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Neural correlates of adolescents' viewing of parents' and peers' emotions: Associations with risk-taking behavior and risky peer affiliations

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Neural correlates of adolescents' viewing of parents' and peers' emotions: Associations with risk-taking behavior and risky peer affiliations

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Social reorientation from parents to same-age peers is normative in adolescence, but the neural correlates of youths' socioemotional processing of parents and peers have not been explored. In the current study, 22 adolescents (average age 16.98) underwent neuroimaging (functional magnetic resonance imaging) while viewing and rating emotions shown in brief video clips featuring themselves, their parents, or an unfamiliar peer. Viewing self vs. other and parents vs. the peer activated regions in the medial prefrontal cortex, replicating prior findings that this area responds to self-relevant stimuli, including familiar and not just similar others. Viewing the peer compared with parents elicited activation in posterior 'mentalizing' structures, the precuneus, posterior cingulate cortex (PCC), bilateral posterior superior temporal sulcus and right temporoparietal junction, as well as the ventral striatum and bilateral amygdala and hippocampus. Relative activations in the PCC and precuneus to the peer vs. the parent were related both to reported risk-taking behavior and to affiliations with more risk-taking peers. The results suggest neural correlates of the adolescent social reorientation toward peers and away from parents that may be associated with adolescents' real-life risk-taking behaviors and social relationships.

Keywords: Parents; Peers; Adolescence; MRI; Social reorientation; Risk-taking behavior.

Adolescents navigate multiple social contexts, including home, where they (typically) live with parents, and school and social situations, where they interact primarily with same-age peers. Unlike younger children, for whom the relationship with parents is paramount, adolescents devote more time and attention to peer networks and may attribute more importance to the appraisals of their peers (Steinberg & Morris, 2001). Indeed, the adolescent "social reorientation," specifically the shift from parent to peer influence that takes place during adolescence, may help facilitate the necessary process of establishing independence and individuating from parents (Nelson, Leibenluft, McClure, & Pine, 2005). However, relationships with parents continue to be meaningful in adolescence (Galambos,

Barker, & Almeida, 2003; Helsen, Vollebergh, & Meeus, 2000; Raja, McGee, & Stanton, 1992) even as youths' social attention moves beyond the family.

While adolescent social reorientation is normative, not all forms of peer affiliation benefit youth development. Many peers encourage healthy behaviors and offer risk-protective friendship; however, other peers may encourage engagement in antisocial and even dangerous behaviors like substance use, unprotected sex, and unsafe driving (Maxwell, 2002). The increasing reward salience of peers in adolescence may fuel adolescent risk-taking (Gardner & Steinberg, 2005; Steinberg, 2008), a possibility supported by evidence that adolescents make riskier decisions in the presence of peers than alone (Chein, Albert, O'Brien, Uckert, &

Steinberg, 2011). Indeed, even adolescent mice, but not adult mice, drink more alcohol in the presence of same-age cagemates (Logue, Chein, Gould, Holliday, & Steinberg, 2014), suggesting a cross-species, evolutionarily conserved tendency for adolescents to engage in more high-risk, potentially rewarding behavior in the presence of peers. At the same time, continued ties to parents appear to help limit risk in the context of positive parent–child relationship quality. For example, adolescents with stronger "family obligation" values (e.g., expectations that they would help with chores and spend time with family members) showed less neural activation to a risk-taking task, which was linked in turn to fewer real-life risk-taking behaviors (Telzer, Fuligni, Lieberman, & Galván, 2013).

The current study is the first, to our knowledge, to compare adolescents' neural responses to video clips of their own parents with clips of unfamiliar peers. Moreover, we explore whether adolescents' relative neural activation to parents vs. to their peers is associated with their real-life risk-taking behaviors and risky peer affiliations.

NEURAL BASES OF ADOLESCENT SOCIAL REORIENTATION

In a review of the neural bases of adolescent social reorientation, Nelson and colleagues (2005) describe a tripartite social brain, comprising regions engaged in detection, cognitive-regulatory functioning, and affective processing. Affective processing regions, which undergo particularly marked growth in adolescence, include the ventral striatum (VS) and amygdala, subcortical regions that appear to mature ahead of the prefrontal cortex (PFC) (Casey, Jones, & Hare, 2008), are innervated by gonadal steroid receptors, and are reorganized in adolescence by pubertal hormones (Scherf, Smyth, & Delgado, 2013). Nelson et al. (2005) speculate that, as the reward salience of peers increases in adolescence and parents' reward value decreases, adolescents may show stronger responses to peer-related stimuli in affective-processing regions in particular.

Affective-processing regions have been associated with adolescents' responding to peers. For example, the VS, which may reflect sensitivity to social reward, is more active when adolescents make risky decisions in the company of peers, e.g., during simulated driving (Chein et al., 2011). Adolescents also recruit VS when anticipating positive peer feedback (Gunther Moor, Van Leijenhorst, Rombouts, Crone, & Van Der Molen, 2010; Guyer, Choate, Pine, & Nelson,

2012), as well as other subcortical areas linked to reward and emotion (including the nucleus accumbens (NAcc; part of the VS), and amygdala; Davey, Allen, Harrison, Dwyer, & Yücel, 2010). In females, responses to peers increase from childhood to adolescence in the NAcc, hypothalamus, and hippocampus (Guyer, McClure-Tone, Shiffrin, Pine, & Nelson, 2009).

In addition to subcortical regions, the development of the adolescent social brain during adolescence also includes cortical structures involved in social emotion processing. These structures include the social or mentalizing network, which comprises cortical midline structures including the medial prefrontal cortex (mPFC), posterior cingulate cortex (PCC), and precuneus, as well as lateral regions including the temporoparietal junctions (TPJ) and posterior superior temporal sulcus (pSTS) (Frith & Frith, 2006; Van Overwalle & Baetens, 2009). These structures are thought to participate in "mentalizing," or making judgments and attributions about others' thoughts or emotions, and show gray matter development in adolescence, with the growth of several structures following a cubic trajectory with an apparent peak in early adolescence (Mills, Lalonde, Clasen, Giedd, & Blakemore, 2014). An anterior-to-posterior shift in the "social brain" appears to take place during adolescence, with activation in the frontal midline decreasing with age and in posterior mentalizing network regions increasing with age (Harenski, Harenski, Shane, & Kiehl, 2012; Pfeifer & Blakemore, 2012).

In addition to their role in mentalizing about others' thoughts or emotions, cortical midline structures have also been associated with processing of self-relevant stimuli (Kelley et al., 2002; Northoff et al., 2006). In the adult literature, the ventral portion of the mPFC has been consistently associated with self-relevant processing (Amodio & Frith, 2006; Denny, Kober, Wager, & Ochsner, 2012), while posteromedial structures (e.g., the PCC and precuneus) may be more involved in processing social information not necessarily specific to the self (Araujo, Kaplan, & Damasio, 2013). Some studies have found greater functional activation of mPFC in adolescents relative to adults, perhaps because of greater inefficiency during a time of cortical growth (Blakemore, 2008). Alternatively, the relative overactivation of the mPFC in adolescence may be linked to a self-focus that shifts toward more other-directed thoughts as perspective-taking abilities develop across adolescence (Crone & Dahl, 2012; Pfeifer, Lieberman, & Dapretto, 2007).

The mPFC appears to be recruited both for self-relevant processing and for social cognition, or

mentalizing. Within the adult literature, similarity to the self has been found to modulate the degree to which mPFC regions are activated when thinking about others. For example, unfamiliar targets with political beliefs more similar to the self appear to elicit more mPFC activation than those with dissimilar beliefs (Mitchell, Banaji, & Macrae, 2005). One possible explanation is that cortical midline structures evolved to guide future behavior by detecting personally salient information and, as a corollary, respond to input that is relevant for, or closely related to, the self (Damasio, 2010; Immordino-Yang, 2011). If this is true, then familiarity might matter even more than self-similarity in activating the mPFC. Indeed, this was found by Krienen, Tu, and Buckner (2010), who asked participants to make judgments about the traits of dissimilar friends vs. similar but unknown others. Regions in the mPFC were more responsive to the friends than to the strangers, even when the friends were dissimilar and the stranger biographies were constructed to be similar to the participant on a variety of demographic, personality, and lifestyle dimensions.

The current study explored the neural correlates of youths' responses to brief video clips featuring either their parents, the youths themselves, or an unfamiliar but similarly-aged, same-gender peer. We attempted to improve ecological validity by using video clips rather than static pictures or trait words and showing participants' clips from their own families. Only one study, to our knowledge, has explored youths' responses to images of their own parents (Whittle et al., 2012) and found activation in affective-processing and mentalizing regions (including the precuneus, anterior and posterior cingulate, and PFC) to video clips of participants' own mothers (vs. other mothers).

The current study also explores whether adolescents' differential neural activation in response to parents and peers is associated with their real-life social affiliations. If adolescent social reorientation is a normative process by which adolescents withdraw social attention from the family and redirect it toward same-age peers, a more extreme version of this reorientation might be marked by a weakening of parents' risk-protective influence and an embrace of peers who reject parental authority. Therefore, we tested whether the difference in magnitude of activation to peers vs. to parents in affective and mentalizing systems was associated with participants' reports of adolescent risk-taking behaviors and their affiliations with risk-taking peers.

Hypothesis 1. We hypothesize that, relative to others (parents, peer), self-stimuli will elicit more activation in cortical midline structures linked to self-relevant processing.

Hypothesis 2. Given that parents are familiar and closely related to the self, we hypothesize that adolescents will show more activation to parents than to an unfamiliar peer in self-relevant regions, specifically regions within the mPFC demonstrated to be more responsive to familiar than to similar others (Krienen et al., 2010).

Hypothesis 3. In keeping with studies of adolescents' viewing peers, we hypothesized that peer stimuli will be linked to greater activation in subcortical areas associated with motivation, reward, and affect, such as the ventral striatum and amygdala, as well as with mentalizing network regions in the PCC, precuneus, pSTS, and TPJs.

Hypothesis 4. Consistent with research suggesting that neural activation in response to peer stimuli may be linked with riskier behavior, we hypothesized that individual differences in adolescents' activation in response to viewing peers vs. parents will be associated with their reported risk-taking behaviors and also their level of social affiliation with risk-taking peers.

METHODS

Participants

Participants were drawn from the second cohort ($n = 69$) of a longitudinal study of family environments and youth development that was conducted in a large US (West Coast) city. Families were recruited from the community via advertising and word of mouth. Eligibility criteria included that the family included a child in middle school (grades 6–8), that the parents had lived together for the past 3 years, and that all three family members could complete measures in English. The study was approved by the Institutional Review Board of the university where it was conducted, and participants were paid.

Forty-three families from this cohort of the longitudinal study took part in a videotaped discussion including both parents and the youth in the second wave of data collection. Our MRI sample was recruited from within these 43 families, with eligibility criteria included that youth be right-handed, not have metal in their body or conditions that would preclude scanning, or not be taking psychoactive medications. Of the 43 families we contacted, seven youth were ineligible, five declined to participate, and seven could not be reached or had scheduling difficulties.

Ultimately, 24 youth participated in the scanning study. Two youth did not have useable data: one because of left-handedness and one because we did not have video clips of his father. A third youth had a brain abnormality (hypointensity in the right occipital lobe) flagged by a radiologist. For that reason, we ran all analyses with and without this individual and included him in the final sample because his inclusion did not change or distort any of the results reported here. The final sample of 22 adolescents (11 males) averaged 16.98 years of age (range 15.47–18.67, $SD = .81$). The sample was diverse, reflective of the urban community from which the sample was drawn: 32% (seven youth) identified as Latino, 32% (seven youth) as Caucasian, 14% (three youth) as African-American, 14% (three youth) as multiracial, and 9% (two youth) as Asian-American.

Creation of functional magnetic resonance imaging (fMRI) stimuli

Video stimuli for the scanning study were drawn from the aforementioned family discussion, which was conducted when the participating youth were average age of 15.12 (range 13.35–16.41, $SD = .88$). The average lag time between the video and scan was 1 year, 10 months (median 1 year, 7 months; range 1.11–4.77; all but two participants did the scan within 2 years of the video). Family triads—mother, father, and youth—were seated together in a room and videotaped for 15 minutes using a split-screen system so that each family member could be viewed individually on a separate screen for coding purposes. In creating stimuli for the MRI study, the software program Adobe Premiere Pro CS 5 (Adobe Systems, San Jose, CA, USA) was used to remove sound and to extract 5-second clips for each family member. We removed sound so that the scanning protocol would focus on nonverbal emotion rather than on the specific verbal content of the discussion. Any clips in which another person was visible (e.g., a parent's hand gesturing in front of the youth) were discarded, so that clips included only the target person. Thirty clips were created for each family member (with only one person visible in each clip) and then rated by the first author on valence (positive and negative affect) and expression (talking or listening). These ratings were used to cull the final clips down to 15 per family member so that each final batch of clips displayed a range of emotions and expression for each target. After clips were selected, at least one undergraduate research assistant (RA), trained in observational coding of emotion, rated each family's clips. Peer clips were rated by three RAs and their ratings were averaged.

An additional set of peer stimuli were created by videotaping two youth, a male and a female, in the same laboratory setting as the family discussion task using the same split-screen camera system, and creating an additional set of 5-s clips, also with sound removed and also with only the target person (either the male peer or the female peer) visible within each clip. As with the family stimuli, the peer clips were rated and then selected to balance positive and negative valence and talking and listening. Before scanning, we established that these youth were unfamiliar to the participant. The "peers" were similarly-aged to the participant, and, because our sample was ethnically and racially diverse, we chose two multiracial youth whose ethnic identity would not appear immediately obvious to participants.

fMRI protocol

Before the scanning protocol began, participants were oriented to the tasks in the laboratory. They were shown a minute-long clip of the triadic family discussion to acclimate them to the potential surprise of seeing themselves or their family members in different clothes and hairstyles. They were told, "You may remember parts of this discussion, but this is not a memory test. Instead, as you watch each person's video, put yourself in their shoes and imagine how they are feeling in that moment." Youth then did a practice version of the task in which they viewed mother, father, youth and peer clips and made ratings using the keypad on the laboratory computer.

In the scanner, adolescents participated in three 5-minute runs of the video task, which used an event-related design. Each run was comprised of five 12-second trials of each of the four conditions —self, mother, father, and peer—along with a 12-second rest condition. Condition order was optimized using a genetic algorithm (Wager & Nichols, 2003) that, because it quantifies the efficiency of multiple designs to distinguish among the modeled conditions, eliminates the need to "jitter" the intertribal interval to create differential overlap among the hemodynamic responses to each condition. The 12-second trials contained a 2-second cue screen in which the word "You," "Mother," "Father," or "Her/Him" (depending on whether the gender-matched peer was male or female) was presented, followed by the 5-second clip, followed by a 4-second rating screen in which participants were asked to rate the valence of the person's emotional expression on a 4-point scale (from Very Negative to Very Positive) using the button box, followed by

a 1-second fixation cross. In analyses, we modeled the whole 12-second trial including the video and emotion rating response.

Whole-brain images were acquired using a Siemens 3 Tesla MAGNETON TIM Trio scanner with a 12-channel matrix head coil. Functional scans were acquired using a T2*-weighted echo planar (EPI) sequence (TR = 2 second, TE = 30 ms, flip angle = 90°) with a voxel resolution of 3 mm × 3 mm × 4.5 mm. Thirty-two continuous transverse slices were continuously acquired to cover the whole brain and brain stem, with breaks between runs. Anatomical images were acquired using a magnetization prepared rapid acquisition gradient (MPRAGE) sequence (TI = 900 ms, TR = 1950 ms, TE = 2.26 ms, flip angle = 7°) with an isotropic voxel resolution of 1 mm.

Data were preprocessed in FSL (fMRI software library). We performed standard preprocessing—slice timing correction, motion correction, brain extraction, spatial smoothing (using a 5 mm kernel), high-pass filtering, and correction for auto-correlation ("pre-whitening")—prior to contrast modeling. Registration to high-resolution structural and to standard space images was carried out using fMRIB's linear image registration tool. Each of the four conditions was modeled with a separate regressor derived from a convolution of a task boxcar function and a gamma hemodynamic response function. Six motion-correction parameters were also included in the model, as was the temporal derivative of each task regressor. After combining the three runs for each subject in a fixed-effect analysis, data were combined across subjects using FLAME mixed-effect analysis with FSL's FEAT (fMRI Expert Analysis Tool), cluster-corrected threshold ($z = 2.3$, $p < .05$). The cluster thresholding technique used by FSL employs Gaussian random field theory to estimate the probability of clusters of a given size, given the smoothness of our data. The $p < .05$ cluster threshold indicates that we accept clusters only which are large enough such that similarly sized clusters occur less than 5% of the time by chance in data with comparable smoothness, after thresholding the images at $Z = 2.3$.

Youths' neural responses to mother clips and father clips did not differ in any of the hypothesized brain regions of interest, so mother and father clips were combined into a single condition ("parents") when analyzing contrasts. Associations between these contrasts and behavioral covariates were tested with a higher-level analysis in which the demeaned behavioral scores were included as cross-subject regressors.

Region of interest (ROI) analysis

In additional to whole-brain analyses, we performed an ROI analysis focusing on two regions known to be important for self-relevant processing and specifically for responding more strongly to familiar vs. similar others. These ROIs, used in the parents vs. peer contrast, were based on the two mPFC ROIs found by Krienen et al. (2010) to be more responsive to familiar than to similar others: one centered around MNI coordinates $x = -4$, $y = 34$, $z = 0$ (labeled a rostral anterior cingulate (rACC) ROI by Krienen and colleagues) and an anterior mPFC (amPFC) ROI centered around MNI coordinates $x = -4$, $y = 56$, $z = 10$. We created each of these ROIs by drawing a sphere of 8 mm around the aforementioned peak coordinates. For these analyses, the same cluster threshold ($p < .05$) was applied, but restricted to voxels within the ROI mask.

Youth risk behavior survey (YRBS)

At another laboratory visit (the third data collection wave of the larger longitudinal study), which took place an average of 3 weeks before the scan (median 7 days before the scan; range 1 year, 4 months before to 1 year, 6 months after the scan; all but three participants did this visit within 10 months of the scan), participants came into the laboratory to fill out additional questionnaires including the YRBS. This widely used measure of adolescent risk-taking behaviors, developed by the Center for Disease Control (CDC, 2009), asks how many times in the previous year the adolescent has engaged in delinquent behaviors (e.g., cheating on tests; breaking or destroying property; shoplifting), substance use (e.g., using alcohol, tobacco, marijuana, or other drugs), and risky sexual behavior (e.g., number of sexual partners; using alcohol or drugs before sex; having sex without a condom). Behaviors within these three domains were summed to create a total score for each adolescent, and these scores were then converted into z scores (mean = 0, $SD = 1$, range = −1.61–1.76).

Peer Behavior Inventory (PBI)

At the same laboratory visit at which participants filled out the YRBS, they also completed the PBI, a 33-item measure developed by Prinstein, Boergers, and Spirito (2001), which assesses the characteristics of adolescents' friends and peers. Participants were asked how many of their friends ("none," "one," "a few," "more than half," and "all") have engaged in each of 19 risky behaviors (e.g., smoking cigarettes,

damaging property, having unprotected sex, skipping school, or cheating on tests) or 12 prosocial behaviors (e.g., helping with chores around the house, volunteering, or getting good grades in school). Cronbach's alpha in this sample was .87. We calculated a risky peer score by averaging the negative and deviant items and then converted these scores into z scores (mean = 0, SD = 1, range =—1.10–2.90).

RESULTS

Behavioral data

Reaction time data indicated that adolescents were slower to rate self-clips than mother clips ($t(21) = 4.79$, $p = .001$), father clips ($t(21) = 2.28$, $p = .03$), and peer-clips ($t(21) = 3.10$, $p = .01$), but reaction time did not significantly differentiate peer and parent clips (peer vs. mother, $t(21) = 1.17$, $p = .26$; peer vs. father, $t(21) = 0.73$, $p = .48$). Emotional valence ratings (made using the button box in the scanner) did not differ between youth, parent, and peer clips (t values ranging from −1.87 to .66; p values ranging from .08 to .78). RA ratings of each family's video clips were positively correlated with participant ratings (mean correlation between participant and RA ratings across the 45 clips shown to each of the 22 participants = .53, $p = .001$; range .21–.72, SD = .14). Additionally, the intraclass coefficient (ICC) for RA and participant ratings was .70, suggesting acceptable reliability of these ratings. Reliability was highest for peer clips (ICC = .75), lowest for self-clips (ICC = .66), and moderate for parent clips (ICC = .70). As with participant ratings, RA ratings did not significantly differentiate youth, parent, and peer clips (t values ranging from –.14 to 1.57; p values ranging from .13 to .89).

Self > others contrast

Since the self vs. parents and self vs. peer contrasts produced similar results, we show both contrasts in one figure (Figure 1) in order to depict whole-brain self vs. other activation. As hypothesized, viewing self-stimuli, relative to other-stimuli, was associated with increased signal in areas associated with self-relevant processing, and also with interoceptive awareness, including the ventral and dorsal regions of the mPFC, anterior cingulate, bilateral insula, bilateral frontal poles, orbital frontal cortex, and right IFG. The self > parents contrast also elicited activation specific to the self in the posterior cingulate/precuneus.

Parents > peer contrast

No significant results emerged from whole-brain analysis of the parents vs. peer contrast. However, as shown in Figure 2, in the separate ROI analyses, both of the a priori ROIs tested in the mPFC showed greater signal in response to parents than in response to peers (peak area of activation for the amPFC ROI: $x = −10$, $y = 52$, $z = 12$, $Z = 3.57$; peak area of activation for the rACC ROI: $x = −2$, $y = 40$, $z = 2$, $Z = 2.97$). No other areas of activation exceeded threshold. As shown in the bar plots of Figure 2 illustrating signal change in these ROIs for peer stimuli vs. resting baseline and parent stimuli vs. resting baseline, participants tended to activate the mPFC ROI to the video stimuli relative to the rest condition (and showed more relative activation to the parent stimuli) and deactivate the rACC ROI relative to rest (but showed less relative deactivation to parents).
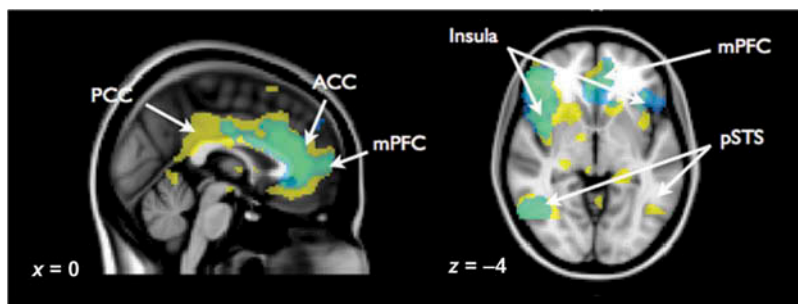

Figure 1. Self > parents (shown in yellow) and self > peer (shown in blue), thresholded at $z = 2.3$, $p < .05$, with activation in cortical midline structures including medial prefrontal cortex (mPFC), anterior cingulate cortex (ACC), and posterior cingulate cortex (PCC), as well as insula and posterior superior temporal sulcus (pSTS).
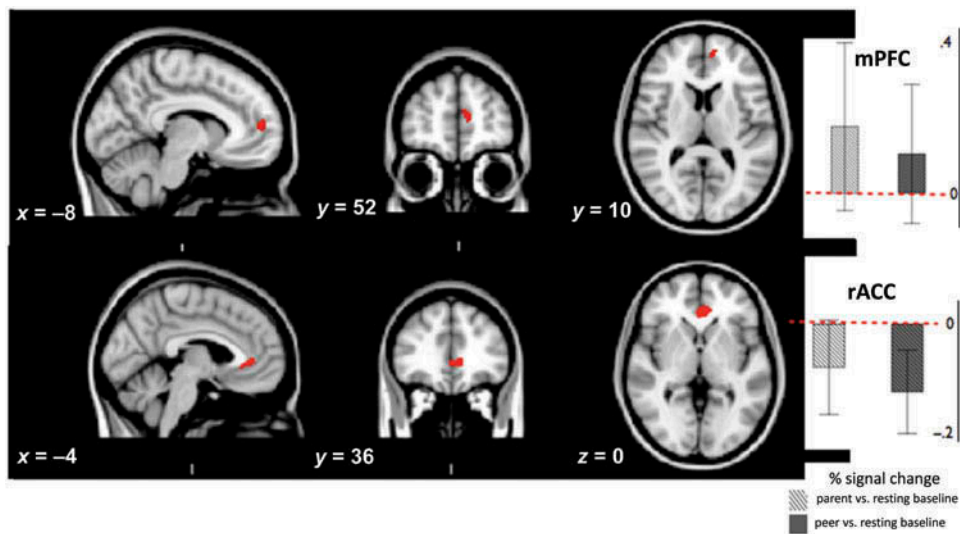
Figure 2. Signal changes for parent > peer contrast in anterior medial prefrontal cortex (amPFC) and rostral anterior cingulate (rACC), within ROIs defined by Krienen et al. (2010) as being more responsive to familiar than to similar others.

Peer > parents contrast

As shown in Figure 3 and in Table 1, whole-brain cluster-corrected analyses revealed clusters that activated more strongly to the peer than parent stimuli in the VS, bilateral amygdala bordering into the hippocampus, PCC, precuneus, bilateral pSTS, and right TPJ, as well as premotor and somatosensory regions. As illustrated by the bar plots in Figure 3, these results included both regions that were more active relative to resting baseline (these regions included the VS and

bilateral amygdala and hippocampus) and those that showed deactivation relative to baseline (including the precuneus and PCC).

Associations with risk-taking behavior and risky peer affiliations

We tested the YRBS risk-taking behavior measure as a regressor in the peer vs. parents contrast, with whole-brain results shown in Figure 4. Higher scores
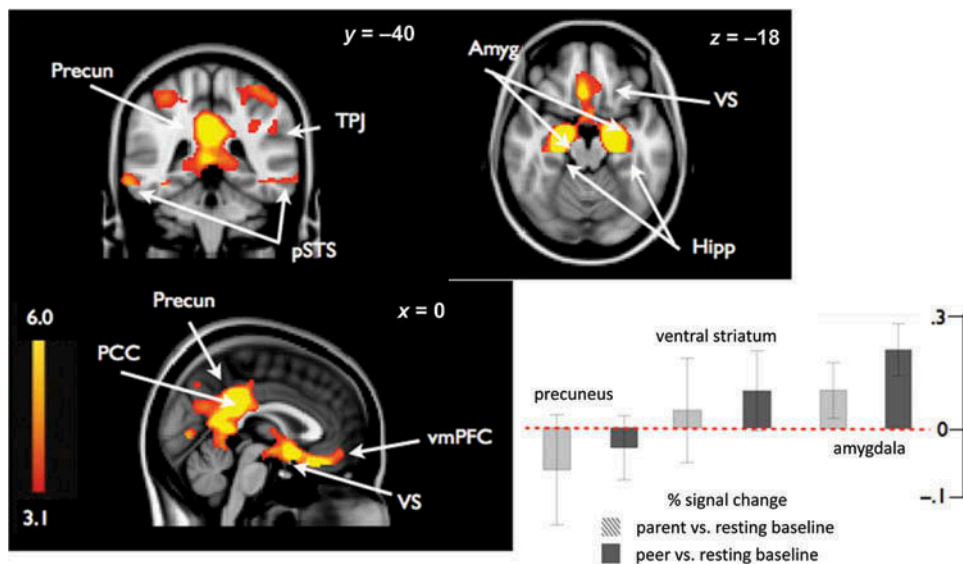

Figure 3. Signal changes for peer > parent contrast in areas including the posterior cingulate cortex (PCC), ventral striatum (VS), and bilateral amygdala-hippocampus formation.

TABLE 1
Clusters showing increased signal in peer condition relative to parent condition

| Cluster	Side	Z	Size	x	y	z
Hippocampus/amygdala	R	10.6	7418	20	−10	−18
Hippocampus/amygdala	L	10.6	394	−18	−10	−18
Ventral striatum		5.44	252	4	4	−6
Posterior cingulate		7.68	1315	2	−36	32
Precuneus		3.64	51	2	−70	42
Temporoparietal junction	R	7.37	1757	36	−66	50
Posterior superior temporal sulcus (pSTS)	R	4.09	91	66	−40	−14
pSTS	L	4.76	79	−52	−46	−10
Lateral occipital cortex	L	6.49	3175	−38	−76	42
Lateral occipital cortex	L	4.12	119	−40	−74	8
Occipital fusiform gyrus	L	3.65	8	−24	−70	−2
Primary somatosensory cortex	L	4.59	792	−46	−14	54
Primary somatosensory cortex	R	3.76	64	36	−42	56
Secondary somatosensory cortex		3.15	1	−54	−12	16
Lingual gyrus		4.51	64	2	−76	2
Premotor cortex	R	4.37	714	34	−6	64
Premotor cortex	L	3.65	66	−8	−18	62
Premotor cortex	R	3.24	5	10	−12	64
Precentral gyrus	R	4.09	67	52	6	46
Precentral gyrus	L	3.97	47	−44	−2	30
Superior frontal gyrus	R	3.57	86	24	34	48
Superior frontal gyrus	R	3.83	26	24	18	62
Superior frontal gyrus	L	3.75	102	−22	16	60
Insula	L	3.41	14	−38	−8	10
Central opercular cortex	R	3.47	13	52	−8	16
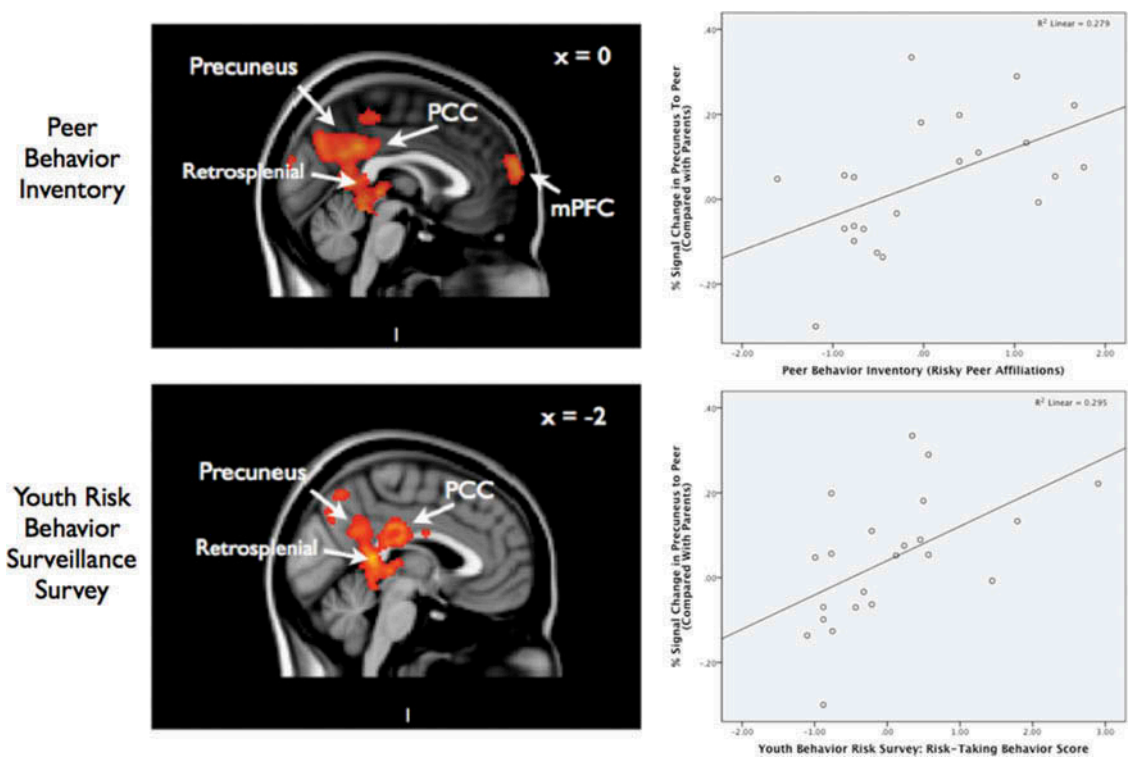
Figure 4. Neural correlates of affiliations with risk-taking peers (Peer Behavior Inventory measure) and youth risk-taking behavior (Youth Behavior Surveillance Survey) and, as shown in the brain (response to peer vs. parent contrast, cluster corrected and thresholded at 2.3, $p = .05$) and accompanying scatterplot of signal change coefficients in the precuneus.

on this measure, indicating greater risk-taking behavior, were associated with more activation in the posteromedial cortices (PCC and precuneus) when viewing and rating peers' emotions relative to parents' emotions. Next, we tested the same contrast with the PBI measure of risky peer affiliations and found a similar pattern of whole-brain results, along with a small region of activation in the mPFC. These results are also depicted in Figure 4. As a follow-up, we used FSL's FeatQuery tool to extract the percentage signal change of the hemodynamic response of the peer > parents contrast in the precuneus and PCC, anatomically defined using Harvard-Oxford Structural Atlas coordinates in FeatQuery (Harvard Center for Morphometric Analysis). YRBS scores were positively correlated with signal change in the PCC ($r(21) = .59$, $p = .004$; Cohen's $d = 1.42$) and precuneus ($r(21) = .54$, $p = .01$; Cohen's $d = 1.26$; scatterplot shown in Figure 4), and PBI scores were also positively correlated with signal change in the PCC ($r(21) = .54$, $p = .01$; Cohen's $d = 1.24$) and precuneus ($r(21) = .53$, $p = .01$; Cohen's $d = 1.21$; scatterplot shown in Figure 4). Because the PBI measure was also associated with activation in the mPFC, we also tested signal change to peer > parents in the same ROIs we used previously in the parents > peer analyses and found PBI scores to be positively correlated with signal change in the amPFC ROI ($r(21) = .43$, $p = .05$; Cohen's $d = .93$), but not with signal change in the rACC ROI ($r(21) = .33$, $p = .13$). The direction of all results was consistent: participants who reported risk-taking behaviors and more affiliations with risky peers showed greater activation when viewing and rating the emotions of peers relative to parents. YRBS and PBI scores were not correlated with signal change coefficients in the precuneus, PCC, rACC, or amPFC ROIs for parent vs. resting baseline or for peer vs. resting baseline (p values ranging from .13 to .84), suggesting that the association between the risk measures and the brain was driven by the relative difference between activation to peer vs. parent stimuli rather than by the absolute magnitude of activation to either peer or parent stimuli.

Potential confounds and moderation by lag time, gender, and age

Since the lag time between when the scan took place and when the video stimuli were created varied, as did the lag time between the scan and the risk-taking measures, we tested correlations between both lag time variables and signal change coefficients (extracted using FeatQuery) for any of the regions

that emerged in the above whole-brain analyses: the amMPFC, rACC, PCC, and precuneus ROIs used for the above analyses, as well as ROIs in the insula, left and right amygdala, left and right hippocampus, and NAcc (all anatomically defined using Harvard-Oxford Structural Atlas coordinates preloaded into FeatQuery). No significant correlations emerged (coefficients ranging from –.31 to .31; p values ranging from .16 to .89).

Next, we ran correlations between signal change coefficients and participant age at the time of MRI scanning and again found no significant correlations (range –.25 to .25; p values ranging from .26 to .79). Splitting the sample by gender and rerunning these correlations also did not yield significant results. We also tested both gender and age separately as regressors or within a two-group difference model for gender with age as a covariate, and again did not find evidence for a moderating effect of gender or age.

Since adolescents' perceptions of the emotion shown in the parent and peer stimuli might be another potential confound, we ran a series of multiple regression analyses in which signal change coefficients in the precuneus and PCC to peer vs. parent stimuli were the outcome variables and YRBS and PBI scores were predictor variables. We then tested participants' in-scanner parent and peer emotion ratings as covariates. The two possible outcomes (precuneus signal change and PCC signal change) and two possible predictors (YRBS scores and PBI scores) were tested in separate models, so that four models were tested with parent emotion ratings included as a covariate, and four models were tested with peer emotion ratings included as a covariate. Results were consistent across these eight regression models: YRBS and PBI scores remained significantly associated with neural signal change, and participants' emotion ratings were not significantly associated with neural signal change coefficients (t values ranging from −1.32 to .50, p values ranging from .20 to .96).

DISCUSSION

In an emotion perception task, we found that adolescents showed more mPFC activation to themselves than to either peers or parents, and more to their own parents than to unfamiliar adolescent peers. However, in other neural regions linked to social processing, including both affective processing structures (the VS and bilateral amygdala bordering into the hippocampus) and posterior "mentalizing" areas (the PCC, precuneus, bilateral pSTS, and TPJ), we found greater BOLD signal change in response to

peers than to parents. Interestingly, the extent to which mentalizing network regions in the posteromedial cortices activated more to peers than to parents was associated with participants' reports of their risk-taking behaviors and their affiliations with risk-taking peers. These findings replicate previous reports that the self and familiar others activate the mPFC more than unfamiliar others (Kreinen et al. 2010) and extend this effect to adolescence. Moreover, the findings suggest that individual differences in neural correlates of the affective, cognitive, and reward salience of unfamiliar peers, relative to one's own parents, might be associated with adolescents' motivation to engage in risky behavior and to seek out more deviant peers. No significant gender or age effects emerged, and the results did not appear to be driven by differences in reaction time, by time elapsed between scanning and other measures, or by adolescents' ratings of the valence of the stimuli.

Taken together, these results are consistent with the extant literature and also suggest new directions for the study of social processing in adolescence. To our knowledge, no other published studies have compared adolescents' responses to parents' and peers' emotions. Our findings suggest that adolescents process these two important social targets differently. Even though adolescents activated self-relevant medial frontal regions more for parents than for peers, they showed more activation while rating peers' emotions than while rating parents' emotions in a broad array of neural regions comprising both subcortical regions implicated in emotion and posterior cortical regions implicated in mentalizing. Specifically, we found greater activation to peer than to parent emotional stimuli in two posteromedial regions that have been associated with thinking about others' thoughts and feelings, the PCC and the precuneus, as well as the right TPJ and the bilateral pSTS. Participants also activated to peers vs. parents in the VS, a region that has been associated with social reward processing in adolescents (e.g., Gunther Moor et al., 2010), and in the amygdala, a structure critically involved in emotion and salience detection that is known to be affected by pubertal hormones and that is thought to play a role in adolescent social reorientation to peers (Scherf et al., 2013). These findings support Nelson et al. (2005)'s prediction that affective-processing structures would be more responsive to peer social stimuli and less responsive to parent stimuli in adolescents. Our preliminary evidence that adolescents show more activation to peers than to parents in mentalizing and subcortical emotion-processing regions is consistent with adolescents' social reorientation toward social networks outside the family and intimate friendships and romantic relationships.

We also found an association with adolescents' self-reported risk-taking behaviors and affiliations with risk-taking peers and their neural activation to peers vs. parents in the precuneus, posterior cingulate, and (for the peer affiliation measure) the mPFC. These findings suggesting that adolescents who devote more processing resources in mentalizing network regions toward an unfamiliar peer, and fewer to parents, may show an exaggerated form of the "social reorientation" from peers to parents described by Nelson et al. (2005) and others. Because close relationships with parents can be risk-protective in adolescence (Rankin & Kern, 1994), adolescents who are less motivated to attend to their parents' emotions than to the emotions of a same-aged stranger may be less attached to their parents, and therefore more likely to seek out risky peers. This accords well with Telzer et al.'s (2013) results that adolescents with stronger family obligation values showed less VS activation to monetary rewards, which was in turn correlated with real-life risk-taking behavior. In another study by the same group, VS activation when choosing to give money to family (rather than to keep it for oneself) was associated with a psychosocial outcome (decreased depressive symptoms over the following year; Telzer, Fuligni, Lieberman, & Galvan, 2014), suggesting that the social cognitive and affective salience of different types of social targets may have relevance for actual social functioning. In our study, differential activation to peer vs. parent stimuli in posterior mentalizing regions was associated with risk-taking, suggesting that engaging in more effortful social cognition toward peers, and less toward parents, may correlate with social motivation toward peer influences outside the scanner.

Developmental studies have found an age-related shift from frontal to posterior midline structures when engaging in social information processing, with older adolescents and adults less likely to engage the mPFC and more likely to engage the posteromedial cortices when thinking about others (Blakemore & Mills, 2014; Pfeifer et al., 2007). Within this sample, we did not find age to be correlated with signal change in these regions, but it is nonetheless interesting that "riskier" adolescents, who may be showing more pronounced reorientation from parents to peers, showed more posterior activation to peers. When analyzed separately, peer vs. rest and parent vs. rest contrasts were not significantly associated with the risk measures, suggesting that our results are not due only to orientation toward the peer or away from the parent but by the relative difference between the two types of stimuli.

This study was limited by not having an unfamiliar adult or a familiar peer condition, so that our peer

condition is conflated with the novelty of the social stimuli. Although a familiar peer condition (e.g., clips of a friend or acquaintance) might have enhanced the interpretability of the results, it also would have introduced new complexities and potential confounds, given natural variability around friendship quality and duration. Given that the relationship with parents has variability as well, we choose to standardize the peer stimuli in order to facilitate the interpretation of the peer vs. parents comparison. Also, we reasoned that the novel peer condition might have ecological validity, in that adolescent social worlds are rapidly expanding and adolescents often encounter unfamiliar peers at school and in social settings. At the same time, friendship and familiarity are particularly important for adolescents, and adolescents may act differently (e.g., they may be more or less prone to engage in risk-taking behavior) with friends rather than with strangers, so this is an important limitation. Indeed, the neural literature has found different brain responses to friends vs. strangers (Campanha, Minati, Fregni, & Boggio, 2011; Wu, Leliveld, & Zhou, 2011). In adults, greater amygdala reactions have been found to novel than to familiar faces in a number of studies (e.g., Schwartz et al., 2003), but conflicting findings have also been reported; for example, mothers show greater amygdala response to their own infants than to unfamiliar infants (Leibenluft, Gobbini, Harrison, & Haxby, 2004) and, among typically developing children, the amygdala responds more strongly to one's own mother than to a stranger (Olavsky et al., 2013; Tottenham, Shapiro, Telzer, & Humphreys, 2012). The posteromedial cortices have been found to activate more strongly to familiar than to famous or unfamiliar faces (e.g., Sugiura et al., 2006), and the only other study, to our knowledge, to use own-parent stimuli found greater activation in the precuneus and PCC to one's own mother rather than to an unfamiliar mother (Whittle et al., 2012). Therefore, though the lack of a friend condition limits our ability to draw conclusions about the distinction between parents and others, and though our findings may have been affected by the familiarity vs. unfamiliarity of our parent and peer stimuli, several of our results (e.g., weaker amygdala response to parent than to the peer; greater posterior mentalizing network activation to the peer) legitimately challenge previous findings.

Future studies with children and adults should also examine the extent to which our findings are specific to adolescents. We hypothesize that parent and peer stimuli have unique significance for adolescents that would not generalize to other age cohorts; however, our current study design does not allow us to directly test this. Children typically spend less time interacting with peers than with parents and are less focused on peer relationships than are adolescents (Steinberg & Morris, 2001), whereas most US adults live independently from their families of origin. Since only adolescents are fully immersed in both social contexts that were examined in this study, a comparison of reactions to peers vs. parents would likely have other factors at play within other age cohorts. However, a study utilizing a larger age range of adolescents would be a useful future test of age effects.

Other limitations of the article include our small sample of only 22 adolescents, which was constrained by recruiting from a longitudinal study with only 43 eligible families, of whom only 24 youth were both MRI-eligible and available for the scanning visit. Another potential confound is introduced by the fact that adolescents participated in the initial discussions with their parents. We edited the video to be as abstracted as possible and to match the peer stimuli (e.g., brief, silent clips with only the target person visible), and we also explicitly instructed adolescents not to focus on their memories of the original discussion but on the in-the-moment emotions displayed within each clip. However, it is possible that adolescents' experience of the initial family discussion biased their responses to own-parent clips. Another limitation is that, because the MRI substudy was inserted into a larger, ongoing longitudinal study with participants coming into the laboratory at different times, the time lag between the creation of the video stimuli, the scan, and the risk-taking questionnaire measures was not standard and in some cases was spaced over several months or more. We tested this time lag as a possible confounding variable and did not find a relationship between either the video-to-MRI or MRI-to-questionnaire time lags and our signal change coefficients, but the lack of standardization is a weakness. At the same time, these limitations are balanced by the leveraging of the data collection efforts of a larger study, and our use of video clips from the participants' own families brings an unusual level of ecological validity to this study. Most fMRI studies of social processing have relied on more standardized stimuli such as trait words and still photographs of strangers, but our use of more dynamic and more personalized stimuli may be more effective at eliciting naturalistic social responses. Using naturalistic data introduces variability in our stimuli, but examining fMRI data in conjunction with real-life, personally meaningful stimuli may represent an important future direction for social neuroscience research (Telzer, Qu, et al., 2014). Our sample of adolescents was ethnically and socioeconomically

diverse, also enhancing the study's external validity. Although it is a limitation that we relied on self-report measures to assess risk behavior rather than on more objective or observational measures, our use of two separate and well-validated questionnaire measures of risk-taking behavior and risky peer affiliations adds convergent validity.

In conclusion, this study compared adolescents' responses to different social targets, parents, peers, and the self, when rating their emotions from video clips. To our knowledge, this is the first study to directly compare adolescents' neural processing of their parents' and peers' emotions, and the results suggest differences in how the brain responds to these stimuli. Moreover, participants' reports of their real-life risk-taking behavior and risky peer group affiliations were associated with individual differences in their neural responding to peer and parent stimuli. This study contributes to knowledge about the neural underpinnings of adolescent social reorientation, a process with critical importance to adolescents' psychosocial functioning and successful transition into adulthood.

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