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Representation of intergroup conflict in the human brain

Yina Ma[1,2,3,4,*] and Huixin Tan[1,2]
[1]State Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, Beijing, 100875, China
[2]IDG/McGovern Institute for Brain Research, Beijing Normal University, Beijing, 100875, China
[3]Beijing Key Laboratory of Brain Imaging and Connectomics, Beijing Normal University, Beijing, 100875, China
[4]Chinese Institute for Brain Research, Beijing, 102206, China
*Correspondence: yma@bnu.edu.cn
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This NeuroView explores intergroup conflict by synthesizing intergroup differences with three group-related neurocognitive processes. We suggest that intergroup differences at the aggregated-group level and interpersonal level are neurally dissociated and independently influence group dynamics as well as ingroup-outgroup conflicts.

Humans are inherently social creatures who thrive in group living. People are inclined to affiliate themselves with various social groups and establish interdependent connections with fellow group members. As a result, the human brain has evolved to specialize in group living, initiating a unique set of perceptual, cognitive, motivational, affective, and neural processes. However, the formation and existence of diverse groups inevitably result in intergroup bias, prejudice, and conflict (Box 1). Investigating intergroup bias and conflicts through the lens of neuroscience to uncover the psychological and neurocognitive processes involved is of particular theoretical and practical importance. This endeavor holds great promise for furthering our understanding of intergroup conflict and shedding light on potential interventions and also offers a unique opportunity to comprehend the human brain specialized for group living.

The human brain is wired to heuristically categorize oneself and others into ingroups and outgroups. This categorization serves as a basis for navigating the social world and defining one's identity. Individuals derive self-esteem and positive identity from group affiliations, resulting in a preference for their own group and a tendency to discriminate against other groups. Our review primarily focuses on ingroup-outgroup conflicts (Box 1), as participants in most existing literature experience intergroup conflict from a first-person perspective. This focus on self-involved intergroup conflict also aligns with the standpoint of social identity theory, a critical theoretical account of intergroup conflict that highlights the importance of self-relevant factors in intergroup conflicts.

We approach intergroup conflict from a neuroscience perspective by reviewing important neuroimaging studies that compare psychological and neurocognitive responses to ingroup and outgroup and to their respective members. We synthesize neural findings on multifaceted intergroup differences by organizing them into three group-related cognitive processes: self-group connection, perception of (in/out)groups, and reaction to (in/out) groups (Figure 1). Furthermore, we analyze how intergroup differences in each of these neurocognitive processes link to the emergence and/or escalation of ingroup-outgroup conflict. Specifically, when individuals join a group or are identified—by themselves or others—as belonging to a group, they establish group membership and *connect the self to a group*. Group membership alters one's relationship with groups and group members: the group one belongs to (and its members) is treated as "ingroup" (ingroup members) and the group(s) one does not belong to (and their members) are treated as "outgroup" (outgroup members). This distinction can further influence how individuals *perceive* and *(re)act* to others belonging to their ingroup and rival outgroups. The differences in the *connections* with groups and in the *perception* and *(re)action* to in- and outgroups may lead to intergroup conflicts.

We propose that groups serve as abstract social collectives that provide group identity and membership (an "aggregated-group level") and also function as interpersonal spaces for group members to interact with their thoughts, emotions, and behaviors (an "interpersonal level"). Therefore, for each of the three cognitive processes, we analyze intergroup differences at both abstract aggregated-group and interpersonal levels, revealing how the two distinct levels link to intergroup conflicts through different neural mechanisms. At the aggregated-group level, we conceptualize each social group as an abstract, aggregated social collective. Social groups that individuals may or may not belong to grant them varying group affiliations and in-/outgroup memberships. These differential group memberships and identities initiate and/or amplify ingroup-outgroup disparities, which can fuel conflicts between ingroup and outgroup. At the interpersonal level, we characterize each social group as an interpersonal space consisting of its group members, who individualize each other during interpersonal interaction, especially among ingroup members. People can navigate interpersonal relationships based on group memberships or simple social heuristics (i.e., "an enemy of a friend is an enemy" and "a friend of a friend is a friend"), marking the social landscape with divisions between ingroup members and outgroup members. The distinct interactions within and between groups can predispose individuals to process ingroup

Box 1. Key terms

Intergroup conflict arises when two or more groups and their members perceive incompatible goals or values, combined with negative attitudes and/or antagonistic feelings toward (members of) rival groups. It serves as a driving force in shaping the evolution of group living and the development of human societies, but it can also be exceedingly destructive and costly to the groups and individuals involved. It is a leading cause of migration, displacement, injury, and death. Besides the environmental stress, political reasons, and resource competition, intergroup conflict is also attributed to the distinct psychological and neurocognitive responses toward ingroups and rival outgroups.

Ingroup-outgroup conflict involves oneself and occurs between ingroups and outgroups, representing one of the most basic and common forms of intergroup conflict.

Neural synchronization refers to the temporal alignment of brain activity among interacting individuals and is suggested to underlie mutual connections and serve as a neural indicator of interpersonal coordination.

Repetitive suppression (RS) reflects attenuated neural responses to repeated perception of stimuli that activate common neuronal populations or engage common neural processes due to habituation.

and outgroup members differently, which may lead to conflicts between "us" and "them."

Together, by highlighting both the aggregated-group and interpersonal levels, we elucidate how the brain (1) *relates* oneself to the ingroup and outgroup (members), (2) *perceives* the ingroup and outgroup (members), and (3) *reacts to* the ingroup and outgroup (members) (Figure 1). With this integrative view, we are approaching a better understanding of the neural underpinnings of intergroup conflicts.

How do people relate the self to group(s)?

People relate themselves to group (members) to fulfill their fundamental need for social belonging, which allows them to identify groups they are part of and distinguish "us" from "them." At the aggregated-group level, group membership initiates a connection between an individual and a specific group. This connection is manifested through the integration of the connected group (i.e., ingroup) into one's self-concept, as evidenced by stronger activation for ingroups than outgroups in brain regions involved in self-related processing. At the interpersonal level, researchers probe the relationship between an individual and group members by asking how one identifies others as in-/outgroup members and interacts neurally with in-/outgroup members, revealing stronger neural synchronization (Box 1) among ingroup members. These distinct neural patterns for ingroups and outgroups further strengthen the sense of belonging to ingroup and foster closer bonds with ingroup members, which may motivate ingroup favoritism and discriminatory behavior toward outgroup and its members, potentially giving rise to intergroup conflict.

Aggregated-group level: Oneself and ingroup/outgroup

In group settings, people relate themselves to ingroups and outgroups differently, which, at the neural level, is reflected by differential engagement of the medial prefrontal cortex (mPFC) when processing the relationship between oneself and ingroups/outgroups. The mPFC is recognized as a central hub of the self-referential network and is integral to self-processing, such as processing one's own traits, mental states, preferences, and goals. When asked to judge whether they belong to various groups, individuals exhibit stronger mPFC activation when the target group is their own group compared with others (Figure 1A), for both pre-existing groups and newly established groups based on trivial categorization.[1] This mPFC activity supports attachment to ingroup and integration of ingroup membership into one's self-concept. The differential mPFC engagement may serve as a potent neural indicator of group belonging and could potentially predict ingroup love and intergroup conflict.

Interpersonal level: Oneself and ingroup/outgroup members

At the interpersonal level, two exciting lines of research are providing new insights into how individuals connect themselves with group members. First, individuals identify others as in-/outgroup members based on functional significance (e.g., whether this person will help me; link to dorsal anterior cingulate cortex [ACC] and anterior insula [AI] activity), dyadic similarity (mediated by mPFC/pregenual ACC activity), or latent group structure (e.g., how people relate to each other, tracked by AI activity).[2] Second, recent developments in simultaneous recordings of neural signals from multiple individuals have motivated investigations of how an individual's neural system interacts with those of ingroup and outgroup members to support interpersonal dynamics in group settings. During group interactions, an individual's brain activity synchronizes with ingroup (versus outgroup) members to a greater extent, as evidenced by stronger neural synchronization in within-group (versus between-group) interactions[3] (Figure 1B). This within-group neural synchronization (GNS) is particularly pronounced when ingroup members share strong social bonds or face common outgroup threats.[4] Furthermore, GNS in the dorsolateral prefrontal cortex (dLPFC) positively associates with hostility toward outgroups, suggesting prefrontal GNS as a potential neural predictor of intergroup conflict and hostility.[4]

How do people perceive ingroup and outgroup and their members?

Group membership serves as a powerful lens that alters the perception of ingroup and outgroup and their members. At the aggregated-group level, we review studies on the neural basis of (in/out) group perception, such as perception of abstract cues or de-individualized stimuli of ingroup and outgroup. This line of research examines neural responses to ingroup and outgroup by averaging across different stimuli within each group

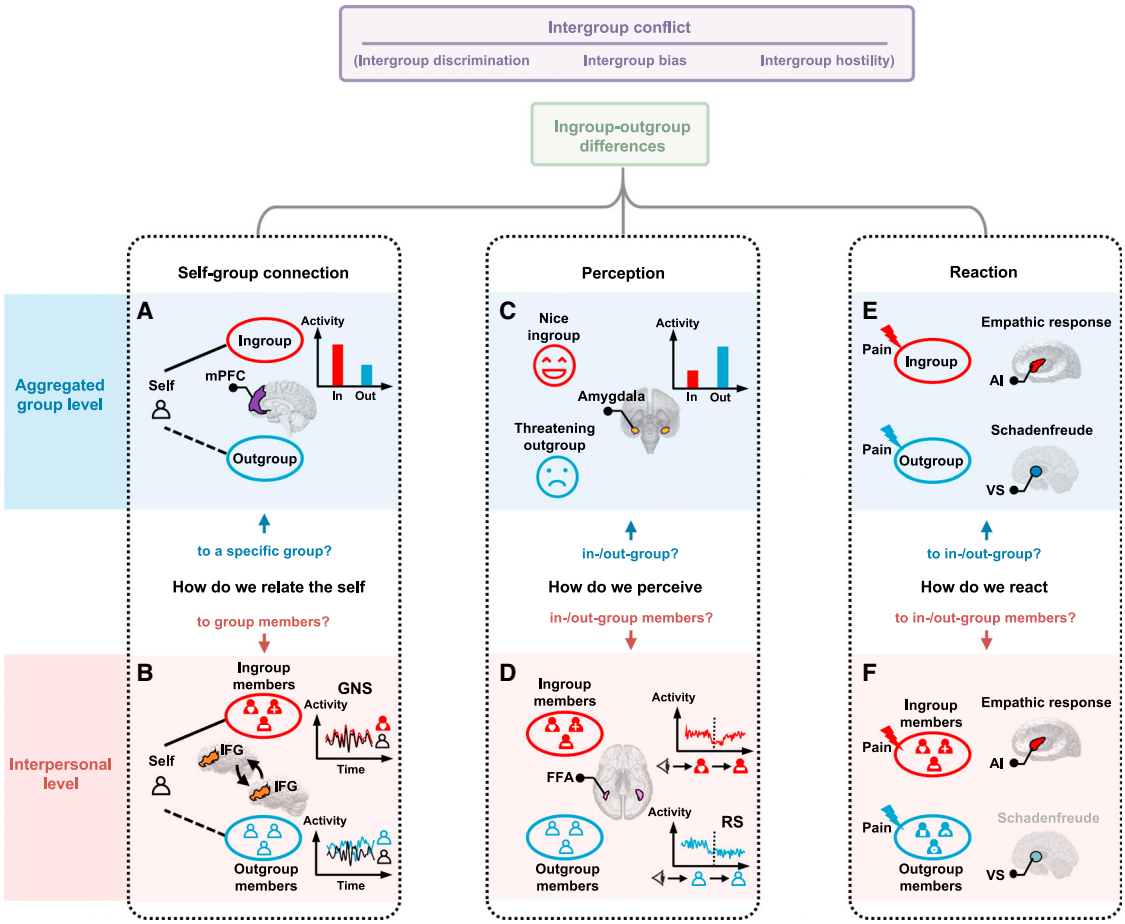

Figure 1. A two-level neurocognitive analysis of ingroup-outgroup differences and conflicts

We synthesize distinct neurocognitive responses toward in-/outgroups and their respective members (ingroup-outgroup differences). We utilize three group-related processes as a scaffold to organize our understanding of intergroup conflicts and analyze each process from both aggregated-group and interpersonal perspectives: (1) self-group connection (A and B), (2) perception of (in-/out)groups (C and D), and (3) reaction of (in-/out)groups (E and F). Solid (hallow) person icons represent individuals whose identities are (not) highlighted.

(A) People connect to ingroup more strongly, and mPFC activation supports self-ingroup connection.

(B) Individuals neurally synchronize with ingroup (versus outgroup) members to a greater degree (illustrated with an example of stronger GNS in the inferior frontal gyrus [IFG]).

(C) Outgroups are often perceived as more threatening, dehumanized, or less trustworthy (illustrated with an example of increased amygdala activity to outgroup).

(D) Individuals perceive ingroup members as distinct individuals and outgroup members as a homogeneous entity, which is captured by stronger RS effect in the FFA during perception of different outgroup (versus ingroup) members.

(E and F) At both aggregated-group (E) and interpersonal (F) levels, individuals exhibit stronger empathy and neural activity in the empathy network (e.g., AI) to the pain of ingroup (versus outgroup). Individuals display schadenfreude and increased VS activity to the pain of outgroup at the group level (E), which is overridden at an interpersonal level, possibly through the individualization of outgroup members (F).

to eliminate the effect of individual identity processing, reflecting ingroup and outgroup perception at an aggregated-group level. At the interpersonal level, we ask how individual members of ingroup and outgroup are perceived by summarizing neural evidence of different sensitivities to individual variations in faces of ingroup versus outgroup members. We expect discriminated, individualized (homogeneous, categorical) neural representations of ingroup (outgroup) members in brain regions sensitive to individual identity, which may pave the way for the development of intergroup bias or even intergroup violence.

Aggregated-group level: Perception of ingroup versus outgroup

Several lines of empirical work have probed how individuals perceive ingroups and outgroups at the aggregated-group level, often suggesting a more threatening, dehumanized, and less trustworthy perception of outgroup as opposed to ingroup.[5,6] Despite some inconsistencies in negatively biased perceptions of outgroups and even instances of outgroup favoritism, our focus is on the heightened perception of threat and dehumanization in outgroups due to its link with intergroup conflicts. One research line examines how group membership modulates perceived threat. The amygdala, a crucial brain region involved in threat detection and processing, plays a key role in perceiving outgroups as social threats.

Previous neuroimaging studies have shown that perception of outgroup (versus ingroup), especially threatening outgroups, is associated with increased amygdala activity[6] (Figure 1C), which in turn predicts more negative attitudes toward outgroups.[5] It is important to acknowledge that amygdala activity related to outgroup perception is complex and affected by factors such as the strength of realistic intergroup threat, individuals' concerns about appearing prejudiced, multivariate (versus univariate) analysis, and specific subregions of interest (e.g., the medial or lateral amygdala).[5,7] Another line of research concerns the dehumanized perception (perceiving others as less than human) of outgroup, characterized by the absence of mPFC activation (similar to perceiving objects) but increased disgust ratings and heightened insula and amygdala activity in response to extreme (low-warmth/low-competence) outgroups.[6] Such dehumanized perception may override the aversion to harming outgroups, thereby enabling violence toward them. Taken together, these findings reveal the neural substrates supporting intergroup biased perception and the tendency to perceive outgroups more negatively, which may also serve as the neural basis for outgroup hate and the escalation of intergroup conflicts.

Interpersonal level: Perception of ingroup/outgroup members

At the interpersonal level, with more interpersonal interactions and stronger GNS, people tend to perceive ingroup (versus outgroup) members as more individualized, which, at the neural level, is captured by more individualized, distinct neural representations of ingroup members in the ventral occipitotemporal cortex including the fusiform face area (FFA). The FFA, a high-level face-processing region, is responsible for the individualizing process and sensitive to individualized features rather than shared perceptual features. One classic approach to characterize the neural representation of different individuals utilizes the repetitive suppression (RS; Box 1) paradigm. Rapid perception of faces of different outgroup (versus ingroup) members elicited stronger RS effect in the FFA, an RS effect even as strong as repeated perception of two identical outgroup faces.[7] This line of research provides neural evidence that people tend to individuate ingroup members, perceiving each as a unique entity, while they categorically perceive outgroup members as similar, interchangeable representatives of the outgroup. This attenuated individualization in the neural representation of outgroup members may link to dehumanized perception and negatively impact the processing of emotions, mental states, and/or behaviors of outgroup members, thereby resulting in intergroup discrimination and ingroup bias across various domains.

How do people (re)act to ingroup and outgroup and their members?

At the aggregated-group level, ingroup attachment and negative perception of outgroup may lead to more caring and considerate (re)actions toward the ingroup but less so or even hostile toward outgroups. Such ingroup-biased psychological and neural (re)actions may further motivate participation in intergroup conflicts. At the interpersonal level, we review neural evidence of how people (re)act to *individualized* ingroup and outgroup members. Interpersonal interaction with specific in-/outgroup members results in the individualization of group members, especially outgroup members, which may attenuate intergroup disparities in neural activity related to caring or hostile (re)actions. Such individualization-attenuated intergroup differences may shed light on potential interventions on intergroup conflicts.

Aggregated-group level: (Re)action to ingroup versus outgroup

At the aggregated-group level, we reveal how group membership shapes our neural (re)actions by looking into studies that have examined neural (re)actions to outcomes endured by the aggregated-group or de-individualized, anonymous individuals with highlighted in- or outgroup membership but diminished individual identities. Converging neural evidence shows that individuals tend to show (1) stronger empathic and neural reactions to the suffering of ingroup (versus outgroup), (2) enhanced understanding and stronger activity in the mentalizing network (e.g., TPJ) to the minds of ingroup (versus outgroup), and (3) increased prosocial behaviors toward the needs of ingroup (versus outgroup).

Take (re)actions in the affect (empathy) and behavioral (trust behavior) domains as examples. First, stronger empathic responses and neural activity in the empathy network when responding to ingroup (versus outgroup) members' suffering from game loss or physical pain, including ACC and AI[7] (Figure 1E). However, outgroup's failure or painful experience activated ventral striatum (VS), which positively correlated with self-reported pleasure and willingness to harm outgroups[7] (Figure 1E). Such differential neural patterns to ingroup and outgroup can be implicated in intergroup harm and intergroup conflict. Second, there is behavioral and neural evidence for intergroup differences in trust. People intuitively trust ingroup (versus outgroup) with more investment.[8] Trusting ingroup is characterized by stronger activity in reward-related brain regions, whereas trusting outgroup requires top-down control to override the intuitive distrust of outgroup and engages activation in the executive control network.[8]

Interpersonal level: (Re)act to ingroup/outgroup members

At the interpersonal level, first, the ingroup-biased psychological and neural (re)action patterns observed at the aggregated-group level are partially evident at the interpersonal level. For example, participants showed similar intergroup bias in empathy, with decreased AI activity to specific outgroup (versus ingroup) members' pain[9] (Figure 1F). Likewise, participants also trusted and activated VS to a greater degree when making donation decisions to already-contacted, specific ingroup (versus outgroup) members.[10] Second, to enable interpersonal (re)actions among group members, researchers have offered participants the opportunity to personally meet, learn about, and/or interact with specific ingroup and outgroup members (e.g., an "ice-breaker" session). Such manipulations to individualize group members, especially outgroup members, reduce intergroup differences, at least in the individualization process, which in turn attenuates intergroup difference in behavioral and neural (re)actions. Indeed, there is no engagement of (1) reward-related regions to individualized outgroup members' pain[9] (Figure 1F)

Box 2. Future extensions

The three cognitive processes and two sets (group and interpersonal levels) of potential neural indicators may inspire and motivate candidate strategies to ameliorate intergroup conflicts and improve intergroup relations, such as fostering positive connections between oneself and outgroup members and between other ingroup and outgroup members, ameliorating individualization of outgroup members, and facilitating the formation of new, shared group memberships.

Moreover, we suggest several possible extensions to understand the group brain. For example, how do the neural indicators from aggregated-group level and interpersonal level interact or shape each other during the development of the group brain? How does the group brain track the dynamics of intergroup relations (e.g., change from peaceful to violent, and vice versa) through the three different cognitive processes? What neurobiological indicators predict the emergence of intergroup conflict, and how could they be used to prevent hostile intergroup relations? And how might long-term exposure to a hostile (versus peaceful) intergroup setting alter the brain function? It would be interesting to examine these questions to help us better understand the group brain.

or (2) executive-control-related regions when donating to individualized outgroup members.[10] Such individualization-attenuated intergroup differences in psychological and neural responses may provide insights into potential interventions on intergroup conflicts.

Conclusions and future directions

In this review, we synthesize how the human brain differently processes information related to ingroup and outgroup (members) from both aggregated-group and interpersonal perspectives, utilizing three neurocognitive processes as a scaffold to organize our understanding of intergroup conflicts. We further review neural evidence that links neuroimaging findings on intergroup differences to ingroup-outgroup conflicts. These three cognitive processes and potential neural indicators at the aggregated-group and interpersonal levels may inspire and motivate effective strategies to ameliorate intergroup conflicts and improve intergroup relations (Box 2).

We reveal distinct neural correlates linked to intergroup conflict at the aggregated-group level and the interpersonal level, suggesting that these two levels are dissociated at the neural level and independently impact group dynamics and ingroup-outgroup conflicts. This neural dissociation helps elucidate scenarios where individuals can establish friendships with individual members of rival outgroups, as well as instances where individuals may strongly dislike specific ingroup members without impacting their overall sense of belonging and favoritism toward the ingroup at an aggregated level. These nuanced distinctions contribute to a more sophisticated understanding of intergroup conflicts. With the existing studies focusing mainly on the aggregated-group level,[7] we call for more attention to the interpersonal level and the relationship between these two levels in future studies of intergroup conflicts.

Although we focus primarily on intergroup conflicts, the analysis of three neurocognitive processes from both aggregate-group and interpersonal levels can be applied to other group-related phenomena, such as group polarization, migration, and intergroup cooperation. We thus provide a perspective for understanding the group brain and ask new questions and hypotheses about the group brain (Box 2). We hope that this review can motivate new directions for future neuroscience research on intergroup interactions and relations, group decision-making, and collective wisdom to further our understanding of the nature of the group brain.

The current review, based on laboratory neuroscience results, only provides a guidepost for investigating, understanding, and potentially intervening intergroup conflict. To extrapolate from neuroscientific findings to real-world intergroup violence is nontrivial. We call for future interdisciplinary efforts to enrich and expand our knowledge of intergroup conflict, opening a promising avenue for solving realistic conflicts.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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