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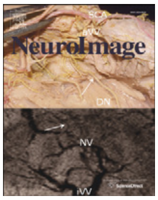

The stimuli drive the response: An fMRI study of youth processing adult or child emotional face stimuli

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ABSTRACT

Effective navigation of the social world relies on the correct interpretation of facial emotions. This may be particularly important in formative years. Critically, literature examining the emergence of face processing in youth (children and adolescents) has focused on the neural and behavioral correlates of processing adult faces, which are relationally different from youth participants, and whose facial expressions may convey different meaning than faces of their peers. During a functional magnetic resonance imaging (fMRI) scan, we compared concurrent neural and behavioral responses as youth ($N = 25$) viewed validated, emotionally varied (i.e., anger, fear, happy, and neutral) adult and child face stimuli. We observed that participants made fewer errors when matching adult, compared to child, face stimuli, and that while similar brain regions were involved in processing both adult and child faces, activation in the face processing neural network was greater for adult than child faces. This was true across emotions, and also when comparing neutral adult versus neutral child faces. Additionally, a valence by stimuli-type effect was observed within the amygdala. That is, within adult face stimuli, negative and neutral face stimuli elicited the largest effects, whereas within child face stimuli, happy face stimuli elicited the largest amygdala effects. Thus, heightened engagement of the amygdala was observed for happy child and angry adult faces, which may reflect age-specific salience of select emotions in early life. This study provides evidence that the relational age of the perceived face influences neural processing in youth.

Introduction

Affective facial displays are central to the human experience. Seminal work by Paul Ekman showed that these displays are universally expressed, unbidden responses to internal feelings of emotion (Ekman, 1993), which largely extended Charles Darwin's early consideration of emotions and their expressions as physiological responses to environmental stimuli (Darwin and Ritter, 1916). Facial displays of others communicate key information, and set the emotional tone of interpersonal interactions. The predilection of infants to readily habituate to facial displays (Simion et al., 2007) suggests that in humans the ability to extract emotion from faces is present early, and perhaps foundational to later social and emotional development. The ability to process facial displays of emotion develops across the first two decades of life, commensurate with brain maturation and with the accumulation of experience (Hoehl and Peykarjou, 2012; Leppanen and Nelson, 2009). Overall, successful transition into adulthood is thought to involve growing capability to understand emotion and to regulate one's response to emotionally evocative stimuli. Because late childhood and adolescence are marked by the emergence of psychiatric illness (Dahl and Gunnar, 2009; Paus et al., 2008), and because aberrant processing of facial displays has been demonstrated in youth at risk for developmental psychopathology (Tottenham et al., 2009), there is reason to further examine the neural and behavioral bases of face processing in youth (children and adolescents). Strong characterization of these processes in typically developing youth will improve our understanding of the emotional armory of childhood, while also providing a means for making future comparisons in at-risk samples.

Studies of the neural and behavioral bases of face processing in adults are numerous. Literature review of the past seventeen years reveals more than 600 published functional magnetic resonance imaging (fMRI) studies of face processing in adults (Fig. 1A). Adult fMRI studies show that regions of the fusiform gyrus, inferior and middle occipital gyrus, lingual gyrus, middle/superior temporal gyrus, limbic, and prefrontal cortex (PFC) are involved in processing emotional facial displays (Fusar-Poli et al., 2009; Palermo and Rhodes, 2007). Adult fMRI and lesion studies corroborate early theories that select areas of the face processing network contribute to

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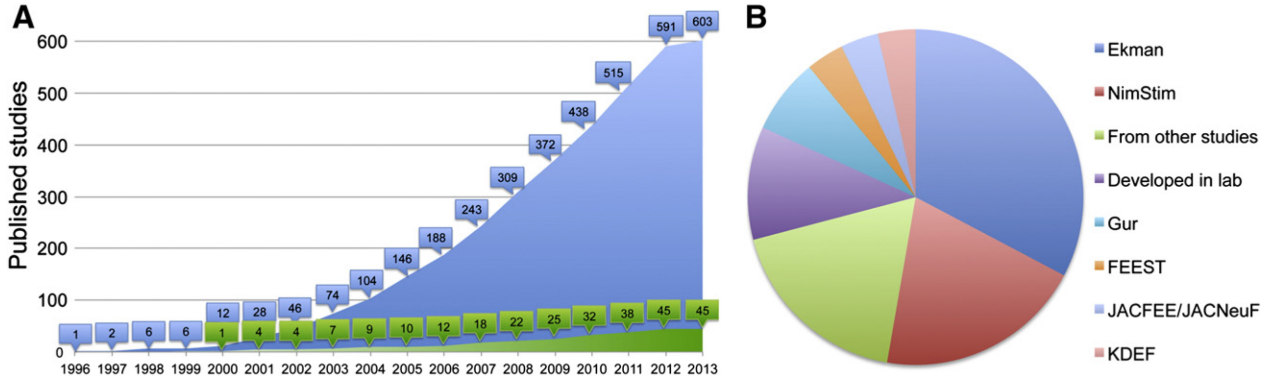

Fig. 1. Growing number of published emotional face processing fMRI studies, and those in youth, almost exclusively employing adult face stimuli. Panel (A) depicts a cumulative summary of published fMRI emotional face processing studies by year (1996–2013). A literature search, performed 2/26/2013, relayed that 648 studies were published overall, with 45 including youth participants. Studies including adult and child/adolescent participants are indicated in blue and green, respectively. Panel (B) indicates the face stimuli used in fMRI emotion face processing studies including youth participants, with only one reporting the use of child face stimuli (Hoehl et al., 2010), which was developed by the researchers for that particular study. Adult face stimulus sets include: Ekman faces (Ekman and Friesen, 1976), NimStim (www.macbrain.org/resources; Tottenham et al., 2009), Gur faces (www.med.upenn.edu/bbl/downloads/2Dfaes/), Japanese and Caucasian facial expressions of emotion (JACFEE/JACNeuF; Biehl et al., 1997), Karolinska directed emotional faces database (KDEF; www.emotionlab.se/resources/kdef; Calvo and Lundqvist, 2008), and Facial expression of emotions: stimuli and test (FEEST; Young et al., 2002).

different aspects of face processing (Adolphs, 2002; Haxby et al., 2002). For example, occipital cortices process perceptual properties of faces (Adolphs, 2002), the amygdala responds to threat-related stimuli (e.g., fearful, angry faces; Breiter et al., 1996; Whalen et al., 2001), and PFC aspects of the response are attributed to emotion regulation processes (Hariri et al., 2000; Phillips et al., 2003). The PFC is also recognized as playing a central role in social cognitive functions such as evaluation of social reinforcement in faces (Haxby et al., 2002). Enhanced responses to emotionally expressive face stimuli have also been observed in the face-selective region of the fusiform gyrus, the fusiform face area (FFA), but this more likely reflects enhanced attention allocation, possibly via feedback from the amygdala to early visual regions (Kanwisher and Yovel, 2006; Vuilleumier and Pourtois, 2007). Taken together, prior evidence in adults indicates that affective facial displays are processed via a distributed neural network, and in a valence-specific manner.

In contrast to the more than 600 adult fMRI studies of face processing, fewer than 50 published fMRI studies have examined face processing in youth. Functional MRI studies of face processing in youth have demonstrated that the same core regions of the brain that process emotional faces in adults also underlie face processing in youth (Hoehl et al., 2010; Lobaugh et al., 2006). Differences between children and adult participants primarily reside in the magnitude and extent to which face regions are engaged during face processing fMRI tasks, and in how particular brain regions respond selectively to specific valences. Indeed, compared to adults, youth show attenuated activation in the PFC to emotional faces (Monk et al., 2003), which has been attributed to protracted maturation of prefrontal regions (Gogtay et al., 2004; Luna, 2009). Youth also show increased selectivity in the FFA (Golarai et al., 2010), and decreased amygdala activity (Guyer et al., 2008; Monk et al., 2003; Thomas et al., 2001) with age, fitting with knowledge that the FFA (Scherf et al., 2007) and amygdala (Giedd et al., 1996; Tottenham and Sheridan, 2009) continue to develop beyond adolescence.

Neural studies of face processing in youth have relied almost exclusively on adult emotion face stimuli (Fig. 1B). The reliance on adult face stimuli for understanding the emergence of neural substrates for face processing in children is a chief limitation recognized by the field (Somerville et al., 2011). This concern arises from observations that age of the face stimuli (Hoehl et al., 2010), familiarity with the actor (Nielson et al., 2010), and relationship of the face to the viewer (Leibenluft et al., 2004; Taylor et al., 2009) alter neural responses in fMRI studies. In a developmental context, the amygdala, in particular, may respond differently to the emotional faces of similarly aged children, so-called “peers”, than to the emotional faces of adults that are inherently authority figures. After all, activation in the amygdala is driven by the emotional significance and behavioral relevance of faces (Anderson and Phelps, 2001; Davis and Whalen, 2001), and adult faces convey specific behavioral relevance to children. Thus, faces of emotional peers may be processed differently than emotion faces of adults, in children.

Indeed, Hoehl and colleagues report evidence for altered processing of adult versus child angry and happy emotion faces in 5–6 year old children (Hoehl et al., 2010). Specifically, activation was observed in the amygdala for angry adult and happy child faces (Hoehl et al., 2010), which was attributed to the regular occurrence of angry expressions of adults to children, and the relevance of peer smiles, respectively. Other recent youth fMRI studies have demonstrated that amygdala response is influenced by learned biases to select races (Telzer et al., 2012). The latter reinforces that experience can alter amygdala response in youth. Together, these findings underscore that prominent features of a face, such as age or emotion, may alter the ways in which that face is processed. Data such as these motivate discussion about the role of experiential learning, or socially relevant cues, in shaping amygdala response (Hooker et al., 2006; Todd and Anderson, 2009).

Behavioral studies of face processing provide further support that characteristics of the stimuli affect speed and accuracy. Recognition memory is best for in-group stimuli (e.g., species, race; Meissner and Brigham, 2001; Scott et al., 2005), and for similarly aged faces (review by Rhodes and Anastasi, 2012). In contrast to a theoretical framework that suggests a processing advantage for own-age face stimuli (see Rhodes and Anastasi, 2012), children appear to be more accurate at recognizing faces of adults (Macchi Cassia, 2011; Macchi Cassia et al., 2012), which may reflect the frequent interaction with adult faces from a young age. In addition, those who interact with children more frequently, such as school teachers, show improved capacity to recognize child faces (Harrison and Hole, 2009), suggesting that these biases are experientially-driven rather than inherent. Hoehl et al. did not find accuracy differences for happy adult compared to happy child faces in a post hoc emotion recognition task, but for angry faces, children were less accurate at recognizing anger in their peers relative to that in adults (Hoehl et al., 2010). Overall, it is apparent that experience or familiarity with select facial stimuli influence processing. This work has motivated interest in how salient aspects of a face affect neural and behavioral processing and raise important questions regarding the exclusive use of adult face stimuli in facial emotion processing studies of youth.

As the transition into adolescence brings about changes in social behavior and the primacy of peer relationships is established, there is need to extend work by Hoehl and colleagues beyond young childhood, using validated child face stimuli. The aim of the present study was to examine differences in brain engagement when late childhood/adolescent participants viewed emotional faces of peers compared to faces of adults. Using a well-vetted experimental paradigm that consists of matching the identity of the face, we compared within-subjects neural and behavioral responses to two variations of a task; one with the most widely used adult emotional face stimuli (Ekman faces; see Figs. 1B and 2A) and the other with newly validated child emotional faces (Fig. 2B; Egger et al., 2011), in which actors used in stimuli closely match the ages of our participants. We examined the following hypotheses: (1) that the same basic neural systems underlie processing of adult and peer faces, (2) that magnitude and extent of response in face processing brain regions will vary between child and adult face stimuli, and (3) that the profile of amygdala response will differ across emotional valences of peer and adult faces. Specifically, we predicted that youth will show more neural activation for adult compared to child emotion faces. This prediction is based on evidence that children's face representation is tuned to adult faces (Macchi Cassia et al., 2012) and also the idea that adult faces should better signal behaviorally relevant outcomes, and thus be associated with enhanced neural processing. Given that Hoehl et al. (2010) observed greater amygdala response for angry adult faces compared to angry child faces, we expected to observe greater amygdala response to negative emotion faces (e.g., fearful, angry) of adults compared to child same-emotion faces. The perception of peer faces, in contrast, may increase amygdala activation for happy faces compared to other peer emotions, as observed in younger children (Hoehl et al., 2010).

Materials and methods

Literature search

A PubMed literature search was conducted to retrieve fMRI studies, published prior to the end of February 2013 that used face stimuli to examine emotion processing. The search terms used were similar to those in a meta-analysis on variations of the emotional faces paradigm (Fusar-Poli et al., 2009) and a meta-analytic comparison of face and natural scene processing (Sabatinelli et al., 2011). The following search string was entered: (“1995/01/01” [Publication Date]: “2013/12/31” [Publication Date] AND (face OR facial OR FFA OR expression) AND (emotion OR mood OR motivation OR affective OR fear OR valence OR pleasantness) AND (fMRI OR neuroimage OR “functional MRI” OR “functional magnetic resonance imaging”)). Exclusion criteria were meta-analyses, and studies that included clinical populations (neurological, psychiatric, or otherwise). Studies assessing pharmacological effects on face processing in nonclinical populations were included. The following parameters were recorded: (a) number of published face processing studies in adults (by year), (b) number of published face processing studies that included children/adolescents (by year), and (c) type of face stimuli that were used. Studies that enrolled both adult and child participants were included in the calculation of total number of child studies, and in assessment of face stimuli frequency. A one-way analysis of variance (ANOVA), implemented in IBM SPSS Statistics ver. 21 (SPSS INC; Chicago, USA), was used to analyze publication frequency across stimuli sets.

Participants

Twenty-eight children and adolescents (18 females/10 males) were recruited from the greater Detroit Area through advertisements on the Wayne State University (WSU) website, Craigslist (Metro Detroit), and printed flyers. All participants and their parents provided written consent or assent as approved by the Institutional Review Board (IRB) of Wayne State University. Exclusion criteria consisted of a history of neurological injury, or significant learning disorder, and all participants were fluent in English. Participants were shown a brief video about MRI experimental procedure to prepare them for the MRI scan session in advance of their appointment. Participants were ages 8–16 with a mean (±sd) age of 12.45 ± 2.26. A chi-square goodness-of-fit test was performed to determine whether participant gender was equally represented across the study population.

fMRI paradigm

A well-established face processing fMRI paradigm was used (see Fig. 2; Hariri et al., 2002a; Hariri et al., 2002b; van Wingen et al., 2008; Carré et al., 2012). During each trial, three stimuli were presented simultaneously, with the stimulus on top indicating the cue. Participants indicated, via button press, which of the two bottom faces was identical to the cued face on the top of the screen. The lure presented was the same gender and emotion, but a different actor. Thus, all stimuli in a single trial were of the same gender and emotional expression (fear, angry, neutral, or happy), and trials were balanced to have stimuli depicting both genders presented equally. In control conditions (Fig. 2C), a horizontally- or vertically-oriented ellipse was presented at the top of the screen as a cue above two ellipses (one vertical and one horizontal), and participants indicated the matching orientation of the ellipse. Blocks were additionally counterbalanced for order of stimulus presentation (faces and shapes conditions) to control for possible habituation effects (Alexander et al., 1986). This task is known to elicit robust responses to facial stimuli, and has been used widely to measure threat-related amygdala function.

Participants were run on two nearly identical versions of the task. The versions varied only in the age of the emotion faces presented. Task order was counterbalanced across participants. Adult faces from the Ekman Pictures of Facial Affect series (Ekman and Friesen, 1976) and child faces from the newly developed and validated National Institute of Mental Health Child Emotional Faces Pictures Set (NIMH-ChEFS; Egger et al., 2011) were used. Importantly, the NIMH-ChEFS child face set shows high agreement and is comparable with values reported for commonly used adult picture sets, including the Ekman Pictures of Facial Affect (Egger et al., 2011). Additionally, actors for the NIMH-ChEFS emotional

Fig. 2. Face matching fMRI paradigm. Example trial from adult (A) and child (B) face runs, where participants select which of the two bottom faces are identical to the top target face. In control conditions (C), participants select which of the two bottom shapes are identical to the top target shape.

face stimuli ranged in age from 10 to 17 years with a mean age of 13.6 years old (Egger et al., 2011). This corresponds well with the age ranges of participants in the present study (ages 8 to 16; mean age of 12.5). All faces were presented in black and white, and framing, contrast, and luminosity were matched.

Each run (adult faces, child faces) consisted of 8 emotion blocks with 2 of each of the following valence conditions: angry, fearful, happy, and neutral. Emotion blocks were interleaved with two control blocks (ellipsoid shapes). Each 42 s block consisted of six 4 s trials. Trials were separated by a jittered (variable length) intertrial interval (ITI) that was on average 3 s. E-prime software v2.0 was used for stimulus presentation (Psychology Software Tools, Inc., Pittsburgh, PA).

Behavioral analysis

To examine behavioral performance, number of errors was calculated across each of the four emotional expressions (angry, fearful, happy, neutral), for adult and child faces, following priors (Easter et al., 2005). Error rates were analyzed using a two-way repeated-measured ANOVA for two factors: age-of-face (child vs. adult) and emotion (angry vs. fearful vs. happy vs. neutral). Post hoc within-participant paired *t*-tests were used for further exploration of significant main effects and interactions evidenced by the ANOVA. Pearson's bivariate correlation was used to test for a relationship between participant age and performance. Statistical analyses were two-tailed and implemented in IBM SPSS Statistics ver. 21 (SPSS Inc.; Chicago, USA). Effects were considered significant at a threshold of $p \le .05$.

fMRI data acquisition and analysis

MRI acquisition

MR scanning was conducted at the MRI Research Center at Wayne State University with a 3.0 Tesla Siemens Verio scanner, equipped with an 8-channel head coil. 217 T2*-weighted blood oxygenation level-dependent (BOLD) images were acquired using echo-planar imaging (EPI) with the following parameters: TR: 2000 ms, TE: 25 ms, matrix: 220 × 220, 29 slices, flip angle: 90°, voxel size: 3.44 × 3.44 × 4 mm. Total scan duration for each functional scan was 7:14. High-resolution anatomical images were acquired for individuals by a T1-weighted sequence with the following parameters: TR: 1680 ms, TE: 3.51 ms, orientation: axial, matrix: 384 × 384, 176 slices, flip angle: 90°, voxel size: 0.7 × 0.7 × 1.3 mm.

Movement

Siemens MRI motion correction (MoCo) software was used (this technique is also known as Advanced Retrospective Technique, or ART) to retroactively reduce the relative motion across the data set by applying post-processing interpolation of frame-to-frame movement. Following this, mean movement and maximum frame-to-frame excursion for each of 6 translational (x, y, z) and rotational (pitch, roll, yaw) movement directions were calculated. Participants that exceeded 3 mm of movement were excluded, resulting in elimination of 3 out of 28 participants. Paired *t*-tests were used to examine within participant movement between child and adult face tasks and between genders. Again, SPSS statistics were thresholded at $p \le .05$.

fMRI data analysis

Preprocessing steps were performed using SPM8 software (Wellcome Department of Imaging Neuroscience, London, UK). After discarding the first 4 EPI volumes to allow for signal stabilization, images were realigned then spatially normalized to the Montreal Neurological Institute (MNI) template, using the participant-specific transformation parameters created by fitting mean functional images to the single reference EPI standard SPM template. Data were not resampled during normalization; thus, data retained the native resolution (3.44 × 3.44 × 4 mm) for subsequent analyses. Following normalization, images were spatially smoothed with a Gaussian kernel of 8 mm full width at half maximum (FWHM).

The general linear model framework (Friston et al., 1995) was used for statistical analyses. Individual participant models included high-pass filtering (to remove low frequency signal components; cut-off, 128 s) and an autoregressive component to account for serial correlations. Subject motion parameters were also included in the model as covariates of no interest. First level contrasts were created to assess effects of all faces over the baseline condition (shapes) and of each valence type (angry, fearful, happy, and neutral) over the baseline condition for both adult and child face runs separately. The shapes condition was used as the baseline condition instead of neutral faces, due to mounting evidence that neutral faces may not be processed as emotionless (Cooney et al., 2006; Herba and Phillips, 2004; Thomas et al., 2001) and because neural response differences between neutral adult and child faces were anticipated and of interest.

Whole-brain group effects for all emotions > baseline were performed separately for adult and child face runs, using one-sample *t*-tests. Additionally, one-sample *t*-tests were performed for individual valences (e.g., angry > baseline); these were performed separately for adult and child face runs. Paired *t*-tests were used to directly contrast adult and child face runs within subject. Specifically, paired *t*-tests were conducted across all emotions (adult faces > child faces and child faces > adult faces) and for each emotion separately. A statistical height threshold of $p < .001$ was used to identify whole brain effects (all faces > baseline), as in previous work (Kim and Hamann, 2007; van Wingen et al., 2008).

Region of interest analyses

Five regions of interest (ROI) were generated for areas in which significant response ($p < .001$) was observed for adult but not child (all faces > baseline) face stimuli (indicated with an asterisk (*) in Fig. 3). ROIs were comprised of 6 mm radius spheres generated using the Wake Forest University (WFU) PickAtlas software (Maldjian et al., 2003). This size represents a more conservative approximation of total amygdala (our smallest brain region of interest) volume without misclassifying voxels (Amunts et al., 2005; Eickhoff et al., 2006). To test for main effects and interactions within each region, percent signal change was extracted for each condition (emotion: 4 levels × age-of-face: 2 levels) and these values were submitted to repeated-measures analysis of variance (ANOVA). Additionally, paired *t*-tests were used to assess significant differences in regional responses between adult and child face stimuli for each emotion (angry, fearful, happy, neutral) within subject. These analyses were two-tailed and implemented in IBM SPSS Statistics ver. 21 (SPSS Inc.; Chicago, USA). Effects were considered significant at a threshold of $p \le .05$.

Following work by Hoehl et al. (2010), we examined the possibility that happy peer faces elicit heightened amygdala response. Specifically, ROI analyses were conducted to examine amygdala response to happy versus other emotions and across age-of-face stimuli. Individual participant effects were extracted from the peak corresponding to faces versus baseline (at $p < .05$, corrected) falling within a bilateral amygdala mask. The peak was located in the right amygdala at $x = 24$, $y = -4$, $z = -18$ (MNI). Statistical correction was performed using AlphaSim, following prior work (Thomason et al., 2009; Thomason et al., 2010). Using repeated-measures ANOVA (emotion: 2 levels × age-of-face: 2 levels; implemented in SPSS), we examined amygdala response for happy versus other emotion pairs: (1) happy versus angry; (2) happy versus fear; and (3) happy versus neutral. Significant interactions were decomposed post hoc by paired *t*-tests. Statistical analyses were two-tailed and performed in IBM SPSS Statistics ver. 21 (SPSS Inc.; Chicago, USA). Again, SPSS effects were considered significant at a threshold of $p \le .05$.

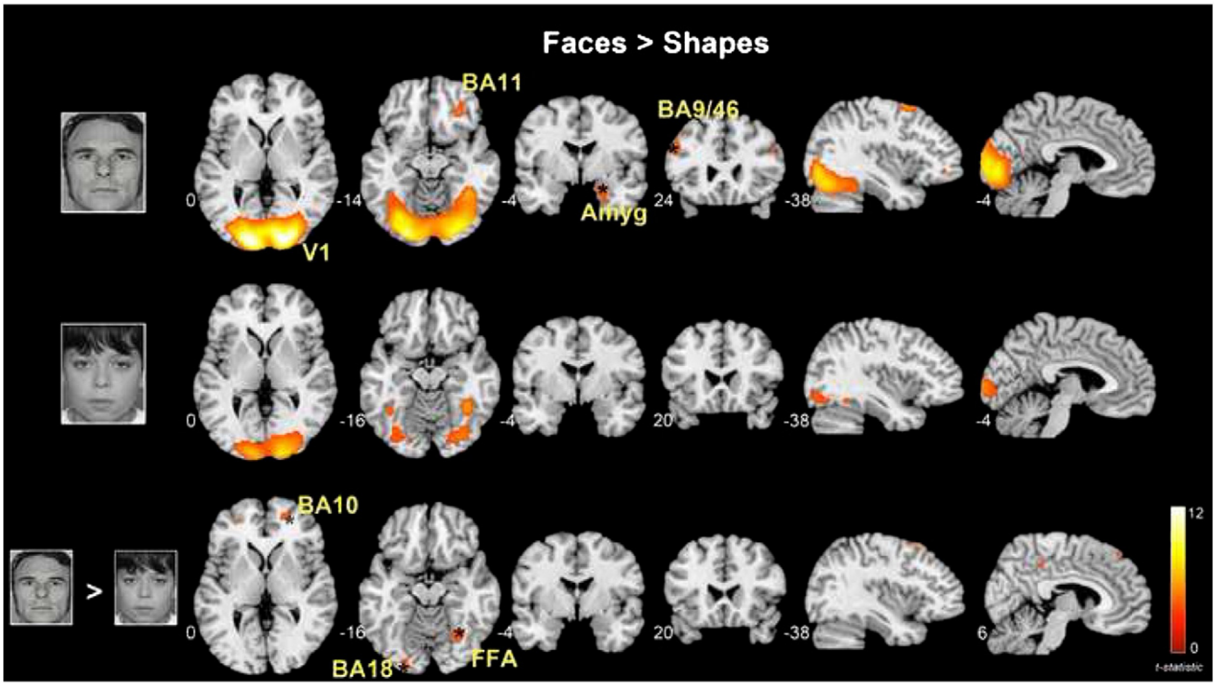

Fig. 3. Enhanced BOLD response in youth to presentation of adult face stimuli. Activation maps are presented for faces – across all valence categories – greater than baseline. Top and middle rows depict response to adult and child face stimuli, respectively. Bottom row depicts the direct comparison of adult > child faces (>baseline). No clusters in the reverse contrast (child > adult) were significant. Corresponding peaks are recorded in Table 1 and asterisks (*) denote areas where ROI analyses were conducted (see Fig. 4). V1 indicates primary visual cortex; BA, Brodmann area; FFA, Fusiform face area; Amyg, Amygdala. Displayed at $p < .001$ uncorrected, cluster threshold = 10 voxels. X, y, and z (MNI) slice levels are denoted adjacent to each image.

Results

Literature search

A review of the literature contained in the PubMed databases yielded 648 fMRI studies on emotional face processing (summarized in Fig. 1A). Of those, 45 included child or adolescent participants. With the exception of one study on 5–6 year old children (Hoehl et al., 2010), studies examining the processing of faces in youth exclusively utilized adult face stimuli. The Ekman series of adult faces (Ekman and Friesen, 1976) was the most frequently reported stimulus set, $F(1,7) = 9.5$, $p = .022$. Refer to Fig. 1B for further detail regarding face stimuli employed in developmental face processing fMRI studies.

Behavioral performance

Participant age was not correlated with error rates for adult or child face runs ($p = .73$ and $p = .31$, respectively). A significant interaction was observed across age-of-face (2 levels) and emotion (4 levels), $F(1,24) = 8.5$, $p < .001$, for error rate. Significant main effects were observed for adult compared to child face stimuli, $F(1,24) = 78.09$, $p < .001$, and across facial emotions, Greenhouse–Geisser-corrected $F(2.06, 49.57) = 5.15$, $p = .009$. That is, error rates were higher for child (6.04 ± 1.52) compared to adult (5.15 ± 1.95) face stimuli, $t(24) = 2.98$, $p = .007$, and error rates were higher for neutral and happy compared to angry and fearful faces. Post hoc paired t-tests comparing adult and child same-emotion faces evidenced that error rates were significantly greater for neutral child compared to neutral adult faces, $t(24) = 7.86$, $p < .001$, but were not significant for any other conditions. Thus, both the age and emotion of the face appeared to modulate observed behavioral responses.

Movement and sex distribution

Average participant movement was less than .08 mm across translational directions, and less than 0.13° across rotational directions. Across both runs, the maximum frame-by-frame displacement was 1.94 mm and 1.66° in translational and rotational directions, respectively. There were no differences in movement between child and adult face runs for either translational ($p = .813$) or rotational ($p = .419$) mean movement. In addition, males and females did not differ in movement for any of the six motion parameters, all $p > .4$. Additionally, although there were more female than male participants, this difference in sex distribution did not reach statistical significance, $\chi^2_{(1)} = 3.24$, $p = 0.072$.

Neural response to emotion face stimuli

Neural responses to face stimuli were significant across a number of regions, including: bilateral occipital cortex, inferior temporal gyrus, fusiform gyrus, cerebellum, right amygdala, right angular gyrus (BA39), and left lateral prefrontal cortex (BA 6/9/46); see Fig. 3 and Table 1. Results obtained here are in good agreement with reports in the literature; see review by Fusar-Poli et al. (2009). The magnitude of response was lessened when youth viewed faces of their peers as compared to adult faces (Fig. 3, Table 1). This result indicates that the same regions are involved in the processing of both peer and adult faces; however they are not recruited to the same extent.

The results of paired t-tests within subject that directly compared adult versus child face activation maps, showed that the most significant effects of age-of-face on neural processing reside in areas of the right FFA (BA19), right superior frontal gyrus (BA10), left inferior occipital gyrus (BA18/17), and cuneus (Fig. 3, bottom row, and Table 1). No voxels were significant for the reverse comparison of child > adult faces at $p < .001$.

ROI analysis in peak regions defined based on significant responses for adult but not child faces (amygdala, BA 9/46, FFA, BA10, BA18; see Fig. 3) confirmed effects observed in activation maps. Specifically, we observed significant main effects for age-of-face across all regions (F-statistics =4.25–17.41, p's .05–<.001) but no main effect

Table 1
Peak areas of activation during the processing of adult and peer faces, across emotions. Asterisks (*) denote peaks within which follow-up region of interest analyses were performed.

Brain region	BA	x	y	z	*t* statistic	Voxels
Adult faces > shapes						
Amygdala*		20	−4	−24	4	77
Middle frontal gyrus*	LBA9/46/6	−48	20	28	4.51	366
Cuneus	R18	16	−96	14	14.54	14041
Middle occipital gyrus	LBA17	−14	−96	0	11.84	
Fusiform gyrus	LBA19	−32	−70	−16	6.55	
Fusiform gyrus	RBA19	32	−70	−16	5.53	
Calcarine	RBA17	16	−96	0	11.88	
Calcarine	LBA17	−10	−96	−2	10.15	
Inferior temporal gyrus		44	−48	−26	4.7	
Declive (cerebellum)		−32	−78	−24	6.44	
Declive (cerebellum)		32	−78	−24	5.79	
Vermis (cerebellum)		6	−80	−16	4.66	
Superior occipital gyrus	BA18	26	−96	18	7.2	
Superior occipital gyrus	BA18	−20	−96	18	5.16	
Inferior occipital gyrus	RBA19	38	−78	−8	6.93	
Lingual gyrus	RBA17	16	−96	0	11.88	
Lingual gyrus	LBA17	−18	−88	−2	9.24	
Inferior parietal lobe	BA39	36	−66	42	4.58	209
Child faces > shapes						
Middle occipital gyrus	RBA18	16	−102	12	8.71	4671
Middle occipital gyrus	LBA19	−20	−100	10	6.56	
Cuneus	RBA18	12	−100	10	7.89	
Calcarine	RBA17	16	−96	−2	7.34	
Inferior occipital gyrus	RBA18	34	−82	−12	5.56	
Inferior occipital gyrus	LBA18	−34	−84	−12	4.12	
Superior occipital gyrus	LBA18	−12	−100	10	6.58	
Fusiform gyrus	RBA19	34	−74	−18	3.5	
Fusiform gyrus	LBA19	−36	−72	−18	3.57	
Lingual gyrus	LBA18	−22	−90	−14	3.68	
Fusiform gyrus	RBA37	38	−52	−18	6.24	329
Fusiform gyrus	LBA37	−46	−56	−18	3.63	72
Inferior frontal gyrus	RBA9/6	60	10	36	5.42	73
Adult > child faces > shapes						
Fusiform gyrus*	RBA19	30	−70	−16	3.67	199
Superior frontal gyrus*	RBA10	24	58	2	3.59	59
Inferior occipital gyrus*	LBA18/17	−28	−94	−18	4.46	91
Cuneus	LBA19	−4	−94	26	3.64	91
Child > adult faces > shapes						
For this contrast, no clusters survived threshold						

Coordinates reported in MNI convention. BA = Brodmann's area. Results presented at a threshold of p < .001. L = left; R = right. All clusters > 66 voxels survive whole-brain correction ($p < .05$).

of emotion, or interaction of emotion × age-of-face. Although the main effect of emotion did not reach significance, paired *t*-tests comparing response to adult versus child faces within each emotion did show statistical strength varied across areas examined (Fig. 4). Thus, there was evidence that the neural systems that process emotions show varied response to different emotions, a result that has been documented previously (Fusar-Poli et al., 2009; Lobaugh et al., 2006). We provide additional evidence that the age of the faces being processed, or their relation to the observer, affects the neural response across emotions.

Neutral faces

Neural responses to neutral faces (>baseline) were significant across a number of regions, including: posterior visual areas, bilateral fusiform gyrus (BA37), cerebellum, bilateral hippocampus, bilateral thalamus, right lateral prefrontal cortex (BA9/46), right orbitofrontal cortex (BA11/47) and left superior/middle frontal gyrus (BA6/8), see Fig. 5. Again, the magnitude of the response was increased when youth processed neutral faces of adults (blue, Fig. 5) compared to neutral peer faces (red, Fig. 5).

The results of paired *t*-tests within subject that directly compared neutral adult versus child faces, showed that the most significant effects of age-of-face on neural processing reside in areas of the left superior frontal gyrus (BA6), right medial frontal gyrus (BA10), and right anterior cingulate cortex (BA32). No voxels were significant for the reverse comparison of neutral child > adult faces.

Amygdala response variation

Following observations that happy emotions are recognized earliest in development (Herba and Phillips, 2004) and that children show enhanced amygdala response for happy faces of other children (Hoehl et al., 2010), we tested for interactions between age-of-face and happy versus other emotions in the amygdala. We observed a significant interaction for happy and angry, adult and child faces, $F(1,24) = 10.67$, $p = .003$ (Fig. 6). Post hoc paired *t*-tests indicated that amygdala response was greater for angry adult compared to happy adult face stimuli, $t(24) = 2.21$, $p = .037$. Amygdala response was also greater for angry adult compared to angry child face stimuli, $t(24) = 2.23$, $p = .035$. When instead processing child face stimuli, amygdala response was greater for happy compared to angry child faces, $t(24) = 2.53$, $p = .018$. We also observed similar interaction effects for happy compared to fearful and neutral faces, such that fearful and neutral adult faces, and happy child faces, elicited the most robust responses in the amygdala, but these interactions were not statistically significant (Fig. 6).

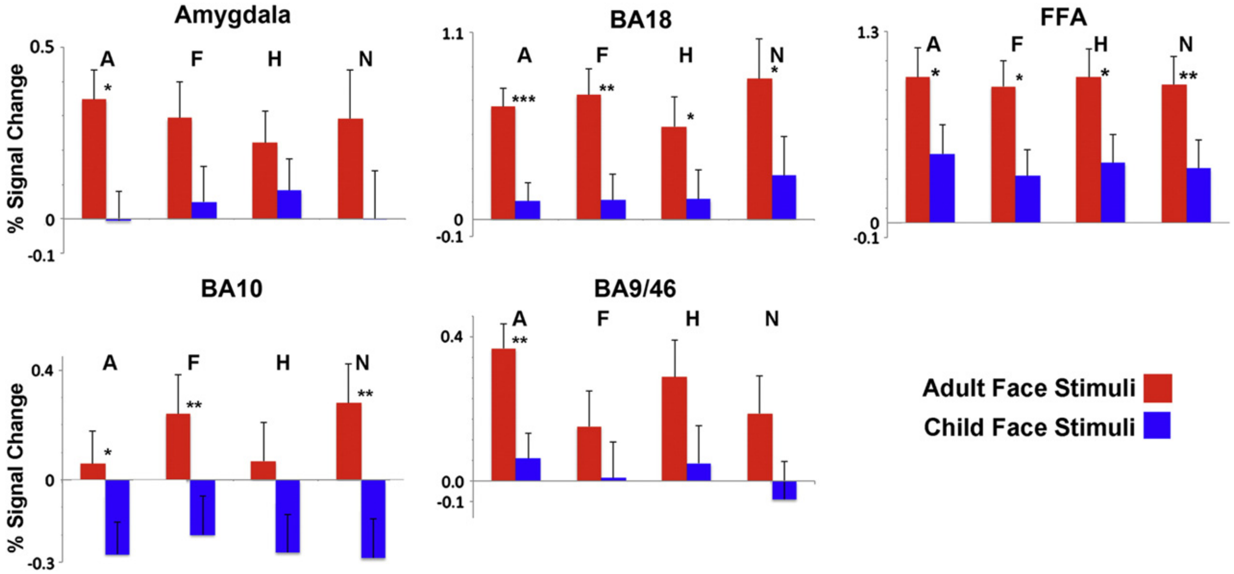

Fig. 4. Increased regional response to adult (red) compared to child (blue) emotional faces across emotions. Mean percent signal change (emotion > baseline; *y*-axis) within each ROI is given for adult and child faces across: (A) angry, (F) fearful, (H) happy, and (N) neutral emotions. ANOVAs indicated significant main effects for age-of-face within all 5 ROIs (p's $\leq .05$). Asterisks indicate significant results from emotion-specific paired *t*-tests: $^*p < .05$, $^{**}p < .01$, $^{***}p < .005$. Error bars represent standard error of the mean. ROIs correspond to areas indicated with asterisks (*) in Fig. 3 and Table 1.

Discussion

Developmental studies of emotional face processing have relied mainly on adult face stimuli, which are relationally varied from child/adolescent participants. Up until this point, no study has explicitly compared neural and behavioral responses when children and adolescents process adult and child emotional faces during an fMRI scan. Here, we show that youth are more accurate for adult compared to child faces, and the same core brain structures are recruited for processing emotional faces of adults and peers. However, the magnitude of response across regions is increased for adult compared to child faces. Importantly, because developmental studies report elevated amygdala (Thomas et al., 2001) or whole-brain (Tahmasebi et al., 2012) responses to neutral compared to fearful or angry adult

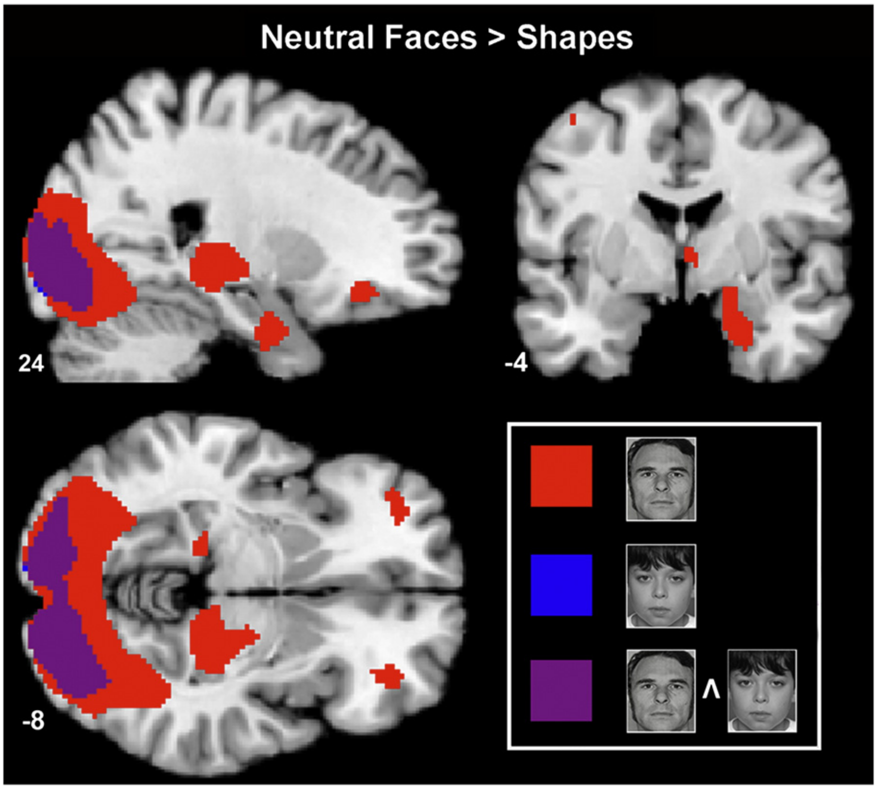

Fig. 5. Regional activation during processing of neutral adult and neutral child faces, and their conjunction (Λ). Magnitude of response to neutral faces was increased for adult compared to child faces. Displayed at $p < .005$, cluster extent threshold = 10 voxels. X, y, and z (MNI) slice levels are denoted adjacent to each image.

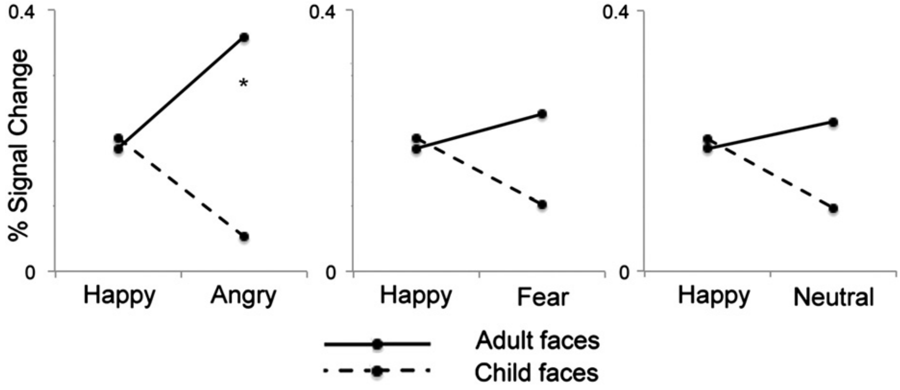

Fig. 6. The amygdala in youth is more responsive to happy versus other emotion faces of peers, and angry expressions of adults. Asterisks (*) indicate significant age-of-face × emotion interaction ($p = .003$), where angry adult faces elicited greater amygdala response compared to happy adult ($p = .037$) and angry child ($p = .035$) faces. In contrast to adult face effects, amygdala response was greater for happy child compared to angry child faces, ($p = .018$). The y-axis shows percent signal change from baseline.

faces, we directly compared the processing of neutral adult and child faces to test whether face processing regions of the brain would be engaged to the same extent for both types of stimuli. We observed greater brain activation to neutral adult relative to neutral child faces. Finally, as response characteristics of the immature amygdala are known to differ from those seen in adults, we probed the amygdala during the processing of happy versus other emotional expressions and found that response patterns differ according to whether the participant is viewing adult or child face stimuli. We found that the amygdala responds preferentially to happy peer faces and also angry adult faces. Together, these findings suggest that youth process emotional displays of adults differently than those of their peers and thus, the source of an emotional expression has relevance for the perception of emotion.

As late childhood and adolescence bring about immense developmental changes in the 'social landscape' (Ernst and Fudge, 2009) and in structure and function of brain regions involved in processing social stimuli (Blakemore, 2008; Burnett et al., 2011), it is important that neural systems are capable of preferentially responding to cues in the environment that are most behaviorally relevant. Although accuracy is typically greater for own-age than other-age faces (see Rhodes and Anastasi, 2012), an emerging developmental perspective emphasizes the salience of an adult face for a child perceiver such that children show improved recognition accuracy for young adult compared to other-age faces (Macchi Cassia, 2011). For the first time, we show greater accuracy (for facial identity matching) and enhanced neural response to adult compared to child affective displays. This may reflect the greater experience that youth have reading emotion from faces of adults than from faces of their peers. That is, with respect to their peers, youth may be less experienced at reading social signals, as facial expressions of peers are less deterministic of reward and punishment outcomes, and thus, less biologically significant. Accordingly, the heightened response for salient faces of adult caregivers/authority figures may be related to the great amount of experience that youth have accumulated with adult individuals since birth.

Previous studies have indicated that youth recruit the same regions as adults when processing emotional faces (Adolphs, 2010; Lobaugh et al., 2006; Moore et al., 2012; Passarotti et al., 2009). Here, we add that while neural responses to adult and peer emotional faces are similar with respect to the involved brain regions, a crucial difference remains in the extent that these regions are engaged. Like prior studies, the profile of the BOLD response differed across regions according to the emotion of the face (Fusar-Poli et al., 2009; Lobaugh et al., 2006). Moreover, our results suggest that emotional expressions of individuals who differ substantially in age from the perceiver are processed differently within the brain. Across development, the significance of certain facial emotions does not follow a linear path and may be shaped by transitions in age-appropriate developmental goals (Scherf and Scott, 2012). There is also evidence that the ability to discriminate certain emotions does not occur altogether developmentally, with some emotions (e.g., happy) recognized earlier in life than others (Herba and Phillips, 2004). This underscores that at different points in development neural systems for processing certain emotions may emerge as more developed, while others may remain in more nascent stages.

It has been suggested that neutral faces hold social meaning, are difficult to interpret, and may not be processed as completely emotionless within the brain (Cooney et al., 2006; Stevens, 2009). Prior developmental work has shown elevated amygdala response to neutral adult faces (Thomas et al., 2001), which has been attributed to the ambiguity of neutral faces during this stage of development (see Somerville et al., 2011). Our data suggest that enhanced neural response is select to neutral faces of adults, who represent omnipresent authority figures and whose expressions are especially salient to children. Thus, a larger amount of neural resources may be recruited in an effort to resolve ambiguity. The amygdala, in particular, is reliably engaged by biologically relevant and ambiguous stimuli, where previously learned cues have been associated with more than one possible outcome. Amygdala engagement is thought to enhance processing of additional stimuli, such as contextual cues, and to potentiate activity of efferent brain regions (Whalen, 1998). Notably, data here suggest that adult but not peer neutral faces enhance amygdala engagement, although this difference did not reach statistical significance. This may be due to the additional recruitment of emotion regulatory signals from the PFC during the perception of neutral adult faces, that may converge on the amygdala and dampen its response (Kim and Hamann, 2007). Children may have more experience with neutral faces of adults, which are likely to be associated with more than one subsequent outcome. Thus, the predictive ambiguity of a neutral adult face should be well established by this point in development. An alternative explanation for an elevated amygdala response to neutral faces of adults is the recent indication of a 'negativity bias' in youth such that neutral faces (of adults) are perceived as negative in valence (Tottenham et al., 2012). Overall, our findings support the notion that neutral faces may not serve as an appropriate baseline in developmental studies (Lobaugh et al., 2006; Thomas et al., 2001; Tottenham et al., 2011).

The amygdala is historically viewed as the brain's central fear processor and within the adult literature, its engagement during the processing of fearful faces is a strong and consistent finding (Morris et al., 1996; Phelps and LeDoux, 2005; Whalen et al., 2001). Recent evidence that the amygdala responds to a range of facial expressions outside of fear has led to a refinement of its role as a putative fear-detector. Increasingly, the amygdala is recognized for its role as a 'salience detector', scanning environmental cues for biological significance (Adolphs, 2010; Cunningham and Brosch, 2012; Santos et al., 2011). Not only is the amygdala sensitive to the emotional significance of a facial expression (Phelps and Anderson, 1997; Sato et al., 2004), but it also mediates attention, memory, and decision making (Adolphs, 2002; LaBar and Cabeza, 2006). In line with previous accounts, we found that the amygdala in youth is responsive to fearful, angry, and neutral expressions of adults (Hoehl et al., 2010; Lobaugh et al., 2006; Tahmasebi et al., 2012; Thomas et al., 2001), although fearful and neutral comparisons did not reach statistical significance (Fig. 6). The engagement of the amygdala by angry expressions of adults vs. children is consistent with observations made by Hoehl et al. (2010) and may be attributed to the greater ability of adult face cues to predict negative social outcomes for a child perceiver. That is, a threatening expression of an adult may act as a conditioned stimulus, signaling an unconditioned aversive outcome for the child (e.g., time out, verbal reproach). These observations are in line with the amygdala's role in vigilance and its ability to associate stimuli with social/emotional value (Whalen, 1998).

When youth processed faces of their peers, the amygdala was more responsive to happy compared to angry expressions. This finding is in agreement with the Hoehl et al. study in 5–6 year olds, and may reflect the behavioral relevance of a peer's smile, which may serve as an important reinforcing cue during development. School-aged children in particular show amplified sensitivity to social acceptance (Blakemore, 2008), and amygdala activation to happy peer faces may correlate with the social relevance of these cues to the young observer. Together, these findings add to a growing body of literature supporting the view of the amygdala as an important hub for learning about socially relevant cues and predicting social outcomes (Hooker et al., 2006; Todd and Anderson, 2009).

In addition to the amygdala, several other brain regions showed enhanced activation for adult compared to child emotional faces. For example, we observed increased activation in the FFA for adult faces. Given that engagement of the emotional system (e.g., involving the amygdala) causes enhanced attention and perceptual processing of emotion-eliciting stimuli (Dolan et al., 2001), elevated processing of adult faces across several regions may result from positive feedback loops. This notion is supported by enhanced activation in the FFA by salient emotional features in adults (e.g., fearful vs. neutral faces), likely via feedback modulation from the amygdala (see Kanwisher and Yovel, 2006). Several prefrontal regions also showed elevated responses to adult emotion faces. In particular, adult but not child faces elicited activation in the lateral prefrontal cortex, a region implicated in cognitive control over emotion-processing systems (Ochsner et al., 2002). This effect was particularly strong for angry faces of adults, a finding that is in line with observations by Hoehl et al (2010), who interpreted this activation as serving to down-regulate negative responses to angry adult faces. Together these findings underscore the idea that age and emotion are salient aspects of a face that broadly affect neural processing.

From a developmental perspective, a child's ability to accurately read emotion from faces is imperative for social functioning. Indeed, prior to the onset of language, 'reading faces' is the primary means by which infants communicate, suggesting that processing facial emotion is an important developmental milestone (Leppanen and Nelson, 2009). As children/adolescents mature, the communicative intent and frequency of emotional faces in the environment change, on a backdrop of major brain maturation (Paus et al., 2008), which in turn is influenced by pubertal change (Moore et al., 2012). Moreover, adolescence is recognized as a time of heightened emotional reactivity paired with reduced emotion regulatory capacity, thus rendering youth particularly susceptible to psychopathology (Pine et al., 1998). Differences in amygdala response to child and adult emotion faces observed here suggest that future studies examining the pathogenesis of affective disorders in youth will benefit from employing both child and adult emotion face stimuli.

The limitations of the present study warrant discussion. We studied a wide age range of participants, which precludes the ability to attribute neural responsiveness to a specific developmental stage. A goal for future research will be to examine how neural biases to face age emerge across development, by interrogating particular developmental stages. An additional limitation of this study was that eye gaze was not monitored during fMRI tasks. Developmental differences in eye gaze may influence neural responses to emotional faces, by altering behavioral response features and subsequent level of processing (see Itier and Batty, 2009 for a review). Thus, an important avenue for future work will also be to perform simultaneous eye monitoring during fMRI to determine whether differences in brain activation are mediated by variation in the location and duration of visual fixation on faces.

Conclusions

The ability to read emotional signals gleaned from the faces of others represents a fundamental aspect of child development. In developmental fMRI research, the current paradigm for examining affective facial processing relies on the use of adult face stimuli, which are relationally varied from youth participants and which represent figures of authority. We addressed this problem by examining neural and behavioral responses differences when youth processed adult and child emotion faces, and found enhanced performance and greater neural activation to adult faces. This result may reflect increased experience youth have reading facial expressions of adults in the rearing environment and beyond. Further, we found that amygdala response was greater for happy peer faces while also greater for angry adult faces, which may reflect social relevance of these cues to the young observer. Our findings hold implications for future developmental work and may also provide insight into reported inconsistencies across face processing studies in different ages (Macchi Cassia, 2011). Accurate characterization of the development of emotional face processing will improve our understanding of how predisposition and experiential factors influence the manifestation of neurodevelopmental and neuropsychiatric disorders.

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Conflict of interest

The authors have no conflict of interest to declare.

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