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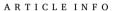


Review article

The neuroscience of intergroup threat and violence

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ABSTRACT

The COVID-19 pandemic led to a global increase in hate crimes and xenophobia. In these uncertain times, real or imaginary threats can easily lead to intergroup conflict. Here, we integrate social neuroscience findings with classic social psychology theories into a framework to better understand how intergroup threat can lead to violence. The role of moral disengagement, dehumanization, and intergroup schadenfreude in this process are discussed, together with their underlying neural mechanisms. We outline how this framework can inform social scientists and policy makers to help reduce the escalation of intergroup conflict and promote intergroup cooperation. The critical role of the media and public figures in these unprecedented times is highlighted as an important factor to achieve these goals.

1. Introduction

The COVID-19 pandemic led to a surge in xenophobic and hostile attitudes toward certain groups (Devakumar et al., 2020). Across the world, minority groups are experiencing an increase in hate crimes, with organisations including the United Nations (United Nations, 2020) and the FBI raising their concerns (Campbell, 2020). Some political leaders encourage animosity toward outgroup members: US President Donald Trump repeatedly called COVID-19 the "Chinese virus" (Viala-Gaudefroy and Lindaman, 2020), Hungary's prime minister Viktor Orbán associated the pandemic with migrants (Rohac, 2020), while Italy's former interior minister Matteo Salvini blamed African refugees for the outbreak in Italy (Tondo, 2020). But the rise in discrimination toward outgroups is not only apparent in Western countries. For example, African people living in China experienced increased discrimination and prolonged periods of forced quarantine (Vincent, 2020), while Muslims have been blamed for the spread of the virus in India, leading to the physical assault of some individuals (Slater and Masih, 2020). In many countries across the globe, perceived threat from the virus is becoming equivalent to outgroup threat.

Associating outgroups with existential threats fosters intergroup violence (Greenberg et al., 2016). Here, we present an overview of social neuroscientific findings from functional magnetic resonance imaging (fMRI) studies related to intergroup threat and violence. FMRI has the potential to uncover automatic neural reactions to stimuli of sensitive nature, such as those tapping into intergroup bias where participants

may be motivated to withhold their honest responses. We organise these findings along classic social psychological theories to provide a framework that illustrates the underlying neural processes that lead from intergroup threat to violence (a graphical representation of the framework and the key brain regions involved are presented in Fig. 1). Finally, we summarise how these findings can be used to develop future research and policy to reduce intergroup conflict.

To ensure that the review is up to date and does not miss out on any key papers, following an initial literature search and identification of key papers based on previous meta-analyses and reviews we additionally searched the American Psychological Association's PsycINFO database in a systematic manner. This database covers nearly 2,500 journals and is updated twice each week. We relied on the search terms 'fMRI OR neuroimaging OR neuroscience AND intergroup threat OR intergroup conflict OR intergroup violence OR moral disengagement OR dehumani* OR schadenfreude'. We ended the search with manuscripts published in July 2021 the date when the literature review was conducted. We included manuscripts that contained original research using fMRI, had an intergroup, rather than interpersonal component, were published in peer reviewed journals, and were written in English language. In addition, we assessed the quality of each target manuscript using the JBI Critical Appraisal Checklist for Analytical Cross-Sectional Studies (Moola et al., 2020). Each manuscript included in the review was written with adequate detail and each study design was of high quality (quality assessment is detailed in the Supplementary Materials). Key characteristics of each target fMRI experiment's design and analyses can

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be seen in Table 1.

2. Responding to intergroup threat

Throughout human evolution, belonging to a group was intimately tied to survival (Kurzban and Leary, 2001). Groups ensured the safety of individual members, while providing them with food and opportunities to reproduce. Members of outgroups often represented threats to the ingroup, for example through competition for scarce resources or the introduction of new diseases. Under such conditions, quickly and automatically categorizing ingroup and outgroup members was highly adaptive to navigate social interactions and ensure survival (Turner, 1975).

Today, we continue to use social categorization and divide the world into 'us' and 'them' (Perdue et al., 1990). Individuals attach great value to certain group memberships, and the social identity obtained through such memberships can become integrated into one's self-concept (Brewer, 2001a; Tajfel and Turner, 1979). An increasing number of studies indicate that information related to ingroup and outgroup members is processed differently, and this is supported by neuroscientific findings as well (Cikara and Van Bavel, 2014; Molenberghs, 2013; Molenberghs and Louis, 2018). For example, individuals perceive

similar actions (Molenberghs et al., 2013) and words (Molenberghs et al., 2017; Westen et al., 2006) of ingroup vs. outgroup members very differently. Multiple neuroimaging studies have also shown greater neural sensitivity for ingroup suffering (for a review see Han, 2018). For example, brain regions involved in pain perception and empathy, including the anterior cingulate cortex (ACC) and anterior insula (AI), exhibit greater activity when seeing ingroup vs. outgroup members in pain (Contreras-Huerta et al., 2013; Xu et al., 2009). Even seemingly trivial tasks, such as the processing of faces in a minimal group context, can result in distinct neural activity depending on the group membership associated with them (Van Bavel et al., 2011). Specifically, participants had an increased neural response in the fusiform face area in response to ingroup (vs. outgroup) faces (Van Bavel et al., 2011). This activity indicates ingroup enhancement (see also Bagnis et al., 2019, 2020).

Yet, ingroup bias or favouritism is not the equivalent of holding hostile attitudes toward outgroup members (Brewer, 1999, 2001b). Additional circumstances and psychological processes are needed to create hostility toward outgroups. Associating an outgroup with a threat is one such factor (Chang et al., 2016). According to intergroup threat theory, outgroup threats can take the form of a realistic or symbolic threat (Stephan et al., 2009). Realistic threats are those presenting direct

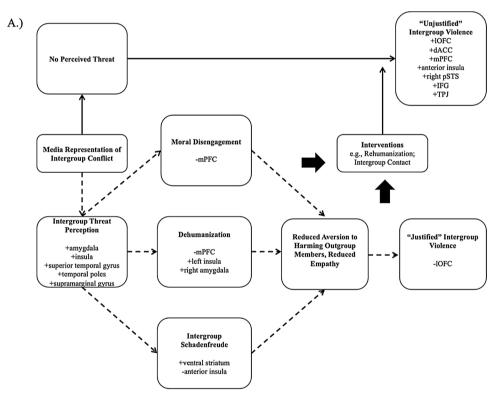


Fig. 1. A) The Neural and Psychological Mechanisms Leading from Intergroup Threat to Intergroup Violence. Breaking the Model at Any of the Dashed Arrows May Ultimately Prevent Intergroup Violence. Some Interventions that May Be Appropriate are Listed. B) The Key Brain Regions Involved in the Neuroscience of Intergroup Threat and Violence.

Note. + = increased activity. - = decreased activity. ACC = anterior cingulate cortex. dACC = dorsal anterior cingulate cortex. IFG = inferior frontal gyrus. lOFC = lateral orbitofrontal cortex. OFC = orbitofrontal cortex. pSTS = posterior superior temporal sulcus. TPJ = temporal parietal junction. The images presented in Figure 1B were created using templates from Somersault18:24's Library of Science and Medical Illustrations (https://somersault1824.gumroad.com/l/library).

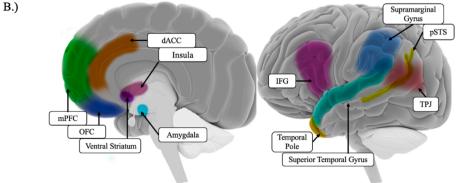


Table 1Key Characteristics of the Design and Analysis of Target Studies.

Paper	Category	N	Whole Brain Analysis or ROI?	Corrections for multiple comparisons and significance levels
Bruneau et al., 2018	Dehumanization	24	Whole brain analyses and ROI analyses for left inferior frontal cortex, precuneus, left inferior parietal cortex, posterior cingulate cortex, mPFC	Whole brain analyses were corrected for multiple comparisons using a permutation-based approach, <i>p</i> < .05. Where appropriate, the significance levels of ROI analyses were adjusted using a Bonferroni correction for multiple comparisons.
Cikara, Botvinick, et al., 2011	Schadenfreude	18	Whole brain analyses	Whole brain analyses were corrected for multiple comparisons using a permutation-based approach, <i>p</i> < .05.
Eberhardt, et al., 2011	Dehumanization	21	Whole brain analyses and ROI analyses for mPFC, posterior cingulate cortex, temporal poles	Whole brain analyses were corrected for multiple comparisons using a permutation-based approach, <i>p</i> < .05.
Cikara and Fiske, 2011	Schadenfreude	21	Whole brain analyses and ROI analyses for anterior insula and anterior cingulate cortex	Whole brain analyses were corrected for multiple comparisons using a permutation-based approach, <i>p</i> < .05.
ikara et al., 2010	Dehumanization	18	Whole brain analyses	Whole brain analyses were corrected for multiple comparisons using a permutation-based approach, <i>p</i> < .05.
Cikara et al., 2014	Moral Disengagement	21	Whole brain analyses and ROI analyses for mPFC	Whole brain analyses were corrected for multiple comparisons using a permutation-based approach, <i>p</i> < .05.
Domínguez D et al., 2018	Intergroup Violence	48	Whole brain analyses and ROI analyses for the lateral orbitofrontal cortex	Whole brain analyses were corrected for multiple comparisons using a permutation-based approach, <i>p</i> < .05.
Harris et al., 2014	Dehumanization	27	Whole brain analyses and ROI analyses for mPFC and medial orbitofrontal cortex	Whole brain analyses were corrected for multiple comparisons using a FDR correction, $q=.001$. Where appropriate, the significance levels of ROI analyses were adjusted for multiple comparisons.
Harris and Fiske, 2006	Dehumanization	Study 1: 10 Study 2: 12	Whole brain analyses and ROI analyses for mPFC	Results significant at $p < .01$
Harris and Fiske,	Dehumanization	18	Whole brain analyses	Results significant at $p < .005$ with at least 10
Jarris and Fiske, 2011a	Dehumanization	20	ROI analyses for anterior insula, left posterior insula, anterior cingulate cortex, visual regions, superior temporal gyri	contiguous voxels Results significant at $p < .001$ with at least 10 contiguous voxels
Hein et al., 2010	Schadenfreude	16	Whole brain analyses and ROI analyses for anterior insula, anterior cingulate cortex, right supplementary motor area, inferior frontal gyri, right temporal gyrus, left middle occipital gyrus	The results of whole-brain analyses are reported at p < .001 (uncorrected) and p < .05 (corrected for multiple comparisons using FDR). Whole brain multiple regression analyses were corrected for multiple comparisons across the nine ROIs. Commonality analyses were corrected for multiple comparisons using a stepwise multiple testing procedure.
ack et al., 2013	Dehumanization	Study 1: 47 Study 2: 40	Whole brain analyses and ROI analyses for temporoparietal junction, left middle temporal gyrus, medial parietal gyrus, precentral sulcus, left parahippocampal sulcus, left lateral parietal gyrus, mPFC, left intraparietal sulcus	Whole brain analyses were corrected for multiple comparisons using a permutation-based approach, p < .05.
Kesner et al., 2020	Intergroup Threat	38	Whole brain analyses	FMRI analyses were corrected for multiple comparisons using a FWE rate threshold of $p < .05$ corrected for the whole brain.
Krendl, 2016	Dehumanization	17 Caucasian-American participants and 17 Chinese participants	Whole brain analyses and ROI analyses for left insula, left mPFC, ventral striatum, parahippocampal gyrus	Whole brain analyses were corrected for multiple comparisons using a permutation-based approach, <i>p</i> < .05.
Krendl et al., 2009	Dehumanization	42 older adults and 23 young adults	Whole brain analyses and ROI analyses for left fusiform gyrus, right anterior cingulate cortex, bilateral amygdala, several prefrontal cortical regions	Results significant at $p < .05$
Grendl et al., 2012	Dehumanization	16	Whole brain analyses and ROI analyses for several prefrontal cortical regions	The results of whole-brain analyses are reported at p < .001 (uncorrected) and p < .05 (corrected for multiple comparisons using a permutation-based approach).
Krendl et al., 2013	Dehumanization	16	Whole brain analyses and ROI analyses for mPFC	Whole brain analyses were corrected for multiple comparisons using a permutation-based approach, p < .05.
antos et al., 2020	Intergroup Threat	30	Whole brain analyses and ROI analyses for amygdala	FMRI analyses were corrected for multiple comparisons using a FWE rate voxel-level threshold of $p < .05$ corrected for the whole brain for the whole brain analyses or for the size of the amygdala for ROI analyses.
Molenberghs et al., 2014	Intergroup Violence	48	Whole brain analyses and ROI analyses for mPFC/ anterior cingulate cortex, IFG/anterior insula, right posterior superior temporal sulcus	FMRI analyses were corrected for multiple comparisons using a FWE rate cluster-level threshold of $p < .05$ corrected for the whole brain for the whole brain analyses or for the size of the amygdala for ROI analyses.

Table 1 (continued)

Paper	Category	N	Whole Brain Analysis or ROI?	Corrections for multiple comparisons and significance levels
Molenberghs et al., 2015	Intergroup Violence	48	Whole brain analyses	FMRI analyses were corrected for multiple comparisons using a FWE rate cluster-level threshold of $p < .05$ corrected for the whole brain.
Molenberghs et al., 2016	Intergroup Violence	48	Whole brain analyses and ROI analyses for the left orbitofrontal cortex	FMRI analyses were corrected for multiple comparisons using a FWE or FDR rate cluster- or voxel-level threshold of $p < .05$ corrected for the whole brain
Schreiber and Iacoboni, 2012	Dehumanization	19	Whole brain analyses and ROI analyses for mPFC and amygdala	For whole-brain analyses, Z -image statistics were performed with a threshold of $Z=2.3$ at voxel level to account for multiple comparisons.

Note. FWE = Family wise error. FDR = False discovery rate. ROI = region of interest. mPFC = medial prefrontal cortex.

danger to the ingroup's physical safety, power, or resources, while symbolic threats risk the ingroup's traditions, values, ideology, religion, and cultural customs. Stephan et al. (2009) suggest that one of the most prominent conditions for perceived intergroup threat is uncertainty. Uncertain situations include those where individuals are unsure about appropriate behaviour, are placed under unfamiliar conditions, lack the support of authority figures, or feel mistrust and suspicion toward outgroups. These conditions might be heightened under the circumstances of the COVID-19 pandemic. Additionally, certain politicians irrationally reinforce the roles of outgroups as active agents in spreading of the virus, thus contributing to heightened perceptions of intergroup threat (Rohac, 2020; Tondo, 2020; Viala-Gaudefroy and Lindaman, 2020).

Previous neuroimaging studies suggest that viewing outgroup faces perceived as threatening is related to increased activity in the amygdala (see Chekroud et al., 2014 for a detailed review). In a recent fMRI experiment, we took this a step further by investigating the neural responses to direct intergroup threat and reconciliation (Lantos et al., 2020). Non-Muslim Caucasian participants observed stereotypically Muslim looking men make threatening or reconciliatory statements toward their ingroup. Threatening statements increased activity in areas previously related to the detection and processing of threat (i.e., amygdala and insula), stereotypical thinking (i.e., superior temporal gyrus and temporal poles), and heightened attention to semantic information (i.e., the supramarginal gyrus). These results suggest quick and automatic processing suitable for decision-making in dangerous situations. Participants' neural responses to outgroup reconciliation offers were vastly different. These responses activated parts of the frontal lobe and ACC. Activity in these regions is associated with higher-order cognitive processing and a conscious evaluation of the situation, a slower process that requires more effort.

Another fMRI study also found increased activity in the amygdala (along increased activity in the visual occipital cortex and right inferior frontal gyrus (IFG)) as participants viewed images of Islamic terrorists in a threatening posture (Kesner et al., 2020). Participants in this study with high xenophobic attitudes toward immigrants had increased neural activity in the fusiform gyrus when viewing close-up images of immigrants' emotional facial expressions taken during the 'European refugee crisis' of 2015. No such activity was observed among participants low in xenophobic attitudes toward immigrants. Participants with increased xenophobia also showed increased fusiform gyrus activity in response to photographs of natural disasters victims' faces. No significant differences were observed in the neural responses of those high vs. low on xenophobia when they viewed photographs of crowds of immigrants taken during the same time period, which suggests the fusiform gyrus activity might not be specific to fearful stimuli.

According to intergroup threat theory, outgroup threats may lead to a range of negative cognitive, emotional, and behavioural consequences toward the outgroup (Stephan et al., 2009). Cognitive consequences include ethnocentrism and dehumanization. Emotional consequences involve a lack of empathy and schadenfreude. Behavioural consequences are direct or indirect aggression, discrimination, and hostility

toward outgroup members. These increased ingroup biases in response to threats also align with research stemming from terror management theory (Greenberg et al., 1990, 2016; Greenberg and Kosloff, 2008). This theory states that individuals strive to achieve literal and/or symbolic immortality as a means of dealing with the anxiety caused by human mortality. Literal immortality is offered by beliefs in concepts such as heaven and reincarnation, while symbolic immortality can be obtained through identification with groups and causes, achievements in the arts and sciences, or raising children. Indeed, ingroup bias in neural responses involved in empathy, that is typically observed in response to observing ingroup vs. outgroup suffering, is more pronounced following mortality primes (Li et al., 2015; Luo et al., 2014). But mortality salience not only strengthens affinity with other ingroup members, it also increases prejudice toward outgroups representing different values (Greenberg et al., 1990, 2016; Greenberg and Kosloff, 2008).

Designating outgroups as the cause of the ingroup's ill fortune instead of facing the deeply embedded fear of death allows leaders to act as though the fears can be controlled and fought against (Greenberg and Kosloff, 2008). This has been apparent during some of the most inhumane acts of collective violence throughout human history. For eaxample, following the social and economic hardship of WWI, Hitler's grandiose speeches emphasised the superiority of the German race and blamed the problems on Jews. Mortality salience leads to an increased support for leaders advocating more aggressive military action than those seeking peaceful resolutions (Cohen et al., 2005, 2017; Pvszczynski et al., 2006). Mortality salience also brings about an increase in negative stereotypes toward outgroups, intergroup hostility, and even violence (Greenberg et al., 2016; Greenberg and Kosloff, 2008; Hirschberger et al., 2016). These findings are in line with increased xenophobia during the COVID-19 pandemic during which death rates are reported daily by the media.

3. Precursors to intergroup violence

While ingroup bias does not in itself lead to outgroup animosity, perceived outgroup threat can set the scene for intergroup violence. Humans are averse to harming other human beings (Cushman et al., 2012), and behavioural as well as developmental social neuroscience findings indicate that this aversion is present from an early age (Decety and Cowell, 2018). Outgroup threat can motivate various psychological processes that enable individuals to overcome this aversion and partake in collective violence, which is violence committed on behalf of a group. Here, we focus on moral disengagement, dehumanization, and intergroup schadenfreude, as these processes have been documented in an intergroup context using fMRI research.

3.1. Moral disengagement

The aversion of causing harm to others can be overcome through moral disengagement (Bandura, 1999, 2002). Moral disengagement is facilitated by a number of processes, including the displacement of responsibility (i.e., the legitimization of harm or even orders to cause harm by authority figures) or a diffusion of responsibility (i.e., acts of violence conducted collectively with other members of the ingroup; Kelman, 1973). Moral disengagement can also happen when one acts 'for the greater good' or in the interest of the ingroup (Pinter and Wildschut, 2012). Acting as the member of a group facilitates a decrease in self-awareness and increases the salience of group identity over personal identity (Diener, 1979; Postmes and Spears, 1998; Reicher et al., 1995).

Cikara et al. (2014) used fMRI to investigate the neural effects of acting in a group vs. alone. Participants competed in a go/no go task either alone or as members of a team. The stimuli included moral statements and control statements presented in a first- or third-person manner. Decreased activity in the medial prefrontal cortex (mPFC) in response to self-referential moral items when acting as a member of the team was positively correlated to subsequent hostility toward outgroup members. This relationship was not present when participants competed alone. The mPFC has been associated with self-referential processing and self-knowledge (Jenkins and Mitchell, 2011). These results support the notion that acting as a member of a group may reduce the salience of personal moral beliefs by reducing self-referential processing overall, thus increasing the readiness to harm outgroup members.

3.2. Dehumanization

We have a tendency to assign uniquely human qualities to members of our species, such as a private mental life encompassing thoughts, desires, and emotions (Harris, 2017). Dehumanization refers to a failure in spontaneously assigning such a mental life to another human, thus associating them with an entity less than human. While we have an aversion toward harming other human beings, this aversion is less for non-human entities, enabling violence toward dehumanized individuals. A dehumanized perspective can be extended to entire outgroups and some of the cruellest examples of mass violence in human history have been conducted in such contexts. For example, the US Constitution valued African slaves as three fifths of a human (Goff et al., 2008), while Nazi propaganda labelled Jews as parasites (Herf, 2008). Today, the media continues to openly represent certain minority groups, such as immigrant and refugees, using dehumanizing language (Esses et al., 2013).

The stereotype content model (SCM) suggests that we categorize people along two main continuums: warmth and competence (Fiske et al., 2002). Those perceived as high on both warmth and competence elicit admiration (e.g., ingroup members), those high on competence but low on warmth elicit envy (e.g., rich people), those low on competence but high on warmth elicit pity (e.g., elderly people), while those low on both warmth and competence elicit disgust (e.g., homeless people). Out of these emotions, disgust is the only one that can be elicited by nonhuman entities and indeed, groups stereotypically placed in the low-low quadrant of the model are often dehumanized (Harris and Fiske, 2011b).

Harris and Fiske (2006) asked participants to lie in an fMRI scanner and simply view photographs of members of groups belonging to each of the four quadrants of the stereotype content model. Results showed diminished activity in the mPFC only in response to viewing pictures of dehumanized groups (Harris and Fiske, 2006). The mPFC is one of the core regions involved in the brain's mentalizing network and is associated with social cognition (Amodio, 2014; Amodio and Frith, 2006). These findings suggest that a basic human-like perception can be withheld from certain individuals simply due to their group membership. Instead, members of groups perceived as low on warmth and competence elicited activity in the amygdala and insula, regions associated with threat and disgust.

In a follow-up study, participants viewed images of individuals belonging to each of the SCM's quadrants whilst undergoing fMRI (Harris and Fiske, 2011a). They then rated each target individual on

human-perception dimensions that were found to differentiate dehumanized targets from targets belonging to the other SCM's quadrants. The results revealed that greater warmth ratings were related to lower activity in the AI. When attributing less humanity to a target, participants also exhibited greater neural activity in the ACC. The authors interpreted this as potentially reflecting the mental conflict between denying one's humanity whilst knowing that in reality they are a human being.

In a cross-cultural replication of Harris and Fiske's (2006), Krendl (2016) found that reduced activity in the mPFC was not apparent among Chinese participants in response to viewing to photographs of homeless people vs. members of control groups, while the effect did replicate among American participants. Increased activity in the insula in response to homeless people did replicate cross-culturally (Krendl, 2016). This indicates that there are cultural similarities and differences in how certain groups are perceived. Other studies with similar designs and aims also found corresponding results. Increased activity in the amygdala in response to photographs of homeless people and substance abusers compared to control images was observed among both young ($M_{age} = 19.53$) and old adults ($M_{age} = 73.13$; Krendl et al., 2009). Schreiber and Iacoboni (2012) found that observing images of individuals violating social norms (e.g., criminals, gang members, homeless people) vs. individuals consistent with social norms (e.g., teachers, families, doctors) was associated with increased amygdala activity and decreased mPFC activity. These neural responses were irrespective of the target's race. Targets allocated as norm violating fit well with the SCM's low warmth-low competence quadrant and are thus likely members of groups which may be stereotypically dehumanized.

Similar neural responses were observed in the context of an experimentally created labor market (Harris et al., 2014). Participants saw profiles of fictious workers (players in a time estimation game). These profiles contained the players' ID numbers, along information about their performance, physical and demographic characteristics, photograph, and price assigned to the player. Participants were requested to purchase five players, aiming to maximise their own monetary profits based on the purchased players' future performance. Participants showed reduced mPFC activity when subsequently viewing the photos of their purchased players vs. randomly selected non-purchased players. The decrease in mPFC activity further predicted activity in the medial orbitofrontal cortex, an area related to valuation (Lin et al., 2012). These findings suggest that assigning economic values to and purchasing human beings may increase dehumanization (Harris et al., 2014). Finally, a similar reduction in mPFC activity was related to hostile sexism among males looking at sexualized images of females, suggesting that the objectification of women is comparable to dehumanization in other contexts (Cikara, Eberhardt, et al., 2011).

Krendl et al. (2012) explored the neural responses to viewing images of stereotypically dehumanized groups (homeless people and substance abusers) compared to viewing affectively negative images of control targets (e.g., a couple in a cemetery or a soldier firing a gun). Participants were asked to either maintain their negative response toward the target individuals or try to regulate it for 8-seconds. When analysing the whole duration of emotional regulation period, results revealed greater activation in the mPFC (along with activity in several temporal and occipital regions) in response to control targets compared to dehumanized targets when regulating emotions. However, focusing on the neural activity only during the first two seconds of each trial revealed a different pattern. Here, mPFC activity (along with activity in several other regions of the PFC) was greater when observing dehumanized (vs. control) targets when regulating emotions and this activity was also positively correlated with participants' implicit bias toward this group. The authors suggested that regulating negative bias to dehumanized groups happens more quickly and automatically compared to other groups. However, in light of the literature summarised above, it is possible that the mPFC plays a unique role here. Upon seeing a dehumanized target, participants may initially perceive them as

a human being, but this may turn into a dehumanized perception once participants are given some time to process the context of the photograph. This is in line with the proposition that humanizing and dehumanizing perceptions are flexibly engaged depending on the social context (Harris, 2017; see also Lantos and Harris, 2021, for a discussion on an underlying dehumanization propensity).

The potential facilitating effects of dehumanization when harming an outgroup member have also been investigated using fMRI (Cikara et al., 2010). Participants were presented with variations of the classic trolley dilemma's footbridge version. In this scenario, a person called Joe sees an empty trolley speeding toward a group of five people. Joe can choose to shove a bystander in front of the car, which saves the lives of the five people but kills the innocent bystander. In the scenarios presented here, Joe always chooses to sacrifice the bystander. However, the group membership of the five people saved and that of the bystander were manipulated. Across trials, all combinations of saved vs. sacrificed group memberships were created corresponding to the SCM's four quadrants. Self-report responses revealed that participants thought it was most acceptable to save members of warm and competent groups, such as the ingroup. They also indicated it was most acceptable to sacrifice a stereotypically dehumanized target, low on warmth and competence. Indeed, the only significant neural response to the interaction between groups saved vs. sacrificed was in response to saving the high-warmth, high-competence group members, whilst sacrificing the low-warmth, low-competence group member. Significant activity was observed across areas of the prefrontal cortex and the ACC. The authors interpreted these findings as related to resolving a complex trade-off, as participants may have an aversion to reporting that some combinations are more acceptable than others across the presented scenarios.

Neuroimaging findings also indicate that rehumanization of targets may be possible when actively trying to engage in mentalization (Harris and Fiske, 2007). Participants asked to infer the vegetable preferences of stereotypically dehumanized individuals showed more activity in the mPFC compared to when asked to infer their age. Learning more about the individual circumstances of dehumanized group members also affects neural responses. Presented with brief vignettes detailing why the individuals on each photograph became homeless revealed distinct neural activity patterns when the cause was within or beyond the target's control (Krendl et al., 2013). Activity in the mPFC increased in response to situations within the target's control, implying an attempt to engage in mentalization to better understand why they chose to act in a way detrimental to their circumstances. Activity in the insula increased in response to situations outside of the target's control. Self-report measures indicated an increased feeling of pity toward such targets rather than disgust, thus this activation likely represents an aversion to the circumstances detailed in the vignette, instead of an aversion to the target individual. Overall, these findings indicate that viewing others as individuals rather than equating them to their group may break the effects of dehumanization.

Blatant forms of dehumanization (i.e., explicitly stating that one is less than human) compared to expressing dislike toward someone have also been differentiated by fMRI research (Bruneau et al., 2018). Participants were presented with social groups (e.g., Europeans), animal species (e.g., puppies), or inanimate groups (e.g., robots) and asked to judge each on a variety of scales. These included the ascent of man scale, displaying an image of five pictograms of the evolutionary trajectory from apes through humanoid figures to the modern human (Kteily et al., 2015). Participants' task was to indicate how evolved they found each presented category using a slider placed under the ascent of man image. Liking was measured using a feeling thermometer. Activity in regions such as the left IFG (previously associated with viewing pictures of animals or humans engaging in animal-like behaviour, such as drinking from puddles; Jack et al., 2013) were associated uniquely with dehumanization ratings. Activity in the posterior cingulate cortex (previously associated with a range of cognitive processes including mentalization, autobiographic memory, and self-referential processing; Spreng and

Andrews-Hanna, 2015) was uniquely associated with liking judgements. These findings suggest that dehumanization and dislike are subserved by different neural processes. The areas with increased neural activity in response to blatant dehumanization, however, do not overlap with those indicated by other research defining dehumanization as a failure of spontaneous mentalization (e.g., Harris and Fiske, 2006, 2007), suggesting that the two phenomena may tap into different processes.

Research differentiating between animalistic (i.e., dehumanization through likening one to nonhuman animals by stripping one of uniquely human characteristics that separate humans from animals) and mechanistic (i.e., dehumanization through likening one to machines by denying characteristics of human nature that separate humans from machines) forms of dehumanization did not replicate the decreased mPFC activity in response to dehumanized vs. nondehumanized targets (Jack et al., 2013; see also Haslam, 2006). Given the numerous studies replicating this finding, it is likely that differences in the employed stimuli or in the procedure may account for this. Nevertheless, the results indicate that animalistic and mechanistic dehumanization are related to different patterns of neural activity. The findings showed that mechanistic dehumanization compared to both animalistic dehumanization and humanization is characterised by decreased activation of the default mode network. On the other hand, animalistic dehumanization compared to mechanistic dehumanization and humanization was related to increased activity across the task positive network.

3.3. Schadenfreude

Schadenfreude refers to positive affect experienced in response to another's ill fortune and is often experienced toward members of disliked outgroups (Cikara, 2015). Repeatedly experiencing pleasure in response to outgroup members' pain may over time reinforce this association. This can lead to desensitisation of outgroup pain, and even endorsement of outgroup pain (Cikara, 2018). Schadenfreude has been associated with activity in the ventral striatum, an area related to both reward processing and reinforcement learning (O'Doherty, 2004).

Hein et al. (2010) used fMRI to investigate participants' neural responses to the physical pain their favourite soccer team's fan (ingroup) experienced compared to a rival team's fan (outgroup). The results showed increased activity in the left AI in response to ingroup vs. outgroup pain. This activity was related to self-report measures of empathic concern and to a willingness to engage in prosocial behaviour that reduced the suffering of the target. Reduced activity in the left AI was additionally related to negative opinions of the outgroup target, suggesting lower empathic processing. Increased activity in the right ventral striatum in response to an outgroup member's suffering was related to participants' negative opinion of the target. This suggests that the more negatively participants felt about the target, the more positive affect they experienced in response to their pain, illustrative of schadenfreude. Activity in the right ventral striatum in response to outgroup pain was further negatively related to prosocial behaviour aiming to ease their suffering.

Another fMRI experiment looked at baseball fans' neural responses to various scenarios occurring during a baseball game (Cikara et al., 2011a). When seeing a despised rival team fail against the supported team, or seeing the supported team succeed against the despised rival team, activity in the ventral striatum increased, indicative of reward processing. A similar activity pattern was observed when the rival team failed against a neutral outgroup team, indicative of pure schadenfreude as the supported team did not directly benefit from this loss. Participants' self-report experiences of pleasure while watching the scenarios correlated to ventral striatum activity. This activity during the rival team's failure further correlated to self-reported willingness to harm the rival team's fans. Witnessing events that were distressing, such as observing the supported team fail against a rival team or the success of the rival team against a third neutral team led to activity in brain regions associated with pain perception, including the ACC. This suggests that

fans experienced pleasure in response to outgroup failure, but also pain in response to outgroup success.

Cikara and Fiske (2011) investigated whether warmth and competence attributed to groups and their members influence how their positive, neutral, or negative experiences are perceived by others. Participants saw photographs corresponding to each of the SCM's four quadrants, paired with short descriptions of various scenarios. Self-report results suggest that participants felt best about negative events, and worst about positive events happening to members of groups high in competence and low in warmth (eliciting envy), compared to groups corresponding to the other quadrants of the SCM. In line with these results, an increase in AI activity was observed in response to envy eliciting targets' good fortune as compared to that of other targets, interpreted by the authors as a counter-empathic response. Decreased AI activity was observed in response to low warmth-high competence vs. high warmth-low competence targets' misfortune, interpreted as schadenfreude. Studies using the SCM may shed light on group processes merely based on warmth and competence ratings, and are thus increasingly useful in making predictions across intergroup contexts.

4. The neural correlates of intergroup violence

Prejudice and intergroup hostility increase under conditions of intergroup threat and mortality salience (Greenberg et al., 2016; Stephan et al., 2009). A range of psychological processes occur under such conditions, ultimately facilitating individual engagement in collective violence. As outlined above, such processes include moral disengagement, dehumanization, and intergroup schadenfreude, each of which have been studied using fMRI (e.g., Cikara et al., 2011a, 2011b, 2014; Harris and Fiske, 2006, 2007). They contribute to harming others simply based on group membership, in the absence of existing interpersonal conflict or even prior contact. But what happens in the brain as one is involved in intergroup violence as a perpetrator?

To investigate this, Molenberghs et al. (2014) asked university students to reward students from their own university or another university if they correctly responded to trivia questions, and punish them for any incorrect responses while undergoing fMRI. Allocating monetary reward to others was related to activity in the dorsal putamen, a region associated with reward processing (Haruno and Kawato, 2006), and the medial orbitofrontal cortex, a region associated with evaluation and decision-making (Berridge and Kringelbach, 2013). These neural responses were stronger when rewarding ingroup members, indicative of ingroup bias. However, punishing others using electric shocks led to activity in brain areas associated with pain perception (dorsal ACC and AI), perspective taking (mPFC and posterior superior temporal sulcus), and moral sensitivity (lateral orbitofrontal cortex, IOFC). There was no difference between these neural responses when harming an ingroup vs. outgroup member (Molenberghs et al., 2014). These findings are in line with the notion that ingroup bias does not in itself lead to increased hostility toward an outgroup. But what about more extreme situations?

To explore this question, Molenberghs and colleagues (2015) investigated the neural processes of justified and unjustified killing. Participants watched short video clips from a first-person perspective as a video game character shot an armed soldier (justified killing), an innocent civilian (unjustified killing), or no one (control) while undergoing fMRI. Although each video was pre-recorded and participants did not have control over the shots fired, they were asked to imagine themselves as the actor. Following the fMRI task, participants indicated how guilty they felt about shooting soldiers and civilians on a self-report scale. The results revealed increased activity in the lOFC in response to killing civilians, but not soldiers. The activity in the lOFC was positively related to the amount of guilt participants expressed about shooting civilians vs. soldiers. This finding supports previous research indicating the role of the lOFC in moral cognition (e.g., Eres et al., 2018; Molenberghs et al., 2014), suggesting that justified and unjustified killing lead to different neural responses. The authors interpreted the absence of IOFC activity in response to killing soldiers as a lack of moral sensitivity because the violence was justified. Effective connectivity analyses with seeds in the left and right IOFC further indicated increased connectivity between the IOFC and bilateral temporal parietal junction (TPJ) when killing civilians versus soldiers. The TPJ is often associated with theory of mind and mentalization (Saxe and Wexler, 2005), which suggests participants were making more inferences about the target's mental state when they were killing innocent civilians.

The limitation of the Molenberghs et al. (2015) study is that participants were watching video clips passively and did not decide themselves to harm or not harm others. Agency plays an important role in moral responsibility. To further investigate whether neural responses in a perpetrator are similar when agency plays a role, Domínguez D et al. (2018) instructed participants to engage in an fMRI shooting task while pretending to be a police officer. Participants were asked to shoot targets whom they believed were holding a gun, but not those holding other objects. The targets were made up of ingroup members (Caucasian targets) and outgroup members (Muslim targets). The neural responses revealed increased activity in the lOFC when participants engaged in unjustified killing (i.e., shooting those holding objects other than guns), likely indicating guilt. These results mirror the results from the Molenberghs et al. (2015) study mentioned above. Interestingly, these results were similar regardless of the victim's group membership. This activity was paired with an increased response in regions related to pain perception and empathy, including the AI and IFG. Activity in the lOFC, AI, and IFG also increased when participants were informed that the target killed them, regardless of the perpetrator's group membership, another example of moral violation. Increased IOFC activity was also observed when participants were confronted by outgroup members holding a gun compared to ingroup members holding a gun, which was interpreted as increased moral sensitivity to outgroup attacks.

This increased sensitivity for outgroup attacks is also supported by the results of another fMRI experiment investigating intergroup violence (Molenberghs et al., 2016). Participants here observed a student from their or another university harm a student from the same university or a competing university. Participants reported increased moral sensitivity when the outgroup member harmed the ingroup member, and exhibited increased activity in the IOFC during this scenario. Together, these results suggest people are highly sensitive to outgroup attacks, which makes sense from an evolutionary point of view as these types of attacks threaten the survival of the ingroup.

5. Implications and future directions: preventing and reducing intergroup conflict

The research presented here holds important implications for social scientists and policy makers aiming to prevent or reduce intergroup threat and violence. FMRI has the capacity to noninvasively measure both conscious and nonconscious neural activity. When exploring topics of a sensitive nature, such as prejudice, researchers often face a challenge. Participants may (sometimes unintentionally) conceal their honest responses on standard psychometric measures to confirm to social norms and desirability. Neuroimaging offers a unique way of uncovering participants' automatic, nonconscious responses to stimuli. Here we presented social neuroscience research suggesting that related psychological processes-moral disengagement, dehumanization, and intergroup schadenfreude-are associated with separate patterns of neural activity. This indicates on a physiological level that these processes are indeed distinct and that different methods may be necessary to counteract them. Here, we focus specifically on the implications that the reviewed research may have for handling the COVID-19 pandemic in a way that promotes intergroup cooperation and peace, but these suggestions can be translated to other scenarios and contexts as well.

The media, public figures, and politicians have great responsibility in how they decide to tackle the discussion around COVID-19. Social neuroscience data suggests that people respond in quick, automatic ways to outgroup threat, and pay increased attention to semantic information in this context (Lantos et al., 2020). Thus, the media can easily (and unintentionally) contribute to creating an environment of anxiety emphasising outgroup blame and threat. Yet the narrative around COVID-19 can just as easily be used to promote cooperation and collaboration between groups. The well-known Robber's Cave Experiment illustrated how groups previously competing against each other and interacting in hostile ways started working together when faced with a common problem to achieve a common goal (Sherif et al., 1961). Similarly, the aim to ensure the safety of people worldwide should be framed as a common goal in everyone's interest that we can work toward jointly.

The Common Ingroup Identity Model suggests that transforming 'us' and 'them' to an inclusive 'we' by highlighting an overarching group identity shared by subgroups fosters intergroup harmony (Gaertner et al., 1993, 2000). Social neuroscience research indicates that the neural representation of ingroup and outgroup members are different, while their actions and words are also processed differently (Bagnis et al., 2020; Cikara and Van Bavel, 2014; Molenberghs and Louis, 2018). Through a common group identity this differential processing is diminished, thus eliminating any former positive or negative bias. For example, Van Bavel et al. (2008, 2011) allocated White participants to a mixed-race (White and Black ingroup members) minimal group. This allowed participants to overwrite their differing neural responses to racial in- and outgroup members. In line with the novel intergroup context, participants' neural activity in response to photographs of faces differed according to in- and outgroup membership, rather than racial categories. Specifically, they exhibited increased responses in the amygdala, fusiform gyri, orbitofrontal cortex, dorsal striatum (Van Bavel et al., 2008), and fusiform face area (Van Bavel et al., 2011) in response to novel ingroup members, interpreted as signalling ingroup bias. These responses were not moderated by the race of the target.

Other research, however, indicates that while emphasising a common identity is associated with some benefits when it comes to intergroup interaction, it can also have some unexpected negative consequences. For example, this type of recategorization leads members who also belong to other, marginalized groups to accept and justify social inequality (Jaśko and Kossowska, 2013). Recategorization to a common ingroup identity further leads to a decreased motivation to engage in collective action aimed at achieving social change for minority groups (Greenaway et al., 2011). Social identity theory (Rubin and Hewstone, 1998; Tajfel and Turner, 1979) suggests that individuals are motivated to uphold a positive image of their ingroup. A positive image of the ingroup contributes to group members' enhanced social identity and personal self-esteem. This explains why marginalized group members might be willing to accept inequality under such circumstances for the sake of the common group's image. This is in line with neuroimaging studies showing that the neural representation of our personal and social identity overlaps (Scheepers and Derks, 2016).

A more effective way of emphasising a shared identity while encouraging individuals to also attend to their subgroup's interests is by introducing a dual identity (Glasford and Dovidio, 2011; Ufkes et al., 2016). For example, highlighting both common humanity and separate nationalities or a shared nationality and separate ethnicities may help foster intergroup peace. Dual identity additionally allows members of various groups to equally promote and attend to the interests of each of their groups. The neural correlates of this type of self-categorization and its effects on intergroup relations should be investigated in more detail in future research.

The phrases that the media and public figures openly use to refer to outgroups also have important consequences when it comes to how people think about those groups. Dehumanizing terminology is often used by the media when referring to minority groups such as refugees and immigrants (Esses et al., 2013). When confronted by dehumanizing terminology repeatedly with reference to a given outgroup, it is possible to internalize the dehumanizing perspective, which in turn decreases

empathy and the aversion to harming members of that group (Harris, 2017; Kelman, 1973). This is evident by the reduction in spontaneous neural responses to dehumanized targets, such as an absence of mPFC activity, an activity related to mentalization, or an increase in amygdala and insula activity, indicating disgust (e.g., Harris and Fiske, 2006; Krendl, 2016; Krendl et al., 2009; Schreiber and Iacobini, 2012). It is thus important to consciously avoid promoting a dehumanized perspective.

However, once a dehumanizing perspective has been adapted, research indicates that rehumanization may be possible. When trying to consciously engage in mentalization toward dehumanized targets such as the homeless, participants exhibited increased activity in the mPFC, whereas activity in the same region was absent when simply observing the target (Harris and Fiske, 2007). Similarly, learning more about the individual circumstances of a homeless person led to increased activation in brain areas associated with mentalising or empathy (Krendl et al., 2013). Thus, encouraging a perspective of others as individuals rather than simply outgroup members may protect against dehumanization. Engaging in intergroup contact may further encourage getting to know outgroup members as individuals, and thus understanding that group membership is not the only thing that defines them (Pettigrew and Tropp, 2006). If the opportunity for intergroup contact is absent, indirect intergroup contact may provide similar benefits (Brown and Paterson, 2016; Reynolds and Klik, 2016). Indirect contact entails experiences such as extended contact (knowing that an ingroup member has a close relationship with an outgroup member) or imagined contact.

Moral disengagement can also be increased by public figures or the media openly associating or even blaming outgroup members for the spread of the COVID-19 virus (Bandura, 1999, 2002; Kelman, 1973). This type of message can shift the perspective about prejudice from socially unacceptable to socially justified (Bandura, 2002). Outgroups devalued this way may face institutionalized discrimination within a society (Bandura, 2002). Thus, in order to prevent intergroup conflict, public statements that suggest the endorsement of prejudice or outgroup hostility should be avoided. Further findings indicate that moral disengagement is most likely when one acts as a part of an ingroup rather than an individual, indicated by a decrease in self-referential neural processing (Cikara et al., 2014). Therefore, an additional technique to reduce moral disengagement may be to continuously and actively emphasise the individual's role as an agent throughout their everyday actions.

By repeatedly pairing the experience of pleasure with outgroup pain, individuals may become desensitised to outgroup pain and even motivated to elicit it (Cikara, 2015, 2018). Research suggests that while ingroup bias leads to an increase in positive affect in response to the success of the ingroup, outgroup failure only leads to an experience of positive affect when further conditions are met. One such instance is when the individual holds particularly negative attitudes about the outgroup (Cikara et al., 2011a; Hein et al., 2010; Molenberghs et al., 2014). Thus, in order to prevent schadenfreude and desensitisation to outgroup pain, it is important to reduce negative outgroup attitudes. Neuroimaging research points to few methods of achieving this. For example, the ACC plays a crucial role in monitoring of cognitive conflict (Amodio, 2014; Etkin et al., 2011). Such monitoring is necessary to detect one's own bias toward an outgroup and to appropriately respond to situations where this bias creates cognitive conflict (Beer et al., 2008; Gonsalkorale et al., 2011). This is in line with behavioural (Payne, 2005) and neuroscientific (Cunningham et al., 2004; Wheeler and Fiske, 2005) research suggesting that control over implicit prejudiced and stereotypical cognitions is related to cognitive control. Training cognitive control may lead to better control of prejudice and stereotypical thinking (Kleiman et al., 2014; Mendoza et al., 2010). The key neural mechanisms that facilitate the progression from intergroup threat to intergroup violence are presented in Fig. 1. This framework also integrates potential interventions at each stage that may break the cycle.

6. Limitation of fMRI research

Though fMRI is a powerful research tool which enables scientists to explore research questions from a novel perspective, it is not without limitations. First, it is not always possible to mimic real-world events realistically inside an MRI scanner. Participants must lie down, they are not allowed to make physical movements, while it is usually noisy and dark. Thus, the ecological validity of these studies should be considered when interpreting their results. Second, although fMRI has great spatial resolution, its temporal resolution is limited. Due to the hemodynamic response, neural activity observed through fMRI is delayed. For this reason, it is difficult to disentangle which brain regions are involved at different time points close together – though in such cases, it is possible to use fMRI in combination with other psychophysiological measures which may address this limitation (Coronel and Falk, 2017).

The analyses and interpretation of fMRI data present further challenges. Brain imaging studies yield hundreds of thousands of datapoints. If corrections for multiple comparisons are not taken into account, the chances of finding false positive results are greatly inflated (Bennett et al., 2009; Kriegeskorte et al., 2009). Furthermore, there are several ways one may conduct data acquisition, pre-processing, and even data analysis (Carp, 2012a, 2012b; Lyon, 2017; Poldrack et al., 2017). Whether one arbitrarily chooses various steps or has a firm rationale behind each step, the final results of each analysis may be significantly altered based on such choices. Finally, the use of reverse inference during the interpretation of the results of fMRI experiments may bias the conclusions drawn (Poldrack, 2006). To avoid such biased conclusions, it is important to keep the limitations of fMRI research in mind. Yet, research also demonstrates that fMRI research can accurately predict real-world human behaviour (Berkman and Falk, 2013), supporting its valuable role in complementing psychological studies.

7. Conclusions

Intergroup conflict poses an important challenge for societies. The complex psychological processes underlying human aggression and violence have been a central question to psychologists for over a century and philosophers for over 2,000 years (Forgas et al., 2011). Despite an ever-growing scientific literature, these phenomena remain present globally, and are increasing during the COVID-19 pandemic (Devakumar et al., 2020). The development of sophisticated neuroimaging techniques provides an unprecedented opportunity for exploring such issues from a novel perspective. By combining social psychological theory with social neuroscientific methods, researchers may gain insight into the physiological mechanisms underlying intergroup threat and violence. Shedding light to these neural mechanisms offers novel guidance to understanding, and thus reducing and preventing intergroup threat and violence. It allows scientists to rely on cross-disciplinary research when developing interventions that target specific mechanism related to intergroup threat and violence (e.g., dehumanization, moral disengagement, schadenfreude). Such interventions may be most effectively developed based on an integrated overview of the unique neural correlates of such processes and additional findings assessed through more traditional research methods (e.g., behavioural data). Such research can provide valuable guidelines for dealing with the COVID-19 outbreak in a way that fosters intergroup harmony.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.neubiorev.2021.09.0 25.

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