is preferentially activated by rewarding stimuli (Diekhof et al., 2012). Viewing the misfortunes of outgroup members is linked to greater activation in the ventral striatum (Cikara et al., 2011). This finding suggests that harm done to outgroup members is not merely less vicariously painful, but that it is indeed pleasurable. Given the robust link between striatal reward responses and heightened aggression (Buades-Rotger et al., 2021; Chester & DeWall, 2016), the ventral striatum is another likely candidate to lie at the heart of intergroup aggression.

Intergroup Exclusion and Retaliation

Intergroup conflicts are characterized and exacerbated by social exclusion. Ingroup members often exclude outgroup members, which widens the intergroup divide and promotes retaliatory aggression (Hales & Williams, 2018; Renström et al., 2020). Yet less is known about *how* intergroup exclusion promotes intergroup aggression. Specifically, the neural correlates of intergroup exclusion, their contribution to intergroup aggression, and how the neural bases of intergroup aggression change post-exclusion remains poorly understood.

The Present Study

Prior research has come close to studying the neural correlates of aggression against outgroup members, yet such studies have used behavioral paradigms that either involve participants as passive witnesses (as opposed to active agents) in harm done to outgroup members or have used proxies of aggression (e.g., stealing points) that do not accurately reflect true aggressive behavior. To fill this gap and investigate the neural correlates of aggression against outgroup members and the role of intergroup exclusion therein, we conducted a functional magnetic resonance imaging (fMRI) study that simulated a competitive, antagonistic encounter between participants and ingroup and outgroup members. In line with decades of past research, we expected that participants would be more aggressive against outgroup, than ingroup, members (though we failed to preregister this prediction). We further predicted that this bias towards aggression against outgroup members would be linked to greater activity in the ventral striatum (representing outgroup schadenfreude) during decisions about how aggressive to be towards outgroup members (Hypothesis 1). We expected that provocation from outgroup members would be met with heightened dorsal MPFC activity (representing 'us' versus 'them' differentiation) and that this neural reactivity would, in turn, be associated with greater aggression towards outgroup members (Hypothesis 2). Finally, we predicted that the links between these patterns of brain activity and their links with outgroup aggression would be exacerbated after experiencing exclusion from outgroup members (Hypothesis 3).

Methods

Open Practices Statement

The preregistration plan for the present research is publicly available (https://osf.io/aj6eg). De-identified behavioral data and de-identified group-level contrast maps are also publicly available (https://osf.io/79jzy/files).

Ethical Practices Statement

Research activities summarized in the manuscript were pre-approved by an institutional review board and carried out in accordance with institutional and national regulations.

Statistical Power Statement

Statistical power was determined by logistical constraints (i.e., data collection continued until the COVID-19 pandemic ended in-person study sessions) and not an *a priori* power analysis. We preregistered a planned sample size of $N = 46$ participants, but due to the COVID-19 pandemic we only achieved a sample size of $N = 35$, which provided our analyses 80% power at $\alpha = .05$ to detect zero-order, between-participants main effects of $r = .44$ and larger. Given that effect sizes in the aggression literature are rarely this large (West et al., 2021), we mostly directed our focus towards the estimation of *within*-participants main effects.

Participants

Participants were 35 young adult, healthy, cisgender men (age: $M = 20.41$, $SD = 2.43$, range = 18-29) with considerable diversity (11.4% Hispanic, 85.7% Non-Hispanic, 2.9% missing ethnicity data; 22.9% Asian, 17.1% Black or African-American, 2.9% Pacific Islander, 45.7% White, 2.9% Multiracial, 5.7% "Other Race", 2.9% missing race data). Potential participants were recruited from the Richmond VA community ($n = 30$) and an introductory psychology subject pool ($n = 5$) via flyers and online

advertisements. We recruited only men because this study was part of a broader project on the neural bases of men's psychopathic aggression. To ensure the validity of our intergroup manipulation, all participants had to be current or former students of the same local university. We used an online screening questionnaire, which assessed the following additional exclusionary criteria that ensured participant safety and MRI data quality: age outside the range of 18 to 35, body mass index above 35, claustrophobia, color blindness, mental or neural pathology, metallic objects in the body, non-right-hand dominance, prior head trauma, and current psychoactive medication use. Each participant received either $40 or research credit for their participation.

Materials

fMRI aggression task. To assess aggression directed towards ingroup and outgroup targets, we adapted the well-established Taylor Aggression Paradigm, which has been effectively implemented in the fMRI environment (Chester & DeWall, 2016; Krämer et al., 2007). This paradigm exhibits good evidence of external, construct, criterion, and convergent validities (Chester & Lasko, 2019; Giancola & Parrott, 2008) and does not elicit excessive distress in participants (Parrott et al., 2015). As in previous iterations of the paradigm, participants repeatedly competed against an opponent to see who could press a button faster when a prompt appeared. In reality, there was no other person and participants completed the task against a computer program. As an ostensible motivational component of the task, participants were punished if they lost a given round of competition by receiving an aversive noise blast through a pair of headphones at the volume their fictitious opponent set for them. Conversely, if participants won the round of competition, their fictitious opponent ostensibly heard the

noise blast at the volume that participants previously set for them and the participant heard nothing. The task was modified to include a within-participants manipulation of aggression target (ingroup [i.e., a male student opponent from their own university], outgroup [i.e., a male student opponent from a local, rival university]; as in prior fMRI research on intergroup hostility: Molenberghs et al., 2014, 2016).

Participants completed two runs of the aggression task (one pre-exclusion, one post-exclusion). Each run of the aggression task consisted of four blocks of eight trials (32 trials total within-run). Two of these four blocks were dedicated to an ingroup opponent (16 trials total within-run) and the other two blocks were dedicated to an outgroup opponent (16 trials total within-run). The order of these four blocks was individually randomized for each participant by the task software within-run. Across both runs, this combined to a total of eight blocks (64 trials across both runs that were categorized into 32 trials per target).

The sequence of each block of the fMRI Aggression Task is depicted in Figure 1. At the beginning of each block, a screen indicated whether participants would be "playing the next 8 rounds against" an ingroup opponent (i.e., "a [same university] student") or an outgroup opponent (i.e., "a [rival university] student"; 4.3s duration). Continuous on-screen reminders of the target's identity were not provided to participants after this initial screen. Each subsequent trial consisted of six events. First, participants passively viewed a fixation cross that modeled baseline neural activity (randomly jittered between 2.15s and 4.3s durations). Then, participants selected the volume of the noise blast to administer to their opponent along a 1 (Low) to 4 (High) scale (3.225s duration). A blank screen then appeared followed by a red square that

indicated to participants that they should press the button as fast as possible to compete against their opponent (3.225s duration). Participants then saw what volume level their opponent set for them (3.225s duration). Finally, participants saw whether they won or lost the competition and, if they lost, experienced the corresponding noise blast (2.15s duration). Opponents' volume settings and the outcome of each trial were randomized with replacement, such that any volume and outcome combination could occur on any given trial.

Figure 1

An Example of One Block of the fMRI Aggression Task
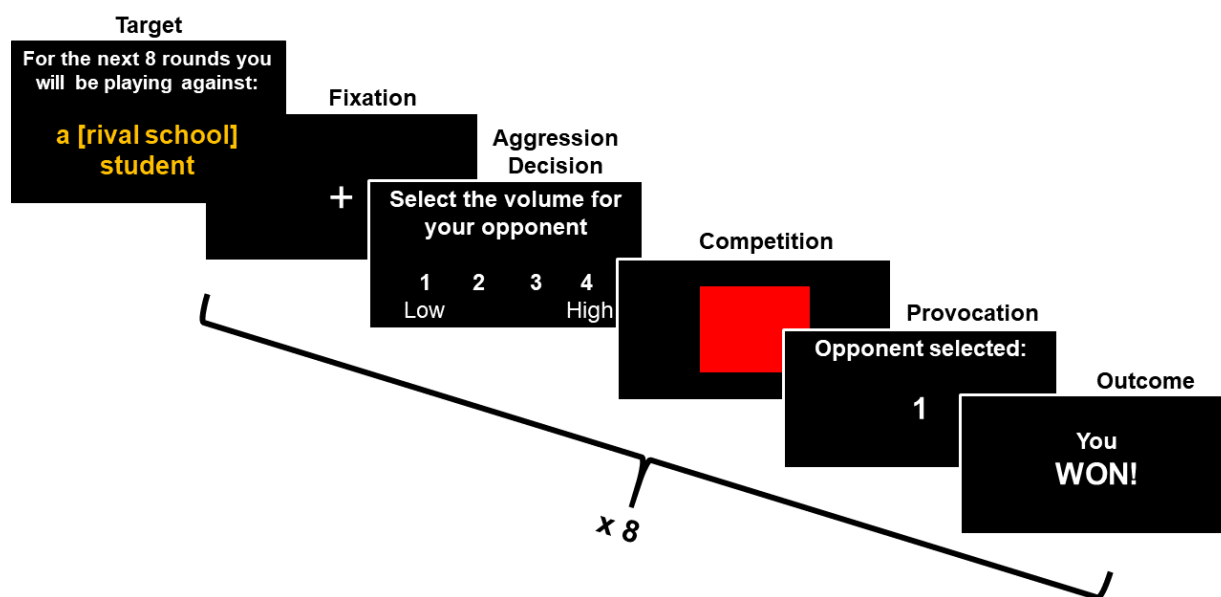
Cyberball task. To induce an experience of social exclusion by outgroup members in the functional neuroimaging environment, we employed the Cyberball social exclusion task (Eisenberger et al., 2003; Williams, Cheung, & Choi, 2000). In this task, participants were instructed to play a virtual ball-tossing game with two fictitious partners who were described to participants as students from the rival university. The ostensible purpose of the task was for participants to mentally visualize the task as if it

were occurring in real life. The task proceeded across three blocks. The first two blocks were 60s in duration and the third block was 91.075s. Each block of ball-tossing was preceded by a 10s rest event (that captured baseline activation) and a 2s 'Get Ready' event (that signaled that each rest period was over and that participants should prepare for the ball-tossing aspect of each block to begin). All participants received an equal number of ball-tosses from their two partners for the full 60s of the first two blocks and the first 30s of the third block (i.e., Outgroup Inclusion). After the inclusionary period of the third block, participants stopped receiving the ball from their partners who continuously threw it back-and-forth to one another for 61.075s (i.e., Outgroup Exclusion). Total task time was 4m 7.25s.

Ingroup and outgroup feeling thermometers. In order to validate whether our group manipulation evoked ingroup positivity and outgroup negativity, we administered two feeling thermometers. The thermometers asked participants how they felt towards students from their own university or a rival university along a 0 (Very Cold) to 50 (No Feeling) to 100 (Very Warm) response scale. Such feeling thermometers are widely used as valid indicators of ingroup positivity and outgroup negativity (e.g., Gonsalkorale & Williams, 2007).

Need threat scale. The 22-item Need Threat Scale served as a manipulation check of the Cyberball paradigm's ability to elicit rejection threat (Riva et al., 2011; Van Beest & Williams, 2006; Williams, 2009). Deviating from our preregistered plan to use all 22 items, we instead focused on the two key items that assessed how excluded participants felt by the Cyberball task ("I was ignored", "I was excluded"). Participants responded to each item along a 1 (Not at all) to 5 (Extremely) response scale. We

computed scores by averaging the two items together. This two-item subscale much more closely captured our construct of interest (i.e., how excluded participants felt by the Cyberball task) than the full, 22-item measure.

Procedure

We recruited participants for a study that ostensibly sought to better understand the neural basis of how different groups make decisions. Participants arrived at the MRI center to complete a three-hour laboratory session. As a broad overview of the procedure, all participants completed an aggression task against both an ingroup and outgroup opponent, then completed a ball-tossing task in which they were included-then-excluded by that same outgroup opponent (and another outgroup member), and then again completed the same aggression task against the same ingroup and outgroup opponents --- all while undergoing fMRI (overview depicted in Figure 2).

Figure 2

Overview of Tasks Completed by All Participants During MRI Scan Procedures
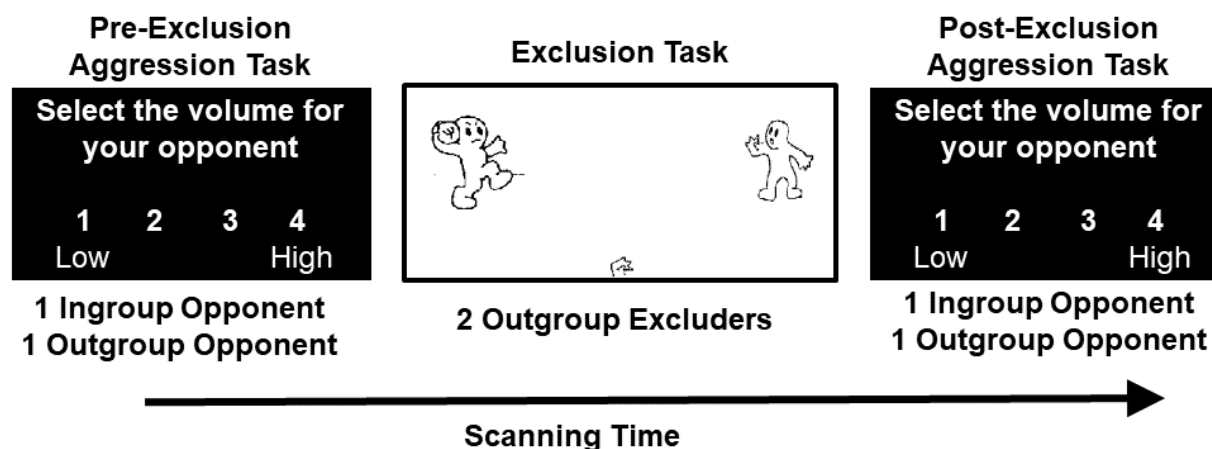
Once participants had arrived, they were verbally given the cover story for our study, that it was focused on "*how people from different groups make decisions and how these differences are represented in the brain. To examine these processes, we*

are going to observe your brain's function and structure while you interact with students from your own university and a rival school." The consent form repeated this cover study. After completing the informed consent form, participants were again screened for MRI safety and then practiced the computer tasks they would complete in the MRI scanner. The practice version of the MRI Aggression Task repeated the cover story with more details (i.e., they would be competing against two male opponents over the internet, one from their own school and one from the rival school). The practice version of the Cyberball Exclusion Task also repeated the cover story with more details (i.e., they would be interacting with two students from the rival school). No confederates were employed in these procedures and participants were not told the exact location of their opponents.

Participants then completed the MRI scanning procedures, which began with several anatomical scans. After the first and second anatomical scans, we verbally informed participants that we were attempting to virtually connect to their partners for the upcoming computer tasks. After the anatomical scans, participants completed an unrelated image viewing and rating task. To begin the pre-exclusion run of the MRI Aggression Task, we verbally informed participants that "*we are going to perform the competitive reaction-time task that we practiced earlier against a student from [the participant's university] and a student from the [rival university]. Your partners are finally all connected to us over the internet so we can begin.*" After the first run of the MRI Aggression Task, we verbally informed participants that "*we are going to perform the virtual ball-tossing task called Cyberball that we practiced earlier with two students from [rival university]. One of your Cyberball partners was your [rival university] opponent*

from the previous competitive reaction-time task." After we verbally pretended to check

to ensure that the new outgroup partner was connected over the internet, participants

completed the Cyberball Task. To then begin the post-exclusion run of the MRI

Aggression Task, we verbally informed participants that "*now we are going to perform*

the competitive reaction-time task again. As before, you are playing against THE SAME

student from [the participant's university] and THE SAME student from the [rival

university]."

Once the MRI scans were complete, participants were removed from the

scanner, and then completed a computerized battery of self-report measures. At the

end of the laboratory session, we gave participants a three-question, funneling

suspicion interview to assess their knowledge regarding the deceptive elements of the

study. No participants indicated suspicion surrounding their fictitious partners when

asked "*did anything seem strange or unusual to you during this study?*" We then

individually debriefed participants as to the deception and true purposes of the study,

provided each with mental health resources, paid them, thanked them, and then

escorted them from the laboratory.

MRI Data Acquisition

All MRI data were obtained using a Philips Ingenia 3.0 Tesla scanner with a 32-

channel headcoil. Echo planar BOLD images were acquired with a T2*-weighted

gradient across the entire brain with: a 3D shim, field of view (FOV) = 240mm x 240mm

x 125.5mm, echo time (TE) = 75ms, repetition time (TR) = 1075ms, slice thickness =

3mm, 36 transverse slices acquired with a multi-band acquisition sequence (MB factor =

4), flip angle = 90°. Eight dummy functional volumes were acquired and discarded from

the beginning of each functional run to allow for signal equilibration. To allow for

registration to native space, a coplanar, magnetization-prepared rapid gradient-echo

(MPRAGE) sequence was also acquired from each participant, with: FOV = 240mm x

259mm x 160mm, slice thickness = 1mm, TE = 3.7ms, TR = 8.1s, 160 sagittal slices, flip

angle = 6°.

MRI Data Preprocessing

The Oxford Center for Functional MRI of the Brain's Software Library (FSL

version 6.0) was used to conduct all preprocessing and fMRI analyses (Smith et al.,

2004). Reconstructed functional volumes underwent head motion correction to the

median functional volume using FSL's MCFLIRT tool. FSL's Brain Extraction Tool was

used to remove non-brain tissue from all functional and structural volumes. After a

series of data-quality checks, functional volumes underwent pre-whitening, spatial

smoothing (using a 6mm full-width-half-maximum Gaussian kernel), and temporal high-

pass filtering (100s cutoff). No slice timing correction was used due to multiband

acquisition. These processed brain volumes were then fed into subsequent data

analyses.

Deviations From Preregistered Analytic Plan

Our preregistration plan included several hypotheses and analyses that

examined between-participants effects. However, given the smaller sample size that we

obtained (and the fact that this would only allow us to detect between-participants that

were too large to reasonably expect [$r > .43$]), we were likely to be too statistically

underpowered to adequately test them. As such, we focused our inferential tests on

within-participants effects excepting our whole-brain regression analyses in which we

examined between-participants variation in neural correlates of outgroup aggression.

MRI Data Analysis

Aggression task - first level (within-participant, within-run). Participants'
whole-brain functional volumes from each run of the aggression task were entered into
a fixed-effects general linear model (GLM) that modeled events using a canonical
double-gamma hemodynamic response function with a temporal derivative. Regressors
of interest for the aggression task included aggression decision events (3.225s duration
per event; i.e., events in which participants decided upon the volume to deliver to their
opponents) towards outgroup targets (i.e., students from their own university) and
outgroup targets (i.e., students from a rival university). We also separately modeled
provocation events (3.225s duration per event; i.e., events in which participants viewed
the specific volume their fictitious opponents selected for them; e.g., 4) from ingroup
and outgroup opponents. In each provocation event, participants viewed the precise
volume level (1 - 4) their opponent provided for them for that particular trial. Accordingly,
provocation was operationalized along this four-point continuum that continuously
ranged from low provocation (i.e., 1) to high provocation (i.e., 4).

All other events were included as nuisance regressors and fixation events were
left unmodeled to create an implicit functional baseline. Linear contrasts compared
Outgroup Aggression Decisions > Ingroup Aggression Decisions (which tested
Hypothesis 1) and Outgroup Provocation > Ingroup Provocation (which tested
Hypothesis 2). Each participant's resulting contrast brain maps from these analyses
were first linearly registered to native space structural volumes and then spatially
normalized to a Montreal Neurological Institute (MNI) stereotaxic space template image

(resampled into 2mm^3 isotropic voxels).

Parametric modulation of provocation. Ingroup and outgroup provocation events were modeled in both non-modulated and parametrically modulated forms. In the modulated form, each provocation event was modulated by the 1-4 volume level selected by the fictitious opponent (i.e., modulated by the software's provocation settings for the participant). Such parametric modulation was not performed for aggression decision events (i.e., in which participants selected the volume for their fictitious opponent), as most participants did not respond within the 3.225s timeframe for all trials, creating missing data.

Aggression task - first level (within-participant, across-runs). A fixed-effects GLM then aggregated the contrast maps from each participant's two pre-exclusion and post-exclusion functional runs into two contrast maps that either combined both runs or modeled a Post-Exclusion > Pre-Exclusion contrast (which tested Hypothesis 3).

Aggression task - second level (across-participants). Participants' contrast maps from the first level were then fed into a second level, mixed-effects GLM that created whole-brain group average maps for each within-run contrast and each across-run contrast (e.g., Post-Exclusion > Pre-Exclusion | Outgroup Aggression > Ingroup Aggression). This GLM also served as a between-participants whole-brain regression analysis that modeled each participant's outgroup aggression. Outgroup aggression values were created by separately averaging participants' volume settings towards their outgroup and ingroup opponents (across both pre-exclusion and post-exclusion runs) and then subtracting the ingroup aggression score from the outgroup aggression score. Higher values on this variable indicated a bias towards greater outgroup aggression.

Clusters were initially defined using a *Z* statistic threshold (i.e., 2.3). Significant clusters were identified from these initial clusters if they were below our cluster probability threshold (i.e., *p* < .05) estimated from Gaussian random field theory and corrected for family-wise error rates (Heller et al., 2006).

Cyberball task - first level (within-participant, within-run). Participants' whole-brain functional volumes from the Cyberball Exclusion Task were entered into a fixed-effects GLM that modeled events using a canonical double-gamma hemodynamic response function with a temporal derivative. Regressors-of-interest included Outgroup Inclusion (150s total duration) and Outgroup Exclusion (61.075s total duration). 'Get Ready' events were included as nuisance regressors and baseline rest events were left un-modeled to create an implicit functional baseline. A linear contrasts compared Outgroup Exclusion > Outgroup Inclusion. Each participant's resulting contrast brain maps from these analyses were first linearly registered to native space structural volumes and then spatially normalized to a MNI stereotaxic space template image (resampled into 2mm^3 isotropic voxels).

Cyberball task - second level (across-participants). Participants' contrast maps from the first level were then fed into a second level, mixed-effects GLM that created a whole-brain group average map. As with the aggression task, the GLM for the Cyberball exclusion task included a whole-brain regression analysis that modeled each participant's outgroup aggression score as a continuous regressor. Cluster-based, family-wise error correction was performed in an identical manner to the aggression task.

Behavioral Analyses

Although we did not preregister any hypotheses relating only to the behavioral and self-report data we collected, we did expect that participants would report greater warmth towards their ingroup than the rival university outgroup (as tested via a paired-samples t-test). We also predicted that participants would select higher noise blasts for outgroup (than ingroup) targets and that this difference would be exacerbated after being excluded by the outgroup, as tested via a 2 (target: ingroup versus outgroup) x 2 (time: pre-exclusion versus post-exclusion) repeated-measures ANalysis-Of-VAriance (ANOVA). These behavioral analyses were conducted using JASP (v. 0.11.1; JASP Team, 2020).

Results

Descriptive statistics are provided in Table 1. Validating our group manipulation, participants felt more warmly towards their own university's students than the rival university's students, $t(33) = 2.98$, $p = .005$, $d = 0.51$ (*95% CI* $= 0.15, 0.87$). Participants reported experiencing substantial variability in their feelings of exclusion via the Need Threat Scale's measure of felt rejection, exhibiting scores that spanned the full range of the response scale, $\alpha = .95$ (Table 1). Yet, participants' mean levels of felt exclusion did not differ significantly from the midpoint of the response scale (i.e., 3), $M = 3.10$, $SD = 1.19$, $t(33) = 0.50$, $p = .618$.

Table 1

*Descriptive Statistics of Key Study Variables, Separated by Target*

Measure	Ingroup			Outgroup		
	M	SD	Range	M	SD	Range
Feeling Thermometer	71.62	17.45	45 - 100	65.85	16.91	40 - 100
Pre-Exclusion Aggression	2.35	1.01	1 - 4	2.33	1.02	1 - 4
Post-Exclusion Aggression	2.28	1.07	1 - 4	2.45	1.13	1 - 4

Aggression Task Behavioral Data

Against our predictions, we observed no main effects of target, $F(1,34) = 2.48$, p = .125, η_p^2 = .07, or time, $F(1,34) = 0.15$, p = .705, η_p^2 = .00 (Figure 3). Further, there was no interactive effect between these two variables, $F(1,34) = 3.25$, p = .080, η_p^2 = .09. Exploratory contrasts demonstrated that there was no significant effect of target pre-exclusion, $F(1) = 0.16$, p = .691, yet participants did exhibit greater aggression towards outgroup (than ingroup) targets post-exclusion, $F(1) = 4.50$, p = .041.

Figure 3

Means and Standard Errors of Aggression, Separated by Target and Time
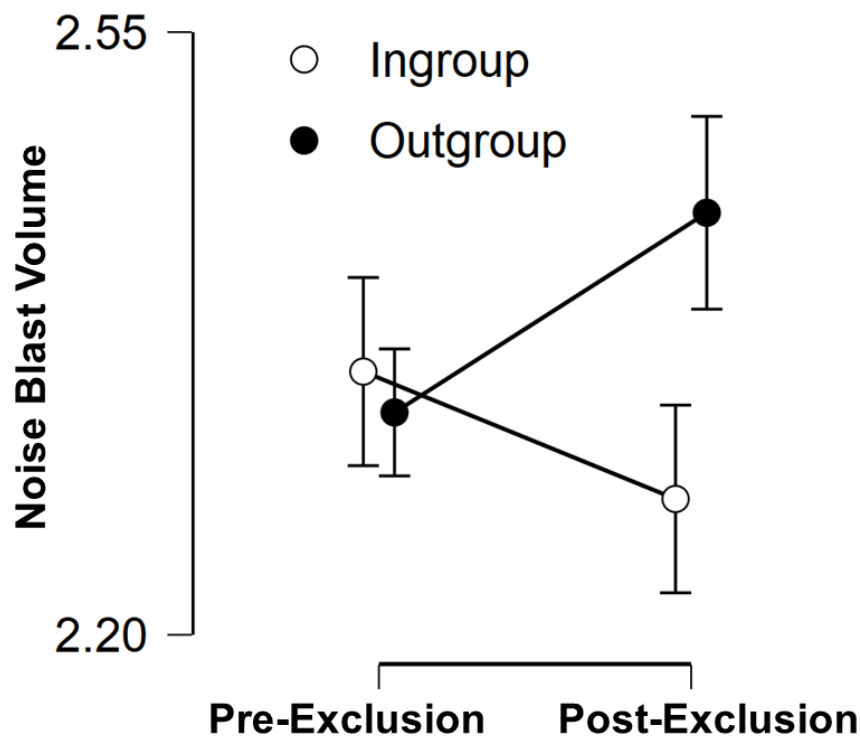
Neural Correlates of Outgroup Exclusion

Outgroup Exclusion (> Outgroup Inclusion) was associated with greater activity in dorsal MPFC, right dorsolateral PFC, as well as left temporoparietal junction and lateral

occipital lobe (Figure 4, Table 2). The continuous outgroup aggression regressor was

unassociated with any exclusion-related brain activity.

Figure 4

Activity in Dorsomedial Prefrontal Cortex and Temporoparietal Junction During
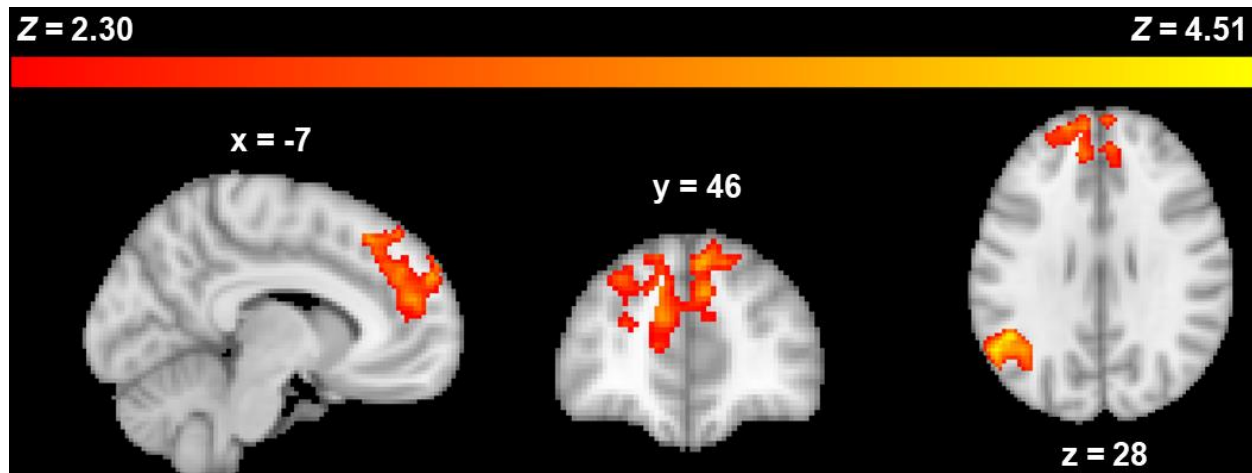
Outgroup Exclusion > Outgroup Inclusion

Table 2

Brain Regions More Active During Outgroup Exclusion > Ingroup Exclusion

Cluster	Voxels	Brain Region	Peak Z	Peak x,y,z
1	1,809	Dorsomedial PFC	4.21	-16, 56, 30
			4.15	10, 56, 38
			4.10	-22, 50, 32
			3.95	-10, 58, 32
			3.90	2, 58, 22
			3.86	6, 44, 42
2	1,440	Temporoparietal Junction	4.51	-46, -52, 26
		Lateral Occipital Lobe	4.44	-54, -62, 12
		Temporoparietal Junction	4.37	-54, -60, 28
			4.25	-52, -56, 28
		Lateral Occipital Lobe	4.15	-54, -64, 26
			4.09	-48, -72, 10
3	453	Dorsolateral PFC	4.32	48, 0, 46
			4.00	46, 8, 40
			3.09	42, -2, 56
			3.05	44, 2, 54
			2.85	34. 2. 38

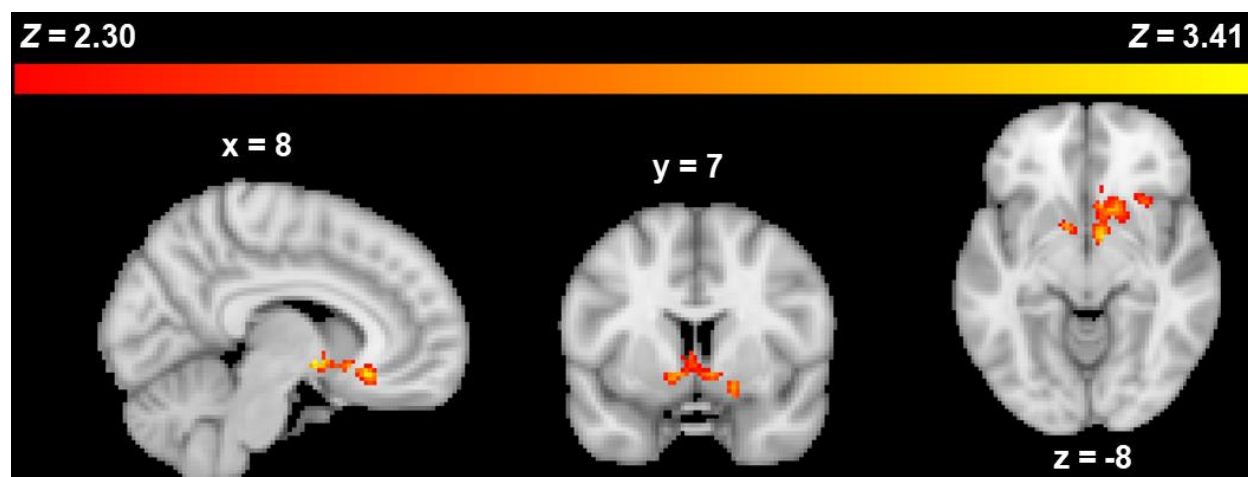*Note.* Each cluster is displayed with rows for all local maxima

Decision-Based Neural Correlates of Aggression Towards Outgroup Targets

Across both the pre-exclusion and post-exclusion runs, the louder that

participants set noise blasts for their outgroup opponent (relative to their ingroup

opponent) during Outgroup Aggression Decisions (> Ingroup Aggression Decisions;

Hypothesis 1), the more activity we observed in the bilateral ventral striatum and

overlying caudate and putamen: 595 voxels; peak voxel: Z = 3.41, MNI coordinates: x =

8, y = 0, z = -6 (Figure 5). This cluster extended rostrally into the neighboring right

hemisphere's anterior insula and orbitofrontal cortex. No such significant outgroup

aggression related brain activity was observed when we compared post-exclusion >

pre-exclusion.

Figure 5

Activity in Ventral and Dorsal Striatum and Insular/Orbitofrontal Cortex during Outgroup

> Ingroup Aggression Decisions, Which was Positively Linked to Outgroup Aggression


Provocation-Based Neural Correlates of Aggression Towards Outgroup Targets

Subsequent fMRI analyses examined the whole-brain correlates of Outgroup

Provocation (> Ingroup Provocation; Hypothesis 2) and their association with

aggression towards outgroup targets. Across both the pre-exclusion and post-exclusion

runs, no significant brain activity was associated with outgroup aggression. However,

when we compared Post-Exclusion > Pre-Exclusion provocation events (Hypothesis 3),

we observed that the louder the noise blasts that participants set for their outgroup

opponent (relative to their ingroup opponent) during Outgroup Provocation (> Ingroup

Provocation), the more activity we observed in the rostral anterior cingulate cortex, the

rostral MPFC, and the dorsal MPFC: 886 voxels; Brodmann's areas 9, 10, 11, 24, 25,

and 32; peak voxel: $Z = 3.70$, MNI coordinates: x = 2, y = 54, z = 15 (Figure 6).

Figure 6

Activity in Dorsal/Rostral Anterior Cingulate and Medial Prefrontal Cortices During

Parametrically-Modulated Outgroup > Ingroup Provocation Events, Which was

Positively Linked to Outgroup Aggression
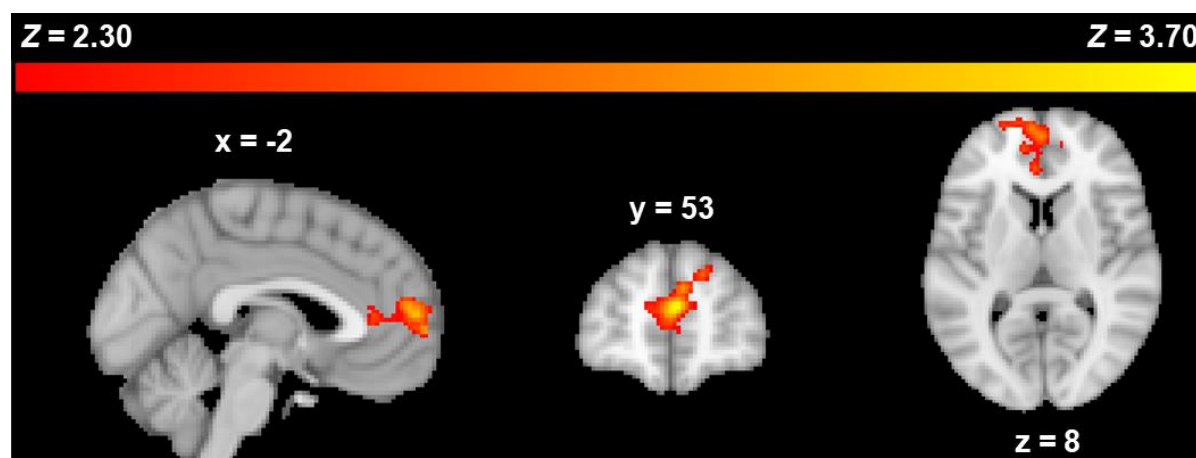
Exploratory Analyses on the Anterior Insula

Given the well-established role of the anterior insula in intergroup cognition

(Cikara et al., 2017; Lau et al., 2020), we re-ran our fMRI analyses in an exploratory

fashion on the MRI Aggression Task as before, except that they were now constrained

to the anterior insula. To do so, we selected an anatomical mask from the automated

anatomical atlas (AAL; Tzourio-Mazoyer et al., 2002) that corresponded to the bilateral

agranular insula using a caudal boundary of y = 8. This analyses did not return any

clusters that were significantly activated in the Outgroup Aggression Decisions >

Ingroup Aggression Decisions or Outgroup Provocation > Ingroup Provocation

contrasts. These null effects were observed pre-exclusion, post-exclusion, when

aggregated across these two runs, and when these two runs were contrasted against

each other.

Discussion

In the present research, we sought to identify the neural mechanisms that

underpinned aggression against provocative and exclusionary outgroup members. We

found an array of frontostriatal correlates of intergroup aggression, exclusion, and

provocation that opened a window into the complex forces driving the harm people often

inflict on members of outgroups.

Behavioral Findings

At a behavioral level, participants were no more aggressive towards outgroup

members than ingroup members prior to exclusion. This failed to replicate past work in

which people typically are more aggressive towards outgroup members (Böhm et al.,

2016; Brewer & Kramer, 1985; Cikara et al., 2011; Haslam, 2006; Jackson, 1993; Lickel

et al., 2006). This may reflect that participants may have forgotten what target they were

aggressing towards (due to the lack of continuous on-screen reminders) or that we did

not select an outgroup that participants felt a significant degree of animosity towards.

Indeed, participants rated the outgroup at a rather balmy 66 degrees. Nonetheless,

participants still were warmer towards the ingroup, allowing us some comparative

degree of outgroup negativity (even if it did not approach 'outgroup hate'). This suggests

that our study was a conservative test of our predictions, obtaining results with this

relatively mild group preference. Future work is needed to seek to replicate our findings

with an outgroup that elicited stronger negativity.

Participants were modestly more aggressive after exclusion, a retaliatory strategy. This post-exclusion increase in outgroup-directed aggression fits with the literature's finding that exclusion by outgroup members is a powerful motivator for retaliatory intergroup aggression (Hales & Williams, 2018). Further, these findings support the broader phenomenon of the rejection-aggression link (Chester et al., 2018).

Outgroup Exclusion

Our Cyberball manipulation was questionably effective in eliciting feelings of exclusion and this is a meaningful limitation of the research. Indeed, self-reports of feelings of exclusion were characterized by ambivalence as evidence by a distribution of scores that centered on the midpoint of the scale coupled with substantial variability. As such, it appears that many participants felt excluded by this paradigm and many did not. This ambivalence does not clearly mesh well with previous research demonstrating that even exclusion from hated outgroup members can elicit social pain (Gonsalkorale & Williams, 2007). It may be that exclusion from outgroup members simply is not that distressing. Indeed, our neuroimaging results suggested the presence of a social pain deficit. More specifically, there was a lack of outgroup-exclusion-related activity in the dorsal anterior cingulate cortex and anterior insula. These two cortical regions comprise an affective pain matrix that reliably indexes social pain in the context of social exclusion (Eisenberger, 2012). Their absence may indicate that the rejection was less distressing than we typically observe during exclusion from ingroup members. This potential social pain deficit would fit with Social Pain Overlap Theory (Eisenberger & Lieberman, 2004), which posits that the distress of exclusion evolved to facilitate our

inclusion in our supportive ingroups. As such, exclusion should be most distressing for

ingroups, who are more likely to provide social support, and less distressing for

outgroups, who are less likely to provide social support.

We did observe heightened activity in key nodes of the default mode or

mentalizing network (i.e., dorsal MPFC, temporoparietal junction) during outgroup

exclusion. Meta-analytic evidence suggests that these are some of the most reliable

neural correlates of social exclusion (Mwilambwe-Tshilobo & Spreng, 2021). The

presence of these default mode network hubs indicates that although outgroup

exclusion may be less distressing than ingroup exclusion, it still contains core, social

cognitive aspects of the exclusionary experience. Sadly, we were unable to include an

ingroup exclusion condition and future research is needed that directly contrasts ingroup

and outgroup exclusion within the same sample. Similarly, our lack of a sub-sample of

participants who were not excluded by outgroup members undermines our ability to

make inferences about the effect of exclusion, as the changes in aggression or neural

activity that we observed may simply be due to the passage of time. Our Cyberball

exclusion task was also limited by the lack of randomized ordering of the inclusion and

exclusion blocks. This leads to a temporal confound in which exclusion always followed

inclusion, which was necessary to avoid the contamination of the inclusion block by any

preceding inclusion (as in Chester et al., 2018). Future work will benefit from event-

related designs that randomly intersperse exclusionary and inclusionary events from

both ingroup and outgroup members.

Striatal Responses to Outgroup-Directed Aggression

Our finding that outgroup aggression was associated with a cluster of activity in

the ventral striatum, dorsal striatum, and medial orbitofrontal cortex all suggest the

presence of a neural reward response. People often enjoy the suffering of outgroup

members (Cikara, 2015), yet our striatal finding is one of the first to suggest that they

enjoy *inflicting* such outgroup harm themselves. Instead of a passive enjoyment of

others' suffering, this striatal finding supports a view of outgroup aggressors as

engaging in reward-driven behavior. This is consistent with a Reinforcement Model of

Aggression (Chester et al., 2018), in which striatal reward responses cause a

subjectively appetitive aggression experience, which promotes future acts of outgroup

aggression seeking. As such, simple reinforcement learning principles may help explain

something as complex as intergroup conflict. More work is needed to examine how

reinforcement learning and reward-based processes promote aggression against

outgroup targets.

The striatal response to decisions to harm outgroup members was observed

across pre-exclusion and post-exclusion runs and was not magnified post-exclusion.

Thus, we failed to support our prediction that such striatal responses would be

magnified after outgroup exclusion. These findings suggest that the reward of outgroup-

directed aggression is largely insensitive to exclusion, though it is unknown why this is

the case. Another unresolved mystery revolves around why we were able to observe

significant clusters of outgroup-aggression-related brain activity when a previous

investigation found no such differences across the brain (Molenberghs et al., 2014).

Dorsal MPFC Response to Outgroup Provocation

We expected to see heightened dorsal MPFC reactivity to outgroup provocation

across both pre-exclusion and post-exclusion runs, and yet we only observed this brain

region's response *after* outgroup exclusion. It is unclear why our prediction was only supported after social exclusion, though this may be due to the relatively weak outgroup we created. Nonetheless, this finding fits well with neuroscientific models of intergroup dynamics that center on the crucial role of the MPFC in social categorization (Molenberghs & Morrison, 2014). These results also mesh with findings from aggression neuroscience that highlight the critical role of the dorsal MPFC in promoting retaliatory aggression in response to provocation (Denson et al., 2009; Lotze et al., 2007; Repple et al., 2017). Unexpectedly, the dorsal MPFC activity we did observe extended considerably into the underlying rostral MPFC. Meta-analyses suggest that the rostral MPFC differs from other MPFC regions in its unique processing of self-related stimuli (Lieberman et al., 2019). As such, self-related processes subserved by the rostral MPFC may be particularly at play in promoting retaliatory responses to exclusionary outgroup members.

Limitations and Future Directions

All of our inferences as to the psychological processes represented by the patterns of brain activity we saw rely on potentially problematic reverse inferences. We did include several manipulation check measures but our sample was too underpowered to adequately test them against their intended brain correlates. Indeed, our sample size was also much smaller than our preregistration plan laid out, rendering it unable to test our preregistered between-participants hypotheses. Future work is needed to replicate these findings and validate them against well-crafted manipulation checks. Additionally, our participants were all men from a specific city in a Western country, severely limiting the generalizability of our findings. Much more research is

needed into the neural mechanisms underlying intergroup aggression with a broader

diversity of participants.

Conclusions

Why does intergroup conflict persist into the modern age? Our findings suggest

that aggression towards outgroup members has a robust brain basis that reflects the

complex psychological processes involved in such intergroup hostility. We implicated

frontostriatal circuits involved in reward processing and social cognition, which may help

us understand and intervene upon group-based violence. We hope that future work will

seek to replicate and extend these findings in the hope of promoting a more peaceful

world.

Author Contributions

DS Chester developed the study concept. DS Chester and EN Lasko developed the study design. EN Lasko, AC Dagher, and SJ West collected the data. DS Chester performed the data analyses with assistance from EN Lasko and SJ West. DS Chester drafted the manuscript and all authors provided critical revisions and approved the final version of the manuscript for submission.

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