The Neural Development of Us and Them
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Abstract

Social groups aid human beings in several ways, ranging from the fulfillment of complex social and personal needs to the promotion of survival. Despite the importance of group affiliation to humans, there remains considerable variation in group preferences across development. In the current study, children and adolescents completed an explicit evaluation task of in-group and out-group members during functional neuroimaging. We found that developmental increases in bilateral amygdala, fusiform gyrius, and orbitofrontal cortex activation predicted greater propensity for in-group favoritism. Additionally, brain regions implicated in social cognition, such as the dorsomedial prefrontal cortex, showed heightened activation when viewing in-group compared to out-group peers. Our findings suggest that the motivational significance and processing of group membership undergoes important changes across development, with peaks in neural sensitivity to in-group members during adolescence, a period when young people are especially concerned with their social identity.

Key words: group membership; social cognition; adolescence; social identity
The Neural Development of Us and Them

Belonging to a group stretches beyond the satiation of immediate social needs, fulfilling the overarching purpose of promoting survival (Brewer, 1991; Hogg, 2003; Parrish & Edelstein-Keshet, 1999; Tajfel & Turner, 1979). Aside from helping establish a personal identity and boosting self-esteem, groups have long been thought to promote behavior aimed at shared desired outcomes, facilitate information and resource sharing, and afford individuals greater protection from predators (Allee, 1931; Bowles, 2006; Brown, Mory, & Kinney, 1994; Silk, Davis, McMakin, Dahl, & Forbes, 2012; Spoor & Kelly, 2004; Tajfel & Turner, 1979). The significant of group membership to humans is highlighted by the recent finding that loneliness has been found to increase the risk for premature death as much as smoking or obesity (Holt-Lunstad, Smith, Baker, Harris, & Stephenson, 2015). The benefits of group membership confer such important survival benefits to humans that group affiliation and in-group preferences emerge very early in development and have been observed in every culture studied on earth (Aboud, 2003; Brown, 1991; Dunham & Emory, 2014; Dunham, Baron, & Carey, 2011). While the tendency for group aggregation and the subsequent importance of group membership is not unique to humans (Parrish & Edelstein-Keshet, 1999), humans do display greater in-group favoritism than other non-human primates (Burkart, Hardy, & van Schaik, 2009). These findings imply that the significance of group membership in humans should be conserved cross-culturally and throughout the life-span. However, empirical evidence suggests otherwise, revealing cultural variations and developmental fluctuations in group affiliation (Baron & Dunham, 2015; Dunham & Emory, 2014; Falk, Heine, & Takemura, 2014; Ma-Kellams, Spencer-Rodgers, & Peng, 2011; Pfeifer et al., 2007; Tanti, Stukas, Halloran, & Foddy, 2011). These variations remain puzzling.
given the importance of groups to human survival. In the current study, we examine changes in neural sensitivity to group membership across childhood and adolescence to better understand the dynamic nature and shifting psychological significance of social groups across development.

**Developmental changes in the significance of groups**

**Infancy and childhood.** For young children and infants, groups help make sense of the different roles and categories that populate the social world, distinguishing between friends and foes (Bar-Haim, Ziv, Lamy, & Hodes, 2006; Hamlin, Mahajan, Liberman, & Wynn, 2013; Hirschfeld, 1995; Kinzler, Dupoux, & Spelke, 2007; Taylor, Rhodes, & Gelman, 2009; Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002; Wynn, 2008). Children utilize groups to facilitate future learning about social category concepts, supporting the premise that group membership allows children to rapidly learn information crucial to navigating their social world (Baron & Dunham, 2015). Such information is useful for survival; young children assume that out-groups are more likely to be hostile than friendly and become aware that in-group members are sources of support and nourishment (Hamlin et al., 2013; Kinzler & Spelke, 2011). Considering this evidence along with findings that young children are biased to remember threatening social stimuli as a means to monitor threat (Baltazar, Shutts, & Kinzler, 2012; Kinzler & Shutts, 2008) it likely that children may display heightened vigilance towards outgroup members. In spite of situational out-group vigilance, infants and children also display in-group preferences. Early conceptions of morality appear to be contingent upon group membership and are ostensibly driven by in-group biases (see Hamlin, 2014). Despite the fact that infants normally favor those who exhibit prosocial behavior, they prefer individuals who harm dissimilar others (Hamlin et al., 2013; Hamlin, Wynn, & Bloom, 2007, 2010; Hamlin, Wynn, Bloom, & Mahajan, 2011). Moreover, infants’ expectations are violated when in-group members fail to display pro-social behavior to one
another, such as when they hinder a fellow in-group member who needs assistance (Baillargeon, Setoh, Sloane, Jin, & Bian, 2014; Baillargeon et al., 2015). The trend of in-group favoritism persists throughout childhood as individuals endorse in-group favoritism and sometimes even retain negative conceptions of out-group members (Bigler, Jones, Lobliner, 1997; Bigler, Spears Brown, & Markell, 2001). Thus, group affiliation and its associated biases in infants and children influence their understanding of the world, imparting them with information necessary for basic social functioning.

**Adolescence.** Although group preferences may emerge at a very young age, there is evidence that the value of group belonging changes across development. While individuals of all ages have demonstrated in-group favoritism—even within arbitrary groups—adolescents appear to be more sensitive to group affiliation and their accompanying social identities than both children and adults (Abrams, Rutland, & Cameron, 2003; Brewer, 1979; Liebkind, 1983; Pfeifer et al., 2009; Tajfel, Billig, Bundy, & Flament, 1971; Van Bavel, Packer, & Cunningham, 2008, 2011). Indeed, adolescents focus on the social aspects of their identity more so than children, and in some instances more than adults (Hart, Fegley, Chan, Mulvey, & Fischer, 1993; Liebkind, 1983; Tarrant et al., 2001). For example, peer groups aid in establishing adolescents’ social and personal identity, with adolescents relying more on the opinions of others when constructing their own self-construals (Brown et al., 1994; Pfeifer et al., 2009). Prominent psychological theories suggest that in-groups may become an increasingly salient and important social identity during adolescence, a developmental period marked by a need to belong and affiliate with peers (Crockett, Losoff,, & Petersen, 1984; Furman & Buhrmester, 1992; Hart & Fegley, 1995; Kroger, 2000; Newman & Newman, 2001; Tajfel & Turner, 1979; Turner, Hogg, Oakes, Reicher, & Wetherell, 1987). Moreover, group membership offers an avenue of social support,
and in doing so, confers benefits to adolescents’ psychological and physiological health (Cacioppo & Cacioppo, 2014; Compare et al., 2013; Holt-Lunstad et al., 2015). Thus, while group membership may be important at all stages of development, groups become more important for youths’ social identity upon reaching adolescence, suggesting that group identity is subject to psychological and motivational changes that peak in adolescence.

Further evidence that the salience of group identity may peak in adolescence comes from developmental neuroscience research. Across rodents, primates, and humans, adolescence is marked by a universal “social restructuring” characterized by an increased orientation towards peers (Nelson, Leibenluft, McClure, & Pine, 2005). Such a social reorientation is mediated by alterations in neural development. In particular, neural regions involved in affective processing (e.g., amygdala, ventral striatum, orbitofrontal cortex (OFC)) show heightened activation to social stimuli among adolescents compared to children or adults, suggesting that adolescents may be particularly sensitive to socioemotional stimuli (Galvan et al., 2006; Hare, O’ Doherty Camerer, Schultz, & Rangel, 2008; Monk et al., 2003; Nelson et al., 2005). This heightened sensitivity is thought to underlie adolescents’ unique attunement towards social evaluation and loss (Nelson et al., 2005). Moreover, neural regions considered part of the “social brain” that are involved in mentalizing or taking the perspective of others (e.g., medial prefrontal cortex (MPFC), temporoparietal junction (TPJ); Blakemore, 2008) show developmental peaks in activation during adolescence compared to adulthood (Blakemore, 2010; Burnett, Bird, Moll, Frith & Blakemore, 2009; Gweon, Young & Saxe, 2011; van den Bos, van Dijk, Westenberg, Rombouts, & Crone, 2011; Wang, Lee, Sigman, Dapretto, 2006). Such activation may explain adolescents’ increased capacities for perspective taking, contributing to their ability to evaluate their experiences as members of groups. Together, neuroscience research underscores how
developmental changes in affective and social cognition regions likely play an important role in directing adolescents’ attention towards social stimuli and increasing the salience of peer groups.

**A Social Neuroscience Approach to Group Membership**

Methodological limitations make self-report and behavioral measures across wide age groups difficult to assess, and so a clear developmental trajectory tracking the psychological significance of groups across children and adolescents has remained elusive. Functional neuroimaging offers insight into the perceptual, cognitive, and affective processes that underlie potential developmental changes in the salience of group membership. Developmental differences may not be adequately captured with self-report measures due to methodological limitations such as ceiling effects in such reports, children’s inability to understand self-report measures adequately, or mischievous responding (Fan et al., 2006; Robinson-Cimpian, 2014; Austin, Deary, Gibson, McGregory, & Dent, 1998). Moreover, the explicit nature of these types of measures fails to capture group processes that occur below the surface of awareness (see Van Bavel, Xiao, & Hackel, 2014). Neuroimaging methods, however, allow for the assessment of implicit processing that goes on to inform broader psychological processes (Cunningham & Van Bavel, 2009; Stanley, Phelps, & Banaji, 2008). Indeed, such methods may allow for a more complete understanding of the contributions of shifting psychological processes—implicit and explicit—that affect the significance of group membership.

Research has identified several brain regions of interest that have previously been implicated in the study of social groups (see Cikara & Van Bavel, 2014 for a review). Specifically, the amygdala and fusiform gyrus are important in understanding the psychological significance of groups (e.g., Van Bavel et al., 2008, 2011). Originally considered to sit at the center of a neural network processing threat (Davis, 1992, 1994; LeDoux, 1996), the amygdala
has been reconsidered to belong to a neural detection network that is sensitive to a broad range of salient stimuli (Cunningham & Brosch, 2012; Vuilleumier & Brosch, 2009). Evidence suggests that the amygdala may capture and direct attention towards noteworthy stimuli, especially emotional ones (Anderson & Phelps, 2001; Cunningham & Brosch, 2012; Cunningham, Van Bavel, & Johnsen, 2008). Moreover, the amygdala has been shown to be more active in response to in-groups than out-groups in adults (Van Bavel et al., 2008) and tracks developmental changes in the salience of social identities including race and gender (Telzer et al., 2013, 2015).

The fusiform gyrus is another key brain region involved in social perception. In particular, early research found the fusiform face area (FFA)—a sub-region of the fusiform gyrus—to be involved in face recognition, responding preferentially to faces compared to other objects (Kanwisher, McDermott, & Chun 1997; Rhodes, Byatt, Michie, & Puce, 2004). More recently however, the fusiform is implicated in categorizing a stimulus as social, compared to non-social (Haxby, Hoffman, & Gobbini, 2002). Because shared social identities may alter the depth with which one processes faces (Hugenberg, Young, Bernstein, & Sacco, 2010; Sporer, 2001), the fusiform may be recruited when viewing in-group relative to out-group faces. Indeed, adults show heightened fusiform activation to in-group faces (Van Bavel et al., 2008, 2011), and adolescents show heightened fusiform activation when receiving positive feedback from peers (Guyer, Choate, Pine & Nelson, 2011), suggesting that group membership facilitates deeper processing of faces.

Because people value group membership and fellow in-group members, group membership also activates brain regions involved in reward value (Baumeister & Leary, 1995; Brewer, 1979, 1991). The ventral striatum and OFC, which encode for and represent subjective value (Kringelbach, 2005), tend to be activated when perceiving and favoring in-group members
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up Membership and Development (Telzer, Ichien, & Qu, 2015; Van Bavel et al., 2008). Further, adolescents show heightened ventral striatum activity both when receiving acceptance feedback from peers (Guyer et al., 2011) and when making risky decisions in their presence (Chein, Albert, O’ Brien, Uckert, & Steinberg, 2011). This research highlights the subjective value of fitting in and belonging to a group.

Finally, successfully navigating group environments requires at least an implicit ability to better recognize and more readily attribute psychological agency and autonomy for in-group relative to out-group members. As such, neural regions involved in mental state reasoning (i.e., mentalizing) and theory of mind may be recruited more when viewing in-group relative to out-group members (see Hackel, Looser, & Van Bavel, 2014). Numerous studies have found that people express greater empathy for in-group compared to out-group members (e.g., Cikara, Bruneau, Van Bavel, & Saxe, 2014), are more accurate at inferring the mental states of their own in-group relative to out-group (Adams Jr. et al., 2014), and engage in less spontaneous mentalizing for out-group members (Harris & Fiske, 2006, 2009). Such increases in mentalizing are facilitated by activation in the dorsomedial prefrontal cortex (DMPFC) when processing in-group relative to out-group targets (Mitchell, Macrae, & Banaji, 2006; Molenberghs & Morrison, 2012; Rilling, Dagenais, Goldsmith, Glenn, & Pagnoni, 2008). Moreover, structural connectivity between the TPJ and DMPFC predicts differences in intergroup bias (Baumgartner, Nash, Hill, & Knoch, 2015). Thus, differences in social group perception and biases may be associated with differential activation of brain regions involved in mentalizing for in-group versus out-group members.

Current Research

Although research with behavioral and neuroscience methods have demonstrated that
children, adolescents, and adults are sensitive to group membership (Bigler et al., 1997; Telzer et al., 2013; Van Bavel et al., 2008), it remains unknown as to how the psychological and neural underpinnings of group membership may differ across these developmental stages. On the one hand, the salience of group membership may be stable, present early in childhood and remaining important across development. On the other hand, the salience of group membership changes developmentally, peaking in adolescence, a time when one’s social identity is forming (Marcia, 1980; Steinberg & Morris, 2001). In order to better understand whether the psychological significance of group membership changes across development, we used functional magnetic resonance imaging (fMRI) with children and adolescents as they observed in-group and out-group peers.

In the current study, children and adolescents ranging from 8-16 years of age were told they would participate in a competition as members of the ‘blue team’ against participants at a rival school who belonged to the ‘red team,’ and that they would view and rate pictures of members from both teams. During an fMRI scan, participants viewed images of in-group (blue team) and out-group (red team) members, one at a time, and were asked to indicate whether they liked or disliked individuals from each team by pressing one button or another. This task allowed us to examine how brain regions involved in detection (amygdala, fusiform), reward processing (VS, OFC) and mentalizing (DMPFC, MPFC, MPPC) vary across childhood and adolescence.

Methods

Participants

Participants included 56 children and adolescents (30 female), ages 8-16 years ($M_{age} = 13.3$ years, $SD = 2.81$ years). Power was determined using GPower (Faul & Erdfelder, 1992). When using an estimated effect size of 0.5, an n of 55 would be needed to properly obtain
statistical power (1-β) of 0.9. Participants self-identified as White (n = 41), Black (n = 4), Asian (n = 3), Latino (n = 2) or mixed race (n = 6). Based on parental report, participants’ total family income ranged from less than $45,000 (n = 11) to greater than $90,000 (n = 29). Parents provided written consent and children provided written assent in accordance with the University of Illinois’ Institutional Review Board. Participants were compensated $50 for participating.

Establishment of Novel In-Group Membership

Participants arrived in the lab one at a time and were told that they would be on a team representing the University of Illinois and that they would take part in a competition with research participants from the Ohio State University, a rival university. To make group membership salient, participants were given a t-shirt with the lab logo in their home university’s colors (blue and orange), and a digital photograph of their face was taken (Figure 1a). The researchers also wore the same t-shirt to increase the salience of team membership. Participants were shown a pictures of rival university members receiving their t-shirts, which were scarlet and grey (Figure 1b). During a learning task, participants were shown pictures of in-group and out-group team members (totaling 72 peers), who were described as participants who had already completed the study. Each face was displayed in random order, one at a time, with a label at the bottom indicating “my team” and “other team.” Participants were instructed to press one of two buttons to indicate the correct team of each peer (Figure 1c). Photos were placed on blue (representing in-group) or red (representing out-group) backgrounds to provide a visual cue to team membership. Participants also saw their own face two times on the colored background and categorized themselves into the appropriate team in order to enhance their in-group identification. The next trial proceeded after participants pressed a button.
The face stimuli were of children and adolescents ranging in age from 8-16 years. The faces were comprised of equal numbers of males and females and one third were White, Black, and Asian. All faces were looking into the camera and smiling. Faces were taken from several databases including the National Institute of Mental Health Child Emotional Faces Picture Set (Egger et al., 2011). The faces of each race were matched based on pilot testing to ensure they were equally attractive (mean attractiveness = 4.1 for each race on scale ranging from 1=“not at all” to 7=“very much”) and ranged equally in terms of perceived age (mean age =5.7 for each race on a scale ranging from 1-9 (1=“5 or younger”, 5=“12 or 13”, 9=“20 or older”). Faces were randomly assigned to the teams ensuring equal representation of race, gender, and age across the teams, and assignment was fully counterbalanced so that participants were equally likely to see each face as an in-group or out-group member. This ensured that any visual differences in the stimuli (e.g., attractiveness, luminance) could not account for observed differences between in-group and out-group members.

fMRI Task

After completing the learning task, participants were placed in the scanner and completed an explicit evaluation task. For each trial of the task, participants were shown the same pictures as the learning task, this time with the instruction to indicate whether they “like” or “dislike” each person (Figure 1d). Participants pressed one of two buttons to indicate their response. The faces were presented on the color background representing team membership. Participants completed 72 total trials, half of which were in-group members and half of which were out-group members. Each face was presented for 3 seconds with an inter-trial interval that was jittered randomly between 1.5 to 3 seconds. On average, participants did not respond to 4.8% (SD=5.8%) of the trials within the 3s response window.
Figure 1. Group Membership Task. (a) participant is told they will be part of a competition between two research teams at different universities, is assigned to their team, provided a t-shirt with the team colors and logo, and a photo is taken, (b) participant is introduced to the rival team from Ohio State, (c) participant completes a short learning task in which they categorize each face into their respective team, (d) during the fMRI scan participants rate each face on whether they like or don't like the person.

fMRI Data Acquisition and Analysis

fMRI data acquisition. Imaging data were collected using a 3 Tesla Siemens Trio MRI scanner. The task included T2*-weighted echoplanar images (EPI) [slice thickness=3 mm; 38 slices; TR=2sec; TE=25msec; matrix=92x92; FOV=230 mm; voxel size 2.5x2.5x3mm³]. Structural scans consisted of a T2*-weighted, matched-bandwidth (MBW), high-resolution, anatomical scan (TR=4sec; TE=64msec; FOV=230; matrix=192x192; slice thickness=3mm; 38 slices) and a T1* magnetization-prepared rapid-acquisition gradient echo (MPRAGE; TR=1.9sec; TE=2.3msec; FOV=230; matrix=256x256; sagittal plane; slice thickness=1mm; 192 slices). The orientation for the MBW and EPI scans was oblique axial to maximize brain coverage.

fMRI Data Preprocessing and Analysis. Neuroimaging data were preprocessed and
analyzed using Statistical Parametric Mapping (SPM8; Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK). Preprocessing for each participant’s images included spatial realignment to correct for head motion (no participant exceeded 2 mm of maximum image-to-image motion in any direction). The realigned functional data were co-registered to the high resolution MPRAGE, which was then segmented into cerebrospinal fluid, grey matter, and white matter. The normalization transformation matrix from the segmentation step was then applied to the functional and T2 structural images, thus transforming them into standard stereotactic space as defined by the Montreal Neurological Institute and the International Consortium for Brain Mapping. The normalized functional data were smoothed using an 8mm Gaussian kernel, full-width-at-half maximum, to increase the signal-to-noise ratio. Statistical analyses were performed using the general linear model in SPM8. Each trial was convolved with the canonical hemodynamic response function. High-pass temporal filtering with a cutoff of 128 seconds was applied to remove low-frequency drift in the time series. Serial autocorrelations were estimated with a restricted maximum likelihood algorithm with an autoregressive model order of 1.

In each participant's fixed-effects analysis, a general linear model (GLM) was created with 12 regressors of interest, modeled as events: in-group and out-group peers broken down by race (Black, White, Asian) and gender (Male, Female). Null events, consisting of the jittered inter-trial intervals, were not explicitly modeled and therefore constituted an implicit baseline. The parameter estimates resulting from the GLM were used to create linear contrast images comparing the conditions of interest (in-group>out-group). Random effects, group-level analyses were performed on all individual subject contrasts using GLMFlex. GLMFlex corrects for variance-covariance inequality, partitions error terms, removes outliers and sudden activation
changes in the brain, and analyzes all voxels containing data 
(http://mrtools.mgh.harvard.edu/index.php/GLM_Flex). We conducted t-tests at the group level to examine overall differences in neural activation when processing group-status and race. In addition, we conducted whole brain regression analyses with age entered as the regressor to examine neural regions that showed increased activation as a function of age.

In addition, given the key role of the amygdala in directing attention to motivationally relevant stimuli (Cunningham & Brosch, 2012), we conducted functional connectivity analyses to examine whether the amygdala shows developmental changes in functional coupling with regions involved in face processing, reward value, and mentalizing. We conducted psychophysiological interaction (PPI) analyses (Friston et al., 1997), using the amygdala as the seed region. The bilateral amygdala was defined structurally using the WFUpickatlas (Maldjian, Laurienti, Kraft, & Burdette, 2003). PPI analyses were run using a generalized form of context-dependent psychophysiological interaction. Specifically, the automated gPPI toolbox in SPM (gPPI; McLaren et al., 2008) was used to 1) extract the deconvolved times series from the amygdala ROI for each participant to create the physiological variables; 2) convolve each trial type with the canonical HRF, creating the psychological regressor; and 3) multiply the time series from the psychological regressors with the physiological variable to create the PPI interaction terms. This interaction term identified regions that covaried in a task-dependent manner with the amygdala. For the first level model, one regressor representing the deconvolved BOLD signal was included alongside each psychological and PPI interaction terms for each condition type to create a gPPI model. At the group level, we conducted random effect, whole brain regression analyses to examine developmental changes in functional coupling between the conditions of interest.
To correct for multiple comparisons, we conducted a Monte Carlo simulation implemented using 3dClustSim in the software package AFNI (Ward, 2000). We used our group-level brain mask, which included only gray matter. Results of the simulation indicated a voxel-wise threshold of $p<.005$ combined with a minimum cluster size of 48 voxels for the whole brain, corresponding to $p<.05$, False Wise Error (FWE) corrected. All behavioral and fMRI analyses control for mean response time (MRT) given large variability in response time across development. Adding this covariate ensures that our developmental effects are due to age differences and not to differences in psychomotor speed. Notably, all analyses remain significant and are robust even without this covariate in the model. We used the MarsBaR toolbox to extract parameter estimates from significant clusters in the group-level analyses.

**Results**

**Behavioral Ratings of In- and Out-group Peers**

As a manipulation check, we first examined whether participants would express in-group favoritism on self-reported liking. We conducted a 3-way repeated-measures ANOVA on self-reported liking (percent liked) with 2 within subject factors representing the face stimuli (group status: in-group, out-group; race: Black, White, Asian) and two covariates representing between-person effects (age and mean response time (MRT)). MRT was entered as a covariate in order to account for age-related variations in task performance, helping ensure our results are specific to age and not differences in response time. As predicted, we found a significant effect of group status ($F(1,53)=37.4, p<.0001, \eta=.31$), such that participants rated liking in-group peers ($M=70.3\%$, $SE=2.7\%$) more than out-group peers ($M=36.4\%$, $SE=3.5\%$). No other effects were significant ($ps >.1$). Thus, regardless of participants’ age or the race of the group member, participants reported liking in-group members significantly more frequently than out-group
members (Van Bavel et al., 2008). For descriptive purposes, we plotted the percent of peers who were rated as liked separated by in-group status, race, and age-group based on theoretically meaningful age categories (children: ages 8-10yrs, N=15; early adolescents: ages 11-14yrs, N=16; mid adolescents: ages 15-16yrs, N=25; Figure 2). See supplemental information for additional findings with MRT.

![Figure 2](image)

**Figure 2.** Behavioral performance on the fMRI task. Participants rated liking more peers in their in-group than out-group, and this did not vary by the age of participants or the race of the stimuli. Error bars represent the standard error of the mean. For the sake of aiding visualization, participants are grouped into three age groups along the x-axis, although it is of note that all analyses were conducted using age using age as a continuous variable.

**Neural Correlates of Liking In-Group Relative to Out-Group Members: Developmental Changes**

Next, we conducted whole-brain interaction analyses to test whether there are differential
neural responses to in-group relative to out-group members as a function of age. To this end, age was entered in a regressor on the contrast of in-group>out-group faces. We found significant effects in several regions, such that participants demonstrated greater activation to in-group>out-group members in the bilateral amygdala, bilateral fusiform gyrus, OFC (Figure 3a), MPFC, MPPC, and pSTS, as a function of age (Table 1). Age was not associated with greater activation to out-group>in-group members. Thus, we found developmental increases in neural activation from childhood to adolescence in regions that code for emotional salience (amygdala), face processing (fusiform), subjective value (OFC), and social cognition (MPFC, MPPC, and pSTS) when rating in-group relative to out-group faces. Together, these neural effects suggest that the salience of in-group members changes across development.

**Linking Neural Correlates of In-group Processing to Behavioral Biases Favoring In-group Members**

Next, we examined whether neural biases (i.e. differential activation to in-group relative to out-group members) were associated with behavioral biases favoring in-group members. Behavioral biases were calculated as the difference in the percent of in-group members who were liked minus the percent of out-group members who were liked, such that higher scores represent a greater bias favoring the in-group. We extracted parameter estimates of signal intensity from each brain region which showed a significant interaction with age to in-group relative to out-group members. We examined whether age was associated with behavioral biases favoring in-group members via greater differential neural activation to in-group relative to out-group members. As shown in Figure 3b, participants who showed greater activation in the amygdala, fusiform gyrus, and OFC to in-group relative to out-group peers showed greater behavioral biases in preference for in-group over out-group peers. No other regions were significantly
associated with in-group bias. Next, we calculated the magnitude and the significance of the indirect effects using the procedures described by Preacher and Hayes (Preacher & Hayes, 2008), in which bootstrapping was performed with 1,000 samples and a bias-corrected confidence interval (CI) was created for the indirect effect. The indirect effects of age on in-group bias through neural activation were significant for the amygdala, fusiform, and OFC. These findings suggest that age is indirectly associated with biases favoring in-group members, such that as youth get older, their greater likelihood to favor their in-group occurs is mediated by heightened amygdala, fusiform, and OFC activation to in-group members.

Figure 3. (a) With age, participants showed greater activation in the amygdala, fusiform, and OFC to in-group relative to out-group faces and (b) each of these neural responses significantly mediated age-related increases in in-group bias. Note. The values in the mediation paths...
represent the standardized coefficients. The indirect effect represents the effect of age through brain activation to in-group bias, calculated using PROCESS (Preacher & Hayes, 2008). CI represents the 95% confidence interval of the indirect effect.

**Neural Connectivity with the Amygdala**

Finally, we examined developmental changes in functional connectivity with the amygdala to in-group>out-group members. Social perception systems in the brain are widely distributed and thought to be organized in networks (Nelson et al., 2005; Van Bavel et al., 2014). Consequently, we conducted psychophysiological interaction (PPI) analyses in order to examine the extent to which our brain regions of interest co-activate in different psychological contexts, thereby allowing insight into the developmental processes that shape social perception and evaluation. In our whole-brain PPI analyses, we entered age as a regressor and found developmental increases in connectivity between the amygdala and the ventral striatum, bilateral TPJ, MPPC, and fusiform gyrus (Figure 4; Table 2). Thus, with age, youth showed greater functional coupling between the amygdala and these neural regions when viewing in-group relative to out-group peers, suggesting a role of the amygdala in directing attention to motivationally relevant cues.
Figure 4. Age-related increases in functional connectivity with the amygdala when rating in-group relative to out-group faces. Increased functional connectivity is found in the ventral striatum, TPJ, and fusiform.

Discussion

Groups are indispensable for survival to several species across the animal kingdom (Allee, 1931; Parrish & Edelstein-Keshet, 1999; Williams, 1964). Favoring in-group members emerges very early in development and is present across development, from infancy to adulthood (Baillargeon et al., 2014, 2015; Baron & Dunham, 2015). However, evidence also shows fluctuations and nuances in this phenomenon and further hints at the possibility that groups adopt different meanings across life (Baron & Dunham, 2015; Dunham & Emory, 2014; Silk et al.,
We found that brain regions implicated in affect, reward, and social cognitive processes show developmental changes in neural sensitivity to novel peer in-groups, peaking in sensitivity during adolescence. Moreover, heightened activation mediated age differences in in-group favoritism. These neural and behavioral results reveal insight into the developmental changes that shape the shifting motivational importance of group membership across early development.

From childhood to adolescence, participants showed linear increases in activation in the bilateral amygdala when rating in-group relative to out-group members. While originally conceptualized as a threat detector (Davis, 1992, 1994), recent work has suggested that the function of the amygdala may instead be to detect and direct attention to motivational relevant stimuli (Cunningham et al., 2008; Cunningham & Brosch, 2012; Lieberman, Hariri, Jarcho, Eisenberger, & Bookheimer, 2005; Vuilleumier & Brosch, 2009). Importantly, the salience of different social identities may change in relevance depending on the context and developmental age of the individual, and so the amygdala will track this changing salience. Indeed, results of our functional connectivity analyses show developmental increases in connectivity between the amygdala and the bilateral TPJ, fusiform, and ventral striatum when participants rated in-group relative to out-group peers. These are regions involved in social cognition, face processing, and reward processing, respectively (Frith & Firth, 2007; Kanwisher et al., 1997; Kringelbach, 2005). Thus, the amygdala may be involved in the detection of meaningful and important stimuli that then alerts and directs attention to relevant brain regions to process the faces in further depth (Hackel et al., 2014; Van Bavel et al., 2011).

Moreover, it is noteworthy that children displayed relatively greater amygdala activation to out-group faces, as evidenced by the scatterplot showing activational patterns below 0 in the
youngest children. This finding, coupled with research showing that children are biased to remember threatening social displays (Baltazar et al., 2012), substantiates the idea that out-groups are salient to children by virtue of their perceived capacity for social threat. By contrast, adolescents become increasingly motivated to learn about in-groups at a time in the lifespan when fitting in is of the utmost importance (Silk et al., 2012). Thus, whereas young children may find out-groups salient, older adolescents may attend more to in-groups as a means of learning about an important social group. Indeed, the amygdala is involved in learning (Morris, Öhman, & Dolan, 1998), in addition to attending to interesting, salient, and important stimuli (Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000; Hamann, Ely, Hoffman, & Kilts, 2002; Telzer et al., 2013, 2015). Overall, these findings provide a novel and unique perspective on the role of the amygdala as a social-salience-detector that communicates with other brain regions, co-activation that increases linearly across development. More broadly, this also serves in characterizing the developmental plasticity of the brain to modulate the processing of social cognitive stimuli in order to accommodate developmental tasks and demands.

In addition, we found age-related increases in fusiform activation when rating in-group relative to out-group peers. These findings are consistent with research on adults, which has shown that adults exhibit greater activation within the bilateral fusiform when viewing novel in-group relative to out-group faces (Van Bavel et al., 2008, 2011). Although the faces of all in- and out-group peers were matched and counterbalanced across participants to ensure neither group was visually distinct than the other, the fusiform nevertheless showed strong differentiation between in- and out-group peers with age. Therefore, classifying faces along group boundaries may alter the depth with which faces are processed, and in-group belonging during adolescence may enhance encoding of in-group members, whereas out-group vigilance may contribute to
enhanced processing of out-group members among younger children. This heightened fusiform differentiation then contributes to developmental biases comparatively favoring novel in-group peers in adolescence. These findings suggest that the amygdala may signal the importance of the social category, and the fusiform may come online to engage in deeper perceptual processing, individuating faces based on their psychological and motivational significance (Van Bavel et al., 2011).

In addition, we found developmental increases in neural regions that code for and represent subjective value. In particular, youth showed developmental increases in OFC activation when rating in-group relative to out-group peers, and the ventral striatum showed developmental increases in functional coupling with the amygdala. Thus, viewing in-group members may activate brain regions involved in reward processing. This finding is consistent with prior work with adults, which has shown that individuals who favor novel in-group members show heightened OFC activity when viewing in-group relative to out-group members (Van Bavel et al., 2008), and rewarding in-group relative to out-group members engages the ventral striatum (Telzer et al., 2015). Thus, heightened OFC and ventral striatum activation when liking in-group relative to out-group peers may be more emotionally satisfying and rewarding.

Establishing intimate platonic and romantic relationships—milestones for teens—fulfills important psychological functions closely associated with well-being (Connolly, Furman, & Konarski, 2000; Levitt, Guacci-Franco, & Levitt, 1993; Steinberg & Morris, 2001). Thus, inclusion in a novel group may be experienced as rewarding during a time when new socioemotional bonds with others are highly sought.

At a time when the development of an identity is necessary for establishing an autonomous sense of self, groups become a source of social information for adolescents to
sample from and build an identity, as evidenced by their reliance on other’s opinions and perspective in crafting their own self-construals (Pfeifer et al., 2009). Indeed we also found developmental increases in activation of the social brain network (Blakemore & Mills, 2014; mPFC, mPPC, pSTS, TPJ) when viewing in-group relative to out-group faces. This neural recruitment highlights the psychological shift in motivational differences of processing group membership between childhood and adolescence. Our results suggest teens are keener to process social cues from in-groups, lending support to the notion that the psychological importance of groups is different between adolescents and children. The increased orientation towards group membership and enhanced social identity development in adolescence results in greater processing of in-group mental states and perspectives.

Interestingly, we did not find age effects in our behavioral analyses of in-group favoritism. That is, while both children and adolescents consistently reported liking in-group peers more than out-group peers, this trend did not change with age. We speculate that this is due to the nature of how we required participants to evaluate group members. By having participants indicate a categorical response (i.e., like/dislike) instead of rating likeability along a wider scale, we alleviated task demands for our younger participants but also removed a source of variability within the data. Most other studies evaluate in-group biases along a continuum (Van Bavel et al., 2008) and subsequently aggregate average ratings for in-group relative to out-group members. Because group membership is important for individuals of all ages, it is likely that children and adolescents do not differ in who they like, but rather how much they like them and the psychological significance of that preference. This is consistent with the notion that, while explicit preferences toward in- and out-group members may not vary with age, other implicit neurocognitive and perceptual processes do. Thus, the motivations and accompanying neural
pathways involved in in-group biases may change while the behavioral output remains relatively constant.

Although we did not find evidence of increases in in-group biases across development, we did find an indirect pathway, such that age contributed to greater neural biases (i.e., differentiation in the amygdala, fusiform, and OFC to in-group>out-group faces), and these neural biases contributed to behavioral biases. These findings suggest that there are important age-related changes in behavioral biases that may be occurring via the changing brain. Our findings suggest that while all age groups report liking in-group peers more than out-group peers, adolescents’ in-group preferences are influenced by the ways in which they respond at the neural level to these social categories. While a direct effect from age to behavioral biases might be expected, statisticians argue that a direct effect is not necessary for establishing statistically significant mediation, particularly in developmental studies that focus on more distal processes (Shrout & Bolger, 2002).

In conclusion, adolescence and childhood are periods marked as having distinct psychological interpretations of group belonging. In particular, childhood is characterized by the need to understand how and why the world works, whereas adolescence is marked by the increased importance of group affiliation to fulfill developmental goals of establishing a social identity (Baron & Dunham, 2015, Marcia 1980; Pfeifer et al., 2009). The latter occurs in tandem with a social reorientation of the teenage brain, a period of unique neural development during which brain regions involved in complex social processes undergo significant maturation (Nelson et al., 2005; Blakemore & Mills, 2014). Together, our imaging data reveal the biological substrates for the shifting psychological importance of groups across the first two decades of life. As individuals develop nuanced conceptions about the world and engage in new developmental
tasks, groups take on new meaning during adolescence.
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Table 1. Neural regions which showed an interaction with age during In-group>Out-group ratings.

| Region           | BA | x  | y  | z  | T    | k  |
|------------------|----|----|----|----|------|----|
| Fusiform         | 37 | R  | 32 | -52| -8   | 4.27| 48 |
| Fusiform         | 37 | L  | -30| -34| -26  | 4.72| 1181 |\(^a\) |
| pSTS             | 40 | L  | -48| -43| 13   | 3.17| 1181 |\(^a\) |
| mPPC             | 31 | L  | -9 | -46| 4    | 3.46| 1181 |\(^a\) |
| Amygdala         |    | L  | -22| -2 | -24  | 3.71| 94  |
| Amygdala         |    | R  | 24 | -1 | -29  | 3.49| 472 |\(^b\) |
| Temporal Pole    | 38 | R  | 39 | 14 | -29  | 4.37| 472 |\(^b\) |
| OFC              | 32/24 | L  | -6 | 35 | -14  | 3.51| 169 |\(^c\) |
| IFG              | 45 | L  | -30| 44 | -14  | 3.79| 169 |\(^c\) |
| Caudate          |    | R  | 21 | -10| 22   | 3.72| 105 |
| Parahippocampus  | 27 | R  | 18 | -31| -14  | 3.56| 84  |
| Cuneus           | 17 | L  | -9 | -85| -5   | 3.55| 127 |
| Cerebellum       |    | L  | -6 | -58| -47  | 3.48| 51  |
| Cerebellum       |    | R  | 36 | -67| -35  | 3.56| 61  |
| Cerebellum       |    | R  | 15 | -61| -50  | 3.20| 51  |

Note. R refers to right and L refers to left. x, y, and z refer to MNI coordinates; t refers to the t-score at those coordinates (local maxima); IFG refers to inferior frontal gyrus; pSTS refers to posterior superior temporal sulcus; OFC refers to orbitofrontal cortex; mPPC refers to medial posterior parietal cortex. Regions that share the same superscript are part of the same cluster.
Table 2. Neural regions which were functionally coupled with the amygdala and showed an interaction with age during In-group>Out-group ratings.

| Region     | BA | x   | y   | z   | T    | k  |
|------------|----|-----|-----|-----|------|----|
| Ventral Striatum |    | 6   | 5   | -2  | 3.86 | 306|
| TPJ        | 39 | R   | 51  | -55 | 4.03 | 87 |
| TPJ        | 39 | L   | -45 | -61 | 3.72 | 48 |
| pSTS       | 40 | L   | -63 | -42 | 3.70 | 70 |
| Fusiform   | 37 | L   | -36 | -46 | 3.33 | 188a|
| Hippocampus|    | L   | -24 | -34 | 4.46 | a  |
| Caudate    |    | R   | 10  | 14  | 4.38 | 168|
| Precuneus  | 31 | R   | 9   | -55 | 3.96 | 232|
| IFG        | 45 | L   | -57 | 14  | 3.65 | 91 |
| IFG        | 45 | R   | 51  | 5   | 3.53 | 73 |

Note. R refers to right and L refers to left. x, y, and z refer to MNI coordinates; t refers to the t-score at those coordinates (local maxima); TPJ refers to temporal parietal junction; IFG refers to inferior frontal gyrus; pSTS refers to posterior superior temporal sulcus; OFC refers to orbitofrontal cortex; MPPC refers to medial posterior parietal cortex. Regions that share the same superscript are part of the same cluster.
Supplemental Information

Behavioral Results with MRT

In the repeated measures ANOVA with group status, race, age, and MRT, we found a significant interaction with MRT x group status ($F(1,52)=22.65, p<.0001, \eta^2=.29$). This effect did not vary by age ($F(2,50)=.98, \text{ns}$) or race ($F(2,49)=2.08, \text{ns}$). To explore this interaction, we computed an in-group bias score, which represents the difference in ratings of in-group relative to out-group peers (i.e., liking in-group members – out-group members), such that higher scores represent liking more in-group members than the out-group members. We then ran correlations with in-group bias with MRT. Faster MRT was associated with a greater bias towards liking in-group members ($r=-.53, p<.001$; Supplemental Figure 1). Thus, individuals who are relatively faster to make a rating are more likely to be biased towards liking in-group members more than out-group members.

Supplemental Figure 1. Individuals with faster mean response times (MRT) show greater behavioral biases liking more in-group members than out-group members. The y-axis represents percent of in-group peers minus percent of out-group peers who were liked.

Neural Correlates of Race

The amygdala is also sensitive to the changing salience of different social identities across contexts. For instance, when race is the most salient social category, adolescents and adults show heightened amygdala activation to Black faces regardless of their own race (Lieberman et al., 2005; Telzer et al., 2013). In contrast, when adults are assigned to a minimal, mixed race group, they show heightened amygdala activation to in-group relative to out-group members regardless of race (Van Bavel et al., 2008). In novel groups, in-group members are particularly motivationally relevant because they afford group members the opportunity to fulfill belonging needs, and therefore the way individuals construe race changes (Van Bavel & Cunningham, 2010; see also Kurzban, Tooby, & Cosmides, 2001). Although we have previously...
shown developmental increases in amygdala activation to Black relative to White faces (Telzer et al., 2013), we hypothesized that by assigning youth to novel, mixed race teams, the salience of race would be diminished.

In whole brain t-tests, we examined differences when viewing Black relative to White faces (B-W), Black relative to Asian faces (B-A), and Asian relative to White faces (A-W). We collapsed across group-status (in-group and out-group) for these analyses. For all three contrasts, we found large clusters of activation in the fusiform gyrus (Supplemental Table 1). Additionally, for B-W we found activation in the TPJ and SMA.

Next, we examined whether there are age-related interactions when viewing different races. To this end, we conducted whole-brain regression analyses with age as a regressor on each of contrast. For B-W, we found age-related increases in activation in the MPFC extending into the DMPFC and the MPPC, for B-A, we found age-related increases in the DMPFC and VLPFC, and for A-W, we found age-related increase in the TPJ and MPFC (Supplemental Table 2). Importantly, we did not find evidence of amygdala activation in any of the contrasts, even at a more liberal threshold of p<.01. Age was not negatively correlated with activation in any region.
Supplemental Table 1. Neural regions which showed activation when viewing Black>White, Black>Asian, and Asian>White faces.

| Region         | BA | x  | y  | z  | t   | k   |
|----------------|----|----|----|----|-----|-----|
| **Black>White**|    |    |    |    |     |     |
| Fusiform       | 37 | L  | -36| -49| -17 | 7.05| 1788 |
| Fusiform       | 37 | R  | 33 | -64| -8  | 5.41| 1391 |
| SMA            | 6  | L  | -9 | 23 | 67  | 3.91| 183 |
| Thalamus       |    | L  | -6 | -19| 7   | 3.84| 52  |
| Cuneus         | 17 | R  | 12 | -73| 13  | 3.50| 75  |
| Angular Gyrus  | 39 | R  | 36 | -67| 49  | 3.39| 48  |
| **White>Black**|    |    |    |    |     |     |
| **Black>Asian**|    |    |    |    |     |     |
| Fusiform       | 37 | L  | -33| -52| -14 | 6.61| 1397 |
| Fusiform       | 37 | R  | 54 | -73| 4   | 4.04| 1012 |
| Thalamus       |    | L  | -9 | -22| 13  | 3.89| 43  |
| Temporal Pole  | 38 | R  | 24 | 14 | -44 | 3.81| 48  |
| **Asian>Black**|    |    |    |    |     |     |
| **Asian>White**|    |    |    |    |     |     |
| Fusiform       | 37 | L  | -21| -40| -14 | 4.32| 206 |
| Fusiform       | 37 | R  | 18 | -43| -11 | 3.60| 88  |
| **White>Asian**|    |    |    |    |     |     |

*Note.* R refers to right and L refers to left. x, y, and z refer to MNI coordinates; t refers to the t-score at those coordinates (local maxima); SMA refers to supplementary motor area. Regions that share the same superscript are part of the same cluster. Contrasts with blank values indicate no significant clusters.
Supplemental Table 2. Neural regions which showed an interaction with age when viewing Black>White, Black>Asian, and Asian>White faces.

| Region        | BA  | x  | y  | z  | t   | k   |
|---------------|-----|----|----|----|-----|-----|
| **Black>White** |     |    |    |    |     |     |
| dmPFC         | 10/11 | R  | 18 | 56 | 19  | 4.79 | 2109^a |
| dmPFC         | 10/11 | L  | -16| 47 | 20  | 4.47 | a    |
| mPPC          | 23   | L  | -24| -43| 28  | 4.34 | 330  |
| Midbrain      |      | L  | -9 | -10| -5  | 3.66 | 63   |
| PCC           | 24/23| 0  | -16| 37 | 3.56| 43   |
| PCC           | 23   | R  | 30 | -34| 31  | 3.49 | 73   |
| **White>Black** |     |    |    |    |     |     |
| pSTS          | 40   | R  | 48 | -76| 19  | 4.48 | 203  |
| Cuneus        | 17   | L  | -15| -76| 16  | 3.56 | 46   |
| **Black>Asian** |     |    |    |    |     |     |
| dmPFC         | 9    | L  | -15| 50 | 22  | 3.04 | 526^b |
| dmPFC         | 9    | R  | 18 | 50 | 19  | 3.35 | b    |
| IFG           | 45   | L  | -51| 26 | 10  | 4.02 | b    |
| IFG           | 45   | R  | 48 | 29 | 16  | 3.19 | b    |
| Midbrain      |      | -9 | -7 | -2 | 5.10| 151  |
| **Asian>Black** |     |    |    |    |     |     |
| pSTS          | 40   | L  | -39| -76| 16  | 3.92 | 270  |
| Temporal Pole | 38   | L  | -39| 5  | -44 | 3.55 | 47   |
| **Asian>White** |     |    |    |    |     |     |
| PCC           | 23   | L  | -20| -42| 25  | 5.18 | 592  |
| PCC           | 26/30| R  | 12 | -43| 19  | 3.75 | 46   |
| mPFC          | 10   | L  | -14| 51 | 3   | 3.75 | 108  |
| **White>Asian** |     |    |    |    |     |     |

**Note.** R refers to right and L refers to left. x, y, and z refer to MNI coordinates; t refers to the t-score at those coordinates (local maxima); dmPFC refers to dorsomedial prefrontal cortex; mPPC refers to medial posterior parietal cortex; PCC refers to posterior cingulate cortex; pSTS refers to posterior superior temporal sulcus; IFG refers to inferior frontal gyrus; mPFC refers to medial
prefrontal cortex. Regions that share the same superscript are part of the same cluster. Contrasts with blank values indicate no significant clusters.