

Brain Activation during Face Perception: Evidence of a Developmental Change

E. H. Aylward¹, J. E. Park¹, K. M. Field¹, A. C. Parsons¹, T. L. Richards¹,
S. C. Cramer², and A. N. Meltzoff¹

Abstract

■ Behavioral studies suggest that children under age 10 process faces using a piecemeal strategy based on individual distinctive facial features, whereas older children use a configural strategy based on the spatial relations among the face's features. The purpose of this study was to determine whether activation of the fusiform gyrus, which is involved in face processing in adults, is greater during face processing in older children (12–14 years) than in younger children (8–10 years). Functional MRI scans were obtained while children viewed faces and houses. A developmental change was observed: Older children, but not younger children, showed

significantly more activation in bilateral fusiform gyri for faces than for houses. Activation in the fusiform gyrus correlated significantly with age and with a behavioral measure of configural face processing. Regions believed to be involved in processing basic facial features were activated in both younger and older children. Some evidence was also observed for greater activation for houses versus faces for the older children than for the younger children, suggesting that processing of these two stimulus types becomes more differentiated as children age. The current results provide biological insight into changes in visual processing of faces that occur with normal development. ■

INTRODUCTION

Behavioral studies suggest that young children perceive and recognize faces in a manner different from older children and adults. Whereas older children and adults encode faces using a gestalt or holistic strategy based on the face's configural information (the spatial relations among the face's features), research suggests that children under age 10 use a piecemeal or analytic strategy reliant on distinctive facial features (Schwarzer, 2000; Carey & Diamond, 1977). These conclusions are based on findings of the face inversion effect in older subjects (≥ 10 years), but not in younger children (≤ 8 years) (Schwarzer, 2000; Carey & Diamond, 1977). The inversion effect refers to the difference in ability to recognize or remember an upright visual stimulus, as compared with an inverted visual stimulus. The magnitude of this effect is greater for faces than for other objects of comparable complexity (Yin, 1969).

Carey and Diamond (1977) propose that when piecemeal face processing is at work, memory for faces is unaffected by the faces' orientation because featural information remains intact (i.e., the same eyes, nose, and mouth appear in both upright and inverted faces). Gestalt processing, however, relies on configural information that changes when faces are inverted, rendering memory for inverted faces poorer than memory for upright faces. Thus, the lack of a face inversion effect

in younger children has been interpreted as reflecting their tendency to use a piecemeal approach rather than a gestalt, or configural, approach in processing faces.

Several studies have attempted to determine which aspects of the relationships among features are essential for configural processing to occur (see Maurer, Le Grand, & Mondloch, 2002, for review), and suggest that this type of processing involves three different steps. First, there must be sensitivity to first-order relations (e.g., recognizing that a face is a face because it contains two eyes above one nose above one mouth); then holistic processing that "glues" the features into a gestalt; and then sensitivity to second-order relations (e.g., perceiving distances that separate each of the facial features from the others).

In EEG research, the adult N170 recorded over occipito-temporal sensors is considered to reflect the classification of a stimulus as a face (Bentin, Allison, Puce, Perez, & McCarthy, 1996). Eyes and upright faces, unlike nonface objects and scrambled faces (where the face features are unrecognizable), have been shown to evoke N170s in viewers of all ages (Taylor, McCarthy, Saliba, & Degiovanni, 1999). In a study of children ages 4 to 15 years, Taylor, Edmonds, McCarthy, and Allison (2001) showed that developmental changes in the N170 response to upright faces continued until adulthood, suggesting slow maturation of configural processing. In contrast, the N170 in children was of shorter latency and greater amplitude in response to eyes alone than to

¹University of Washington, ²University Of California, Irvine

faces and was mature by 11 years. This suggests that the N170 responds to individual features of faces as well as to configural information, and that this featural processing is in place much earlier than the configural processing.

Many functional MRI (fMRI) studies have demonstrated that the region of the brain that is most activated in adults during viewing of human faces is the fusiform gyrus (e.g., Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Asgari, Gore, & McCarthy, 1995). Further research has suggested that the fusiform gyrus is also activated during viewing of nonface stimuli with which the viewer has particular expertise (e.g., birds viewed by birdwatchers; Gauthier, Skudlarski, Gore, & Anderson, 2000). It has been argued that such expertise, like face perception, involves configural processing of the visual stimuli (Gauthier & Tarr, 2002). Furthermore, it has been argued that the emergence of the face inversion effect results from the development of an “expert means” of representing upright faces that encodes, no longer simply individual features, but the configural information of upright face (Carey & Diamond, 1977). The emergence of the face inversion effect in later childhood may therefore result from the development of an “expert means” of representing upright faces that develops as a result of experience in viewing faces.

Studies suggest that the fusiform region is involved not only in second-order processing, but in first-order processing as well. In fMRI studies, viewing inverted faces causes little or no change in the level of fusiform activation (in comparison to viewing upright faces), suggesting that the fusiform gyrus is involved in first-order processing (recognizing a face because of specific key features), as well as its more traditional role of configural processing (Aguirre, Singh, D’Esposito, 1999; Haxby, Ungerleider, et al., 1999; Kanwisher, Tong, & Nakayama, 1998). These fMRI studies suggest that inverted faces also increase activation in parts of the brain known to be involved in object perception, presumably because of increased difficulty in perceiving the first-order features. N170 data also support the notion that the fusiform gyrus is involved in processing inverted faces (Rossion et al., 2000; Bentin et al., 1996), and therefore must be responding to featural as well as configural data.

Thus, evidence from behavioral studies suggests that young children process faces using a featural strategy and that a configural strategy slowly emerges with age. EEG studies demonstrate that the N170 response to faces decreases in latency and increases in amplitude, with the adult pattern of face processing appearing to be fully in place in the mid-teens. fMRI studies indicate that the fusiform gyrus is the region of the brain that is most activated during face perception in adults. There is as yet no evidence for developmental changes in the fusiform gyrus during viewing of faces.

The current study was designed to assess developmental changes in activation of the fusiform gyrus

during face perception. We hypothesized that older children would demonstrate greater activation of the fusiform gyrus than younger children for faces versus houses because the older children process the configural aspects of the faces. We also hypothesized that levels of activation in the fusiform would correlate positively with a behavioral measure of memory for upright faces and would correlate negatively with memory for inverted faces. Activation of the fusiform was also expected to correlate with a measure of configural processing, the difference in memory accuracy for upright versus inverted faces. These hypotheses were based on the assumption that fusiform activation during viewing of faces reflects the use of configural strategies for viewing faces that should, in turn, yield better face memory.

Previous research suggests that the fusiform gyrus may be involved in processing featural information as well as configural information. We, therefore, hypothesized that younger children would demonstrate more fusiform activation for faces than for houses, but that the level of activation for younger children would be lower than the level of activation for the older children who process configural information as well as featural information.

RESULTS

Behavioral Data

Results of the behavioral testing are shown in Table 1. As expected, older children remembered more upright faces than inverted faces [$t(8) = 3.2, p = .01$]. This difference approached significance for the younger children [$t(8), p = .07$]. Neither group showed significantly poorer memory for inverted versus upright houses. For younger children, the percent difference score for faces (percent correct for faces minus percent correct for inverted faces) was not significantly different from the percent difference score for houses (percent correct for houses minus percent correct for inverted houses) [$t(8) = -0.95, p = .37$]. For the older group, this difference was significant [$t(8) = 3.6, p = .007$], with greater difference between face and inverted face than between houses and inverted houses.

fMRI Results

Results for the faces versus houses comparison are shown in Figure 1 for the younger group, in Figure 2 for the older group, and in Figure 3 for the older versus younger comparison. Functional maps have been registered on a composite of the structural brains for the appropriate age group. As can be seen in Figure 2, activation in the bilateral fusiform gyrus was observed for the older group, with greater activation on the right than on the left. Other regions of activation included

Table 1. Behavioral Data

<i>Group</i>	<i>Stimuli</i>	<i>Percentage Correct ± SD</i>
Younger (<i>n</i> = 9)	Faces	79.6 ± 21.7
	Inverted faces	66.7 ± 12.5
	Difference between faces and inverted faces	13.0 ± 18.7
	Houses	65.7 ± 21.8
	Inverted houses	64.8 ± 16.0
	Difference between houses and inverted houses	0.9 ± 23.4
	(Difference between faces and inverted faces) minus (Difference between houses and inverted houses)	12.4 ± 38.0
Older (<i>n</i> = 9)	Faces	77.8 ± 7.2
	Inverted faces	63.9 ± 17.9
	Difference between faces and inverted faces	13.9 ± 13.2
	Houses	60.2 ± 10.0
	Inverted houses	67.6 ± 17.9
	Difference between houses and inverted houses	-7.4 ± 19.3
	(Difference between faces and inverted faces) minus (Difference between houses and inverted houses)	21.3 ± 17.7

bilateral middle and inferior temporal and occipital gyri. For the younger group, no activation was observed in the fusiform gyrus, but there was activation more laterally in the left inferior temporal gyrus, bilateral occipital gyri, and bilateral anterior temporal lobe. Table 2 presents Talairach coordinates of these regions. Figure 3 demonstrates that the right fusiform region showed significantly more activation for the older children than for the younger children. Other regions that were more activated in older children than younger children included the right middle and inferior temporal and occipital gyri. A separate *t* test showed no areas of greater activation for the younger children in comparison to the older children.

We also assessed differences between younger and older children in level of activation for the houses versus faces comparison. Although neither group showed any regions that were significantly more activated for houses than for faces, the group comparison showed a small

region of greater activation for the older group than for the younger group for houses versus faces in a region medial and superior to the region activated by faces (Figure 4). No other regions of increased activation for the older versus younger group comparison were observed, and there were no regions where younger children showed more activation than older children for the houses versus faces comparison.

Activated Voxels within the Fusiform Gyrus

Within the fusiform gyrus, the number of activated voxels and average *z*-score were determined, and then a ratio was calculated by dividing the number of activated voxels within the fusiform by the number of activated voxels within the total brain. Table 3 shows data for the younger and older groups for the faces versus houses comparison.

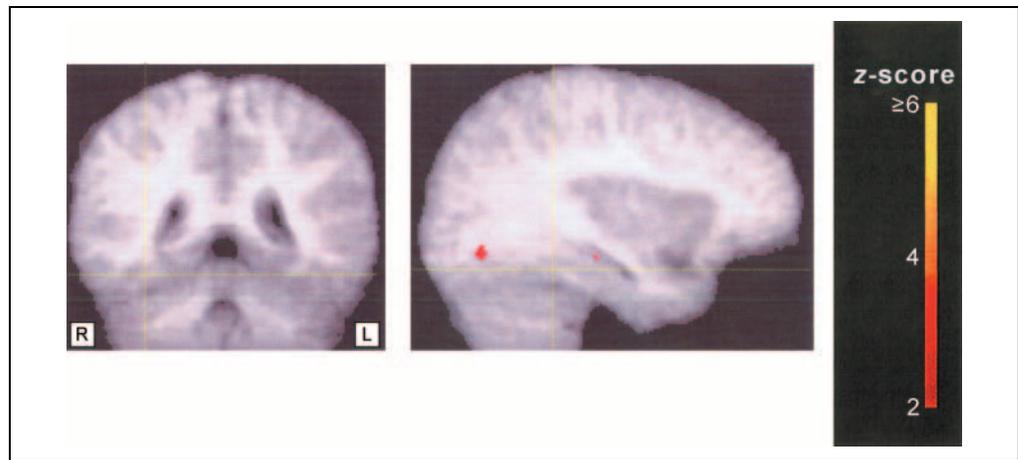
For the faces versus houses comparison, groups did not differ on the number of activated voxels or on the average *z*-score in the fusiform gyrus. The groups did differ, however, on the percentage of fusiform activation (the number of activated voxels in the fusiform divided by the number of activated voxels in the total brain times 100) [$t(16) = 2.2, p < .05$], with older subjects having greater proportional activation. Because of concern that left- and right-handers might show different patterns of results, we repeated the analyses with the three left-handers omitted. We again found that the older children had significantly greater percentage of activated voxels for fusiform gyrus ($p < .05$). No group differences were found for the houses versus faces comparison on average *z*-score, number of activated voxels, or percentage of total brain activation.

There were no significant age group differences for any of the fusiform gyrus measurements for the houses versus faces comparison. There was, however, an Age group (older vs. younger) × Comparison (comparing the activation for houses vs. faces with the activation for faces vs. houses) interaction for percent fusiform gyrus activation [$F(1,16) = 4.9, p < .05$]. Post hoc paired *t* tests revealed no difference between the houses versus faces comparison and the faces versus houses comparison in percent fusiform activation for the younger group, suggesting that the fusiform is essentially processing houses and faces at the same level of activation. The paired *t* test for the older group revealed significantly greater percent fusiform activation for the faces versus houses comparison ($19.8 \pm 13.2\%$) than for the houses versus faces comparison ($12.9 \pm 9.0\%$).

Associations between Behavioral and fMRI Results

Fifteen subjects (9 older and 6 younger) had both behavioral and scan data. Correlations were performed between the behavioral measures (accuracy for faces,

Figure 1. For younger subjects, brain activation during viewing of faces was contrasted with brain activation during viewing of houses. Activation for the group is superimposed upon the averaged structural brain of the younger subjects, warped into stereotaxic space. The significance of activation is indicated by the color bar to the right. Images are in radiological convention. Note that there is no activation in the fusiform gyral region, the center of which is at Talairach coordinates 33, -39, -15, indicated by the cross-hair.



inverted faces, difference between faces and inverted faces, houses, inverted houses, and difference between houses and inverted houses) and: (1) average z-score in the left and right fusiform, (2) number of activated voxels in each region, and (3) percentage of activated voxels in each region (the number of activated voxels in the region divided by the number of activated voxels in total brain).

For the faces versus houses fMRI comparison, the face difference score (faces minus inverted faces) correlated positively with the average z-score in the fusiform gyrus ($r = .65, p < .01$) (Figure 5) and left fusiform ($r = .68, p < .005$), as well as with the number of activated voxels in the fusiform ($p = .66, r < .01$) and left fusiform ($r = .74, p < .005$). Percent fusiform activation in the fusiform also correlated with age ($r = .53, p < .05$) (Figure 6).

Memory for faces or inverted faces alone did not correlate significantly with any of the fusiform measures, although the correlations between memory for inverted faces and fusiform measures were in the predicted directions (positive for faces and negative for inverted faces). Memory for houses or inverted houses (or the

difference score between these measures) did not correlate with activation in the fusiform.

DISCUSSION

This fMRI study is one of the first to demonstrate a developmental change in the way faces are processed in the brain. As shown in Figure 1, there was no significant difference in brain activation in the fusiform gyrus of younger subjects when contrasting viewing of faces versus viewing of houses. Figure 2 shows both right and left fusiform gyral activation for older children when viewing faces versus houses, and Figure 3 shows the contrast between older and younger children. A significant correlation between age and the percent fusiform activation (Figure 6) also suggests that the involvement of the region is developing with age. Activation for faces versus houses was also observed in both the older and younger groups in bilateral inferior temporal and occipital gyri, regions that have been found to be involved in featural processing.

Our results for older children showing greater activation on the right than on the left are consistent with the

Figure 2. The analysis from Figure 1 is shown here in older subjects, with the z-map superimposed upon the averaged structural brain of the older subjects, warped into stereotaxic space. Note activation in the fusiform gyral region when contrasting brain activation during face versus house viewing. Color bar and Talairach coordinates of the cross-hair are the same as for Figure 1.

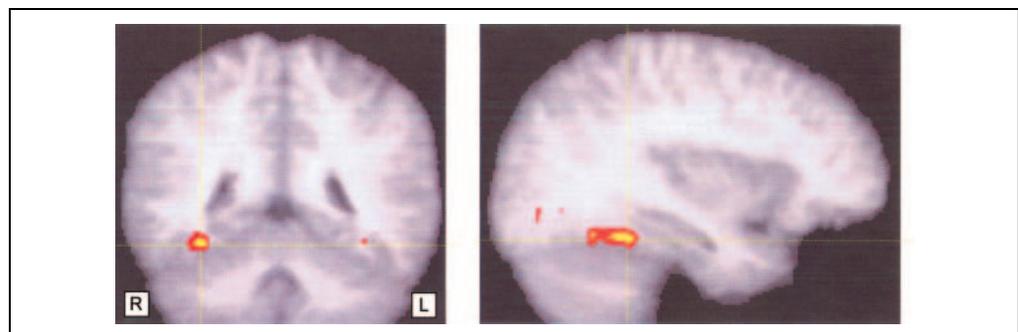
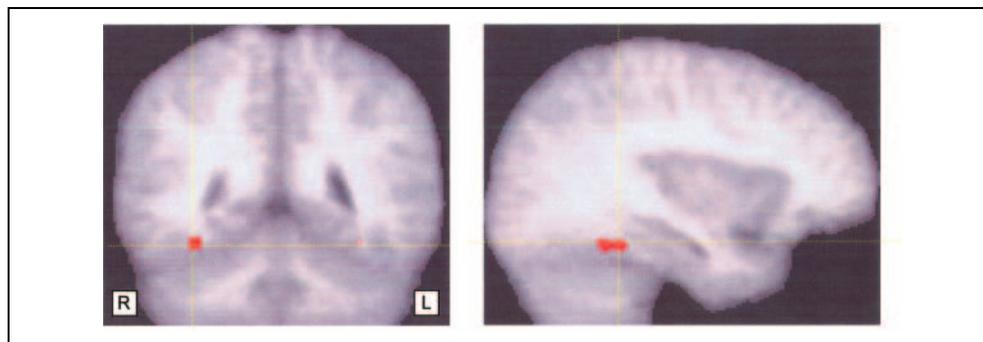


Figure 3. Older subjects contrasted with younger subjects for face versus house viewing. Data are presented on the averaged structural brain from the entire sample, warped into stereotaxic space. Older subjects show greater activation in the right fusiform gyrus. Color bar and Talairach coordinates of the cross-hair are the same as for Figure 1.



adult pattern observed in previous studies (Kanwisher, McDermott, et al., 1997; Puce et al., 1995). The level of activation in the fusiform gyrus for the older children is not, however, as robust as is observed in most other studies with adult subjects. This could suggest that the fusiform is still not functioning at an adult level in children who are 12 to 14 years of age, and that further development will eventually lead to the adult level of activation. This conclusion is consistent with ERP studies showing that developmental changes in the N170 response to upright faces continue until adulthood (Taylor, Edmonds, et al., 2001), suggesting slow maturation of configural processing. Alternatively, the relatively low level of activation in the fusiform may reflect a lack of attention to the stimuli in our study. No behavioral response to the stimuli was required in our fMRI study. Several studies have shown greater levels of activation of the fusiform for active versus passive viewing.

Neither the younger group nor the older group showed significantly greater activation for viewing houses than for viewing faces in any brain region. The lack of activation for houses versus faces in the younger children would be consistent with our conclusion that faces and houses are basically being represented equivalently, although featural processing demands might be somewhat greater for faces than for houses, as suggested by increased activation of inferior temporal and occipital gyri. The older children, unlike adults in pre-

vious studies (Gorno-Tempini & Price, 2001; Epstein & Kanwisher, 1998), showed no areas of greater activation for the houses versus faces comparison in the parahippocampal place area (PPA), or anywhere else in the brain. Previous studies showing PPA activation for places suggest greater activation for scenes than for houses or other buildings, and greater activation for familiar places than for unfamiliar places. Epstein, Harris, Stanley, and Kanwisher (1999) conclude that familiarity of landmarks (campus buildings) increases PPA activity by encouraging scene elaboration. Lack of PPA activation in our study may be associated with the lack of familiarity of the house stimuli.

Although neither younger nor older subjects showed significant activation for houses versus faces, the older group did show more activation for this comparison than did the younger children in a region lateral to the right hippocampus (Figure 4) that has been associated with object perception (Haxby, Ungerleider, et al., 1999). This group difference provides some indication for a developmental trend for processing of house stimuli, with the assumption that even the older children are not yet processing houses in exactly the same region (or to the same extent, in comparison with faces) as adults. This developmental trend, along with increased activation in the fusiform for the faces versus houses comparison, suggests an increasing differentiation of how faces and houses are processed.

Figure 4. Older subjects contrasted with younger subjects for house versus face viewing. Data are presented on the averaged structural brain from the entire sample, warped into stereotaxic space. Older subjects show greater activation in a region just medial to the right hippocampus. Color bar is the same as for Figure 1. Talairach coordinates of the cross-hair are 36, -21, -11.

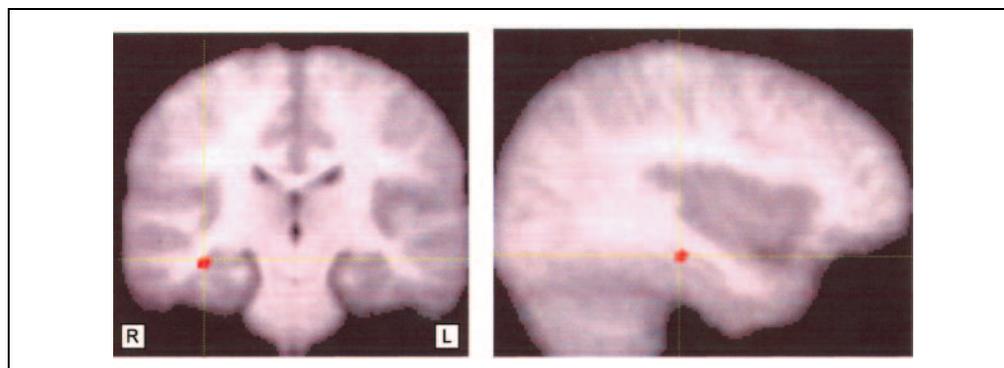


Table 2. Tailarach Coordinates of Regions Other than the Fusiform that were Activated by the Face versus House Comparison for Each Group

<i>Older Group</i>			
R Middle Temporal	56	-33	-6
L Middle Temporal	-55	-10	-7
R Inferior Temporal	42	-48	-6
L Middle Occipital	-39	-70	-7
R Middle Occipital	42	-70	-7
L Inferior Occipital	-35	-64	-5
R Inferior Occipital	43	-72	-6
R Lingual	11	-82	-14
L Lingual	-18	-83	-14
<i>Younger Group</i>			
R Inferior Temporal	43	-44	-10
L Inferior Occipital	-40	-66	-9
R Inferior Occipital	39	-59	-8
R Middle Occipital	36	-68	9
L Superior Temporal	-49	-20	3
R Superior Frontal	7	13	46
<i>Older > Younger</i>			
R Middle Temporal	40	-64	-1
L Middle Temporal	-48	-60	-4
R Lingual Gyrus	13	-82	-10
L Lingual Gyrus	-20	-85	-4

One possible interpretation of our data is that the differentiation of brain regions activated in older versus younger children reflects different “levels” of face processing, such as proposed by a model of a distributed

human neural system for face perception (Haxby, Hoffman, & Gobbini, 2000). Based on a review of many fMRI and evoked potential studies of face perception, Haxby et al. identified three core regions that perform different functions in processing face information. According to this model, the inferior occipital gyri are involved in the most basic processing of featural aspects of the face; the lateral fusiform gyrus processes the invariant aspects of faces; and the superior temporal sulcus appears to be involved in the representation of changeable aspects of faces (e.g., eye and lip movement, expression). Additional areas of the brain are recruited to process the significance of information gleaned from the face, such as emotions (amygdala), or personal identity (anterior temporal). In our study, both the older and younger children demonstrated activation of the inferior occipital gyri, which would be consistent with the role of this region in processing the basic featural aspects of the face. Only the older children, however, showed significant activation of the fusiform gyrus, the second level of the hierarchical model, for the faces versus houses comparison. This study was not designed to test response to changeable aspects of faces (e.g., emotions, eye movement), so we are unable to conclude whether developmental changes would occur in the amygdala or superior temporal gyrus in response to facial movement or expression.

A multiple-component model of face processing is supported by EEG studies suggesting that whole faces, face parts, and even moderately scrambled faces (i.e., where facial parts are easily identifiable) are initially processed in the same regions, although latencies are slightly longer for face parts and scrambled faces (George, Evans, Fiori, Davidoff, & Renault, 1996). Shibata et al. (2002) found two different visual evoked potentials with similar latencies (i.e., N170) that are sensitive to faces in general and human eyes, respectively. Dipole source localization analysis indicated that dipoles for the N170 elicited by eyes were located in the posterior inferior temporal gyrus, and those for faces, located initially in the same region, but moved toward the fusiform and lingual gyri at the late phase of the N170.

Table 3. Activated Voxels within the Fusiform for Faces versus Houses in Younger and Older Subjects

<i>Group</i>	<i>Region</i>	<i>Mean Number of Activated Voxels</i>	<i>Percentage Total Brain Activation</i>	<i>Average z-score of All Voxels within Region</i>
Younger (<i>n</i> = 8)	Right Fusiform	146.7 ± 161.6	3.5 ± 4.2	0.13 ± 0.12
	Left Fusiform	228.5 ± 305.7	4.1 ± 5.9	0.19 ± 0.19
	Total Fusiform	375.2 ± 426.4	7.6 ± 9.0	0.16 ± 0.14
Older (<i>n</i> = 10)	Right Fusiform	340.4 ± 462.9	8.5 ± 11.3	0.25 ± 0.28
	Left Fusiform	503.3 ± 526.7	11.3 ± 10.3	0.32 ± 0.31
	Total Fusiform	843.7 ± 818.0	19.8 ± 13.2*	0.28 ± 0.25

**p* < .05 for comparison of older versus younger subjects.

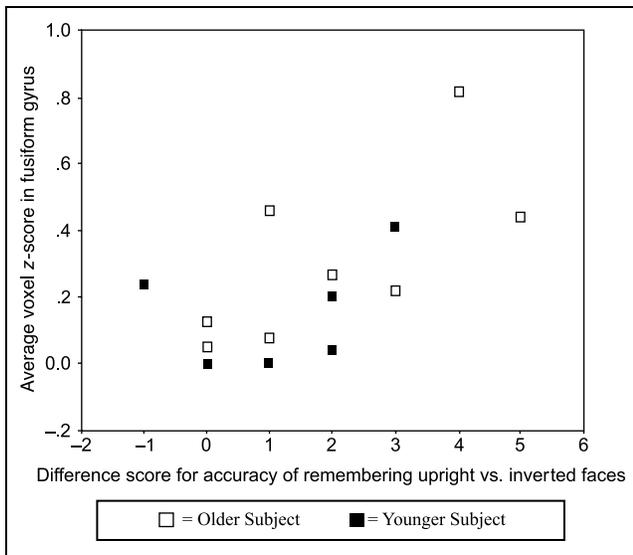


Figure 5. Correlation between difference score for accuracy of memory for upright versus inverted faces and average z-score within the fusiform gyrus. Positive scores reflect better memory for upright than for inverted faces. White squares represent older children and black squares represent younger children.

Our finding of activation of the fusiform and lingual gyri in the older children, but not in the younger children, again suggests that the brains of younger children may be responding more to the features of the face than to the whole face.

Our results are also consistent with an ERP study of children ages 4–14 years and adults (Taylor, McCarthy, et al., 1999) that supports a multicomponent model of face processing. An N170 was recorded to faces at posterior temporal sites across age groups, but at steadily increasing latencies in the younger children. In children under 12 years of age, the frontal P170 could not reliably be seen, leading the investigators to conclude that the underlying neural basis associated with processing faces matures in a gradual, quantitative manner throughout childhood. De Haan, Pascalis, and Johnson (2002) found a putative “infant N170” that distinguished human faces from nonhuman primate faces, but did not respond to the orientation of the face, again suggesting a slowly developing system that grows in specificity in its response to faces.

Although our findings suggest that the brain areas used to process faces and houses change as children get older, we cannot necessarily conclude that increased activation of the fusiform reflects a more “configural” approach to face processing in the older children. The hypothesis that younger children process faces with a more piecemeal approach than a configural approach was only marginally supported by our behavioral data. The difference in accuracy for remembering upright versus inverted faces was only slightly greater in older subjects than in younger subjects, and this group differ-

ence was primarily due to better performance by the older subjects for inverted houses than for upright houses. Our behavior data are, however, consistent with results from other studies that suggest steady progress toward using a configural approach to process faces (Bruce et al., 2000; Carey, Diamond, & Woods, 1980) in children between ages 6 and 10, rather than a sudden strategic shift after age 10. Indeed, previous behavioral studies suggest that a face inversion effect may be seen under certain circumstances at much younger ages (Mondloch, Le Grand, & Maurer, 2002; Bruce et al., 2001; Freire & Lee, 2001), possibly even in infants (Cohen & Cashon, 2001), and that a steady improvement occurs in upright face-encoding efficiency in children from age 6 to age 10 (Carey & Diamond, 1994). We suspect that a younger sample of children would be required to show a total lack of memory difference for upright versus inverted faces. Similar to our older group of subjects, the older subjects (10-year-olds) in the study by Carey and Diamond (1977) also showed somewhat better performance on inverted houses than on upright houses.

Our correlational data support to some extent the hypothesis that the developmental increase in fusiform activation may be associated with a greater configural (as opposed to “piecemeal”) approach to face processing. Activation in the fusiform for the faces versus houses comparison was significantly correlated with the difference in memory for faces versus inverted faces. If one accepts the assumption that the discrepancy in memory for upright versus inverted faces reflects the extent to which a configural approach is being used, our correlational data provide some evidence that children with greater fusiform activation are more successful at using configural processing (Figure 5). Gauthier, Skudlarski,

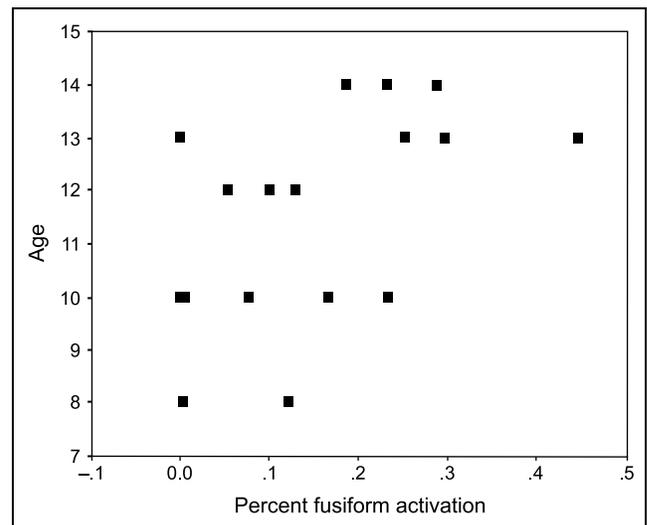


Figure 6. Correlation between age and percent fusiform activation (the number of activated voxels in the fusiform divided by the number of activated voxels in the entire brain, multiplied by 100).

et al. (2000) found similar results, with relative expertise for birds or cars (as measured by tests that required matching of bird species or car model year) positively correlated with relative percent signal change for birds versus cars in the right fusiform face area. Although we hypothesized negative associations between fusiform activation and memory for inverted faces, and positive associations between fusiform activation and memory for faces, these correlations were not significant. Thus, it appears that activation in the fusiform gyrus is associated with use of a configural strategy, but that it is not necessarily associated with accuracy of memory for faces, as many other factors must certainly affect this type of memory. In this sample, neither memory for upright nor memory for inverted faces was correlated with the face difference score ($r = .14$ and $.004$, respectively), which is assumed to reflect use of a configural strategy.

Recent studies have suggested that the fusiform gyrus is activated by stimuli with which the viewer has “expertise” (Gauthier, Skudlarski, et al., 2000). Furthermore, an “inversion effect” can be observed for stimuli other than faces with which the viewer has expertise (Gauthier, Skudlarski, et al., 2000; Carey & Diamond, 1986). Carey and Diamond (1977) theorize that the substantial effect of face inversion that emerges after age 10 results from the development of an expert means, based on experience, of representing upright faces that encodes not simply individual distinctive features, but the configural information of upright faces. Alternatively, it could be argued that the fusiform gyrus is not developmentally “ready” to deal with stimuli in a configural manner until the child is older, and this maturation may be somewhat independent of the number of faces encountered in one’s lifetime. According to this view, the child must rely on a piecemeal approach for perception until the fusiform gyrus matures. Our results cannot clearly adjudicate between these alternative hypotheses.

Previous research suggests that the fusiform gyrus is activated when adults view inverted faces as well as upright faces (Aguirre et al., 1999; Haxby, Ungerleider, et al., 1999; Kanwisher, Tong, et al., 1998), suggesting that this brain region is involved in featural processing as well as in configural processing. We did not, however, find significant differences in fusiform activation for the younger children when they viewed faces versus houses, suggesting that the fusiform gyrus is not even being used for featural processing in younger children. In addition, for the young children, the percent fusiform activation (the number of activated fusiform voxels divided by the total number of activated voxels in the brain) was not significantly different for the faces versus houses comparison ($7.6 \pm 9.0\%$) than for the houses versus faces comparison ($6.5 \pm 8.9\%$; $t = .68$, $p = .52$). This finding might lend support for the interpretation that the fusiform gyrus is not yet fully functionally developed,

as it is not yet responding specifically to faces, either to their featural or configural aspects.

Developmental studies involving training of subjects to increase “expertise” with either face or nonface stimuli may be able to determine whether the limited fusiform activation in the younger children is the result of limited experience with faces, or due to developmental immaturity of the fusiform. [Studies with adults suggest that training on nonface stimuli may activate the fusiform (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999), but these studies have been performed in subjects whose fusiform presumably is functioning in a mature fashion.] Furthermore, such training studies may be helpful in understanding disorders such as autism, in which perception and memory for faces are deficient. Previous research has demonstrated abnormal activation of the fusiform gyrus in adolescent and adult autistic subjects during face perception (Pierce, Muller, Ambrose, Allen, & Courchesne, 2001; Schultz et al., 2000). Similar to the younger children in this study, viewing of faces activated the inferior temporal gyrus in the subjects with autism. Studies of people with autism involving training them with a novel set of faces may be useful in determining whether their lack of focal activation during face processing is the result of: (a) a “faulty” or developmentally immature fusiform gyrus, or (b) a lack of experience with faces, perhaps due to failure to look at people’s faces in early childhood.

The extent to which memory for faces and inverted faces should be associated with fusiform activation is unclear. Although many studies with adults show less fusiform activation for viewing inverted than for upright faces (or trained stimuli), there is little known about the relationship between memory for these stimuli and fusiform activation. However, because it is assumed that the difference in accuracy of recognition for upright versus inverted faces reflects use of configural processing, and activation of the fusiform gyrus is associated with configural processing, it is reasonable to hypothesize that increased activation of the fusiform during viewing of upright faces (as compared with nonface stimuli) will be correlated with better accuracy for face recognition. Based on these assumptions, we hypothesized that levels of activation in the fusiform would correlate positively with memory for upright faces, as well as for the difference in memory accuracy for upright versus inverted faces, and would correlate negatively with memory for inverted faces.

As indicated above, our measure of configural processing (memory for upright vs. inverted faces) correlated significantly with activation in the total fusiform gyrus and in the left fusiform, but not in the right. Most studies with adults suggest fusiform activation on the right is more strongly associated with configural processing. A recent study with children who had restricted vision in the right or left visual fields as infants suggests that input to the right, but not to the left, visual field

caused impaired second-order relational processing (Le Grand, Mondloch, Maurer, & Brent, 2003). There is, however, evidence that both right and left fusiform areas are involved in face processing. Measuring PET response during viewing of faces and nonface stimuli, Rossion et al. (2000) concluded that face-specific processing occurs in both the right and the left middle fusiform gyrus, and show that the response in the left fusiform can be greater than that in the right during face perception if attention is directed toward individual facial features. This is consistent with other behavioral, clinical, and EEG studies (Tovée, 1998; Rhodes, 1993) which suggest that recognition of faces by the left hemisphere of the brain occurs when processing involves more of a piecemeal approach.

Several limitations of this study must be addressed. It could be argued that age group differences in fusiform gyral activation might potentially be explained by a lesser degree of attention to faces for the younger subjects. If this were the case, one would not expect to find any regions of activation for the faces versus houses comparison. The regions that were found to have greater activation for faces than houses for the younger children—the bilateral inferior temporal gyri and inferior posterior occipital region, and the anterior temporal lobe—include regions associated with object perception (Ishai, Ungerleider, & Haxby, 2000). In a PET study of 2-month-old infants, Tzourio-Mazoyer et al. (2002) found that faces activated the same bilateral inferior occipital area that corresponds to an occipital face area previously identified in adults as involved in perceiving featural aspects of faces. Furthermore, one would have expected greater activation for older children than younger children for the faces versus fixation comparison (see Methods, fMRI Techniques). Although the activation for faces versus fixation was somewhat more localized to occipital regions in older children than in younger children, the total number of brain voxels activated for this comparison was not significantly different for the two groups [$t(16) = 0.96, p = .35$]. The potential of differential attention to faces versus houses could be tested in future studies by conducting memory tests for stimuli observed during scanning or by including a test of face matching or working memory during the scan session.

Another possible consideration in interpreting the age group differences would be potential differences in hemodynamic response for the two age groups. Although this was not assessed in this study, previous research has found that peak amplitudes of hemodynamic time courses were comparable between adults and children (ages 7–8) on a simple visual reaction time task in all eight brain regions studied, and that time courses were comparable in seven of eight regions (Kang, Burgund, Lugar, Petersen, & Schlaggar, 2003). These investigators concluded that their findings validate the feasibility of direct statistical comparison of

children and adult fMRI data, suggesting no evidence of developmental changes in the level of general hemodynamic response.

In this study, we did not include children younger than 8 years due to concerns regarding cooperation among younger children during scanning. Because some activation of the fusiform occurred in children age 8–10 years (Table 3), it would be ideal to repeat this study with children who are even younger. Understanding the development of brain function for face processing in normal children will be important in understanding and treating atypical face processing strategies in developmental disorders.

METHODS

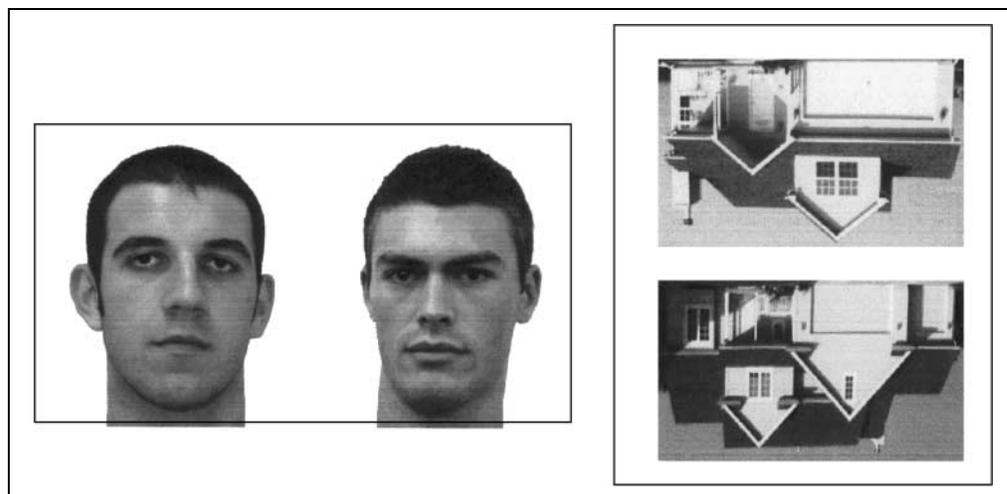
Participants

Participants were 11 children age 8–10 years (7 boys, 4 girls; mean age = 9.3 ± 0.86 years) and 10 children age 12–14 years (6 boys, 4 girls; mean age = 13.0 ± 0.86 years). All but two older girls and one younger boy were right handed. Three of the younger boys could not tolerate the scanning procedure, but behavioral data were available. Behavioral data were not available for one of the older boys and two of the younger boys because of computer problems. Participants were recruited through flyers posted at local schools and in the hospital, and through personal contacts. Children with a neurological disorder or unremovable foreign metal such as oral braces were excluded from the study. Children and their parents gave informed consent prior to the study, which was approved by the University of Washington Human Subjects Institutional Review Board.

Behavioral Techniques

As in the developmental study by Carey and Diamond (1977), participants were presented with two memory tasks. In the first, subjects were asked to remember 15 faces randomly intermixed with 15 houses, each picture shown individually in upright orientation for 2 sec (Figure 7). Immediately afterward, subjects were shown 12 pairs of faces and 12 pairs of houses and indicated via arrow keys which picture in each pair had been previously presented. The second memory task was identical to the first except that faces and houses were presented upside down. The pictures for the two tasks (upright and inverted) were different, with sets counterbalanced across subjects. Thus, the pictures that were presented upright for half of the subjects were presented upside down for the other half of the subjects, and vice versa. Face stimuli were gray-scale digital photos of Caucasian men who were 18–35 years old and without facial hair, glasses, or jewelry. E-Prime (Version 1.0, Psychology Software Tools, Pittsburgh, PA) was used to present the stimuli and to record the participants' responses.

Figure 7. Example of upright and inverted face and upright and inverted house. For the behavioral task, subjects saw individual faces (upright and inverted) and houses (upright and inverted). These are examples of the stimuli used for the forced-choice test condition in which subjects were required to indicate which face or house in the pair was the one they had previously viewed.



Behavioral data were analyzed using the same method used by Carey and Diamond (1977). Percent correct was calculated for each type of stimuli (upright faces, inverted faces, upright houses, inverted houses). A difference score was calculated by subtracting percent correct for inverted faces from percent correct for upright faces, and the same was done for inverted houses and upright houses. Within each group, paired *t* tests were used to determine whether there were differences in memory for upright versus inverted stimuli, and whether difference scores (upright minus inverted) were different for the two types of stimuli.

fMRI Techniques

Scan Acquisition

Structural and functional MRI were performed on a 1.5 T MR imaging system (General Electric, Waukesha). Scanning included a 21-slice axial set of anatomical images in plane with functional data (TR/TE 200/2.2 msec; fast spoiled gradient-echo pulse sequence; 6 mm thick with 1 mm gap; 256 × 256 matrix). Anatomical imaging was followed by an fMRI series using two-dimensional gradient-echo echo-planar pulse sequence (TR/TE 3000/50 msec, 21 slices; 6 mm thick with 1 mm gap, 64 × 64 matrix, 114 volumes total; time = 342 sec). During the scan the subject viewed pictures of faces for a 36-sec epoch, followed by a 36-sec epoch of pictures of houses. Each pair of epochs was repeated 4 times, with novel stimuli used for each epoch. Each picture was presented for 6 sec, with no interstimulus interval. In addition, an 18-sec fixation condition (crosshair) was presented at the beginning, middle, and end of the 342-sec scan. Face stimuli were digital photos of 24 Caucasian adult men and women without glasses or jewelry. No pictures were used as stimuli for both the behavioral and fMRI studies. The conditions were counterbalanced so that faces were shown before houses to

half of the participants in each age group, and houses were shown first to the other half.

Image Processing and Analysis

fMRI scans were analyzed using MEDx (version 3.4.1) (Sensor Systems, Sterling, VA). The data were motion corrected, linear detrended, and a *t* test was performed contrasting the two conditions within each scan, with results expressed as a *z*-score. Each subject's activation *z*-map was spatially smoothed with a 4-mm gaussian filter and converted to standard stereotaxic space of Talairach and Tournoux (1988) using FLIRT (www.fmrib.ox.ac.uk/fsl/). Maps showing significant activation for each group were generated (Bosch, 2000). Activated voxels with $z > 2.4$ and belonging to an activation cluster with size greater than that expected by chance ($p < .05$) were identified (Friston, Worsley, Frackowiak, Mazziotta, & Evans, 1994). This approach considers the significance of activation in the voxel of interest as well as in adjacent voxels to identify a voxel as significantly activated, and also corrects for multiple comparisons. In order to compare *z*-maps between the two age groups, we calculated a *z*-map contrasting respective values using the two-sample test statistic for comparison of means (Rosner, 1995).

In addition to group comparisons of *z*-maps, we also quantified the average *z*-score and the number of activated voxels (i.e., those reaching threshold of ≥ 2.4) in the fusiform gyrus. These activation measures were obtained for each hemisphere and for the two comparisons (faces vs. houses and houses vs. faces). The regions were outlined manually on the stereotaxic space anatomical template, then converted to a mask and applied to each individual subject's *z*-map in stereotaxic space. (Brain volumes for the two groups were not significantly different, $t(16) = 1.8$, $p = .65$, making it unlikely that any systematic variance in the warping

procedure would falsely result in group differences. In addition, visual inspection showed that regions of activation on individual maps were in the same structures as on the group maps.) The total number of significantly activated voxels within the whole brain was also calculated, and ratios were computed (activated voxel count in each region /total brain activated voxel count). Pearson correlations were performed between behavioral data (e.g., memory for upright vs. inverted faces) and the activation data.

Acknowledgments

This work was funded in part by research support generously provided by the UW Center for Mind, Brain & Learning, the Talaris Research Institute, and the Apex Foundation, the family foundation of Bruce and Jolene McCaw. We thank Kenneth Maravilla, director of the Diagnostic Imaging Science Center, MR technicians James Anderson and Gerald Ortiz, and electrical engineers Cecil Hayes and Mark Mathis. We also thank Hunter Hoffman for his assistance in developing our MRI visual presentation system.

Reprint requests should be sent to Elizabeth Aylward, Department of Radiology, Box 357115, University of Washington, Seattle, WA, 98195, USA, or via e-mail: eaylward@u.washington.edu.

The data reported in this experiment have been deposited in the fMRI Data Center (<http://www.fmridc.org>). The accession number is 2-2004-117KC.

REFERENCES

- Aguirre, G. K., Singh, R., & D'Esposito, M. (1999). Stimulus inversion and the responses of face and object-sensitive cortical areas. *NeuroReport*, *10*, 189–194.
- Bentin, S., Allison, T., Puce, A., Perez, A., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, *8*, 551–565.
- Bosch, V. (2000). Statistical analysis of multi-subject fMRI data: Assessment of focal activations. *Journal of Magnetic Resonance Imaging*, *11*, 61–64.
- Brace, N. A., Hole, G. J., Kemp, R. I., Pike, G. E., Van Duuren, M., & Norgate, L. (2001). Developmental changes in the effect of inversion: Using a picture book to investigate face recognition. *Perception*, *30*, 85–94.
- Bruce, V., Campbell, R. N., Doherty-Sneddon, G., Import, A., Langton, S., McAuley, S., & Wright, R. (2000). Testing face processing skills in children. *British Journal of Developmental Psychology*, *18*, 319–333.
- Carey, S., & Diamond, R. (1977). From piecemeal to configurational representation of faces. *Science*, *195*, 312–314.
- Carey, S., & Diamond, R. (1986). Why faces are and are not special: An effect of expertise. *Journal of Experimental Psychology: General*, *115*, 107–117.
- Carey, S., & Diamond, R. (1994). Are faces perceived as configurations more by adults than by children? *Visual Cognition*, *1*, 253–274.
- Carey, S., Diamond, R., & Woods, B. (1980). Development of face recognition: A maturational component? *Developmental Psychology*, *16*, 257–269.
- Cohen, L. B., & Cashion, C. H. (2001). Do 7-month-old infants process independent features or facial configurations? *Infant and Child Development*, *10*, 83–92.
- De Haan, M., Pascalis, O., & Johnson, M. H. (2002). Specialization of neural mechanisms underlying face recognition in human infants. *Journal of Cognitive Neuroscience*, *14*, 199–209.
- Epstein, R., Harris, A., Stanley, D., & Kanwisher, N. (1999). The parahippocampal place area: Recognition, navigation, or encoding? *Neuron*, *23*, 115–125.
- Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature*, *392*, 598–601.
- Freire, A., & Lee, K. (2001). Face recognition in 4- to 7-year-olds: Processing of configural, featural, and paraphernalia information. *Journal of Experimental Child Psychology*, *80*, 347–371.
- Friston, K. J., Worsley, K. J., Frackowiak, R. S. J., Mazziotta, J. C., & Evans, A. C. (1994). Assessing the significance of focal activations using their spatial extent. *Human Brain Mapping*, *1*, 214–220.
- Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience*, *3*, 191–197.
- Gauthier, I., & Tarr, M. J. (2002). Unraveling mechanisms for expert object recognition: Bridging brain activity and behavior. *Journal of Experimental Psychology: Human Perception and Performance*, *28*, 431–446.
- Gauthier, I., Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (1999). Activation of the middle fusiform “face area” increases with expertise in recognizing novel objects. *Nature Neuroscience*, *2*, 568–573.
- George, N., Evans, J., Fiori, N., Davidoff, J., & Renault, B. (1996). Brain events related to normal and moderately scrambled faces. *Cognitive Brain Research*, *4*, 65–76.
- Gorno-Tempini, M. L., & Price, C. J. (2001). Identification of famous faces and buildings: A functional neuroimaging study of semantically unique items. *Brain*, *124*, 2087–2097.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, *4*, 223–231.
- Haxby, J. V., Ungerleider, L. G., Clark, V. P., Schouten, J. L., Hoffman, E. A., & Martin, A. (1999). The effect of face inversion on activity in human neural systems for face and object perception. *Neuron*, *22*, 189–199.
- Ishai, A., Ungerleider, L. G., & Haxby, J. V. (2000). Distributed neural systems for the generation of visual images. *Neuron*, *28*, 979–990.
- Kang, H. C., Burgund, E. D., Lugar, H. M., Petersen, S. E., & Schlaggar, B. L. (2003). Comparison of functional activation foci in children and adults using a common stereotactic space. *Neuroimage*, *19*, 16–28.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 4302–4311.
- Kanwisher, N., Tong, F., & Nakayama, K. (1998). The effect of face inversion on the human fusiform face area. *Cognition*, *68*, B1–B11.
- Le Grand, R. L., Mondloch, C. J., Maurer, D., & Brent, H. P. (2003). Expert face processing requires visual input to the right hemisphere during infancy. *Nature Neuroscience*, *6*, 1108–1112.
- Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Sciences*, *6*, 255–260.
- Mondloch, C. J., Le Grand, R., & Maurer, D. (2002). Configural face processing develops more slowly than featural face processing. *Perception*, *31*, 553–566.

- Pierce, K., Muller, R., Ampbrose, J., Allen, G., & Courchesne, E. (2001). Face processing occurs outside the fusiform “face area” in autism: Evidence from functional MRI. *Brain*, *124*, 2059–2073.
- Puce, A., Allison, T., Asgari, M., Gore, J. C., & McCarthy, G. (1995). Face-sensitive regions in human extrastriate cortex studied by functional MRI. *Journal of Neurophysiology*, *74*, 1192–1199.
- Rhodes, G. (1993). Configural coding, expertise, and the right hemisphere advantage for face recognition. *Brain and Cognition*, *22*, 19–41.
- Rosner, B. (1995). *Fundamentals of biostatistics*. Belmont, CA: Duxbury Press.
- Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S., & Crommelinck, M. (2000). The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: An electrophysiological account of face-specific processes in the human brain. *Cognitive Neuroscience*, *11*, 69–74.
- Schultz, R. T., Gauthier, I., Klin, A., Fulbright, R. K., Anderson, A. W., Volkmar, F., Skudlarski, P., Lacadie, C., Cohen, D. J., & Gore, J. C. (2000). Abnormal ventral temporal cortical activity during face discrimination among individuals with autism and Asperger syndrome. *Archives of General Psychiatry*, *57*, 331–340.
- Schwarzer, G. (2000). Development of face processing: The effect of face inversion. *Child Development*, *71*, 391–401.
- Shibata, T., Nishijo, H., Tamura, R., Miyamoto, K., Eifuku, S., Endo, S., & Ono, T. (2002). Generators of visual evoked potentials for faces and eyes in the human brain as determined by dipole localization. *Brain Topography*, *15*, 51–63.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the brain*. New York: Thieme Medical.
- Taylor, M. J., Edmonds, G. E., McCarthy, G., & Allison, T. (2001). Eyes first! Eye processing develops before face processing in children. *NeuroReport*, *12*, 1671–1676.
- Taylor, M. J., McCarthy, G., Saliba, E., & Degiovanni, E. (1999). ERP evidence of developmental changes in processing of faces. *Clinical Neurophysiology*, *110*, 910–915.
- Tovée, M. J. (1998). Face processing: Getting by with a little help from its friends. *Current Biology*, *8*, R317–R320.
- Tzourio-Mazoyer, N., de Schonen, S., Crivello, F., Reutter, B., Aujard, Y., & Mazoyer, B. (2002). Neural correlates of woman face processing by 2-month-old infants. *Neuroimage*, *15*, 454–461.
- Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, *81*, 141–145.