Research Article

The Neural Substrates of In-Group Bias

A Functional Magnetic Resonance Imaging Investigation

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ABSTRACT—*Classic minimal-group studies found that people arbitrarily assigned to a novel group quickly display a range of perceptual, affective, and behavioral in-group biases. We randomly assigned participants to a mixed-race team and used functional magnetic resonance imaging to identify brain regions involved in processing novel in-group and out-group members independently of preexisting attitudes, stereotypes, or familiarity. Whereas previous research on intergroup perception found amygdala activity—typically interpreted as negativity—in response to stigmatized social groups, we found greater activity in the amygdala, fusiform gyri, orbitofrontal cortex, and dorsal striatum when participants viewed novel in-group faces than when they viewed novel out-group faces. Moreover, activity in orbitofrontal cortex mediated the in-group bias in self-reported liking for the faces. These in-group biases in neural activity were not moderated by race or by whether participants explicitly attended to team membership or race, a finding suggesting that they may occur automatically. This study helps clarify the role of neural substrates involved in perceptual and affective in-group biases.*

People who accurately identify, value, and cooperate with in-group members enjoy numerous functional benefits, including the fulfillment of their basic psychological needs (Allport, 1954; Correll & Park, 2005). The value humans place on group membership is illustrated by the ease with which humans form groups and favor in-group members. Mere assignment to an arbitrary group (i.e., the *minimal-group* paradigm) elicits strong preferences for in-group relative to out-group members in the absence of factors typically thought to account for intergroup

discrimination, such as prior contact with in-group or out-group members and competition over resources (Tajfel, 1970). Such minimal-group research laid the foundation for two seminal concepts in intergroup relations: People rapidly and flexibly categorize themselves in terms of currently salient social groupings (Turner, Hogg, Oakes, Reicher, & Wetherell, 1987), and social identities are a central motivational force in human life (Tajfel, 1982).

In-group identities shape not only preferences, thoughts, and behavior, but also basic social perception. For example, people are better at recognizing members of their own race or ethnicity than at recognizing members of other races—the *own-race bias* (ORB; Malpass & Kravitz, 1969; Sporer, 2001). Although the ORB was originally explained in terms of experience with racial in-group members (i.e., people have a lifetime of experience recognizing members of their own race), there is increasing evidence that self-categorization with a group leads to in-depth or individuated processing of in-group members (Sporer, 2001). Indeed, the so-called ORB has been replicated across a variety of nonracial social categories, including minimal groups. These studies demonstrate that mere categorization with a group is sufficient to produce greater recognition of in-group than of out-group faces when prior exposure to members of the two groups is equivalent (Bernstein, Young, & Hugenberg, 2007). This suggests that self-categorization may motivate in-group biases in social perception (Balcetis & Dunning, 2006), including the more in-depth or individuated processing of in-group members.

Extending this research, Golby, Gabrieli, Chiao, and Eberhardt (2001) found that Black and White participants showed heightened activity in the fusiform face area while viewing own-race faces during functional magnetic resonance imaging (fMRI). Participants exhibiting the strongest effect also displayed the greatest ORB on a subsequent recognition task. Because the fusiform face area appears to play an important role in processing and individuating faces (Kanwisher, McDermott, & Chun, 1997; Rhodes, Byatt, Michie, & Puce, 2004) and

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in perceptual expertise (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999), Golby et al. concluded that own-race biases in fusiform activity were due to superior perceptual expertise with own-race faces. However, it remains unclear whether own-race biases in fusiform activity stem from perceptual expertise with own-race faces, motivated aspects of self-categorization, or some combination of these factors.

The amygdala is also believed to play an important role in processing faces from different social groups. Viewing images of racial out-group members activates the amygdala more than does viewing images of racial in-group members (Hart et al., 2000), and this difference in amygdala activity correlates with implicit measures of racial bias (Cunningham et al., 2004; Phelps et al., 2000). These correlations with racial bias, coupled with evidence linking the amygdala and fear conditioning (LeDoux, 1996), have led researchers to interpret differences in amygdala activation in intergroup contexts as evidence of negativity toward certain groups (e.g., Harris & Fiske, 2006; Lieberman, Hariri, Jarcho, Eisenberger, & Bookheimer, 2005). However, recent research has shown that the amygdala is sensitive to representations of any valence when they are motivationally relevant (Cunningham, Van Bavel, & Johnsen, 2008). Accordingly, when race is the most salient social category, the amygdala may respond to members of groups that are stereotypically associated with threat or novelty (Dubois et al., 1999). However, when race is *not* salient, the amygdala may be responsive to members of groups that are currently relevant, including the in-group (Allport, 1954).

The present study was designed to clarify the role of neural substrates involved in intergroup processing. We used a variant of the minimal-group paradigm in which White participants were randomly assigned to a mixed-race team without a history of contact or conflict (see Kurzban, Tooby, & Cosmides, 2001, for a similar paradigm). To enhance intergroup encoding, we showed faces to the participants and told them that the teams were competing, unlike in the classic minimal-group paradigm. In previous studies, participants had different experiences and associations with the social groups, so it was possible that familiarity or novelty elicited the observed fusiform (Gauthier et al., 1999) or amygdala (Dubois et al., 1999) activity, respectively. However, the mixed-race teams in the present study were equated in familiarity-novelty, so these variables were eliminated as potential explanations. Assigning participants to mixed-race teams allowed us to examine the role of self-categorization in neural processing (Turner et al., 1987): Would a current team membership—however minimal—override racial biases in social perception? On the basis of previous research, we hypothesized that in-group, compared with out-group, members would be associated with greater activity in the fusiform gyri; however, it was unclear whether fusiform activity would increase in response to familiar racial in-group members (Golby et al., 2001) or in response to current in-group members (Sporer, 2001) regardless of race. Previous research suggested that amygdala activity might be greater in response to out-group members, or at least racial

out-group members, than in response to in-group members (Hart et al., 2000). However, recent research linking the amygdala to motivational relevance (Cunningham et al., 2008) led us to propose that the most relevant faces—those of novel in-group members—would be associated with heightened amygdala activity.

METHOD

Participants

Twenty-two White participants (8 males, 14 females; mean age = 25 years, $SD = 4$) were paid $50 for completing the study.[1] Participants reported no abnormal neurological history and had normal or corrected-to-normal vision.

Materials and Procedure

Group Assignment
Participants arrived at the imaging center and posed for a digital photograph. They were informed that they were in a study exploring learning about groups and that they had been (randomly) assigned to the Leopards ($n = 11$) or Tigers ($n = 11$).[2] They were also told that it was important for them to learn the members of their team and a competing team before moving to other phases of the study. Participants then completed two learning tasks taking about 15 min. During the first learning task, participants spent 3 min memorizing the team membership of 24 faces presented simultaneously: 12 members of the Leopards and 12 members of the Tigers. Race was orthogonal to team membership; there were 6 Black and 6 White males on each team. Faces were randomly assigned to the teams, and assignment was fully counterbalanced so that nothing in the appearance of the faces allowed participants to visually sort them into teams (the experimental design logically guaranteed that participants were equally likely to see each face as an in-group or out-group member).

During the second learning task, the faces were shown one at a time, and participants categorized each according to whether it was affiliated with the Leopards or the Tigers. We had participants categorize their own face as part of this task, to enhance their identification with their team. Thus, during this task only, each participant viewed his or her own face, which was randomly interspersed at three points within each block of learned faces. During the first block of trials, a label reminded participants whether each face was a Leopard or Tiger. Participants categorized each face once and their own face three times during the first block, for a total of 27 trials. During the second block of trials, the label was removed so that participants needed to rely on their memory. Following each trial in the second block, feedback indicated if the response was correct. Participants categorized each face three times and their own face three times during the second block, for a total of 75 trials.

[1]None of the observed effects were moderated by participants' gender.

[2]There were no main effects of team assignment.

Categorization Task
Next, participants completed a categorization task during fMRI. This phase of the experiment included six runs of four blocks; each block contained 12 trials, for a total of 288 trials. In each block, 12 of the 24 faces were randomly selected and presented to participants. Participants categorized each face according to team membership or race (see Fig. 1). During explicit blocks, pictorial labels representing the teams (Leopards and Tigers) appeared in the top corners of the screen, and participants categorized 12 faces according to team membership. We refer to these blocks as "explicit" because participants' attention was explicitly focused on group membership. During implicit blocks, pictorial labels representing race (Black and White) appeared in the top corners of the screen, and participants categorized 12 faces according to skin color. At the beginning of each block, participants saw a 4-s directions screen calling attention to the new labels at the top corners and then a 2-s fixation cross. The directions screen appeared only at the beginning of each block and was designed to cue the categorization required on the following 12 trials. On each trial, participants saw a face for 2 s and categorized that face according to team membership or race (depending on the block), using two buttons on a button box held in their right hand. Each face was followed by a fixation cross to allow for estimation of the hemodynamic signal. The duration of this fixation cross varied (2, 4, 6, or 8 s, in pseudo-random order). This pattern was repeated for the 12 trials in each block. The left/right positions of team and race labels were counterbalanced within runs. Blocks were presented in random order within each run. Each of the 24 faces was categorized twice in each run (once by team membership and once by race). The fMRI acquisition parameters were identical to those in our previous research (see Cunningham et al., 2008).

Rating and Memory Tasks
After scanning, participants completed two computerized questionnaires. First, participants completed a face-rating task in which they were told that "people can often quickly determine who they like or dislike based on subtle facial features and expressions" and then rated each of the 24 faces on a 6-point liking scale (1 = *dislike*, 6 = *like*). Second, participants completed a memory task in which they reported whether each face was a Leopard or a Tiger. Faces were presented in random order in both tasks.

RESULTS

Behavioral Results

fMRI Categorization Speed and Accuracy
We examined reaction time (in milliseconds) and accuracy (proportion of trials with a correct categorization) as a function of team membership and race during each fMRI categorization
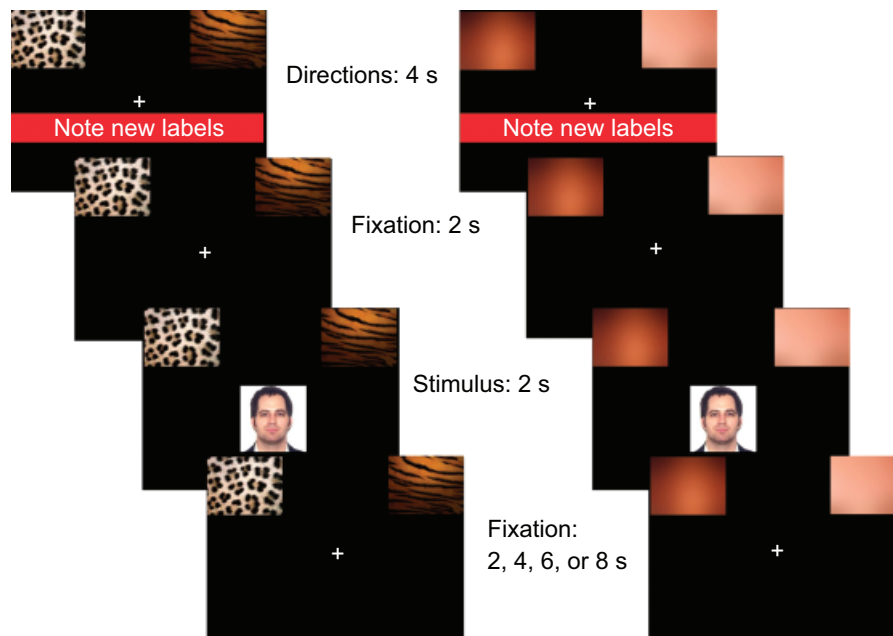

Fig. 1. The team-categorization task (left) and race-categorization task (right) performed during functional magnetic resonance imaging. Each block started with a directions screen. After the directions screen, participants completed 12 trials. On each trial, participants categorized a randomly presented face according to the pictorial labels (representing either team membership or race, depending on the task) shown at the top corners of the screen and then saw a fixation cross. After the completion of each block, directions for the next block appeared. Each of six runs contained two blocks in which the race-categorization task was performed and two blocks in which the team-categorization task was performed.

TABLE 1

Accuracy and Reaction Time During the Categorization Tasks

Task and face category	Accuracy		Reaction time (ms)	
	Mean	SD	Mean	SD
Implicit (race) task				
White, in-group	.96	.19	896	298
White, out-group	.95	.22	902	310
Black, in-group	.94	.24	862	282
Black, out-group	.96	.19	849	264
Explicit (team) task				
White, in-group	.86	.35	1,210	329
White, out-group	.79	.41	1,250	322
Black, in-group	.79	.41	1,233	319
Black, out-group	.79	.41	1,270	316

Note. Accuracy is the proportion of trials responded to correctly during the 2-s face presentation. Reaction time is the time in milliseconds between the presentation of a face and the response to it. Trials on which the reaction time was less than or equal to 300 ms are excluded.

task (see Table 1). We first removed all trials on which the response time was less than or equal to 300 ms. Responses were faster, $F(1, 21) = 113.29$, $p_{rep} > .99$, and more accurate, $F(1, 21) = 19.40$, $p_{rep} > .99$, during the implicit than during the explicit categorization task. As in previous research (Levin, 1996), a Task × Race interaction indicated that participants were faster to categorize Black than White faces during the race-categorization task, $F(1, 21) = 5.05$, $p_{rep} = .90$, but not during the team-categorization task. A Task × Team interaction indicated that participants were faster to recognize and categorize in-group than out-group faces during the team-categorization task, $F(1, 21) = 7.73$, $p_{rep} = .95$, but not during the race-categorization task. There were no other main effects or interactions for either reaction time or accuracy (p_{rep}s < .77).

Ratings and Memory

We analyzed participants' ratings of accurately recalled faces (as determined from the memory task).[3] Rating and memory results for 1 participant were lost because of a data-collection error. The mean rating of the sample was used as a rating score for this participant in subsequent brain-behavior correlations. Excluding this participant did not change the correlations or main effects.

To determine if ratings were characterized by in-group bias, out-group derogation, or some combination of the two (see Fig. 2), we subtracted the midpoint of the rating scale, 3.5, from every rating and analyzed these adjusted scores. As in previous research (see Brewer, 1979), participants preferred novel in-group to out-group members, $F(1, 20) = 4.59$, $p_{rep} = .89$. Moreover, this preference for in-group members was not moderated by race ($p_{rep} < .68$). Specifically, it was driven by in-group liking

[3]Although participants were more accurate at recognizing the team membership of White than Black faces during the final memory task, $F(1, 20) = 5.43$, $p_{rep} = .91$, there were no differences in accuracy between novel in-group and out-group faces, regardless of race (p_{rep}s < .77).

($M = 0.40$), $t(20) = 3.23$, $p_{rep} = .97$. There was no evidence of out-group disliking ($M = -0.03$), $t(20) = -0.15$, $p_{rep} = .20$. These data are consistent with the view that in-group bias and out-group derogation are not necessarily reciprocal—liking an in-group does not necessitate disliking an out-group (Allport, 1954; Brewer, 1999).

fMRI Results

fMRI Preprocessing and Analysis

Data were preprocessed and analyzed using SPM5 (Wellcome Department of Cognitive Neurology, London, United Kingdom). They were corrected for slice-acquisition time and motion, co-registered to structural images, transformed to conform to the default T1 Montreal Neurological Institute (MNI) brain interpolated to $3 \times 3 \times 3$ mm, and smoothed using a 9-mm full-width/half-maximum kernel. The blood-oxygenation-level-dependent (BOLD) signal was modeled as a function of a canonical hemodynamic response function and its temporal derivative, using a 128-s high-pass filter. First-level images were analyzed at the second level using a 2 (team membership: in-group, out-group) × 2 (race: Black, White) × 2 (categorization task: explicit, implicit) repeated measures analysis of variance. BOLD activity during directions screens was modeled using separate regressors so they would not affect analyses.

For whole-brain analyses, the level of significance was a p_{rep} value of at least .99, $p \leq .001$ (uncorrected), and a significant effect was reported if activity in at least 10 contiguous voxels met this criterion. For region-of-interest (ROI) analyses, the level of significance was a p_{rep} value of at least .95, $p \leq .01$ (uncorrected), and a significant effect was reported if activity in at least 10 contiguous voxels met this criterion. ROIs were based on voxels from 5-mm spheres centered on the maxima of the amygdala (defined using an anatomical mask) and significant regions identified in the whole-brain analysis. To examine moderation and correlations, we exported ROI data from SPM5 to SAS.

Data from 17 participants (7 males, 10 females; 9 Tigers, 8 Leopards) who successfully learned the group membership of the faces (average = 87% correct) and completed the categorization task were included in the fMRI analyses. The other 5 participants were excluded because of head motion (> 3 mm; $n = 1$), random responding during implicit categorization (> 3.6 standard deviations below the mean in accuracy; $n = 1$), and failure to learn the teams (< 71% correct, with 50% = chance; $n = 3$).

Novel Group Membership

Neuroimaging results were consistent with the idea that self-categorization motivates social perception (see Table 2 for all statistically significant effects of self-categorization on brain activity). Novel in-group members were associated with greater activity in bilateral fusiform gyri than were novel out-group members (see Table 2 and Fig. 3a). These results converge with
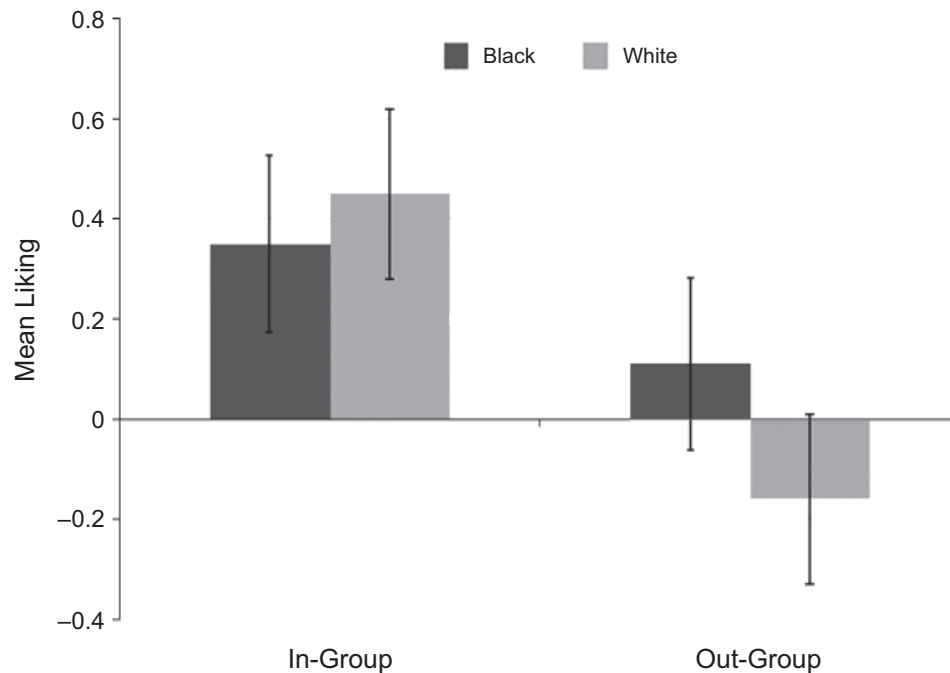
Fig. 2. Mean liking of in-group and out-group White and Black faces. Participants rated each face on a 6-point scale (1 = *dislike*, 6 = *like*). Ratings were centered on the scale's midpoint (3.5) such that more positive scores represent greater liking and more negative scores represent greater disliking. Error bars show standard errors.

those of previous studies showing greater fusiform activity in response to racial in-group members than in response to racial out-group members (Golby et al., 2001; Lieberman et al., 2005). These earlier studies suggested that fusiform activity in response to racial in-group members may be due, at least in part, to familiarity (Golby et al., 2001), whereas the present data suggest that

aspects of self-categorization other than familiarity contribute to this relationship (Sporer, 2001). Indeed, self-categorization with a minimal group leads to greater individuation of novel in-group, relative to out-group, members (Bernstein et al., 2007), and the fusiform gyri has been shown to play a role in individuation (Rhodes et al., 2004).

TABLE 2

Areas With Statistically Significant Blood-Oxygenation-Level-Dependent (BOLD) Activation

Brain region	BA	Hemisphere	No. of voxels	Coordinates x	y	z	t(16)
Greater activity in response to novel in-group relative to novel out-group faces							
Amygdala	34	Left	10	−24	3	−15	3.53
Orbitofrontal cortex	47	Left	16	−30	39	−6	5.18
Fusiform gyrus	37	Right	61	39	−48	−15	5.50
Fusiform gyrus	37	Left	46	−36	−42	−24	4.96
Putamen	48	Right	32	27	−6	15	5.65
Inferior temporal cortex	37	Left	20	−54	−57	−6	4.88
Greater activity in response to Black relative to White faces							
Angular gyrus	39	Left	18	−36	−54	30	5.34
Inferior occipital cortex	19	Left	85	−48	−78	−6	5.38
Inferior occipital cortex	19	Right	43	42	−75	−6	5.10
Inferior occipital cortex	18	Right	10	33	−93	−9	5.15
Inferior occipital cortex	18	Left	31	−30	−96	−9	5.04

Note. All parameters are based on cluster maxima. The x, y, and z coordinates are in Montreal Neurological Institute space. The t values are from full-brain analyses ($p \leq .001$) and region-of-interest analyses ($p \leq .01$); an effect was considered significant if activity in 10 or more contiguous voxels met at least one of these statistical thresholds. No regions showed significantly greater activity in response to novel out-group faces than in response to novel in-group faces or significantly greater activity in response to White than in response to Black faces. BA = Brodmann's area.
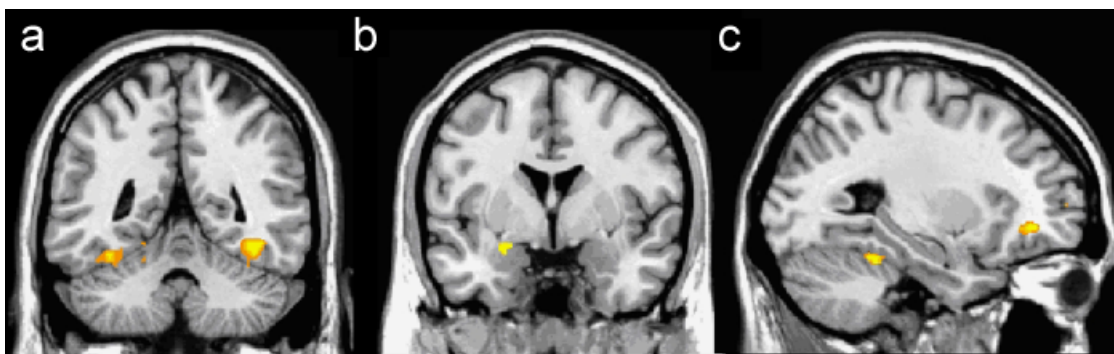
Fig. 3. Maps showing brain areas in which activity was greater for in-group than for out-group faces. Areas showing this effect were (a) the fusiform gyri (coronal view; $y = -48$), (b) the amygdala (coronal view; $y = 0$), and (c) orbitofrontal cortex (sagittal view; $x = -24$).

Although previous research has suggested that amygdala activity in response to Black faces reflects the processing of negative information, recent models posit a more general role for the amygdala in processing motivationally relevant stimuli (e.g., Cunningham et al., 2008). Results were consistent with this latter model in that novel in-group members were associated with greater amygdala activity than were novel out-group members (see Table 2 and Fig. 3b). Although this result may appear to differ from experimental results showing greater amygdala activity in response to racial out-group faces relative to racial in-group faces (e.g., Cunningham et al., 2004; Hart et al., 2000), racial attitudes and stereotypes are likely to be motivationally relevant in some intergroup contexts and irrelevant in others. For example, amygdala activity is greater for racial out-group faces than for racial in-group faces when people think of the faces in terms of their social category membership, but amygdala activity is greater for racial in-group faces than for racial out-group faces when people think of the faces as individuals (Wheeler & Fiske, 2005).

The contention that amygdala activity in response to novel in-group members may reflect motivational consequences of belonging to a group rather than negativity is corroborated by our finding of greater activity associated with novel in-group members, relative to out-group members, in the orbitofrontal cortex (OFC; see Table 2 and Fig. 3c) and dorsal striatum (putamen). The OFC plays a key role in linking social and appetitive stimuli to hedonic experience (Kringelbach, 2005), and the dorsal striatum is active during acts of mutual cooperation (Rilling et al., 2002) and viewing of pictures of loved ones (Bartels & Zeki, 2000).

No regions showed significantly greater activity for out-group than for in-group faces.

Correlations Between Neural Activity and In-Group Bias

We tested whether the greater neural activity in response to viewing novel in-group, relative to out-group, members was associated with individual differences in in-group bias (i.e., liking in-group members more than out-group members). For

each ROI (fusiform gyri, amygdala, OFC, and striatum), we calculated individual differences in brain activity (in-group − out-group) and then correlated these scores with individual differences in self-reported liking of the faces (in-group − out-group). Participants with greater in-group bias in OFC activity reported a stronger preference for in-group over out-group members ($r = .54$, $p_{rep} = .94$).[4] Moreover, OFC activity mediated the in-group bias in self-reported liking for the faces. Specifically, in-group bias was significantly reduced (from $b = 0.389$, $p_{rep} = .92$, to $b = -0.131$, $p_{rep} = .63$) when we controlled for increases in OFC activity (in-group − out-group; Sobel $z = 2.22$, $p_{rep} = .94$).

Racial Group Membership

To further examine the neural components involved in processing social groups, we compared brain activity in response to Black and White faces. Black faces were associated with greater activity in the visual cortex than were White faces (see Table 2); no regions were more active in response to White faces than in response to Black faces.[5] These data are consistent with studies showing that race may be largely ignored when it is orthogonal to current group membership (Kurzban et al., 2001).

Interactions of Team With Race and Task

To examine the automaticity of these in-group biases in neural processing, we tested whether the observed in-group biases in brain activity were moderated by race (Black vs. White), attention (explicit vs. implicit) to team membership, or both. For each ROI (i.e., fusiform gyri, amygdala, OFC, and dorsal striatum), we compared mean activity for Black versus White faces

[4]As in previous research, in-group bias (in-group − out-group) in self-reported liking was not correlated with amygdala activity (Phelps et al., 2000), or with activity in other regions showing in-group bias. We also conducted correlations between activity in regions showing in-group bias. Activity in the left fusiform gyrus was correlated with activity in the right fusiform gyrus ($r = .62$, $p_{rep} = .97$) and in the putamen ($r = .59$, $p_{rep} = .97$). No other correlations were statistically significant.

[5]We extracted an ROI from each brain region showing in-group bias, and race (Black vs. White) did not have a significant effect on activity in any of these regions.

and the implicit versus the explicit categorization tasks. In-group biases in neural activity were not moderated by race, categorization task, or a Race × Task interaction. Whereas previous studies have shown that activity in these regions can be modulated by explicit processing goals (Cunningham, Johnson, Gatenby, Gore, & Banaji, 2003), the in-group biases in neural activity reported here do not appear to require explicit attention to team membership, nor do they pertain strictly to Black or White faces.

GENERAL DISCUSSION

This study reveals a constellation of neural activity consistent with models of flexible self-categorization (Turner et al., 1987). Viewing novel in-group members was associated with greater activation in the fusiform gyri, amygdala, OFC, and dorsal striatum, relative to viewing novel out-group members. More-over, OFC activity mediated the in-group bias in self-reported liking for the faces. In-group biases in neural processing occurred within minutes of team assignment, in the absence of explicit team-based rewards or punishments, and independently of preexisting attitudes, stereotypes, or familiarity. In-group biases in neural processing were not moderated by the target's race or by the categorization task, which suggests that they did not require explicit attention to team membership and may have occurred relatively automatically.

This study provides neural evidence that in-group members are processed in greater depth than out-group members—placing in-group biases in perception firmly within the realm of motivated social perception (Balcetis & Dunning, 2006). By virtue of their motivational significance in a variety of contexts (e.g., economic, psychological, and evolutionary), in-group members often warrant greater, or deeper, processing than out-group members (Brewer, 1979, 1999). By assigning participants to novel groups and providing equal exposure to in-group and out-group faces, we were able to minimize the roles of familiarity and novelty as causal variables in the observed neural in-group biases. The absence of expertise with the faces also raises the possibility that the fusiform gyri may be associated with attentional biases (Wojciulik, Kanwisher, & Driver, 1998) toward in-group members, greater individuation (Rhodes et al., 2004) of in-group relative to out-group members, or both.

Whereas earlier studies reported greater amygdala activity in response to racial out-group, relative to in-group, faces—often interpreted as reflecting negativity or fear toward out-group or stigmatized-group members (e.g., Lieberman et al., 2005)—participants in the current study had greater amygdala activity in response to novel in-group, relative to out-group, members (see also Chiao et al., in press). Wheeler and Fiske (2005) found both patterns: Amygdala activity was greater in response to racial out-group faces during a social categorization task (deciding whether a person was young or old), but was greater in response to racial in-group faces during an individuation task. Wheeler

and Fiske's study captures the flexibility of the amygdala, which can respond to positive and negative stimuli, stimulus intensity, and, more generally, the motivational relevance of stimuli (Cunningham et al., 2008). The amygdala may be involved in segregating relevant from irrelevant stimuli in order to enhance perception of important stimuli (Anderson & Phelps, 2001; Vuilleumier, 2005; Whalen, 1998). This view of amygdala function offers an alternative explanation for previous results showing that amygdala activity of both White and Black participants is greater for Black than for White faces (Lieberman et al., 2005). Amygdala activity among White participants may reflect negative stereotypes toward Blacks, whereas amygdala activity among Black participants (who generally have a stronger racial identity and may therefore view Black faces as more relevant than White faces; Crocker, Luhtanen, Blaine, & Broadnax, 1994) may reflect increased processing of in-group members. In other words, different psychological mechanisms may guide the processing of racial in-group and out-group members. We propose that the amygdala activity in response to in-group members in the current study stemmed from their motivational relevance and salience in the current group context.

The relevance of most social category memberships also varies according to social context (Turner et al., 1987). Assigning people to mixed-race teams may change the way they construe race, and sensitize perceptual and affective processes to the currently-salient social category (i.e., team membership). Indeed, people categorize others according to race when it is the salient social category, but categorize according to team membership (and ignore race) when team membership is salient (Kurzban et al., 2001). Whereas race was the most salient difference between faces in previous fMRI studies, team membership was highly salient in the study reported here. In the current study, in-group biases in neural activity were not moderated by race; however, in contexts in which race provides the most salient group distinction, attitudes, cultural stereotypes (especially threat), and personal values (egalitarianism) may provide the most relevant motivational guides to perception, evaluation, and behavior. Moreover, people may process others according to race when these others are unaffiliated with the in-group or out-group (Van Bavel & Cunningham, in press).

The pattern of in-group bias in the current study extended to self-reported preferences for in-group members. Participants with a stronger preference for in-group members exhibited stronger OFC activity in response to in-group relative to out-group members. This brain-behavior relationship is consistent with a recent study showing a strong correlation between activity in a similar region of the OFC while participants tasted liquids and self-reported pleasantness of the liquids (Kringelbach, O'Doherty, Rolls, & Andrews, 2003) and, more generally, with the idea that this region plays a central role in representing and processing subjective value (Kringelbach, 2005). To our knowledge, this is the first fMRI study to identify the neural mediators of self-reported intergroup biases, and it demon-

strates an important link between the pervasive preference for novel in-group members (Brewer, 1979) and brain regions that process reward and subjective value (Kringelbach, 2005).

In-group biases in neural activity did not require explicit attention to team membership. Although the tasks differed in difficulty (judging by the faster reaction times and higher accuracy in the implicit task), neural in-group biases did not differ across tasks. This finding suggests that these biases are relatively automatic. Similarly, Bernstein et al. (2007) proposed that "ingroup faces are processed in a default, automatic manner, characterized by holistic processing" (p. 711). Indeed, several regions activated by in-group members respond automatically to social stimuli; for example, the amygdala responds to subliminal presentations of arousing faces (Whalen et al., 1998), and the fusiform gyri respond to faces within 100 to 200 ms (Liu, Harris, & Kanwisher, 2002). Future research will need to use electroencephalography and other techniques to examine the time course of the in-group biases demonstrated in this study and whether or not they emerge prior to conscious awareness.

CONCLUSION

This study elucidates the neural substrates that underlie in-group biases in perceptual and affective processing and clarifies the role of the fusiform gyri and amygdala in intergroup contexts. Although we have referred to the observed patterns of activity using the term *in-group bias*, future research will need to include neutral control faces to more precisely dissociate the neural components of perceiving and evaluating both in-group and out-group members. Humans are a fundamentally social species, and understanding the neural processes that underlie intergroup perception and evaluation promises to yield important insights into how people navigate their complex social worlds.

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