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The Neuroscience of Intergroup Relations: An Integrative Review

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Abstract

We review emerging research on the psychological and biological factors that underlie social group formation, cooperation, and conflict in humans. Our aim is to integrate the intergroup neuroscience literature with classic theories of group processes and intergroup relations in an effort to move beyond merely describing the effects of specific social out-groups on the brain and behavior. Instead, we emphasize the underlying psychological processes that govern intergroup interactions more generally: forming and updating our representations of “us” and “them” via social identification and functional relations between groups. This approach highlights the dynamic nature of social identity and the context-dependent nature of intergroup relations. We argue that this theoretical integration can help reconcile seemingly discrepant findings in the literature, provide organizational principles for understanding the core elements of intergroup dynamics, and highlight several exciting directions for future research at the interface of intergroup relations and neuroscience.

Keywords

cognition, intergroup relations, neuroscience, social cognition

The human brain is “truly social,” which is to say specialized for group living (Caporael, 1997; Dunbar, 1998). People who accurately identify, value, and cooperate with in-group members enjoy numerous benefits, including the fulfillment of many basic psychological needs (Allport, 1954; Correll & Park, 2005; Kurzban & Neuberg, 2005; D. S. Wilson & Wilson, 2007). The value humans place on group membership is illustrated by the ease with which humans form groups and favor in-group members. Indeed, the propensity to prefer one’s in-group has been observed in every culture on earth (D. E. Brown, 1991) and in children as young as 5 (Dunham, 2011; Fehr, Bernhard, & Rockenbach, 2008).

The functional benefits of group membership notwithstanding, group life is also a source of social strife and destruction (e.g., pressure to conform within groups, protracted conflict between groups; Brewer, 1999; Cosmides, 1989; Hewstone, Rubin, & Willis, 2002; Neuberg & Cottrell, 2006). Intergroup conflict, in particular, has been described as “one of the greatest problems facing the world today” (Cohen & Insko, 2008). For example, it has been estimated that over 200 million people were killed in the last century in acts of genocide,

war, and other forms of group conflict (Woolf & Hulsizer, 2004). The social and economic obstacles of group living have attracted the attention of scholars and scientists from social, developmental, evolutionary, and cognitive psychology, social neuroscience, and biological and cultural anthropology, among others.

In the last few decades, there has been a surge of interest in the effects of group membership on cognitive and biological processes with the goal of better understanding how these processes, in turn, contribute to parochialism, prejudice, and intergroup conflict. This interdisciplinary approach—termed *social neuroscience* (Cacioppo, Berntson, Sheridan, & McClintock, 2000) or *social cognitive neuroscience* (Ochsner & Lieberman, 2001)—to the study of intergroup relations has captured the attention of the scientific community (e.g., Kubota, Banaji, & Phelps, 2012; Molenberghs, 2013), as well as that of the popular media and society more broadly (e.g.,

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Brooks, 2009). This approach builds on the assumption that complex social phenomena, such as intergroup relations, may be better understood by combining social and biological theories and methods that traverse multiple levels of analysis (Cacioppo & Cacioppo, 2013). Researchers in this area have already helped to bolster and refine existing psychological theories of intergroup relations (e.g., Derks, Scheepers, & Ellemers, 2013), highlighted the contextual flexibility of seemingly “hardwired” biological responses (e.g., Van Bavel, Packer, & Cunningham, 2008; Wheeler & Fiske, 2005), and challenged popular interpretations of biological systems (e.g., De Dreu, Greer, Van Kleef, Shalvi, & Handgraaf, 2011). In the domain of intergroup relations, this approach may ultimately inform the design of better targeted interventions (including pharmacological interventions) for mitigating prejudice and intergroup conflict (e.g., Terbeck et al., 2012).

To date, intergroup and cultural neuroscience has focused largely on specific social groups rather than studying the dynamics that govern group formation and intergroup interactions. Several excellent reviews have examined the neural basis of social categorization along boundaries marked by visual cues to targets’ group membership, such as race, sex, and age (e.g., Eberhardt, 2005; Ito & Bartholow, 2009; Kubota et al., 2012); however, broader inferences about group processes are often difficult to make on the basis of these social categories because of confounding variables (e.g., differences in the visual appearance of target stimuli, associated stereotypes and prejudices, and perceivers’ personal experience with groups in question). Furthermore, research that focuses exclusively on a single, static category boundary fails to account fully for the flexible nature of social identity representation (e.g., the effects of context on self-categorization, the effects of task on person construal; Freeman & Ambady, 2011). Thus, the next phase of intergroup neuroscience research must account for the fact that not all out-groups are equivalent, not all group memberships are static, and which group identities are salient is highly context dependent (Turner, Oakes, Haslam, & McGarty, 1994).

We therefore focus our attention on research examining (a) how the basic concepts of “us” and “them” are represented in the mind and brain and (b) the factors that drive people to flexibly update these representations, including social identity (Tajfel & Turner, 1979; Turner, Hogg, Oakes, Reicher, & Wetherell, 1987), cooperation (Deutsch, 1949), and competition (Sherif, Harvey, White, Hood, & Sherif, 1961). Building on these classic perspectives, we emphasize the processes by which social groups are defined (e.g., self-categorization, common fate) as well as the forces that intensify group identities and intergroup conflict (shared versus competing goals, status

threat). We argue that focusing on these elemental features, rather than on specific, static social groups in isolation, will help to resolve seemingly discrepant findings in the emerging literature, generate novel hypotheses, and offer a more general framework for understanding the neuroscience of intergroup relations.¹

Overview

In order to integrate major theories of intergroup relations with research on the neural systems implicated in maintaining and updating our representations of in-group and out-group members, we examine how these representations affect fundamental psychological processes, including perception, emotion, motivation, and decision making, as well as subsequent behavior. We also review some of the scientific advantages of assigning people to novel groups (Tajfel, Billig, Bundy, & Flament, 1971) and manipulating group features and intergroup dynamics. To illustrate the utility of this approach, we highlight instances in which studying intergroup phenomena in the context of novel groups has incited a revision of existing psychological and neuroscience theories. Our hope is that this approach can better account for findings across multiple contexts and levels of analysis.

We begin by reviewing the influence of social identity and self-categorization on the biological bases of group formation and evaluation. We describe how people move from categorizing themselves as individuals to identifying with a group and representing others as “us” versus “them.” We then review the social forces that unite and divide groups, with a specific emphasis on functional relations between groups, relative group status, and the effects of these dynamics on empathy and social behavior (i.e., help, harm). Finally, we outline an agenda for future research to address gaps in this growing area of inquiry and to foster greater collaboration between psychologists and neuroscientists.

Representing “Us” and “Them”

Psychologists have long conceded that prejudice may be an inevitable aspect of human life (Allport, 1954). Categorizing people into social groups—termed *social categorization*—allows us to simplify the social world and generalize our existing knowledge about certain groups and new people (Bruner, 1957). Although social categorization serves an important cognitive function, it can also lead to the activation and application of inaccurate stereotypes and prejudices, unless people are able to individuate specific social targets (Brewer, 1988; S. T. Fiske & Neuberg, 1990). As many models of person perception posit, this problem is magnified by the fact that

categorizing others according to their age, gender, or race can be reflexive and difficult to override (Brewer, 1988; Devine, 1989; Ito & Urland, 2005; Macrae & Bodenhausen, 2000; Taylor, Fiske, Etcoff, & Ruderman, 1978). To help understand how people perceive and evaluate targets from different social categories, scientists have used neuroimaging and other psychophysiological methods to examine how social categories are represented, evaluated, and integrated with ongoing psychological processes (see Amodio, 2008; Cunningham & Van Bavel, 2009; Eberhardt, 2005; Ito & Bartholow, 2009; Kubota et al., 2012; Phelps & Thomas, 2003; Wheeler & Fiske, 2005).

This relatively recent application of neuroscience to the study of social categorization has already provided important insights into the specific component processes that underlie intergroup categorization (e.g., Golby, Gabrieli, Chiao, & Eberhardt, 2001), evaluation (e.g., Phelps et al., 2000), and motivation (e.g., Amodio et al., 2004) and illuminated the time course of intergroup processing (e.g., Cunningham, Van Bavel, Arbuckle, Packer, & Waggoner, 2012; Ito & Urland, 2003, 2005). Social group memberships do, indeed, affect neural processes automatically and unconsciously, and these processes have important implications for discriminatory behavior (Cunningham, Johnson, et al., 2004).

Most research that has examined the neural bases of social categorization has focused on static social groups and categories, such as race, rendering the findings ecologically valid while obscuring inferences about the underlying processes. Differences in the groups, context, and experimental method have often produced inconsistent results. These inconsistencies reflect the fact that race and other social categories are confounded with a variety of factors that might affect neural responses. For instance, participants in previous neuroimaging studies of social categorization often have strong associations with existing social groups, introducing the possibility that factors ranging from low-level visual features of stimuli (e.g., luminance and contrast) to stereotypes can account for differences in neural responses to same versus specific other-race targets. Furthermore, most studies examine how majority group members respond to minority group members; relatively few have directly compared the responses of members of different racial groups to same- versus other-race targets within a single study (c.f., Golby et al., 2001; Hart et al., 2000; Lieberman, Hariri, Jarcho, Eisenberger, & Bookheimer, 2005).

In this section, we introduce a different approach to studying the biological bases of group processes. We review self-categorization and social identity theory to explain how people develop and maintain representations of “us” and “them,” in the real world and in the laboratory. We then contrast early findings from

intergroup neuroscience research (using existing social groups) against more recent findings, which have generated significant reinterpretation of earlier results by incorporating novel groups and classic theories of intergroup relations. We believe this approach complements research with existing social groups by emphasizing the context-dependent nature of social identity representation and identifying organizational principles for understanding the core elements of group formation and conflict.

Self-categorization, social identity, and minimal groups

There is no doubt that certain social categories, such as age, gender, and race, play a major role in shaping neural responses as well as the biases and stereotypes that people bring to bear on their social judgments and behavior. However, work on social identity theory (Tajfel & Turner, 1979) and self-categorization theory (Turner et al., 1987) has argued that how people categorize themselves as members of a group is also fundamental to understanding intergroup relations. Tajfel and Turner conceptualized a group as “a collection of individuals who perceive themselves to be members of the same social category, share some emotional involvement in this common definition of themselves, and achieve some degree of social consensus about the evaluation of their group and their membership of it” (1979, p. 40). From this perspective, aggregates of individuals become meaningful social groups by virtue of the fact that the members choose to identify with groups and their other members (see Sherif, 1966).

When people categorize themselves as part of a group or coalition, their self-concept shifts from the individual (“I” or “me”) to the collective level (“we” or “us”)—a process termed *social identification* (Brewer & Gardner, 1996). Social identities represent individuals’ knowledge that they belong to certain groups, along with the psychological significance of these groups, their relationship to these groups and group members, and associations they have with these groups (Tajfel, 1982). As such, social identities fulfill a number of basic human motives, including belonging (Brewer, 1991), self-esteem (Tajfel & Turner, 1979), and certainty (Hogg, 2000) needs.

The act of categorizing one’s self as a group member has a significant influence on basic intergroup perception, evaluation, and behaviors (e.g., Ashburn-Nardo, Voils, & Monteith, 2001; Otten & Wentura, 1999; Van Bavel & Cunningham, 2009, 2011). The nature of the effects depends on which social identity is made salient, which is determined in large part by the social context. Social identities become more inclusive as the context makes more abstract identities salient (e.g., shifting from local to national to global identities), leading to the inclusion of others who would otherwise be deemed as

distinct from the self (S. L. Gaertner, Mann, Murrell, & Dovidio, 1989; Turner et al., 1994). Conversely, the social context can heighten the accessibility of a more specific social identity (e.g., university affiliation, sports team allegiance), which in turn elicits perceptions and evaluations consistent with the activated aspects of this identity. Specific identities can become integrated with the representation of one's self (Smith & Henry, 1996), especially among people who strongly identify with the in-group (Brewer & Pickett, 1999). Identification with specific groups may even override automatic responses to orthogonal categories like race (Van Bavel & Cunningham, 2009). In other words, when people identify with a group, their in-group members may be seen as valuable regardless of their race or other seemingly important category memberships.

One important consequence of the social identification process is that humans reliably divide the world into *us* and everyone else: *them*. The mere act of categorizing people into groups has profound implications for intergroup preferences (Brewer, 1979). Group membership matters because it reliably predicts intergroup bias: prejudice and discriminatory behavior that favors the in-group relative to an out-group (Hewstone et al., 2002). Perhaps most fascinating is that individuals construct intergroup boundaries and discriminate in favor of in-group members in the absence of any factors typically posited to account for intergroup bias.

Creating “Us” and “Them” in the Laboratory: The Minimal Group Paradigm. The ease with which one can generate intergroup bias is best illustrated by the minimal group paradigm (Tajfel, 1970; Tajfel et al., 1971). In these studies, people are told they are assigned to minimal groups on the basis of arbitrary group differences, such as a preference for abstract art or dot estimation abilities (in fact, they are randomly assigned). Once they are assigned to groups, participants typically have no face-to-face interaction within or between groups, which prevents any sense of competition or the potential for stereotype activation. Remarkably, randomly assigning participants to minimal groups (even when participants know one another prior to the study) produces discrimination in favor of in-group members. These findings underscore how readily people identify with social groups as well as the context-dependent nature of these identities.

Creating novel groups is a powerful tool for intergroup neuroscience research because it can be used to isolate the effects of social identification processes: (a) Participants do not have any preexisting stereotypes or associations regarding the in-group and out-group prior to group assignment, (b) theoretically irrelevant group features (e.g., majority or minority status, power, familiarity) can

be matched between groups, (c) theoretically relevant group features (e.g., current threat, perceived cohesion) can be effectively and ethically manipulated between groups, (d) there is a natural mechanism for creating neutral targets who are not associated with either group to help differentiate in-group favoritism from out-group derogation (e.g., Van Bavel, Packer, & Cunningham, 2011), and (e) individuals can be randomly assigned and then reassigned to groups, allowing researchers to examine the flexibility of self-categorization processes (e.g., Cikara et al., 2014). Furthermore, novel groups are easy to implement in the lab (e.g., easier than collecting equal numbers of ethnic minority and majority participants). Finally, in our experience, most participants take to their identities quickly and maintain them until another identity becomes salient.

Neural responses to “us” and “them”

Early results in the neuroscience of intergroup evaluation. The initial neuroimaging research on social categorization focused on the amygdala—a small structure in the temporal lobe (see Fig. 1). The amygdala has been implicated in a host of social and affective processes, including fear conditioning and processing negative stimuli (for a review, see Phelps, 2006). Building on this work, several functional magnetic resonance imaging (fMRI) studies of social categorization found that Black and White perceivers exhibited relatively greater amygdala activity when viewing other-race faces than own-race faces (Hart et al., 2000) and that individual differences in amygdala activity to other-race faces were correlated with implicit measures of racial bias—including startle eye blink and the Implicit Association Test (IAT; Cunningham, Johnson, et al., 2004; Phelps et al., 2000). These correlations with racial bias, coupled with studies demonstrating a link between the amygdala and fear conditioning (LeDoux, 1996), led some researchers to interpret differences in amygdala activity to other-race faces as evidence of negativity (including disgust and fear) toward stigmatized groups.

Despite the robust relationship between the amygdala and negative stimuli, several studies have shown that the amygdala also responds to highly arousing stimuli more generally (Anderson et al., 2003; Cunningham, Raye, & Johnson, 2004), including positively arousing stimuli (Hamann, Ely, Grafton, & Kilts, 1999). As such, the amygdala may play a role in directing attention to any motivationally relevant stimuli, regardless of valence (Cunningham & Brosch, 2012; Cunningham, Van Bavel, & Johnsen, 2008; Vuilleumier & Brosch, 2009). When race is the most salient social category—as is often the case in experiments where participants are presented with hundreds of Black and White faces—the amygdala may

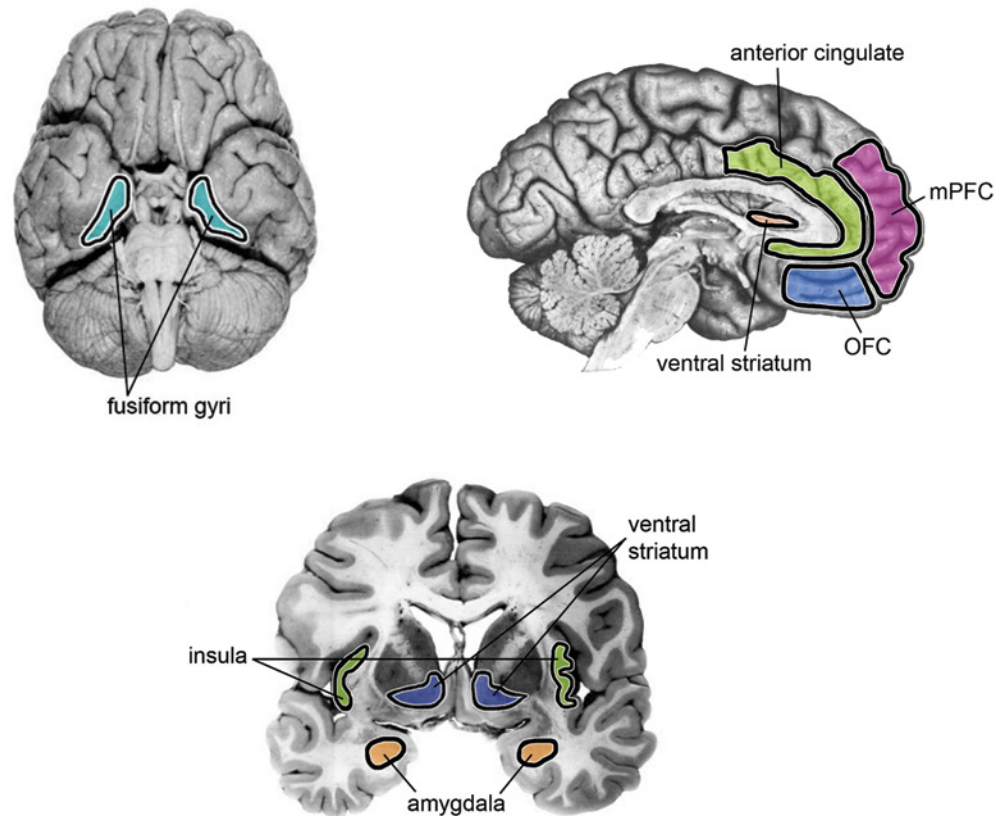


Fig. 1. Anatomical images of several key brain regions associated with group categorization and evaluation, functional relations between groups, empathy, and prosocial and antisocial behavior. As such, this figure is meant to serve as a guide to the location of various regions we reference frequently (not to represent a neural circuit supporting one process in particular). mPFC = medial prefrontal cortex; OFC = orbitofrontal cortex.

indeed be responsive to members of groups that are novel (Dubois et al., 1999) or associated with threatening stereotypes or prejudice (Phelps et al., 2000). However, when race is not the most salient social category, the amygdala may be responsive to members of groups, who are motivationally relevant for other reasons (see Van Bavel & Cunningham, 2011).

Reinterpreting findings from the neuroscience of intergroup evaluation. In minimal groups, in-group members tend to be motivationally relevant because they afford group members the opportunity to fulfill belonging needs and other core social motives; furthermore, minimal out-group members are not associated with any specific stereotypes (Hugenberg, Young, Bernstein, & Sacco, 2010; Van Bavel & Cunningham, 2012; Van Bavel, Swencionis, O'Connor, & Cunningham, 2012). To test the hypothesis that the amygdala would respond more to a novel in-group members as compared with out-group members, one study randomly assigned White participants to a minimal mixed-race group, had them briefly

learn the members of each group, and then presented them with in-group and out-group faces during fMRI (Van Bavel et al., 2008). Crossing race and group membership provided a clean investigation of the role of group membership in neural processing because it diminished differences between in-group and out-group members on familiarity, novelty, and other factors. Likewise, the novel groups had no preexisting stereotypes, and the images were counterbalanced to rule out any visual differences between in-group and out-group members.

Whereas earlier studies had often interpreted amygdala activity to other-race faces as reflecting negativity or fear, perceivers in this experiment had greater amygdala activity in response to members of their novel in-group. Specifically, people exhibited greater amygdala activity in response to in-group than to out-group faces. There was no main effect of race, nor was this pattern of in-group bias moderated by target race. Strikingly, this pattern of in-group bias in neural processing occurred within minutes of group assignment, in the absence of explicit team-based rewards

or social interaction, and independent of preexisting racial bias, stereotypes, or familiarity. This suggests that social identification with a group—even a seemingly trivial group—can guide neural responses to social targets. Subsequent studies confirmed that assigning people to mixed-race teams can even override racial biases on relatively automatic measures of evaluation (see Van Bavel & Cunningham, 2009) and that the effects of novel group membership can influence perceptual processes within the first few hundred milliseconds of perception (Ratner & Amodio, 2012; Van Bavel, Earls, Morris, & Cunningham, 2013).

This research underscores the idea that the relevance of different social categories varies according to the immediate social context (Turner et al., 1987). In contexts where race provides the most salient group distinction, racial attitudes, cultural stereotypes, and personal values (e.g., egalitarianism) may provide the most relevant frameworks for perception and action. Assigning people to mixed-race groups, in contrast, may change the way people construe race and other social categories and sensitize perceptual and evaluative processes to other contextually relevant group memberships (Kurzban, Tooby, & Cosmides, 2001).

Perceiving “us” and “them.” For nearly a century, scientists have known that people are better at recognizing faces from their own racial or ethnic groups compared with faces from other racial groups (Feingold, 1914). This phenomenon, typically termed the *own-race bias*, has largely been explained in terms of experience with own-race faces (i.e., people have a lifetime of experience identifying members of their own race; Malpass & Kravitz, 1969; Sporer, 2001). For instance, one influential neuroimaging study found that Black and White participants showed heightened activity in the fusiform face area (FFA) to own-race relative to other-race faces (Golby et al., 2001). The FFA—a face-sensitive subregion of the fusiform gyri (see Fig. 1)—plays an important role in processing and individuating faces (Kanwisher, McDermott, & Chun, 1997; Rhodes, Byatt, Michie, & Puce, 2004) and perceptual expertise (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999). Participants with the strongest FFA activity to own-race (relative to other-race) faces also displayed the greatest own-race bias on a subsequent recognition memory task, leading the authors to suggest that own-race biases in fusiform activity may have been due to superior perceptual expertise with own-race faces (Golby et al., 2001; see also Feng et al., 2011).

Although studies have shown that lifelong experience with own-race faces is associated with own-race bias (Sangrigoli, Pallier, Argenti, Ventureyra, & De Schonen, 2005), interracial contact (a proxy for expertise) explains only 2% of the own-race bias effect (Meissner & Brigham,

2001). As a result, researchers have sought alternative theoretical frameworks to explain own-race bias. Sporer (2001) and others have argued that categorizing others as own-group versus other-group members may alter the depth or type of processing the targets receive, such that own-race faces are processed as individuals (encoded at a subordinate level) and other-race faces are processed as interchangeable representatives of a social category (encoded at a superordinate level; see also Hugenberg et al., 2010; Levin, 1996, 2000). Indeed, the own-race bias has been replicated across a variety of nonracial social categories, including minimal groups, demonstrating that mere categorization with a group can enhance the recognition of in-group relative to out-group faces, even when prior exposure to in-group and out-group members is equivalent (Bernstein, Young, & Hugenberg, 2007; Van Bavel & Cunningham, 2012). This suggests that social identity may also motivate enhanced encoding of in-group members' faces.

Building on this work, Van Bavel and colleagues (2008, 2011) examined whether members of novel groups would encode in-group members at an individuated, subordinate level and out-group members at a categorical, superordinate level. Specifically, they predicted that deeper encoding of in-group members would be reflected in differences in fusiform activity for in-group compared with out-group members, despite similar exposure to members of both groups. Given the role of the fusiform gyrus—especially the FFA—in perceptual expertise, White participants might have been expected to show greater fusiform activity to own-race relative to other-race faces. However, given the role of the fusiform in individuation (see Kanwisher et al., 1997; Tarr & Gauthier, 2000), the authors expected that participants would show greater fusiform activity to in-group relative to out-group faces, regardless of race. Consistent with the latter hypothesis, participants exhibited greater activation within the bilateral fusiform gyri for novel in-group than out-group faces (Van Bavel et al., 2008). It is important to note that there was no main effect of race, nor was this pattern of in-group bias moderated by race (see also Hehman, Maniab, & Gaertner, 2010; Van Bavel & Cunningham, 2012). These results provided evidence that the fusiform may be sensitive to shifts in self-categorization, individuating faces imbued with psychological significance by virtue of their group membership.

Subsequent research has linked this pattern of in-group bias directly to behavior. In a follow-up experiment, the same authors examined the FFA using a face-localizer task. They not only replicated the pattern of in-group bias reported above, but they also found that FFA activity was associated with the effects of group membership on recognition memory—a behavioral index of individuation. Specifically, there was a positive

correlation between the individual differences in FFA activity to in-group versus out-group faces and recognition memory differences for in-group versus out-group faces (Van Bavel et al., 2011). Similarly, several electroencephalography (EEG) studies have found that novel group membership can influence very early components of face processing (i.e., within the first few hundred milliseconds). For instance, a recent study found that people have greater N170 responses—an event-related potential implicated in facial identity encoding—to minimal in-group than out-group faces (Ratner & Amodio, 2012). Other work suggests that in-group members are perceived faster than out-group members (Zheng & Segalowitz, 2013) and that these group affiliations can override initial racial biases in perceptual processing (Van Bavel et al., 2013). Taken together, these findings imply that once people identify with a group, in-group members are more likely to be processed as individuals than out-group members. However, the time course of these signals suggests that motivational concerns may influence face processing earlier than many social cognitive models suggest.

Consistent with these findings, recent research suggests that social memory is also sensitive to the extent of social identification (see Hugenberg et al., 2010, for a review), and the motivational aspects of the perceiver's social identity shape social attention and memory over and above mere categorization into groups (Van Bavel & Cunningham, 2012; Van Bavel et al., 2012). For instance, people, who have a high need to belong or who are highly identified with their in-group appear to have the largest memory advantage for in-group versus out-group faces. However, social roles can attenuate in-group bias: For example, memory for out-group faces was heightened among participants who were assigned to be a "spy," a role that required greater attention toward out-group members. This research suggests that many aspects of social identity—from collective identification to specific social roles—influence social perception and memory.

More generally, there is evidence that the influence of social identity extends far beyond face perception. Confirming the experience of countless sports fans, one classic study found that students from two different universities had very different perceptions of the same football game, recalling different "facts" about the game (e.g., irrespective of team allegiance, fans recalled with great certainty that the other team had played dirty; Hastorf & Cantril, 1954). A related, recent neuroimaging study found evidence that groups might indeed bias basic perceptual processing of in-group versus out-group targets' actions (Molenberghs, Halasz, Mattingly, Vanman, & Cunningham, 2012). The authors randomly assigned participants to the red team or blue team and had them

judge the speed of hand movements performed by both in-group and out-group members. Participants judged the actions of in-group members as faster than the identical actions of out-group members; this intergroup bias was associated with activity in the left inferior parietal lobule—a region that has previously been implicated in transforming visual representations of actions to the motor system for action (see Rizzolatti & Craighero, 2004; Rizzolatti & Fabbri-Destro, 2008). This work converges with several recent behavioral studies suggesting that group allegiances can play a role in structuring basic perceptions of the social and physical world (Caruso, Mead, & Balcetis, 2009; Xiao & Van Bavel, 2012; Young, Ratner, & Fazio, 2014).

Effects of "Us" and "Them" on Higher Order Social Cognition.

It is important to note that differences between processing in-group and out-group targets are not confined to perceptual and evaluative processes. Higher order social cognition also appears to be sensitive to social identity concerns: For example, people are more accurate when inferring the mental states of own-race relative to other-race targets (Adams et al., 2010). Building on the hypothesis that "we" is represented similarly to "I," several neuroimaging studies have attempted to identify an overlap between the brain regions implicated in self-referential processing, such as the medial prefrontal cortex (mPFC, adjacent to the pregenual anterior cingulate cortex; Kelley et al., 2002; Mitchell, 2009; see Fig. 1), and representation of in-group members. For instance, people assigned to a minimal group showed greater activation in the dorsal mPFC when they had to choose between allocating points to an in-group versus out-group member (as opposed to two in-group or two out-group members); this activation was correlated with in-group bias (i.e., awarding more points to in-group than out-group players; Volz, Kessler, & von Cramon, 2009). Other research has found that in-group relative to out-group labels of both real social groups (e.g., "male," "Australian"; Morrison, Decety, & Molenberghs, 2012) and novel groups (e.g., red team vs. blue team; Molenberghs & Morrison, 2012) were associated with greater activation in the mPFC.

Although the regions reported in these studies are more dorsal than the region of mPFC that is usually associated with self-referential processing (e.g., Denny, Kober, Wager, & Ochsner, 2012; Jenkins & Mitchell, 2011), these findings led the authors to infer that social and personal identity processes draw on overlapping neural substrates (see also Scheepers et al., 2013). It is important to keep in mind that the "self" is not a static representation stored in an isolated region of the brain but rather an online construction derived from contextually determined patterns of activation across networks

involving many different regions of the brain (Smith, Coats, & Walling, 1999). As such, social identities and specific group memberships also involve the dynamic construction of a collective self-representation (Aron, Aron, Tudor, & Nelson, 1991; Packer & Van Bavel, in press; Turner et al., 1987).

Summary

Taken together, these studies support the notion that social identification involves a highly flexible shift in self-representation from the personal to the collective and that this shift can override the influence of visually salient social categories on perception, evaluation, and other aspects of cognition. One important implication is that many social categories are poor proxies for group membership because they are associated with a host of other variables. This research marks the initial phase of work on novel groups in social neuroscience, and future work will likely continue to revise existing theories of the neural bases of social categorization and intergroup relations. It is important to note, however, that work with novel groups should complement, rather than replace, work with existing social groups (e.g., race-based categories). Intergroup relations are complex, and inviting a synthesis of both perspectives likely offers the greatest hope for understanding and attenuating intergroup conflict.

Forces That Unite and Divide “Us” and “Them”

An integrative theory of intergroup relations must appreciate not only that group membership is flexible and highly context dependent but also that not all out-groups are equivalent. People today encounter a far greater number and variety of out-group members than their ancestors did; however, the fundamental questions that govern social interactions remain the same. Whenever we encounter a novel person or group, we are motivated to answer two questions as quickly as possible: the first is “friend or foe?”; the second is “is this agent capable of enacting his or her intentions toward me?” Specifically, functional relations between groups—are your goals concordant, discordant, or entirely independent of ours?—and status—do you have access to resources?—largely determine the course of intergroup interactions (Cuddy, Fiske, & Glick, 2007; S. T. Fiske, Cuddy, & Glick, 2007; Fiske, Cuddy, Glick, & Xu, 2002). As such, one alternative to studying intergroup relations with existing social groups and categories is to manipulate these structural variables among novel groups. The primary strength of this approach is that it provides experimental control over confounding factors and allows for more precise inferences about the causal influences of different aspects of

the intergroup context. Accordingly, insights from this approach should have greater generalizability across intergroup contexts and may allow for greater specification of potential interventions (see Billig, 1976). Here we review the effects of functional relations (i.e., cooperation, competition) and relative group status on the neural bases of intergroup interactions. We then explore some of the effects of these structural variables on intergroup interactions, including effects on empathy, help, and harm between groups.

Role of Functional Relations in Intergroup Dynamics

Extensive evidence suggests that random assignment to minimal groups can elicit intergroup bias—even in the absence of intergroup hostility. Beyond mere group membership, one key amplifier of intergroup bias is the perception of a zero-sum relationship between the respective groups’ goals (S. T. Fiske & Ruscher, 1993; see also Struch & Schwartz, 1989). Even in the absence of actual competition, the mere perception of groups as competitive engenders negative emotions toward them (S. T. Fiske et al., 2002). Making competition explicit increases intergroup hostility in part because it makes social identity more salient (Hogg, 1992, 1993; Mullen, Brown, & Smith, 1992). For all these reasons, competitive functional relations increase intergroup conflict and out-group derogation (Deutsch, 2006; D. W. Johnson & Johnson, 1989; Sherif & Hovland, 1961).

In addition to the flexibility of social identification with groups (Turner et al., 1994), the functional relations between groups (and the consequences thereof) are also malleable (Sherif, Harvey, White, Hood, Sherif, 1961; Tajfel & Turner, 1979). Groups that have previously had cordial relations may become competitive. The fluid nature of functional relations between groups, however, is also reason to be optimistic about interventions in intergroup conflicts: If perceptions or the salience of intergroup relations can be changed, individuals may overcome hostility toward previous enemies (Sherif et al., 1961), even in the context of socially meaningful identities that are linked to deeply held political beliefs, gender, or race. For example, during the fiercely contested 2008 Democratic presidential primary process, Hillary Clinton and Barack Obama supporters gave more money in a dictator game to strangers who supported the same primary candidate (compared with the rival candidate). Two months later, after the Democratic National Convention, the supporters of both candidates coalesced around the party nominee—Barack Obama—and this bias disappeared (Rand et al., 2009). Along with the findings that novel teams can override race categorization (e.g., Kurzban et al., 2001; Van Bavel & Cunningham,

2011), these findings fit well with decades of research on common in-group identity (S. L. Gaertner & Dovidio, 2000; Sherif et al., 1961). The moment-to-moment motivational salience of specific functional relations can modulate attitudes, emotions, and behaviors.

It is surprising that very little research has explored the biological bases of intergroup competition and cooperation as well as group-based social status inference. In the sections that follow, we review the relevant literature and include some of the recent work on these topics in the context of interpersonal interactions as the basis for generating novel hypotheses about these processes at the group level.

Neuroscience of Competition and Cooperation

The last decade has seen an explosion of research examining the neural substrates of cooperation and competition between individuals (see Rilling & Sanfey, 2011). By some accounts, people cooperate because it is inherently rewarding (Zaki & Mitchell, 2013). For example, in one study, playing a game with another person in both cooperative and competitive contexts (relative to playing alone) recruited the frontoparietal network, which is associated with executive control (e.g., Vincent, Kahn, Snyder, Raichle, & Buckner, 2008); however, when the two social interaction conditions were contrasted against one another, cooperation, relative to competition, elicited a relatively greater response in orbitofrontal cortex (among other regions), which the authors interpreted as reflecting a reward response (Decety, Jackson, Sommerville, Chaminade, & Meltzoff, 2004). Several other studies support the cooperation-as-reward theory: For example, ventral striatum (also associated with reward registration in the service of optimizing future behavior) responds when individuals observe cooperation (Rilling et al., 2002) and fair resource distribution (Tricomi, Rangel, Camerer, & O'Doherty, 2010), as well as when individuals choose to act equitably (Zaki & Mitchell, 2011). Somewhat surprisingly, the same neural mechanisms associated with cooperative behavior are also associated with antisocial responses in competitive contexts.

People experience pleasure when they have the ability to punish or watch the punishment of a disliked or competitive other. When a partner behaved unfairly (i.e., defected) in a game, the dorsal striatum—a region implicated in action selection on the basis of reward value—was relatively more active when people administered punishments that reduced defectors' payoffs, as compared with punishments that did not (De Quervain et al., 2004). Moreover, subjects with stronger activations in the dorsal striatum were willing to incur greater costs in order to punish. Other work has found that seeing the

pain of a cooperative confederate activated a network of brain regions associated with firsthand experience of pain; however, seeing the pain of a competitive confederate activated ventral striatum. Further, ventral striatum activation correlated with an expressed desire for revenge (Singer et al., 2006). Thus, in interpersonal contexts, competition (even among strangers, for low-stakes outcomes) fundamentally changes people's social preferences and corresponding neural responses.

One open question is how moving from an interpersonal to intergroup context affects these processes. Is observing out-group punishment or failure rewarding in competitive intergroup interactions? There are several reasons to think interpersonal and intergroup processes will manifest differently in degree and possibly in kind. People trust groups less than individuals and expect interactions with groups to be more hostile than person-to-person interactions (Bornstein & Ben-Yossef, 1994; Insko & Schopler, 1998; Pemberton, Insko, & Schopler, 1996; Wildschut, Pinter, Vevea, Insko, & Schopler, 2003). In competitive contexts, people cooperate less with out-groups relative to individual competitors (Insko, Wildschut, & Cohen, 2013) and behave more aggressively (e.g., Goette, Huffman, Meier, & Sutter, 2012; Hugh-Jones & Leroch, 2011; Meier & Hinsz, 2004; Wildschut et al., 2003). Relative to interpersonal contexts, people seem to abandon their preferences for equity and disdain for harming others to an even greater extent when "we" are competitive with "them" (Cohen, Montoya, & Insko, 2006).

These findings suggest that the biological bases of social preferences may manifest differently in the context of intergroup interactions (particularly competitive interactions) because the expectations and attributions are fundamentally different. For example, as we noted above, several studies have illustrated that participants show increased activity in dorsomedial prefrontal cortex when thinking about the mental states of other individuals (Mitchell, 2009). Activation in this region is higher in response to in-group relative to out-group targets in the absence of overt competition (Mitchell, Macrae, & Banaji, 2006; Molenberghs & Morrison, 2012; Rilling, Dagenais, Goldsmith, Glenn, & Pagnoni, 2008). These results dovetail nicely with the finding that people engage less in spontaneous mentalizing for extreme out-group members (Harris & Fiske, 2006, 2009). Putting people in competitive intergroup contexts, in contrast, may show the exact opposite pattern. In competitive or threatening contexts, out-group members, by virtue of the fact that they are more likely to arouse suspicion, may elicit even larger responses in regions associated with mentalizing than in-group members (see Hackel, Looser, & Van Bavel, 2014). One possible explanation of this discrepancy is that the minimal group context specifically facilitates

in-group preference without any out-group derogation (Brewer, 1999; Jetten, Spears, & Postmes, 2004), whereas an overtly competitive context, in which out-group members' actions are more motivationally relevant (see Ackerman et al., 2006), might increase consideration of out-group members' mental states—especially their agentic capacity. This hypothesized pattern is reflected in recent research that reported that people exhibited greater motor resonance, indexed by mu-suppression in EEG recordings, with racial in-group members (relative to out-group members) when the targets made benign gestures. However, the pattern was reversed when targets made offensive gestures (i.e., “giving someone the finger”; Gutsell & Inzlicht, 2013). Thus, people exhibited greater motor resonance with out-group members when those targets became threatening. Related recent evidence suggests that the emotional suffering of a threatening out-group member not only elicits as much activity in mentalizing regions as in-group suffering does but also more activity than neutral out-group suffering (Bruneau, Dufour, & Saxe, 2012). Processes ranging from motor resonance to empathy for emotional suffering can be brought online when out-groups pose an active threat.

Recent work in an intergroup context using different relational structures has also revealed new insights about oxytocin—a hormone that acts as a neuromodulator in the brain. Interest in the effects of oxytocin on human behavior has boomed in the last decade, with several researchers and media outlets referring to it as the “love hormone” because of its role in facilitating social affiliation and prosocial behavior (Bartz & Hollander, 2006). However, the effects of oxytocin are inconsistent and highly context dependent (Bartz, Zaki, Bolger, & Ochsner, 2011). Rather than promoting universal other concern and affiliation, once people are divided into groups (both ethnic and arbitrary groups), oxytocin administration yields greater in-group favoritism relative to a placebo. Specifically, people exhibit greater positive associations with their in-group and contribute more resources to an in-group pool in an intergroup prisoner's dilemma game (De Dreu et al., 2010; De Dreu et al., 2011). However, there is no difference between people who receive oxytocin and controls with regard to negative associations with the out-group or contribution of resources to an “out-group harm” pool. Together these findings indicate that oxytocin administration selectively enhances in-group love but does not engender out-group derogation (Brewer, 1999).

Subsequent research has examined the effects of oxytocin when the out-group represents an active threat. When the payoffs in the prisoner's dilemma game were structured so that the out-group had the potential to hurt the in-group, participants who received oxytocin were more likely to defect on behalf of their in-group.

Self-report data revealed that oxytocin recipients engaged in these “preemptive strikes” against the out-group, not because they thought out-group defection was more likely, but because they wanted to minimize harm to the in-group (see also De Dreu, Shalvi, Greer, Van Kleef, & Handgraaf, 2012). Thus, by some accounts, oxytocin's facilitation of this response is largely parochial, leading to in-group favoritism and ethnocentric behavior (De Dreu, 2012). Conversely, a recent study reported that administration of oxytocin increased Israeli Jewish participants' empathy for individuated Palestinian targets' pain (Shamay-Tsoory et al., 2013); this finding supports the hypothesis that oxytocin heightens the salience of social information (Heinrichs, von Dawans, & Domes, 2009), which may increase prosocial responses toward identifiable victims, even if they are members of an out-group (Chen, Kumsta, & Heinrichs, 2011). These findings clearly indicate that we need to conduct further research to understand the circumstances under which oxytocin exacerbates rather than reduces intergroup prejudice and conflict.

More recent research has started to investigate the neuroendocrine substrates of overt out-group aggression. Building on findings demonstrating that human and many other nonhuman vertebrate males exhibit increases in testosterone—a steroid hormone—in anticipation of fighting another male (Gladue, Boechler, & McCaul, 1989; Hirschenhauser & Oliveira, 2006; Salvador, 2005; Wingfield, Hegner, Dufty, & Ball, 1990; Wobber et al., 2010), a recent study investigated whether testosterone levels after competition were modulated by the participant's relationship with the competitor. In the community of Bwa Mawego, Dominica, men who defeated an out-group team member in a game of dominoes exhibited significant increases in testosterone, whereas men who beat their friends did not (Flinn, Ponzi, & Muehlenbein, 2012). Without studying these hormones in intergroup contexts—specifically competitive and cooperative contexts—researchers would not have revealed the parochial nature of the neuroendocrine processes that underlie fundamental help and harm behavioral tendencies. This is yet another example of how the study of intergroup relations can provide important contributions to our understanding of basic biological processes.

Role of Status in Intergroup Dynamics

Once the question “friend or foe?” is answered, people want to know to what extent a group is capable of enacting their intentions. Status refers to one's position in a social hierarchy; those higher in the hierarchy have greater access to resources, which can make them a more credible threat (A. P. Fiske, 1992; Sidanius & Pratto, 2001).

As such, individual and group survival is contingent on members' abilities to infer others' social status and protect or better their own status. These inferences help to "optimize" group behavior (e.g., groups are better able to avoid engaging dominant groups in contests they are sure to lose).

Given the centrality of status to intergroup dynamics, it is not surprising that sensitivity to dominant and submissive cues is present in infancy (Thomsen, Frankenhuys, Ingold-Smith, & Carey, 2011) and that by the time humans are adults, status inference is reflexive and ubiquitous—even between groups (see Jost & Banaji, 1994; Sidanius & Pratto, 1999). Status inference is supported, in part, by social comparison (comparing oneself against others in order to determine one's standing), which occurs across human societies (Festinger, 1954; S. T. Fiske, 2011; Olson, Herman, & Zanna, 1986; Suls & Wheeler, 2000). Social comparisons about status happen quickly, consume few cognitive resources, and can occur outside of subjects' control (Gilbert, Giesler, & Morris, 1995; Pelham & Wachsmuth, 1995; Wedell, 1994). Indeed, evidence from EEG studies suggests that inferences of social status from facial cues occur within 170 ms (Chiao et al., 2008). Whether or not we intend it, we register others' social status immediately.

The trouble with automatic status comparisons is that they often highlight one's own (or one's group's) relatively lower status, which can have negative cognitive and affective consequences (e.g., Brickman & Bulman, 1977; Tesser, Millar, & Moore, 1988) and induce stress, which has negative health implications over the long term (Segerstrom & Miller, 2004). Conditions are not entirely rosy for groups with high status either. Competitive, high-status social groups elicit emotions like envy, which attracts punishment and aggression, both overt and subtle (Cuddy et al., 2007). For example, women who occupy high-power positions in the workplace are frequently targets of backlash (e.g., hiring discrimination, harsher appraisals, and sabotage; Rudman & Fairchild, 2004). In general, targets that are seen as high status are also perceived as being capable of defending themselves, so it seems more acceptable to harm them (Cikara, Farnsworth, Harris, & Fiske, 2010; Glick, 2002).

Neuroscience of Social Status Inference

Understanding the biological bases of social status inference is important for several reasons, not least because status has implications for personal well-being and intergroup conflict (Fiske, 2011). Neuroimaging studies document a reliable network of brain regions associated with social status inference, including the inferior parietal lobe

(IPL; for review, see Chiao, 2010). The IPL is associated with the representation of scalar magnitudes; thus, its role in social status inference makes sense: People track rank like they track higher versus lower numerical values (Chiao, Harada, et al., 2009). However, social status inference is not a cold, cognitive process; people have associated affective and motivational responses because social status is imbued with value. Accordingly, viewing higher ranked compared with lower ranked individuals (relative to oneself) is associated with greater responses in the ventral striatum, which, again, is associated with the salience and registration of rewarding stimuli (Zink et al., 2008). One of the nicest features of these studies is that the researchers manipulated status rather than just measuring it. It is worth noting, however, that follow-up studies revealed that these effects are moderated by participants' own socioeconomic status (SES). Individuals with lower SES actually showed a greater ventral striatum response to lower status targets, whereas individuals with higher SES replicated the original finding (Ly, Haynes, Barter, Weinberger, & Zink, 2011). This is not surprising in light of the fact that low- and high-status groups have divergent goals. Low-status groups are motivated to improve their standing, whereas high-status groups are driven to defend their position in the hierarchy; as such, groups of differing status respond differently, especially to threat (Derks, Scheepers, Van Laar, & Ellemers, 2011; Ellemers, Spears, & Doosje, 2002).

The stability of the hierarchy also plays an important role. When relations are stable, low-status group membership (even among arbitrary groups) is associated with cardiovascular indices of threat (i.e., higher blood pressure, lower cardiac output, higher total peripheral resistance); however, when hierarchies are seen as unstable, low status is associated with a challenge response, and the high-status group members exhibit threat responses instead (Scheepers, 2009; Scheepers & Ellemers, 2005). Experimental manipulations of stability have revealed that people who operate in an unstable hierarchy exhibit greater activation in the amygdala and mPFC in response to pictures of higher status individuals, which the authors interpret as increased status-related reactivity (Zink et al., 2008). Though most hierarchies that affect our day-to-day lives are quite stable (i.e., SES), these studies suggest that changing perceptions about the stability of a given hierarchy may mitigate the stress response that plagues low-status groups.

Implications for Empathy, Helping, and Harm

Understanding how people represent and process intergroup functional relations and group status is paramount for understanding downstream phenomena such as

empathy, help, and harm. Empathy has received a great deal of attention from social and developmental psychologists and from cognitive neuroscience as of late (Cikara, Bruneau, & Saxe, 2011). “Empathy” as a construct has been used to refer to several distinct but interrelated processes (Batson, 2009, in Decety & Ickes, 2009): knowing or feeling what another person is feeling; experiencing compassion in response to another person’s distress; feeling motivated to help or improve another’s welfare; and so on. Because it promotes prosocial behavior, empathy is an integral element of human experience. Despite its centrality to social life and early emergence in development (Preston & de Waal, 2002), empathy is not a universal response. Instead, apathy and antipathy, rather than empathy, are common responses when the target belongs to an out-group.

Most of the extant research explores intergroup empathy bias in the context of existing social and cultural groups (e.g., Cuddy et al., 2007; Decety, Echols, & Correll, 2010; J. Johnson et al., 2002). Both behavioral and neuroscience studies have found that people show decreased and sometimes absent empathic responses when witnessing a racial out-group relative to an in-group member in physical and emotional pain. Even motor-simulation responses, which are theorized to support empathic responding via perception–action coupling, vary by target group membership (Gutsell & Inzlicht, 2010). For example, Black and White participants show sensorimotor resonance when an in-group member’s hand (even an artificially colored, purple hand) is pricked by a pin; however, this response is not just reduced but absent when the hand belongs to an out-group member (Avenanti, Sirigu, & Aglioti, 2010). A convergent study reported that White participants exhibited comparable skin conductance responses—an index of autonomic arousal—to images of White and Asian targets’ painful experiences but significantly lower responses to Black targets’ painful experiences (Forgiarini, Galluci, & Maravita, 2011). Finally, a recent EEG study reported that participants’ patterns of neural responses when they felt sad were similar to those exhibited when they saw an in-group but not an out-group member expressing sadness (Gutsell & Inzlicht, 2012). Across these studies, people reliably exhibit decreased (if not absent) physiological traces of empathy, broadly defined.

It is interesting to note that the fMRI research on intergroup empathy reveals a pattern of discrepant effects. Most of these studies have examined the influence of group membership on responses in the so-called pain matrix or shared neural circuit for pain (Decety, 2011; Eres & Molenberghs, 2013), which includes the anterior cingulate cortex, supplementary motor area, and the insula (see Fig. 1). In line with the studies described above, two fMRI studies report that the pain matrix was

more responsive when participants viewed same-race faces (Xu, Zuo, Wang, & Han, 2009) and hands (Azevedo et al., 2013) relative to other-race faces and hands being pricked with a needle. In another fMRI study, however, White participants’ responses in the pain matrix were equivalent for White and Black targets’ emotional suffering, whereas Black participants showed an even greater response to Black relative to White targets’ suffering—a response that the authors termed “extraordinary empathy” (Mathur, Harada, Lipke, & Chiao, 2010). In a third fMRI study, Israelis and Arabs reported feeling similar amounts of compassion for South American protagonists and protagonists from the in-group but less compassion for members of the threatening out-group (e.g., Israelis reported less compassion for Arab targets). However, responses in the pain matrix were equivalent for in-group and threatening out-group members and decreased for South American targets (Bruneau et al., 2012). Again, the lack of consistent effects across studies likely reflects the fact that race, ethnicity, and nationality covary with multiple dimensions of intergroup context, including perceived competitiveness, social status, and majority–minority status—all of which could affect the intergroup empathy bias. Isolating and testing the effects of these dimensions independently will help reconcile these seemingly discrepant findings.

A few studies have examined real social groups that are defined almost uniquely by a competitive context—sports fans. Sports fans are interesting to study because sports is one of the few domains in which it is acceptable to express overt antipathy toward out-group members. It is therefore unsurprising that sports fans are characterized by robust intergroup empathy bias, including both dampened empathy and overt counterempathic responses (i.e., Schadenfreude: pleasure in response to rivals’ misfortunes). In one study, Boston Red Sox and New York Yankees fans—archrival baseball teams—reported pleasure and exhibited activity in ventral striatum when watching rivals fail to score (even against a lower ranked team, the Baltimore Orioles; Cikara, Botvinick, & Fiske, 2011). These findings extend to individuals merely associated with the rival team: Soccer fans exhibited activity in ventral striatum when watching a rival team’s fan receive a painful electric shock (Hein, Silani, Preuschoff, Batson, & Singer, 2010). Greater ventral striatum response to a rival’s suffering was associated with an increased desire to harm rival team fans (Cikara, Botvinick, & Fiske, 2011) and a decreased willingness to relieve a rival fan’s pain (by accepting a proportion of the pain for oneself; Hein et al., 2010). These behavioral responses illustrate the implications of group membership for pro- and anti-social behavior.

Only one series of studies to date has focused on assessing the effects of competitiveness and status of

stereotyped social groups on empathy and harm. Although these studies also used existing social groups (e.g., homeless people, investment bankers, elderly targets), the analyses collapsed across the specific groups and analyzed the data using competitiveness and status as the predictors. In one study, participants read about positive and negative events befalling members of groups that were independently identified as high or low competition and high or low status (yielding four types of targets). In the first study, participants reported that they felt least bad about negative events and least good about positive events when they befell competitive, high-status group members as compared with other targets: Participants did not, however, explicitly report feeling better (i.e., experiencing *Schadenfreude*) when negative events befell competitive, high-status group members as compared with other targets. Facial electromyography simultaneously recorded facial muscle responses, focusing on the zygomaticus major (the cheek muscle), because it correlates with positive affect (S. L. Brown & Schwartz, 1980) and indicates the presence of positive, and not just the absence of negative, affect. Participants exhibited the greatest zygomaticus responses (i.e., smiles) when negative events befell competitive, high-status group members relative to other targets (Cikara & Fiske, 2012). A follow-up fMRI study replicated the self-report data and further found that participants exhibited greater anterior insula activation in response to competitive, high-status group members' good fortunes. One interpretation is that this insula activation represents a counterempathic reaction (i.e., envy or resentment). In line with the findings from the Red Sox–Yankees fans study, this “counterempathic” response was correlated with a willingness to harm competitive, high-status targets (Cikara & Fiske, 2011).

Summary

Once people have determined that someone is an out-group member, they need to determine *what kind?* Rather than examine how one or two different combinations of social groups represent and interact with one another, we suggest focusing on social structural variables—functional relations and status. The strength of this approach is that it is not restricted to specific targets; examining the effects of competitiveness and status allows for predictions about emotional and behavioral responses to any social group about which people harbor stereotypes. In addition to measuring these factors among existing social groups, future studies should manipulate functional relations and relative social status among novel groups in order to control for confounding factors.

Future Directions

A central assumption of our approach is that organizing future research around classic theories (e.g., social identity, self-categorization theory, realistic conflict theory) and contemporary models of intergroup relations (e.g., stereotype content model) with recent research on the neural systems underlying social cognition will move the field toward a more comprehensive theory of the neuroscience of intergroup processes. Although initial, exploratory research was necessary to establish empirical foundations for the field, the mere demonstration that some process or outcome changes depending on whether the target of that process is an in-group or out-group member is only partially informative because most groups vary on many different dimensions. Therefore, we recommend exercising caution against using existing social groups to make more general inferences about group processes.

As we have already outlined, one way to investigate intergroup processes so that the results are more generalizable is to use novel groups and manipulate the features of interest (e.g., functional relations; relative status). Another approach is to examine many different in-group versus out-group identities (e.g., race, nationality, religion) within a single experiment (Cikara & Fiske, 2011, 2012; Lewis & Bates, 2010; Morrison et al., 2012). If the process or outcome in question is fundamentally about “us” and “them” rather than any specific identity, the results should average out across groups. However the groups are instantiated, we believe this approach offers an important complement to the extant intergroup neuroscience literature on existing social groups and categories (e.g., Kubota et al., 2012). In particular, this approach will allow investigators to test how specific aspects of a person's social identity and intergroup context shape the responses of his or her nervous system. In turn, they can study how neural, neuroendocrine, metabolic, and immune systems dynamically influence specific social perceptions, motivations, and behaviors (Cacioppo, Berntson, & Decety, 2010). Here, we highlight several other areas of inquiry that we believe are ripe for investigation.

Future Directions in Neuroscience

Structural and Functional Connectivity. The research covered in this review documents the widely distributed network of brain regions involved in maintaining and updating our representations of “us” and “them.” To date, however, most of the research on intergroup neuroscience has focused on the effect of intergroup contexts on circumscribed brain regions (and individual hormones), in isolation from the systems in

which they are embedded. This approach neglects the fact that each discrete region supports many psychological processes, and each psychological process engages a complex network of interconnected brain regions, the components of which have both excitatory and inhibitory effects on one another (see Phillips, Zeki, & Barlow, 1984). It remains an open question whether the documented findings are better characterized as reflecting functionally discrete processes (e.g., face perception in the FFA) or integrated and distributed processes mediated by anatomical connections (e.g., the extended face processing network; see Friston & Buchel, 2003, for discussion; Pyles, Verstynen, Schneider, & Tarr, 2013). As such, it is inappropriate to infer psychological processes from activation of isolated brain regions (Poldrack, 2006). This type of “reverse inference” does a disservice to the field because it engenders inappropriate speculation about the psychological mechanisms underlying intergroup cognitions, affect, and behavior (particularly when activation is considered in the absence of any convergent self-report or behavioral indices of said processes).

We believe that an important future direction in the nascent field of intergroup neuroscience will be the examination of structural and functional connections among constellations of brain regions. Examining connectivity is fundamental not only for understanding the psychological processes supported by specific patterns of activation but also for shedding light on the interactions between processes that are central to many psychological models. For instance, social psychologists have exerted considerable effort trying to understand the relationship between automatic and controlled processing in the expression of racial bias (Devine, 1989; Fazio, Jackson, Dunton, & Williams, 1995; Greenwald, McGhee, & Schwartz, 1998). Initial work in social neuroscience has suggested that regions associated with cognitive control—including the lateral prefrontal cortex (PFC)—might play a role in inhibiting racial bias in regions such as the amygdala, promoting more egalitarian judgments and behavior (e.g., Amodio, Harmon-Jones, & Devine, 2003; Cunningham, Johnson, et al., 2004; Richeson et al., 2003). Recent research has used functional connectivity to provide a more direct assessment of the relationship between the amygdala and the lateral PFC during the perception of Black and White faces (Forbes, Cox, Schmader, & Ryan, 2012). As expected, activity in the amygdala was negatively correlated with activity in the orbitofrontal cortex (OFC) and lateral PFC, suggesting that regions associated with control have been recruited to suppress responses associated with racial bias. However, this pattern was reversed when participants were exposed to violent rap music, suggesting that controlled processes may also be recruited to increase—or even up-regulate (Ochsner et al., 2004)—racial bias in certain contexts (see

Crandall & Eshleman, 2003). This research highlights the potential value for using functional connectivity to test and develop process models of intergroup relations.

The effects of individual differences in anatomy on intergroup bias have also garnered increasing interest as of late. For example, individual differences in biological structure (i.e., decreased gray matter volume in dorsal mPFC) are associated with increased intergroup bias (Baumgartner, Schiller, Hill, & Knoch, 2013). Future research could examine how individual differences in white matter microstructural integrity—particularly of pathways within hypothetically relevant networks—relate to representation of in-group and out-group boundaries and relations. The growing popularity of neuroimaging techniques that visualize the anatomical connections between different parts of the brain (e.g., diffusion tensor imaging) will likely promote a greater appreciation of the role of structural networks in intergroup relations.

Networks of Brain Regions. Shifting the focus from isolated brain regions to collections of functionally and/or anatomically connected brain regions should also generate greater interest in well-established networks that are likely engaged in intergroup cognition and behavior. The reverse-inference problem we discussed above applies to networks in the same way it does to individual brain regions; however, framing research questions in terms of how networks associated with a given psychological process respond in intergroup contexts can generate more specific hypotheses and better constrain post hoc theorizing about whole-brain activations. To date, few investigations have taken this approach (Mathur, Harada, & Chiao, 2012, represent one notable exception).

Although research on networks has been somewhat neglected in intergroup neuroscience, many of the core psychological processes we have discussed—representing “us,” “them,” related affective and semantic associations, generating emotional and behavioral responses to in-group and out-group targets—are associated with well-articulated networks. First, there are networks that have, by some accounts, evolved or been co-opted specifically to support social interaction. For example, the default mode network (DMN) is a system of regions that is activated when individuals engage in conscious or unconscious introspection and mind wandering (Buckner, Andrews-Hanna, & Schacter, 2008; Christoff, Gordon, Smallwood, Smith, & Schooler, 2009; Mason et al., 2007; Raichle et al., 2001). It is interesting that the mentalizing network, which includes regions associated with action perception and inferring others’ beliefs and traits, largely overlaps with the DMN (e.g., Aichhorn et al., 2009; Frith & Frith, 2000; Saxe & Kanwisher, 2003). This has led some researchers to speculate that our “default” is to

think about other people (e.g., Mitchell, 2009; Schilbach, Eickhoff, Rotarska-Jagiela, Fink, & Vogeley, 2008). What is fascinating about this network is that it is recruited when people engage truly social cognition (e.g., impression formation as opposed to memorizing a list of facts about a person; Mitchell et al., 2006). In complement, evidence suggests that a specific region of this network is less active when people view images of extreme out-group targets (Harris & Fiske, 2006). These networks likely mediate a considerable amount of intergroup cognition and behavior and are therefore prime targets for investigation.

Likewise, several domain-general networks, which are not dedicated specifically to social processes, are likely implicated in the detection and identification of in-group and out-group members, as well as the generation of approach and avoidance motivations and behaviors. For instance, dissociable networks have been implicated in the detection of salient or novel stimuli (Hughes, 2007; Kiehl, Laurens, Duty, Forster, & Liddle, 2001; Ranganath & Rainer, 2003; Squire, Stark, & Clark, 2004), reward processing and appetitive behavior (Delgado, 2007; Grabenhorst & Rolls, 2011; Kable & Glimcher, 2009; Knutson & Cooper, 2005; Levy & Glimcher, 2012; Montague & Berns, 2002; O'Doherty, 2004; Peters & Büchel, 2010), avoidance and aversive responses (Barrett & Wager, 2006; Yamada & Decety, 2009), and executive function and cognitive control (Amodio, 2008; Forbes & Grafman, 2010; Richeson et al., 2003). The last two decades of intergroup neuroscience research have seen an explosion of foundational but somewhat exploratory brain mapping. Our belief is that future research, which places an emphasis on hypothesis testing in networks, will make significant strides toward building predictive, multilevel models of a variety of intergroup phenomena.

Genetic Approaches. Though both “nature” and “nurture” contribute to neural anatomy, studies exploring individual differences in anatomical structure (and their relationship to prejudice) have increased interest in the heritability of intergroup biases. A recent study with an adult, German twin sample reports that monozygotic twins were more highly correlated than dizygotic twins on nationalism, patriotism, and generalized prejudice scores; however, further modeling accounting for (non) shared environmental effects found evidence only for the heritability of in-group love, not out-group derogation (Lewis, Kandler, & Riemann, in press). Findings like these have sparked the search for the genetic bases of bias. For example, one study examined the interaction between OFC lesions and single nucleotide polymorphisms on implicit gender bias. These findings suggest that increased neural plasticity in OFC, facilitated by certain polymorphisms, may contribute to the inhibition of stereotype

activation (Forbes et al., 2011). In another study, which examined the interaction between genetics and the environment on intergroup bias, participants with at least one short allele of serotonin transporter gene polymorphism (5-HTTLPR) were more prejudiced and exhibited more discriminatory behavior toward a threatening out-group relative to a nonthreatening out-group; participants with two long alleles, in contrast, did not respond to the two out-groups differently (Cheon, Livingston, Hong, & Chiao, 2013). These recent studies build on a rich literature based on animal models of social behavior (e.g., Robinson, Fernald, & Clayton, 2008) and represent the beginning of a new branch of human social neuroscience, integrating molecular, cellular, and systems levels of analysis. This work has the potential to elucidate more precise biological mechanisms that give rise to biased attitudes and behaviors.

Enthusiasm for this approach, however, must be tempered by the understanding that there is not a one-to-one mapping between single candidate genes and particular behaviors. Individual genes do not, in isolation, determine behavior; they interact with other genes, and these complex interactions further interact with an individual's environment (including other people, who have their own genetic constitutions). As such, a correlation between a particular polymorphism and, for example, prejudicial or discriminatory tendencies should not be taken as evidence of the hard wiring of a given psychological or behavioral phenomenon (Ratner & Kubota, 2012).

Other Tools and Approaches. Though EEG and fMRI are currently the most popular methods for investigating the neural bases of intergroup relations, many other complementary methods may help refine and revise existing theories. For instance, magnetoencephalography (MEG) is a technique for mapping brain activity that offers the best of both worlds: the temporal resolution of EEG and the spatial resolution of fMRI. MEG affords the possibility of examining the activity of neural systems as it unfolds in real time. This is particularly exciting in the context of networks of brain regions, as one could examine how the temporal dynamics of hypothesized networks (e.g., salience → evaluation) vary as a function of the target and the task at hand. This tool also captures a recent paradigm shift in systems neuroscience as conceptualizations of human cognition have shifted from emphasizing the role of discrete regions to the dynamic interactions among multiple regions unfolding over time (e.g., Cunningham, Zelazo, Packer, & Van Bavel, 2007; Honey et al., 2012; Lerner, Honey, Silbert, & Hasson, 2011).

Work with lesion patients has also had a huge impact on the neuroscience of judgment and (non)social decision making (e.g., Bechara, Tranel, & Damasio, 2000; Koenigs et al., 2007; L. Young, Bechara, et al., 2010). Two

studies have already used this approach to examine the role of the amygdala and OFC in race (Phelps, Cannistraci, & Cunningham, 2003) and gender (Milne & Grafman, 2001) bias, respectively. In addition to brain lesions, more work could be done using techniques like temporary transcranial magnetic stimulation and transcranial direct current stimulation to examine the causal role of different brain regions in target psychological processes (e.g., L. Young, Camprodon, Hauser, Pascual-Leone, & Saxe, 2010), and to provide greater specificity about the necessity and sufficiency of certain regions.

Several other recent and exciting findings highlight additional avenues for future research. Work in psychopharmacology highlights the possibility of administering drugs as intergroup conflict interventions: For example, exogenously administered propranolol has been shown to reduce implicit racial bias (Terbeck et al., 2012). Studies in comparative psychology and neuroscience have revealed that neural circuits, which support the function of nonsocial behaviors critical for survival (e.g., escape), similarly support social cognition, decision making, and behavior (e.g., gaze aversion; Chang et al., 2013). Finally, we believe that there is a lack of work at the computational level of analysis, which is ultimately necessary to bridge the neural and psychological levels of analysis in intergroup neuroscience (Freeman & Ambady, 2011). Ultimately, a complete understanding of the neuroscience of intergroup relations will require the efforts of scientists using all of these methods.

Future Directions in Psychology

From Categories to Groups. One relatively unexplored avenue for future intergroup neuroscience research is the difference between the representation of social categories versus social groups (Asch, 1952; Brewer, Hong, & Li, 2004). Social categories are inclusive structures that require merely that all members share some feature (e.g., brunettes), whereas more “purposive groups . . . [are] intact social system[s], complete with boundaries, interdependence for some shared purpose, and differentiated member roles” (e.g., a sports team; Hackman & Katz, 2010, p. 1210). Note that this difference is better characterized as a continuum than a dichotomy; many important social identities lie somewhere in between the two extremes (e.g., Red Sox fans, a category whose members have a shared purpose but do not constitute a purposive group). And as we have stressed throughout this article, the salience of different social identities, be they categories or groups, depends largely on the social context.

Many studies have explored the differences between processing a target as a group member (e.g., stereotype activation; Mitchell, Ames, Jenkins, & Banaji, 2009) as

opposed to an individual (e.g., trait attribution; Mende-Siedlecki, Cai, & Todorov, 2012; see Andersen, Klatzky, & Murray, 1990, for direct comparison of the processes); however, few have looked at the features that make some categories and groups more cohesive than others. Extensive research has documented that not all social categories possess the features that give groups their potency: joint actions, shared goals, perceptual or psychological cohesion, group members' similarity to one another, and so on (e.g., Campbell, 1958; Hamilton & Sherman, 1996; Yzerbyt, Castano, Leyens, & Paladino, 2000). These features matter because they shape how people respond to members of these groups, including increasing stereotyping, intergroup bias, and hostility (Abelson, Dasgupta, Park, & Banaji, 1998; L. Gaertner & Schopler, 1998; Lickel, Miller, Stenstrom, Denson, & Schmader, 2006; Waytz & Young, 2012). One priority for future research lies in untangling how our minds and brains extract this information in intergroup contexts. Specifically, intergroup neuroscience research may want to (a) consider the biological substrates of Gestalt laws of perceptual organization as a target system for future research (not unlike the work on social status and IPL, which is associated with representing numerical magnitude; Chiao et al., 2008) and (b) examine how this system interacts with other neural systems to evaluate and guide social interactions in group contexts.

The Self in Social Groups. Another important avenue for future research is the investigation of how acting as a member of a group changes representations of one's self (Ellemers, 2012; Packer & Van Bavel, in press). There is a large literature on how the self and similar versus dissimilar others (in-group and out-group members) are represented in the mind and brain; as we have already noted, representations of similar others and in-group members show greater overlap with self-representations than do representations of out-group members (e.g., Jenkins et al., 2008; Mitchell et al., 2006; Volz et al., 2009). But people's behavior changes when they join groups. For example, individuals tend to engage in more hostile behaviors toward opponents when acting as part of a group than when acting alone (e.g., Meier & Hinsz, 2004). How and to what extent do self-representations change in intergroup contexts?

A recent fMRI study demonstrated that acting with a group in a competitive context reduces neural responses associated with self-referential thought. Consistent with previous competitive groups research, participants harmed out-group members more than they did in-group members. Critically, the degree to which participants were willing to carry out such harm was associated with the degree to which they exhibited reduced activity in a region of mPFC implicated in self-referential processing

in response to moral statements. This pattern was observed only when participants were competing in a group, not when competing alone. These results suggest that acting as part of a competitive group may reduce the salience of one's own moral standards and, in turn, enable out-group harm (Cikara, Jenkins, Dufour, & Saxe, in press). Future research should examine what other aspects of self-representation change when individuals act as representatives of their groups rather than as agents on their own behalf.

A Second-Person Intergroup Neuroscience. The third psychological future direction we highlight is a greater incorporation of enriched social stimuli and intergroup interaction in real time. Most of the literature in intergroup neuroscience can be fairly criticized for focusing on individuals' responses to static images, words, or games representing in-group or out-group members and their behavior. However, social cognition is fundamentally different when people actually interact with others rather than merely observing them or being led to believe they are interacting with them (Schilbach et al., 2012). Real-world intergroup interactions are far richer than current methods appreciate and likely engage a far broader network of biological substrates. Recent forays into "brain-to-brain" methods and analyses have demonstrated that researchers do not necessarily relinquish experimental control or analytical precision by studying real social interactions (Hasson, Ghazanfar, Galantucci, Garrod, & Keysers, 2012). For example, in one fMRI experiment, participants played a cooperative game with a partner, knowing that in one condition the partner's behavior was prerecorded and in the other that they were interacting in real time via a video feed. Relative to the prerecorded condition, playing the game in real time elicited greater responses in brain regions associated with social cognition and reward (Redcay et al., 2010). These results suggest that incorporating actual interaction in the neuroscience of intergroup relations may reveal new targets for investigation, including systems that support communication and shared understanding (or a lack thereof between groups in conflict; Cikara, Honey, Paluck, & Hasson, 2013). Future work should therefore move toward dyadic interactions and ultimately large group interactions to understand how social identities create emergent "group-level" cognitive phenomena. This work not only captures the essence of group contexts, but it may also have important implications for understanding and cultivating successful leaders and educators who are tasked with coordinating collective cognition.

Societal and Cultural Factors. An examination of the influence of societal and cultural backgrounds will continue to play a large role in understanding the boundary

conditions of many findings in the neuroscience of intergroup relations (e.g., Chiao, Mathur, Harada, & Lipke, 2009; Jost & Amodio, 2012; Moran et al., 2011). For example, both Korean and White American participants exhibited increased mPFC and bilateral temporoparietal junction activation when viewing same-race versus other-race targets' emotional suffering; however, Korean participants reported a significantly larger empathy gap relative to White American participants. This difference was correlated with a cultural preference for hierarchy among Korean participants (Cheon et al., 2011).

All intergroup interaction occurs within a broader societal or cultural context, and work that examines group processes within these broader contexts—including social dominance hierarchies and system-level factors (Jost & Banaji, 1994; Sidanius & Pratto, 1999)—is necessary for providing a complete account of intergroup neuroscience. We believe that studying the fundamental structures and features of intergroup relations, using all of these approaches, will continue to advance our understanding of how and why groups and their members behave as they do.

General Discussion

Throughout this article, we have highlighted recent findings in the neuroscience of intergroup relations, emphasizing cases in which existing psychological and neuroscience theories have been revised once the relevant phenomena have been investigated in intergroup contexts or with novel groups (see Table 1 for a review). Work in this area has already refined extant models of intergroup relations and documented the widely distributed network of brain regions that supports intergroup cognition. It is important to note that identifying the biological bases of these processes does not suggest that specific in-group and out-group effects are "hard-wired." On the contrary, one of the major contributions of this recent work is the demonstration of how flexibly these biological systems represent the self and others, carving up the social world into "us" and "them" at the toss of a coin. This is an especially important message to communicate to lay consumers of research on the psychology and neuroscience of intergroup relations because it implies considerable promise for reducing prejudice and intergroup conflict.

Work on racial bias is often interpreted as evidence of more general in-group and out-group processes. Although the investigation of social categories such as race is important for understanding pervasive social inequities and obstacles, using this work to make broad inferences about group processes can be problematic for several reasons. First, race is confounded with many other factors, including visual properties of the stimuli, familiarity, and

Table 1. Summary of Relevant Brain Regions and Neuroendocrine Systems, Their Associated General Functions, and Original or Updated Theories of Function From Intergroup Relations Research

Biological target	Task	Moderator	General function	Groups application	Citation
Amygdala	Viewing other-race faces in Black ^a and White ^b participants	Individual differences correlated with IAT (Cunningham, Johnson, et al., 2004) and startle eye blink (Phelps et al., 2000)	Fear conditioning; processing negative stimuli	Negativity (disgust and fear) toward stigmatized groups	Hart et al., 2000
	Viewing in-group faces in a mixed-race minimal group paradigm ^b		Segregation of relevant from irrelevant to enhance perception of important stimuli	Responsive to the most motivationally relevant stimuli in the absence of other salient groups (e.g., race)	Van Bavel et al., 2008
	Playing an interactive game in an unstable (vs. stable) hierarchy ^b		Processing social emotional stimuli; threat response	Emotional arousal related to the possible social hierarchical consequences of performance	Zink et al., 2008
Fusiform gyrus	Viewing own-race faces in Black ^a and White ^b participants	Correlated with own-race bias on recognition memory task	Processing and individuating faces; perceptual expertise	Superior perceptual expertise with own-race faces may moderate the own-race bias	Golby et al., 2001
	Viewing in-group faces in a mixed-race minimal group paradigm ^b		Flexible involvement in individuation of faces' motivational relevance	Sensitive to shifts in self-categorization, aiding response to motivationally relevant faces, regardless of expertise	Van Bavel et al., 2008
- FFA	Greater recognition memory for minimal in-group (vs. out-group) faces ^b		Flexible involvement in individuation of faces' motivational relevance	In-group members are processed as individuals more than out-group members—or individuating in-group members is more automatic than out-group	Van Bavel et al., 2011
mPFC	Playing a game with another in a competitive condition (as compared with cooperative condition) ^c		Mentalizing	Competing with another requires maintenance of the perspectives of both self and others	Decety et al., 2004
	Playing an interactive game in an unstable (vs. stable) hierarchy ^b		Mentalizing; person perception	Social cognition related to the possible social hierarchical consequences of performance (including reputation)	Zink et al., 2008
	Salience of personal moral standards while competing in a group (independent self-reference task) ^c	Correlated with willingness to harm competitors	Self-referential processing	Competing as a group can reduce the salience of one's own moral standards and enable harm	Cikara et al., in press
	Viewing in-group members in a painful situation, in Black participants only ^a	Correlated with in-group bias in empathic ratings	Cognitive empathic processing	In addition to affective empathic processing normally occurring with empathy, regardless of group, extraordinary empathy for one's in-group involves cognitive empathic processing	Mathur et al., 2010

(continued)

Table 1. (continued)

Biological target	Task	Moderator	General function	Groups application	Citation
	Playing a prisoner's dilemma game with an in-group member ^c	Correlated with greater report of in-group bias	Mentalizing	Mentalizing about an in-group member is facilitated by perceived similarities with oneself	Rilling et al., 2008
TPJ - lTPJ	Viewing same-race vs. other-race targets' emotional suffering, in Koreans ^b and Caucasian Americans ^b	Greater activity in Koreans correlated with preference for social hierarchy	Mentalizing	Cultural values may directly modulate the systems involved in representing others' mental states and, in turn, empathic processing	Cheon et al., 2011
- rTPJ	During a prisoner's dilemma game with a minimal-groups in-group member ^c	Correlated with greater report of in-group bias	Mentalizing	Mentalizing about an in-group member is facilitated by perceived similarities with oneself	Rilling et al., 2008
OFC	Playing a game with another in a competitive condition (as compared with cooperative condition) ^c		Making behavioral choices; encoding relative value	Cooperating with others is socially rewarding	Decety et al., 2004
	Choosing to allocate monetary resources equitably in a dictator game ^c		Value representation	Choosing to act prosocially has high reward value	Zaki & Mitchell, 2011
Ventral striatum	Engaging in mutually cooperative social interactions in a prisoner's dilemma game ^c		Reward processing	Engaging in a mutually cooperative social interaction has high reward value	Rilling et al., 2002
	Distributing monetary resources to self and others ^c		Reward processing	Reward signals are modulated by social factors (e.g., inequality-averse preferences)	Tricomi et al., 2010
	Seeing the pain of an unfair confederate in a prisoner's dilemma game ^c	Correlated with expressed desire for revenge	Reward processing	Serving justice is rewarding	Singer et al., 2006
	Viewing higher ranked compared with lower ranked individuals (compared to oneself) ^b	Those with low SES show greater activity to lower status targets; those with high SES replicate original findings (Ly, Haynes, Barter, Weinberger, & Zink, 2011)	Reward salience; valuation	Social status inference involves valuation dependent on motivational factors	Zink et al., 2008
	Watching rival teams failing to score (correlates with reported pleasure) ^c	Effect holds even against a lower ranked team	Valuation; motivation	Increased reward value of out-group failure may contribute to counterempathic responses	Cikara, Jenkins, et al., 2014
	Watching a rival team's fan experience pain ^c	Correlated with a decreased willingness to accept a proportion of the fan's pain	Reward processing	Increased reward value of out-group failure may contribute to counterempathic responses	Hein et al., 2010
Dorsal striatum	Administering punishments that reduced a defector's payoff ^c	Correlated with greater will to incur a self-cost in order to punish	Reward processing	Punishing a norm violation is rewarding	De Quervain et al., 2004

(continued)

Table 1. (continued)

Biological target	Task	Moderator	General function	Groups application	Citation
IPL	During comparison of people who are closer to one another in a social hierarchy ^b		Representation of scalar magnitudes (processing higher vs. lower numerical values)	Social status inference recruits regions involved in numerical processing	Chiao et al., 2008
Cortical midline subsystem of DMN	Viewing racial in-group members in painful situations, in African American participants ^a	Correlated with greater racial identification	Self-referential processing (e.g., introspection, personal significance, affective processing)	Highly identified minority group members may empathize by accessing their own feelings and having a personal, affective experience	Mathur et al., 2012
ACC	Viewing same-race (vs. other-race) faces experience pain in Chinese ^b and Caucasian ^a participants	Differences not reflected in self-report ratings of pain intensity others experience	First-person pain experience	Enhanced sharing of pain for in-group members may result in increased empathy concern	Xu et al., 2009
Anterior insula	Viewing others in painful situations, regardless of group, in Black ^a and White ^b participants	"Extraordinary" response among Black participants seeing in-group	Affective empathic processing		Mathur et al., 2010
	Viewing same-race (vs. other-race) faces experience pain in Chinese ^b and Caucasian ^a participants	Differences not reflected in self-report ratings of pain intensity others experience	First-person pain experience	Enhanced sharing of pain for in-group members may result in increased empathy concern	Xu et al., 2009
	Viewing others in painful situations, regardless of group in Black ^a and White ^b participants		Affective empathic processing		Mathur et al., 2010
	Reading descriptions of physically painful (vs. nonpainful) events, in Israeli, Arab, and South American immigrants or visitors ^a		Generalized processing of pain experience	Shared pain network may be influenced by current task goals and is not tied to specific modality (e.g., verbal vs. pictorial representation)	Bruneau et al., 2012
	Viewing competitive, high-status targets' good fortunes ^c	Correlated with willingness to harm competitive high-status targets	Shared neural circuit for pain	Shared pain network is influenced by group distinctions and status, with potential effects on behavior (e.g., harm)	Cikara & Fiske, 2011
Oxytocin	Playing trust game ^c		Facilitates affiliative motivation and prosocial behavior	May help to reduce conflict	Kosfeld et al., 2005
	Playing trust game ^{a,b}		Facilitates "tend and defend" behavior toward the in-group in particular	Supports parochial behavior that undergirds several instantiations of in-group bias	De Dreu et al., 2010

Note: IAT = Implicit Association Test; FFA = fusiform face area; mPFC = medial prefrontal cortex; TPJ = temporoparietal junction; lTPJ = left TPJ; rTPJ = right TPJ; = OFC = orbitofrontal cortex; SES = socioeconomic status; IPL = inferior parietal lobe; DMN = default mode network; ACC = anterior cingulate cortex.

^aDenotes majority subject population. ^bDenotes minority subject population. ^cDenotes that majority and/or minority status of subject population was not reported in the study.

stereotype content. Thus, it is difficult to know whether the effects are driven by group identification per se. Second, self-categorization is extremely flexible, meaning that existing theories of the neural bases of intergroup relations are likely limited to specific contexts. We argue that using mixed-race and novel groups, in complement with real groups, and manipulating features of interest (e.g., motivational salience of the in-group versus out-group) will prove useful for advancing theories of the cognitive, affective, and neural bases of intergroup relations.

Integrating classic theories and contemporary models of intergroup relations with the investigation of the biological bases of intergroup dynamics will benefit both psychologists and neuroscientists. Not only does our proposed approach account for discrepancies in the existing research, it generates a number of hypotheses and directions for future research. This approach also confers greater consilience; theories that operate at multiple levels of analysis are more likely to stand the test of time and present several opportunities for collaboration between psychologists and neuroscientists (E. Wilson, 1998). Furthermore, the exchange of knowledge is bidirectional: We emphasize both how biological processes support social cognition and behavior and how social influences modulate biological processes. The work on intergroup neuroscience should not be construed as a brain-mapping exercise; it is about developing models that can be tested using cognitive and behavioral tasks. Specifically, this research has the potential to benefit the psychological study of intergroup relations, especially when predictions from neural models contradict or adjudicate among multiple psychological models (Mather, Cacioppo, & Kanwisher, 2013).

Conclusion

In summary, initial work on intergroup neuroscience highlights the dynamic nature of social identity and the contextual factors that shape intergroup relations. We believe an understanding of these factors will resolve discrepant findings in the literature, provide organizational principles for understanding the core elements of intergroup dynamics, and help generate novel insights for social, developmental, evolutionary, and cognitive psychologists. Although it is beyond the scope of this article, it is our hope that greater integration across methods and levels of analysis will ultimately lay the foundation for superior interventions and social policy.

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Note

1. Relationship partners (i.e., dyadic partners) can also become strongly integrated with the representation of one's self (Aron et al., 1991; Beckes, Coan, & Hasselmo, 2013). However, dyads differ from groups in several important respects (e.g., dyads are more ephemeral and evoke stronger emotions; several key group phenomena, including coalitions and minority influence, cannot occur in dyads; Levine & Moreland, 1990; Moreland, Hogg, & Hains, 1994), placing a thorough analysis of dyads outside the scope of the current review. The neuroscience of social relationships is a rapidly growing area of inquiry (see Beckes & Coan, in press); exactly how dyadic relationship phenomena relate to intergroup phenomena in the brain is a wide open question.

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