Neural developmental changes in processing inverted faces

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We explored developmental changes in neural substrates for face processing, using fMRI. Children and adults performed a perceptual-matching task with upright and inverted face and animal stimuli. Behaviorally, inversion disrupted face processing more than animal processing for adults and older children. In line with this behavioral pattern, the left middle occipital gyrus showed a stronger face than animal inversion effect in adults. Moreover, a superior aspect of this region showed a greater face inversion effect in older than in younger children, indicating a developmental change in the processing of inverted faces. The visual regions recruited for inverted face processing in adults also overlapped more with brain regions involved in the viewing of upright objects than with regions involved in the viewing of upright faces in an independent localizer task. Hence, when faces are inverted, adults recruit regions normally engaged for recognizing objects, possibly pointing to a role for the featural processing of inverted faces.

Humans have a remarkable competence for perceiving, recognizing, and identifying countless faces over the course of a lifetime. An enduring issue concerns the development of this capacity (for recent reviews, see Gauthier & Nelson, 2001; Maurer, Le Grand, & Mondloch, 2002; Pascalis & Slater, 2003). There is general agreement that face recognition accuracy increases from childhood to adulthood (Gauthier & Nelson, 2001; Maurer et al., 2002; Want, Pascalis, Coleman, & Blades, 2003). However, there is less agreement on what aspects of face recognition change with development (Carey & Diamond, 1994; Freire & Lee, 2001, 2003; Itier & Taylor, 2004a; Mondloch, Le Grand, & Maurer, 2002, 2003; Pellicano & Rhodes, 2003; Schwarzer, 2000; Want et al., 2003).

One aspect of face processing that may change with development is a shift from the processing of faces in a piecemeal or feature-based manner in childhood to a reliance on the processing of face patterns more relationally (i.e., with more configural and/or holistic information) in adulthood (Carey & Diamond, 1994; Freire & Lee, 2001, 2003; Itier & Taylor, 2004a; Mondloch et al., 2002, 2003; Schwarzer, 2000; Want et al., 2003). A key piece of evidence for this conclusion comes from the examination of performance when face patterns are inverted (Yin,

1969). Research suggests that inversion disproportionately interferes with the processing of relational information (Bartlett & Searcy, 1993; Carey & Diamond, 1977, 1994; Diamond & Carey, 1986; Freire, Lee, & Symons, 2000; Murray, Rhodes, & Schuchinsky, 2003; Searcy & Bartlett, 1996; Tanaka & Farah, 1993, 2003; Young, Hellawell, & Hay, 1987). Researchers such as Carey and Diamond (1977, 1994) have found that inversion affects performance less in children than in adults. On the basis of this and other evidence (e.g., Mondloch, Dobson, Parsons, & Maurer, 2004), many researchers have argued that children rely less on relational information than do adults to process faces.

However, the notion that the developmental change in face processing is driven by the increased use of relational information in adulthood, in comparison with childhood, is not universally accepted. For instance, Itier and Taylor (2004b; see also Pellicano & Rhodes, 2003; Want et al., 2003) failed to find a disproportionately greater effect of inversion on adult performance than on that of children and argued that the developmental change in face processing involves a general across-the-board increase in performance accuracy, rather than a qualitative change in the use of relational information.

As the debate concerning the cognitive and perceptual mechanisms of face recognition development continues, the neural basis for developmental changes in face recognition in humans is just starting to be explored with functional neuroimaging techniques (Aylward et al., 2005; Gathers, Bhatt, Corbly, Farley, & Joseph, 2004; Itier & Taylor, 2004a; Passarotti et al., 2003; Taylor, Edmonds, McCarthy, & Allison, 2001). Gathers, Bhatt, Corbly, et al. used functional magnetic resonance imaging (fMRI) to examine face processing in adults and two groups of

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school-aged children 5–8 and 9–11 years old. A region of the fusiform gyrus was activated bilaterally when adults passively viewed photographs of faces, in comparison with the viewing of objects. Likewise, children 9–11 years of age showed a similar region of activation for viewing faces versus objects. This region was very similar to a face-preferential region that responds more strongly to faces than to other, nonface stimuli, reported in numerous other studies of face processing in adults (e.g., Kanwisher, McDermott, & Chun, 1997; see Joseph, 2001, for a review). However, the youngest children did not show face-preferential activation in the fusiform gyrus but did show activation in a more posterior visual association area, in the right and left occipital gyri. Gathers, Bhatt, Corbly, et al. suggested that the anterior shift in face-processing regions with age may reflect the developmental change in face processing reported by Carey and Diamond (1977). This anterior shift could be the neural correlate for a shift away from a reliance on processing faces featurally (in younger children) toward a reliance on processing faces relationally (in older children and adults).

Indeed, in another fMRI study, Aylward et al. (2005) showed that 8- to 10-year-old children did not preferentially activate the fusiform gyrus when viewing faces versus houses, whereas older children (12–14 years of age) did show fusiform activation. Moreover, the magnitude of the fMRI signal in the fusiform gyrus for viewing faces versus houses correlated with the magnitude of the face inversion effect in a recognition task conducted outside of the scanner. Younger children activated more posterior visual-processing regions, such as the inferior occipital gyrus, for viewing faces versus houses, similar to the finding by Gathers, Bhatt, Corbly, et al. (2004). In both of these studies, younger children showed face-preferential activation in brain regions outside of the fusiform gyrus, but it is not clear what aspect of face processing is subserved by the more posterior versus the fusiform regions in younger children. Therefore, we examined brain activation patterns in adults and in two groups of children defined on the basis of a median split of the age range: children under 9.7 years of age (younger group) and children over 9.7 years of age (older group). In addition, in the previous two studies, passive-viewing tasks were used, and neither study manipulated face inversion in the scanner. Consequently, the present study manipulated face inversion while the participants were in the fMRI scanner and employed an active-matching task to further explore developmental changes in neural correlates for face recognition.

In addition to using inverted faces as stimuli, we also examined brain activation patterns in children and adults in response to inverted and upright animal stimuli. The comparison of face stimuli with animal stimuli is critical for assessing claims that face processing selectively recruits a region in the fusiform gyrus (e.g., Kanwisher et al., 1997), at least in adults. In addition, previous studies in which face inversion has been used to study the development of configural-processing or face-specific-processing mechanisms have not always included an appropriate comparison category (Want et al., 2003), which

further motivated the need to use a nonface category in the present study.

We used a perceptual-matching task in which two stimuli were presented simultaneously and the participant decided whether they were the same or different. We chose this matching task, rather than old/new recognition or identification, because we were interested in perceptual processing of faces, rather than in mnemonic aspects of face processing. Simultaneous matching of stimuli emphasizes perceptual analysis and has no memory load. Therefore, the present matching task allowed us to assess developmental changes in perception and cognition apart from developmental differences in memory capacity (Want et al., 2003). We predicted that, behaviorally, adults would show the classical face inversion effect first reported by Yin (1969); specifically, inversion would disrupt face processing more than it would animal processing. Children were not expected to show a strong inversion effect, given previous behavioral findings that inversion does not disrupt face processing in children to the same degree that it does in adults (Carey & Diamond, 1977, 1994; Donnelly, Hadwin, Cave, & Stevenage, 2003). In line with the behavioral prediction, we also expected that adults would show a dissociation of brain activation patterns between upright and inverted face matching but no dissociation for upright and inverted animal matching. Children were expected to show minimal differences between upright and inverted matching for either faces or animals, given that, behaviorally, their face recognition performance is not strongly disrupted by inversion.

In addition to the matching tasks, we also used a passive-viewing face localizer task commonly used in brain activation studies of face recognition. This task can isolate a fairly well circumscribed region in the fusiform gyrus that responds more strongly to faces than to nonface objects and is referred to as the *fusiform face area* (FFA; Kanwisher et al., 1997). However, because findings are mixed as to whether inversion of faces has no effect on FFA response (Aguirre, Singh, & D'Esposito, 1999; Haxby et al., 1999) or a slight reduction in FFA response (Yovel & Kanwisher, 2004) in adults, more studies of face inversion are needed. Moreover, only one study to date has examined the effect of face inversion on FFA response in children (Aylward et al., 2005). Consequently, more studies of face inversion are needed to further characterize the response properties, cognitive processing, and developmental time course associated with functionally defined cortical regions such as the FFA.

METHOD

Participants

Twenty-eight 5- to 11-year-old healthy children with no significant medical histories were compensated for participation. Two children did not complete the study, due to equipment problems (a 5- and a 7-year-old). Data from 9 other participants were omitted due to excessive head motion (these children ranged in age from 9 to 11 years), and 1 child was omitted for less-than-chance performance (a 6-year-old). Thus, data from 16 participants (11 males; age range, 7–11 years; median age, 9 years, 8 mos.) were submitted to

further analyses for the fMRI tasks. The *younger* group of children consisted of those 8 individuals below the median age (mean age = 8 years, 8 mos.), and the *older* group consisted of those 8 individuals above or equal to the median age (mean age = 10 years, 7 mos.). Eighteen adults (7 males; mean age, 28 years, 8 mos.) were compensated for participation, but 2 were omitted for excessive head motion. Thus, data from 16 adults were submitted to analyses in both the face localizer and the matching tasks. All the volunteers had normal visual acuity, were fluent in English, and showed a right-hand preference on the basis of an adaptation of the Edinburgh Handedness Survey (Oldfield, 1971). The receptive and expressive language skills of the adults and children were within normal age limits, as determined by the Peabody Picture Vocabulary Test (Dunn & Dunn, 1997) and the Expressive Vocabulary Test (Williams, 1997). In accordance with the guidelines of the University of Kentucky Institutional Review Board, the adult participants gave written consent, the child participants gave written assent, and the parents of the children gave written consent.

Stimuli

For the face- and animal-matching tasks, the stimuli were 26 grayscale photographs of unfamiliar faces (14 female and 12 male faces) scanned from a high school yearbook and 37 line drawings of animals used in previous studies (e.g., Joseph, 1997). Because we had similarity rating, reaction time (RT), and error data for both face photographs and animal line drawings, we used the line drawings of animals for our control stimuli, which allowed us to equate faces and animals for difficulty prior to scanning. The stimuli were presented in pairs, with one stimulus presented above and one below a fixation cross in the center of the screen (Figure 1). The pair of images was enclosed in a box, and the entire display subtended a visual angle 2.6° in height. Twenty-four *different* pairs of faces and animals and 8 *same* pairs from each category were constructed. For face *same* pairs, the same face was presented, but one of the faces was a left-right reversal of the other. For animal *same* pairs, two different exemplars, views, or positions of the animal were presented (for 5 adult and 3 children participants), or left-right reversals of the same version of the animal were presented (for 11 adult and 13 children participants).¹ The *different* animal pairs consisted of two different animals that did not evoke the same name, as determined by previous name agreement data (Joseph & Gathers, 2003). Animal and face pairs were chosen on the basis of previous similarity ratings (Gathers, Bhatt, & Joseph, 2004; Joseph, 1997). To optimize task performance in the children, only low-similarity pairs were used.

Each stimulus pair appeared in both an upright and an inverted orientation once throughout the experimental session. For the passive-viewing face localizer task, the stimuli consisted of 30 grayscale photographs of human faces, 30 natural objects (e.g.,

fruits and vegetables), and 30 manufactured objects (e.g., tools and household objects; for more details, see Gathers, Bhatt, Corbly, et al., 2004; Joseph & Gathers, 2002). Each stimulus was presented individually in the center of the screen and subtended a visual angle of 2.17° .

Design

The participants performed one run of animal matching, one run of face matching, and one face localizer run, with task order counterbalanced across participants. We collected 100 brain volumes in each animal- or face-matching run, which was organized in a block fashion. Each experimental block consisted of eight trials, with two match and six mismatch pairs randomly ordered within a block. The orientation of the images (upright vs. inverted) was manipulated across blocks, with upright and inverted blocks alternating with each other. Experimental blocks were interleaved with blocks of four fixation trials (16 sec each).

We collected 90 brain volumes for the face localizer run, which consisted of 270 trials, organized into nine 42-sec, pseudorandomly ordered task blocks: three of each stimulus type (unfamiliar faces, natural objects, and manufactured objects). A task block consisted of 30 randomly ordered stimuli. The 9 task blocks were interleaved with 8 fixation blocks 18 sec in duration. The individual face, manufactured, and natural stimuli were repeated three times during the face localizer run.

Procedure

During the training session for the matching task, the participants were trained to identify which pairs of objects or faces constituted a match by viewing each pair at a self-paced rate. They were also trained to use the response pad by pressing one button for match trials and another button for mismatch trials. In these 24 practice trials (2 categories $\times$ 2 orientations $\times$ 2 match conditions [match/mismatch] $\times$ 3 repetitions), the timing parameters were the same as those used during the fMRI session (see below). Training for the passive-viewing face localizer task (15 practice trials) required the participants to press a button with their index finger each time they saw a stimulus, regardless of the category.

During the fMRI matching tasks, the experimental trials were synchronized with the fMRI scans with a trigger pulse from the scanner that started each trial. Each trial lasted for 4,000 msec, with the stimulus pair displayed for 2,500 msec and a fixation crosshair for 1,500 msec. This stimulus duration was determined on the basis of pilot data, showing that children have greater-than-chance performance and minimum anxiety at a 2,500-msec exposure duration. The participants were instructed to respond to a match pair with the index finger and a mismatch pair with the middle finger of their

Figure 1. Sample face and animal pairs used in the present study.

right hand and to respond as accurately and quickly as possible. The participants could respond at any time during the presentation of the picture, so they had a maximum time of 2,500 msec to respond.

For the face localizer task, each stimulus was presented for 1,000 msec, followed by a 400-msec crosshair fixation (trials were not triggered by the scanner). The participants were instructed to view the pictures, to push a button beneath their index finger each time a picture appeared, and not to respond to fixation. All the stimuli were presented using a high-resolution rear projection system (Avotec, Stuart, FL) and an MRI-compatible response glove. A Dell Dimension XPS T800t computer running E-Prime 1.0 (Psychology Software Tools, Pittsburgh) controlled stimulus presentation and the recording of responses.

fMRI Image Acquisition

A 1.5 T Siemens Vision magnetic resonance imaging system located at the University of Kentucky Magnetic Resonance Imaging and Spectroscopy Center (MRISC) equipped for echo-planar imaging (EPI) was used for data acquisition. For each matching task, 100 EPI images were acquired (TR = 4,000 msec, TE = 40 msec, flip angle = 90°), each consisting of 44 axial slices (matrix = 64 × 64, FOV = 228 × 228 mm, thickness = 3 mm, gap = 0.6 mm) to yield images with 3.6-mm³ voxels. Acquisition of the face localizer data differed from matching task acquisition in three parameters. A total of 90 EPI images were acquired (TR = 6,000 msec), each consisting of 46 contiguous axial slices. At the end of the experiment, a high-resolution T1-weighted MP-RAGE anatomical scan (150 sagittal slices for the adults and 76 sagittal slices for the children, matrix = 256 × 256, FOV = 256 × 256 mm², slice thickness = 1 mm for the adults and 2 mm for the children, no gap) was collected for each participant.

fMRI Data Analysis

The fMRI data were analyzed in two phases: individual-subject analysis and mixed effects group analysis. For the individual-subject analysis on the matching tasks, the first four volumes of each run were discarded, to allow the MR signal to reach steady state (the first three volumes for the face localizer task). Using FMRIB's FSL package (www.fmrib.ox.ac.uk/fsl), images in each participant's time series were motion corrected with the MCFLIRT module of the FSL package. Functional runs were discarded when uncorrected head motion exceeded half a voxel (1.7 mm). Using the mean of each individual's residual motion following implementation of MCFLIRT, a one-way between-subjects ANOVA indicated no significant difference [$F(1,31) = 0.901, p < .350$] in corrected head motion between age groups (children vs. adults). Images in the data series were then spatially smoothed with a 3-D Gaussian kernel (FWHM = 7.5 mm) and were temporally smoothed using a high-pass filter (192 sec for the matching task and 360 sec for the face localizer task). The FEAT module of the FSL package was used for image processing and statistical analyses.

Customized square waveforms (on/off) were generated for each participant according to the order of experimental conditions that he or she completed. These customized waveforms were generated for each condition (e.g., upright face) representing the blocks in which the participant encountered that condition (i.e., on), in comparison with the blocks in which he or she did not (i.e., off). These waveforms were then convolved with a double-gamma hemodynamic response function. For each participant, we used FILM (FMRIB's Improved Linear Model) to estimate the hemodynamic parameters for different explanatory variables (face inverted, face upright, animal inverted, and animal upright) and to generate statistical contrast maps of interest (face inverted vs. face upright and animal inverted vs. animal upright). Considering the relatively greater head motion in the localizer data from the children, we also added six movement parameters (three rotation values in radians and three translation values in millimeters) as covariates of no interest, in order to model the variance in the fMRI signal induced by head motion.

After statistical analysis for each participant's time series, contrast maps were normalized into common stereotaxic space before mixed effects group analyses were performed. This involved registering the average EPI volume to the MP-RAGE volume and the MP-RAGE volume to the ICBM152 T1 template, using FLIRT (FMRIB's Linear Image Registration Tool) module of the FSL package.

In the mixed effects group analysis, the spatially normalized contrast maps from individual participants were used. Given previous reports of differences in face processing between older and younger children (e.g., Gathers, Bhatt, Corbly, et al., 2004), we added a binary age covariate to model the age difference when we performed the group analyses on the face localizer and matching task data from the children. To identify the regions of brain activation, we defined regions of interest (ROIs) first by clusters of 10 or more contiguous voxels (Xiong, Gao, Lancaster, & Fox, 1995) in which parameter estimate (PE) values differ significantly from zero ($p < .01$, two-tailed). Using the Mintun peak algorithm (Mintun, Fox, & Raichle, 1989), we further located the local peaks (maximal activation) within each ROI. We then obtained an activation map for each effect alone.

RESULTS

Behavioral Results

To characterize behavior, we used four dependent measures: RT, error rate, sensitivity, and bias. To satisfy the normality assumption for multivariate analysis, we applied a log-transformation to the RT data to normalize the RT distribution. Log-transformed RTs from individual trials greater than three standard deviations from the overall group mean were considered outliers (0.1% of the data). Only correct log-transformed RTs were submitted to analyses (93% of the data). Due to constraints on the length of fMRI studies, the number of trials per cell of the design was not sufficient to use a parametric approach to signal detection (Macmillan & Creelman, 1991); hence, we used a nonparametric approach to compute bias and sensitivity (Donaldson, 1992). Bias values could range from -1 to 1 , with negative values indicating a bias to respond *same*, or a liberal bias. Higher sensitivity values indicate greater discrimination between *same* and *different* pairs, and a sensitivity value of .5 indicates chance performance. We analyzed the inversion effect for each dependent variable in a separate three-way mixed ANOVA, using the multivariate approach (O'Brien & Kaiser, 1985), with category (animals or faces) and orientation (upright or inverted) as repeated factors and age (adult, older children, or younger children) as a between-subjects factor. For these ANOVAs, results from multivariate tests are reported because they are identical to the results from univariate tests.

Figure 2 shows the group-averaged RT, errors, bias, and sensitivity values as a function of age, category, and orientation. Face matching was more difficult than animal matching. Face matching took longer [$F(1,26) = 24.0, p < .0001$], produced more errors [$F(1,26) = 12.1, p < .002$], and reduced sensitivity [$F(1,26) = 14.4, p < .001$], relative to animal matching. The reduced sensitivity for faces was especially pronounced for the younger children [category × age interaction, $F(2,26) = 3.6, p < .04$], as would be expected on the basis of previous findings in the literature (e.g., Carey & Diamond, 1977). Inverted matching was more difficult than upright matching in that

Figure 2. Behavioral performance as a function of age (adults, older children, or younger children), category (faces or animals), and orientation (upright or inverted) for (A) error rate, (B) reaction time (RT), (C) sensitivity, and (D) response bias. An asterisk indicates a significant simple effect of category at $p < .05$.

it took longer [$F(1,26) = 18.7, p < .0001$], yielded more errors [$F(1,26) = 16.8, p < .0001$], and reduced sensitivity [$F(1,26) = 8.7, p < .007$], but these effects were not different for adults and children (orientation $\times$ age interaction, n.s.). The effect of age did not reach significance

for any dependent measure but was marginally significant for RT [$F(2,26) = 2.8, p = .082$].

We expected to replicate the oft-reported face inversion effect (e.g., Yin, 1969) with a significant category $\times$ orientation interaction in which inversion affected face

matching more than it did nonface (i.e., animal) matching. Indeed, the category $\times$ orientation interaction was significant for RT [$F(1,26) = 6.4, p < .018$], errors [$F(1,26) = 9.5, p < .005$], and bias [$F(1,26) = 4.4, p < .05$]. As is shown in Figure 2, inverting animal pairs had less impact on these dependent measures than did inverting faces. Face inversion was associated with longer RTs, more errors, and a shift away from a bias to respond *different* (indicated by a positive value for the bias measure) toward an unbiased response (a value close to 0). The three-way interaction of category, orientation, and age was marginal for RT [$F(2,26) = 2.5, p = .10$] but was not significant for the other dependent measures. When the two child groups are combined into a single group, the three-way category $\times$ orientation $\times$ age interaction is significant [$F(1,27) = 4.3, p < .05$], suggesting clear differences between adults and children in terms of the face inversion effect. The smaller group sizes that resulted from dividing the children into separate age groups likely reduced the power to detect age effects and interactions.

Although the three-way interaction of category, age, and orientation was marginal only when we used two subgroups of children, we proceeded to explore face inversion effects separately within each age group because (1) prior findings have clearly indicated developmental changes in the face inversion effect (e.g., Carey & Diamond, 1977, 1994; Mondloch et al., 2002), (2) age did interact with category (for the sensitivity measure), and (3) the fMRI results (presented below) suggested interactions with age. Within each age group, we conducted paired t tests (or

simple main effects; see Keppel & Zedeck, 1989) contrasting inverted versus upright faces and inverted versus upright objects. Significant contrasts are indicated with an asterisk in Figure 2. In the adults, inversion disrupted performance for faces, but not for animals, in terms of RT ($p < .0001$) and errors ($p < .01$). In the older children, inversion disrupted performance for faces ($p < .042$), but not for animals, for RT.

In summary, the behavioral data show that inversion disrupts matching of faces more than it disrupts matching of animals in the case of performance accuracy and RT for adults. Older children also showed poorer performance with inverted faces than with upright faces for RT. Younger children, however, did not show a face inversion effect for any dependent measure. Hence, there was a developmental change in the face inversion effect, as has often been reported in other studies.

Brain Imaging Results: Regions Involved in Matching Tasks

Given that the adults showed significant face inversion effects behaviorally but the youngest children did not, we expected that the adults would show more dissociated brain activation for inverted versus upright face matching in visual-processing regions than would the children. However, neither the children nor the adults were expected to show dissociated activation for inverted versus upright animal matching. This hypothesis was confirmed. Figure 3 shows the inverted versus upright contrast for face matching in the adults, with all the visual-processing

Figure 3. Brain activation results for inverted versus upright face matching at $p < .01$, two-tailed, and cluster size >10 voxels for adults (top row) and children (bottom row). Axial slices are labeled by the MNI z -coordinate. The three regions indicated with circles showed developmental changes: (A) the left superior occipital gyrus ($x = -26, y = -86, z = +24$; BA 19), (B) the left middle occipital gyrus ($x = -36, y = -86, z = +4$; BA 18), and (C) the right fusiform gyrus ($x = +28, y = -42, z = -12$; BA 37). Labels A–C correspond to the graphs in Figure 4.

regions outlined in Table 1. The adults showed extensive differential activation between inverted and upright face matching in the ventral processing stream (VPS) and other visual association areas centered primarily in the inferior and middle occipital gyri, with a small region emerging in the right anterior fusiform gyrus. Importantly, the adults did not show this same extent of dissociated activation for inverted versus upright animal matching (see Table 2). In fact, only one visual-processing region (the right middle occipital gyrus) emerged for inverted versus upright animal matching in the adults.

The children as a group showed some differential activation for inverted versus upright face matching in visual-processing regions, but it was not as extensive as that for the adults. Moreover, the children showed no differential activation for inverted and upright animal matching in any visual-processing regions (Table 2). Two regions in the group analysis of face matching for the children showed a significant effect of age (indicated with an asterisk in Table 1). A left superior occipital region that overlapped slightly with the adult left middle occipital region emerged as significant (Region A in Figure 3). In addition, a small right anterior fusiform region that was somewhat ventral to a similar adult region also showed a significant age effect for upright versus inverted faces.

To confirm these qualitative differences in brain activation as a function of inversion in the two age groups, we directly compared the face-inverted versus face-upright statistical map for the adults with the face-inverted versus face-upright statistical map for the children, using a mixed effects analysis. This direct group comparison yielded essentially the same pattern of results as the within-group contrasts. Namely, the four visual-processing regions that were recruited for inverted face matching in the adults (Table 1) also emerged in this analysis, providing quantitative support for a greater dissociation between upright and inverted face matching in adults than in children.

Table 1
Visual Processing Regions Recruited for Face Matching

Age	Region	BA	Size	<i>x</i>	<i>y</i>	<i>z</i>
Inverted > Upright Faces						
Adult	R. inferior occipital gyrus	19	22	+46	-72	-16
	R. fusiform gyrus	37	22	+28	-42	-10
	L. middle occipital gyrus	18	759	-36	-86	+4
	R. middle occipital gyrus	19	29	+34	-80	+14
Child	L. fusiform gyrus	37	11	-46	-58	-14
	L. inferior occipital gyrus	18	11	-26	-92	-10
	L. middle occipital gyrus	18	13	-26	-82	+10
	L. superior occipital gyrus*	19	79	-26	-86	+24
Upright > Inverted Faces						
Adult	L. calcarine sulcus	18	11	-12	-88	-6
Child	R. fusiform gyrus*	37	16	+38	-42	-20
	L. lingual gyrus	18	36	-18	-54	+4

Note—All activated regions are significant at $p < .01$, two-tailed, and cluster size > 10 voxels. BA, Brodmann's area. *Regions in which age explained a significant amount of variance at $p < .01$, two-tailed.

Table 2
Brain Regions Recruited for Animal Matching

Age	Region	BA	Size	<i>x</i>	<i>y</i>	<i>z</i>
Inverted > Upright						
Adult	R. hippocampus	20	11	+40	-28	-6
	R. middle occipital gyrus	18	56	+32	-80	+12
	R. supramarginal gyrus	40	180	+38	-46	+40
	L. superior parietal lobule	7	80	-22	-66	+50
	R. superior parietal lobule	7	389	+22	-64	+54
	R. precentral gyrus	6	14	+26	-14	+60
Child	R. cerebellum		21	+36	-44	-46
	R. cerebellum		14	+24	-62	-42
	R. cerebellum	37	69	+54	-52	-30
	L. cerebellum	37	10	-24	-30	-30
	L. cerebellum	19	35	-18	-62	-14
	L. putamen	48	19	-32	+6	-4
	R. inferior frontal gyrus	44	21	+44	+4	+24
	R. superior parietal lobule	7	16	+22	-64	+52
Upright > Inverted						
Adult	R. putamen	48	12	+36	-4	-2
	R. precuneus	30	17	+16	-50	+18
Child	R. hippocampus	20	16	+38	-28	-6
	R. middle frontal gyrus	10	16	+30	+66	+6
	R. insula	48	19	+30	+16	+12
	L. middle frontal gyrus	10	257	-22	+62	+10
	L. superior temporal gyrus	22	54	-64	-38	+22
	R. precentral gyrus	6	42	+34	-24	+68

Note—All activated regions are significant at $p < .01$, two-tailed, and cluster size > 10 voxels. BA, Brodmann's area.

The group analysis of the data for the children indicated that some visual-processing regions showed differential effects of age for inverted versus upright face matching, perhaps indexing an important developmental change in the processing of inverted faces. However, these analyses do not indicate whether the face inversion effect was greater for the younger or the older children. In addition, it is possible that either group of children produced a greater face inversion than animal inversion effect in the same regions that the adults did, but below the statistical cutoff that we used. To explore these possibilities, we conducted ROI analyses on the four adult face-matching regions (inverted > upright faces) and on the two face-matching regions that showed age effects in the child group analysis (inverted > upright faces) in Table 1. Given that the group-level fMRI analyses suggested interactions of age with face inversion effects, we submitted the fMRI signal (expressed as a PE relative to baseline) from the two face conditions (upright and inverted) in each cluster to a two-way ANOVA with orientation as a repeated factor and age as a between-subjects factor.

A significant orientation $\times$ age effect emerged in the left superior occipital gyrus region ($x = -26$, $y = -86$, $z = +24$) that showed an age effect for inverted versus upright faces in the children [$F(2,28) = 4.0$, $p < .03$]. The fMRI signal in this region is plotted in Figure 4A. Both the adults and the older children showed a greater signal for inverted than for upright faces, whereas the younger children showed a greater signal for upright faces. The face inversion effect (inverted - upright faces) was greater in the older

Figure 4. fMRI signal for face matching in regions that showed developmental changes illustrated in Figure 3: (A) the left superior occipital gyrus ($x = -26, y = -86, z = +24$; BA 19), (B) the left middle occipital gyrus ($x = -36, y = -86, z = +4$; BA 18), and (C) the right fusiform gyrus ($x = +28, y = -42, z = -12$; BA 37). An asterisk indicates that the difference between inverted and upright faces was significant according to paired t tests ($p < .05$; A–C) or that the face inversion effect was greater in older than in younger children (A) at $p < .05$.

children than in the younger children (Tukey's honestly significant difference test: $p < .05$) but was not different between the older children and the adults ($p = .228$).

Two of the adult regions that showed a greater response to inverted than to upright faces showed marginal orientation $\times$ age interactions. The left middle occipital gyrus region ($x = -36, y = -86, z = +4$) showed a gradual increase in face inversion effect with age [orientation $\times$ age interaction, $F(2,28) = 2.5, p = .10$], and this interaction became significant when the two child age groups were combined [$F(1,29) = 4.7, p < .04$], indicating that the age effect was largely between the adults and the children, rather than between the two child groups. Hence, only adults showed a significant difference between inverted and upright faces in this region, as was shown by a paired t test ($p < .001$; indicated by an asterisk in Figure 4B). In the right fusiform gyrus region ($x = +28, y = -42, z = -10$), the adults showed a greater face inversion effect than did either group of children [orientation $\times$ age interaction, $F(2,28) = 2.7, p = .087$], and the interaction became significant when the two child age groups were combined [$F(1,29) = 5.2, p < .03$; see Figure 4C]. As for the left middle occipital region shown in Figure 4B, the age difference was largely between the adults and the children, rather than between the two child groups. Not surprisingly, the difference between inverted and upright faces was significant in this region only for the adults ($p < .002$).

Although the children showed minimal dissociated brain activation patterns for inverted versus upright face processing in visual-processing regions, the children did show extensive differential activation for upright and inverted faces in other brain regions (Table 3). This activation was most prominent and extensive in the frontal lobe but also emerged in parietal regions. We examined the magnitude of fMRI response in one of these regions—the right middle frontal gyrus—to demonstrate that children produce fMRI signals that are on par with those of adults. In this region, the youngest children produced the greatest activation (PE = 30.5 for inverted faces, relative to baseline) followed by older children (PE = 27.1), followed by adults (PE = 11.3). The age effect was not significant, indicating that children produce robust fMRI activation that is comparable to that of adults.

Brain Imaging Results: Face Localizer Task

Previous studies have implicated the FFA in many aspects of face processing, but the findings are mixed as to whether the FFA is sensitive to inversion (Aguirre et al., 1999; Aylward et al., 2005; Kanwisher, Tong, & Nakayama, 1998; Yovel & Kanwisher, 2004). In the present study, the contrast of upright versus inverted face matching (Table 1) did not implicate a VPS region that was close to the FFA in adults. Hence, it is possible that the FFA was active when both upright and inverted faces were processed, so that the contrast between the two conditions might not reveal differential FFA activation. To further examine the response of the FFA to inversion and to explore potential developmental changes as suggested by a previous study (Aylward et al., 2005), we used the face localizer run to isolate the FFA in both the adults and the children. Following our previous studies (Gathers, Bhatt, Corbly, et al., 2004; Joseph & Gathers, 2002), we isolated the FFA by using face-preferential

Table 3
Other Brain Regions Recruited for Face Matching

Age	Region	BA	Size	<i>x</i>	<i>y</i>	<i>z</i>
Inverted > Upright Faces						
Adult	L. middle frontal gyrus	44/48	17	-38	+16	+30
	R. suppl. motor area	6	12	+10	+10	+52
	L. precentral gyrus	6	15	-38	-8	+42
	L. inferior parietal cortex	40	21	-42	-42	+46
	R. precuneus	7	336	+18	-76	+44
Child	L. precuneus	7	189	-12	-64	+50
	L. cerebellum		84	-28	-56	-48
	R. cerebellum		22	+36	-66	-44
	R. precuneus	17	86	+28	-48	+12
	R. anterior cingulate gyrus	32	165	+14	+32	+16
	R. middle frontal gyrus	46	468	+30	+50	+36
	L. precentral gyrus	6	137	-38	-6	+30
	R. precentral gyrus	6	149	+54	+8	+40
	L. middle frontal gyrus	9	998	-24	+48	+28
	L. precentral gyrus	6	74	-34	-12	+44
	L. superior parietal lobule	7	707	-42	-56	+56
	R. superior frontal gyrus	8	150	+36	+24	+50
	R. superior parietal lobule	7	142	+20	-74	+56
Upright > Inverted Faces						
Adult	L. hippocampus	28	16	-16	-4	-16
	L. putamen	48	25	-20	+8	-8
	R. superior frontal gyrus	11	11	+18	+52	+8
	R. insula	48	41	+34	+20	+16
Child	R. gyrus rectus	25	98	-4	+10	-18
	L. gyrus rectus	11	10	-4	+30	-24
	R. orbito-frontal gyrus	10	53	+10	+48	-4

Note—All activated regions are significant at $p < .01$, two-tailed, and cluster size > 10 voxels. BA, Brodmann's area.

activation in which faces activate a region more than do nonface objects and more than does the baseline task (see Table 4). Within these five regions, we then extracted PEs, relative to baseline, for inverted and upright faces and for inverted and upright animals. We explored face inversion effects and potential developmental differences with a three-way ANOVA in which category (faces or animals) and orientation (upright or inverted) were repeated factors and age (adults, older children, or younger children) was a between-subjects factor. Neither the category $\times$ orientation interaction nor the category $\times$ orientation $\times$ age interaction was significant in any of the five regions. Hence, face-preferential regions, including the classically defined FFA, did not show face inversion effects, in line with previous findings, nor were these regions implicated in developmental changes in face processing.

Combined Face Localizer and Face Inversion Effects

One hypothesis that has emerged in the literature is that inverted faces are processed more like objects than are upright faces (Aguirre et al., 1999; Haxby et al., 1999). With the present data set, inverted faces were processed differently than upright faces, potentially by recruiting the neural substrates used for object processing. To explore this hypothesis directly with the present data set, we used the data from the face localizer run in combination with the data from the face-matching task run. We asked whether inverted face processing overlapped more with

upright object processing or with upright face processing. Specifically, we overlaid the inverted versus upright face contrast (from the matching run) with the activation map for upright faces (i.e., face-preferential activation from the localizer run) and with the activation map for upright objects (i.e., the manufactured objects vs. faces contrast from the localizer run) in the adults. As is shown in Figure 5, inverted face matching overlaps more with passive viewing of upright objects (184 voxels of overlap, indicated in purple) than with passive viewing of upright faces (16 voxels of overlap, indicated in green), despite the fact that low-level image characteristics of upright face stimuli are more similar to inverted face stimuli than to photographs of manufactured objects.

DISCUSSION

The goal of the present study was to examine both behavioral and cortical developmental changes in face processing by comparing upright face matching with inverted face matching, as well as with upright and inverted animal matching. In general, our findings indicate that inversion disrupts face processing more for adults than for children. Adults and older children showed greater disruption in performance with inverted versus upright faces, whereas the youngest children did not. These results concur with other findings in the literature that adults show greater face inversion effects than do children (Carey & Diamond, 1977) and that the face inversion effect increases with age (Carey & Diamond, 1994).

The brain-imaging data mirror this behavioral pattern in that adults showed greater differences in brain activation for inverted versus upright face processing than for inverted versus upright animal matching. Activation in the left middle/superior occipital gyrus was particularly prominent for the processing of inverted faces in adults, and a superior aspect of this region showed greater face inversion effects in older children than in younger children. Taken together, the present findings indicate that inverted face processing changes with development; specifically, the adult face-processing system may be more tuned to upright faces than to inverted faces, whereas the developing face-processing system does not show this preference as strongly. We suggest that when faces are inverted, adults recruit a posterolateral region that is more often engaged in the processing of objects, as is illustrated in Figure 5. This left posterolateral activation may reflect

Table 4
Visual Processing Regions Showing a Face-Preferential Response From the Logical Combination Approach

Age	Region	BA	Size	<i>x</i>	<i>y</i>	<i>z</i>
Adult	R. fusiform gyrus	37	103	+36	-52	-24
	R. cuneus	18	650	+26	-98	-6
	L. middle occipital gyrus	18	1,265	-32	-96	-2
Child	R. fusiform gyrus	37	7	+40	-50	-18
	R. inferior occipital gyrus	19	56	+38	-78	-12

Note—All activated regions are significant at $p < .01$, two-tailed, and cluster size > 6 voxels. BA, Brodmann's area.

Figure 5. Overlapping regions of activation in adults for inverted versus upright face matching ($p < .01$, two-tailed; rendered in blue), upright objects (manufactured objects > faces, $p < .01$, two-tailed; rendered in red), and face-preferential activation [i.e., (faces > baseline) and (faces > natural objects or faces > manufactured objects); $p < .01$, two-tailed; rendered in yellow]. Inverted face activation overlaps more with upright object activation (purple voxels) than with face-preferential activation (green voxels).

featural processing of faces when they are inverted, in accord with other suggestions in the literature (e.g., Carey & Diamond, 1977; Mondloch et al., 2002), but we acknowledge that this does not necessarily imply that inversion disrupts relational processing of faces. In the following discussion, we will elaborate on the suggestion that posterior visual regions are engaged for featural processing, on the basis of evidence that these regions are more strongly engaged for the processing of objects and inverted faces. In addition, we will discuss the role of these posterolateral occipital regions in the development of face processing.

fMRI studies in adults have shown that the regions engaged for inverted face processing are more similar to the regions engaged for the processing of upright objects than to those engaged for the processing of upright faces (Aguirre et al., 1999; Haxby et al., 1999). Yovel and Kanwisher (2004) showed that a region that responds more strongly to objects than to texture patterns (the lateral occipital complex; Malach et al., 1995) was also more responsive to a task that required the processing of parts of upright faces or houses than to a task that required the processing of configural information (i.e., spacing among the parts of the stimulus) of the same stimuli. Marotta, Genovesi, and Behrmann (2001) showed that faces activated more posterior regions of the fusiform gyrus in prosopag-

nosics than in normal adults. Marotta et al. speculated that the prosopagnosics were recruiting posterior regions for feature-based face recognition, which is less efficient than relational processing and may underlie their face recognition deficit. Collectively, these findings suggest that the posterolateral occipital regions that were recruited in the present study for inverted face matching may reflect the processing of face parts, which is more strongly engaged when faces are inverted than when they are upright.

There is also accumulating evidence that younger children or infants engage relatively more posterior visual regions than do older children or adults for face processing. We suggest this may be associated with a greater reliance on featural processing for faces in younger children or infants. For example, de Haan, Pascalis, & Johnson (2002) examined ERPs in adults and 6-month-old infants in response to upright and inverted human and monkey faces. Scalp distributions of event-related activity showed no differences between upright and inverted monkey face processing and differences between upright and inverted human face processing only for adults. For infants, scalp distributions did not differentiate between upright and inverted face processing for either human or monkey faces. In other words, only adults were sensitive to inversion effects for human faces, for which they have much expertise. Interestingly, pos-

terior electrodes showed the greatest difference between inverted and upright face processing in adults. Likewise, in the present study, posterior occipital regions showed the greatest difference between inverted and upright face matching in adults.

Our previous developmental fMRI study of face recognition (Gathers, Bhatt, Corbly, et al., 2004) and the study by Aylward et al. (2005) have shown that younger children recruit more posterior VPS regions for the processing of upright faces. Gathers, Bhatt, Corbly, et al. showed that children 5–8 years of age did not recruit the fusiform face area when passively viewing faces versus nonface objects. Instead, these children recruited the lateral occipital cortex bilaterally in the face condition. Older children 9–11 years of age, however, recruited the right fusiform face area, similar to the region recruited in adults. Likewise, Aylward et al. showed that older children (12–14 years of age) recruited the FFA when passively viewing upright faces versus houses, but younger children (8–10 years of age) recruited the inferior occipital gyrus. Gathers, Bhatt, Corbly, et al. suggested that the similarity in neural correlates for face recognition may reflect the behavioral finding that older children process faces in a way that is more similar to that of adults than do younger children (Carey & Diamond, 1977). Interestingly, the lateral occipital regions recruited for face recognition in the younger children are similar to the areas recruited for inverted face matching in adults in the present study. We speculate, then, that these posterolateral VPS regions may emerge for inverted face processing in adults because they are recruited for featural or parts-based processing of stimuli. Likewise, young children may not have developed relational face-processing abilities fully and will, instead, recruit brain regions involved in featural processing during face recognition tasks. This speculation is supported by other studies (Carey & Diamond, 1994; Mondloch et al., 2002) indicating a gradual development of configural processing in face recognition.

We also explored whether the FFA was affected by inversion and whether there was a developmental change in face processing in this region, but we found no evidence to support either of these hypotheses. This is somewhat at odds with the finding in Aylward et al. (2005), in which the magnitude of FFA activation for viewing faces versus houses was correlated with the magnitude of the behavioral face inversion effect. One reason for the lack of face inversion effects in the FFA may be that we used a perceptual-matching task that made minimal demands with respect to differentiating an individual face from a set of other faces. In contrast, the task used by Aylward et al. was a recognition memory task, which would have made greater demands on individual-face recognition. Hence, the FFA may not have been strongly implicated in face inversion in the present study because we used a perceptual-matching task that did not require individual-face recognition. Another possibility is that the failure to implicate the FFA in the present face inversion task may be that the FFA, instead, serves to discriminate faces from objects, but it may not

be differentially involved in the aspects of face processing that are believed to be affected by inversion (such as configural processing). The latter proposal is consistent with previous reports of no inversion effects in the FFA in adults (Aguirre et al., 1999; Haxby et al., 1999) and the finding that the FFA does not respond differentially to configural and featural processing of faces (Yovel & Kanwisher, 2004).

Although we have developed the idea that the posterolateral occipital activation during inverted face processing in adults reflects featural or parts-based processing of faces, alternative explanations must be addressed. Matching of inverted faces was more difficult than matching upright faces or animals, so the posterolateral occipital activation in adults may have, instead, reflected task difficulty. However, children also had difficulty in matching inverted faces, but they did not show the extensive posterolateral occipital activation that adults did. Another consideration is that face matching requires differentiating stimuli at a subordinate level, whereas animal matching requires differentiating stimuli at a basic level. Had the animal matching required subordinate-level differentiation, perhaps the same pattern of inversion effects for faces would have been observed for animals. This is an interesting possibility, which cannot be addressed with the present data. However, previous studies have implicated more anterior VPS regions or medial temporal lobe regions as involved with subordinate categorization, rather than more posterolateral regions (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Gerlach, Law, Gade, & Paulson, 1999; Joseph & Farley, 2004; Joseph & Gathers, 2003; Price, Noppeney, Phillips, & Devlin, 2003; Rogers, Hocking, Mechelli, Patterson, & Price, 2005; Tranel, Damasio, & Damasio, 1997). Nevertheless, this is an interesting question for future research.

CONCLUSION

The present study showed that face processing undergoes both behavioral and neural changes with development. Performance on a face-matching task was more disrupted by inversion in adults and older children than in younger children. This pattern of results was accompanied by a similar dissociation in brain activation. Namely, the more difficult inverted-face-matching condition recruited the lateral, posterior occipital cortex, in comparison with upright face matching in adults. Older children showed a greater face inversion effect than did younger children in a superior aspect of the posterolateral occipital cortex, pointing to a developmental change in the processing in this region. We propose that for inverted face processing, adults recruit brain regions that are more strongly implicated in featural or parts-based processing that is normally engaged for recognizing objects. Older children show evidence of such processing in similar brain regions, but younger children do not, perhaps due to engaging featural processing for both upright and inverted faces.

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NOTE

1. Although we intended to test for developmental differences in exemplar and left-right reversal match processing, the final number of participants in the exemplar condition was too low to properly test the effects of this variable. Therefore, we collapsed across this variable in subsequent analyses.

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