Cortical Representations of Symbols, Objects, and Faces Are Pruned Back during Early Childhood

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Regions of human ventral extrastriate visual cortex develop specializations for natural categories (e.g., faces) and cultural artifacts (e.g., words). In adults, category-based specializations manifest as greater neural responses in visual regions of the brain (e.g., fusiform gyrus) to some categories over others. However, few studies have examined how these specializations originate in the brains of children. Moreover, it is as yet unknown whether the development of visual specializations hinges on "increases" in the response to the preferred categories, "decreases" in the responses to nonpreferred categories, or "both." This question is relevant to a long-standing debate concerning whether neural development is driven by building up or pruning back representations. To explore these questions, we measured patterns of visual activity in 4-year-old children for 4 categories (faces, letters, numbers, and shoes) using functional magnetic resonance imaging. We report 2 key findings regarding the development of visual categories in the brain: 1) the categories "faces" and "symbols" doubly dissociate in the fusiform gyrus before children can read and 2) the development of category-specific responses in young children depends on cortical responses to nonpreferred categories that decrease as preferred category knowledge is acquired.

Keywords: development, fMRI, fusiform gyrus, pruning

Introduction

In adulthood, visual expertise exists for all sorts of shapes, including natural categories (e.g., animals and faces) and cultural artifacts (cars, tools, letters, and other symbols). Expertise in these different domains likely begins to emerge early in development as children assimilate visual and semantic category information. However, very few neuroimaging studies have examined the status of visual expertise in children who are this young (Scherf et al. 2007). In the present study, we partially fill this gap by examining the organization of the ventral visual pathway for basic processing of symbols and objects in 4-year-old children.

There are well-defined expectations of how brain activity related to visual object processing should be organized in adulthood (Dehaene and Cohen 2007; Martin 2007). Faces and letter strings are 2 visual categories that have been studied extensively in adults. In adulthood, faces and letter strings elicit distinct responses in ventral temporal cortex. Faces evoke selective activity in the mid-fusiform gyrus relative to other objects (Allison et al. 1994; Kanwisher et al. 1997; Kanwisher 2000). In contrast, the lateral mid-fusiform/inferior temporal gyrus shows a bias for processing words, letters, and letter strings over digits and other objects (Allison et al. 1994; Polk and Farah 1998; Dehaene et al. 2002; Polk et al. 2002; Cohen and Dehaene 2004; Hashimoto and Sakai 2004; Pernet et al. 2005; Baker et al. 2007). Both categories are hypothesized to recruit specialized neural processes that best suit the features that define the category (Polk and Farah 1998; Kanwisher 2000). The developmental origins of their specializations, however, are presumably quite different.

Faces have an evolutionary significance and spontaneously attract children's attention from birth. Infants who are just days old prefer to look at images of faces instead of nonfaces and familiar rather than novel faces (Johnson et al. 1991; Nelson 2001). On the other hand, letters are a relatively recent cultural innovation and only become relevant to children when someone attempts to prepare them for literacy, usually in early childhood (i.e., 4–5 years of age). Children gradually master the visual forms of letters, their corresponding sounds, and, over the course of many years, the correct uses of letters for reading and writing (Schlaggar and McCandliss 2007). It might be expected that faces elicit neural selectivity earlier in development than letters. The exact pace of development, however, depends on whether the brain segregates its responses to a given category as soon as experiences with that category begin or only after that category is perceptually or conceptually defined.

Current evidence indicates that face-selective neural processing is already present in the fusiform gyrus by 6 years of age and becomes increasingly robust throughout adolescence (Tzourio-Mazoyer et al. 2002; Aylward et al. 2005; Golarai et al. 2007; Scherf et al. 2007; Grill-Spector et al. 2008; Libertus et al. 2009). The gradual refinement of face-related neural processing over development parallels the well-known changes in children's face recognition abilities (Carey and Diamond 1994). However, it is not clear how the neural development of face-selectivity relates to processing of culturally defined symbolic classes such as letters or numbers.

Early in development, letter identification is the single most reliable predictor of reading ability in young children (Scarborough 1998; Shaywitz et al. 2004). Some evidence suggests that letter-related activity in occipitotemporal cortex is connected to successful reading development. Children with dyslexia exhibit reduced activation relative to typically developing children on letter identification tasks in the left fusiform regions that selectively respond to words, letters, and letter strings in adults (Shaywitz et al. 2004; Schlaggar and McCandliss 2007). Letter-selectivity in the brain may emerge slowly over development, as children accumulate reading and

writing experience (Maurer et al. 2006). However, given that letter strings universally recruit a similar subregion of the left lateral occipitotemporal sulcus across adults (Jobard et al. 2003; Cohen and Dehaene 2004; Bolger et al. 2005), it has been suggested that this area might exhibit early biases for processing the shapes of symbols (Dehaene and Cohen 2007; Dehaene 2009). Symbol-specific processing may therefore emerge rapidly in development and shape the acquisition of reading and writing skills.

A second important question is to what extent observed changes in cortical organization relate to knowledge of the categories. Some evidence indicates that face-selectivity in the fusiform gyrus is related to face recognition memory in children (Golarai et al. 2007). Children who perform better on face recognition tasks exhibit a greater spatial extent of face-related activity, defined as the difference in activity between faces and nonface objects. Importantly, however, it is as yet unknown whether the refinement of face-related processing hinges on "increases" in the fusiform response to faces, "decreases" in the responses to nonfaces, or "both." This question is critical for understanding the nature of the developmental process underlying category-selectivity in the brain. In fact, a long-standing debate in the developmental literature concerns the question of whether neural development is driven by building up or pruning back representations in the brain (Changeux and Danchin 1976; Changeux 1985; Changeux and Dehaene 1989; Bourgeois and Rakic 1993; Purves et al. 1996; Dehaene-Lambertz and Dehaene 1997; Quartz and Sejnowski 1997; Quartz 1999).

In the constructivist view, experience-dependent input specifies the connectivity and functions of cortical regions and thereby gradually builds up specialized cortical functions (Quartz 1999). Selectionism, in contrast, postulates that redundant and irrelevant neuronal connections exist from birth and are gradually eliminated on the basis of experience-evoked activity in order to define specialized cortical functions (Changeux and Danchin 1976). In principle, these 2 developmental processes can be distinguished in the category-selective brain responses of young children. For instance, in the case of face representation, a constructivist pattern of activity would predict an increase in face-related activity with increasing face recognition ability, whereas a selectionist pattern would predict a decrease in nonface activity with increasing face recognition ability. Naturally, both patterns are non-exclusive and may jointly occur, either simultaneously or at different ages.

To examine the nature of children's face and letter representations in relation to the pattern predicted by previous studies of adults, we tested 4-year-old children's and adults' responses to faces, letters, numbers, and shoes in occipitotemporal cortex. Subjects viewed exemplars of these categories along with scrambled versions of the stimuli in a picture-viewing functional Magnetic Resonance Imaging (fMRI) paradigm (Fig. 1). Then, we tested children on a series of identification and naming tests with the stimuli presented in the fMRI session to test the relationship between children's developing category knowledge and their category-related brain activity.

Material and Methods

Subjects

Fifteen typically developing children (7 females, mean age = 4.9 years, standard deviation [SD] = 0.52, range = 4.0-5.8 years) and 14 adults (8 female, mean age = 26 years, SD = 3.9) were tested in our fMRI study. All subjects were right-handed (according to parental report) and had normal or corrected to normal vision with no history of neurological impairment or abnormality. All guidelines and requirements of the Duke University Institutional Review Board were followed for subject recruitment and experimental procedures. Originally, 22 children participated in this study; however, the data from 7 children were excluded due to excessive motion (i.e., >5 mm). Four additional children declined participation.

fMRI Stimuli, Task, and Procedure

Prior to the actual scanning session, children were given a half-hour training session in a mock scanner to familiarize them with the scanner environment, experimental task, and to prepare them to remain motionless throughout the scan. During training, subjects talked about the scanner with the experimenter for 10 min, they were put into the mock scanner to watch a movie while staying still for 10 min, and they practiced the experimental task for 10 min. Immediately following the training session, children were tested in the actual Magnetic Resonance Imaging (MRI) scanner. In the actual scanner, medical tape (sticky side up) and foam padding were used to secure children's head position. Adults did not receive a mock-scanner training session prior to the experimental session but were given verbal instructions and a brief practice session prior to the actual MRI scanning session.

During the MRI scanning session, we measured neural activity (indexed by blood oxygen level–dependent [BOLD] activity) in response to pictures of faces, letters, numbers, shoes (we chose "shoes" as a control for face-related responses in the fusiform gyrus.

Figure 1. The picture-viewing fMRI task. Children and adults viewed pictures of faces, shoes, letters, numbers, and scrambled stimuli while performing the incidental task of pressing a response button for pictures with green borders. Stimuli were presented in a random order for 500 ms each with a variable 2- to 10-s intertrial interval.

Shoes was chosen because it is a basic-level category that is familiar to young children and a category that did not show correlated activity with faces in Haxby et al. [2001]), and scrambled versions of each class. The design was event related (Fig. 1): each picture was presented for 500 ms with a 2- to 10-s jittered intertrial interval; the order of presentation was random across all classes (faces, letters, numbers, shoes, and scrambled stimuli). Stimuli were presented across two 9.7-min runs (one with faces, shoes, and their scrambled counterparts and a second with letters, numbers, and their scrambled counterparts). Each run consisted of approximately 150 trials, 50 per condition. The order of the runs was counterbalanced across subjects. Subjects fixated a central crosshair throughout the scanning session.

On each trial, a stimulus was randomly selected from a database of 26 pictures per category. Stimuli were taken from The Psychological Image Collection at Stirling database (http://pics.psych.stir.ac.uk/). The letters presented were from A to Z, and the numbers were Arabic numerals from 1 to 26. Stimuli were black and white photographs of faces (adults, neutral expression, mixed ethnicity, half male and half female) and shoes on a black background and pictures of letters and numbers in 300-point gray font on a black background. Each stimulus was 300 × 300 pixels, presented on a 640 × 820 resolution monitor. Stimuli were positioned centrally, within a 5° radius around fixation. The square border around each stimulus was randomly colored one of 3 colors (green, red, or blue) on each trial.

Subjects were given the task of pressing a response button whenever a green border appeared around a picture (but not a red or blue border). Subjects responded with their right index finger. Green borders were presented on 30% of all trials at random and were evenly distributed over all stimulus classes. The purpose of this task was to keep subjects attending to the stimuli throughout the session.

Image Acquisition
Whole-brain BOLD imaging was conducted on a 3-T General Electric Signa Excite scanner at the Duke University Brain Imaging and Analysis Center. High-resolution structural T_1 contrast images were acquired at the beginning of each session (time repetition [TR] = 7.4 ms, time echo [TE] = 3 ms, flip angle = 12°, field of view [FOV] = 256 mm, matrix = 256 × 224, slice thickness = 2 mm, 60 axial oblique slices). An echo-planar imaging pulse sequence was used for T_2^* contrast (TR = 2000 ms, TE = 27 ms, flip angle = 60°, FOV = 256 mm, matrix = 64 × 64, slice thickness = 4 mm, 30 slices). The first 4 TRs were discarded to allow for signal equilibration. Functional imaging was conducted over 2 functional runs with 290 volumes collected per run. Total scanning time was approximately 25 min (including time for anatomical image collection).

Image Processing and Analysis
Functional images were processed and analyzed in SPM2 (Statistical Parametric Mapping, Wellcome Department of Cognitive Neurology). Images were slice time corrected, spatially aligned to the mean image in each run, spatially smoothed with a 6-mm full-width at half-maximum kernel, normalized to the Montreal Neurological Institute (MNI) template, and high-pass filtered. All coordinates are reported in MNI space.

During the functional scan sequence, the included children moved, on average, 1.4 mm more than adult subjects. The overall amount of translational motion in the x, y, and z axes, calculated from the realignment parameters for each subject over each scanning run, was significantly greater for children than adults ($t_{27} = 2.99$, $P < 0.01$; child mean = 3.12 mm, range = 0.81–4.8 mm; adult mean = 1.69 mm, range = 0.3–3.5 mm). There was no difference between adults and children in rotational motion ($t_{27} = 1.63$, $P = 0.11$; child mean = 0.028 radians, adult mean = 0.043 radians). The amount of motion in children was correlated with their age (translation: $r = -0.62$, $P < 0.01$; rotation: $r = -0.60$, $P < 0.01$). However, it also should be noted that realignment algorithms were applied to all data, and motion parameters were included as regressors in the functional data analysis. Additionally, we have included analyses for a subset of the children whose motion estimates were in the same range as those of the adults (child subset mean = 2.1 mm, range = 0.81–3.87 mm), and the results nicely overlap with those of the full child sample (see Figs 2 and 3 in Results). We also report in Results that there was no correlation between children's motion estimates and their BOLD responses in our regions of interest (ROIs).

The general linear model applied to the processed images included a hemodynamic response function convolved with trial onsets for each stimulus class (faces, letters, numbers, shoes, and scrambled stimuli), a temporal derivative parameter, and 6 motion parameters. The resulting beta maps were subjected to paired t-tests for each category > scrambled, for each subject. These individual contrast images for each category versus scrambled were used as the dependent measure in the Group-level analysis of variance (ANOVA) and the individually defined ROI analyses described below.

At the Group level, we conducted 1) hypothesis-driven random effects contrasts and 2) individually defined ROI analyses.

Group-Level ANOVA
A random effects Group (Children, Adults) × Category (Faces, Letters, Numbers, and Shoes) ANOVA was conducted over the individual contrasts of each category versus scrambled ($P < 0.005$ at the voxel level, minimum cluster threshold 20 voxels, $P < 0.05$ corrected for multiple comparisons at the cluster level). In order to isolate object-selective occipitotemporal cortex, this ANOVA was constrained by a mask ($P < 0.005$ at the voxel level, corrected at the cluster level, $P < 0.05$) of the linear contrast of All Whole Stimuli (Faces, Letters, Numbers, and Shoes) > Scrambled (Scrambled Faces, Letters, Numbers, and Shoes) across both adults and children. We implemented the ANOVA to test for main effects of Category across groups and then tested specific Group × Category interactions to identify group differences.

Individually Defined ROI Analyses
In parallel, we conducted individually defined ROI analyses. The center of each ROI search area was uniformly placed at an anatomically relevant peak that emerged from the Group-level contrast of All Whole Stimuli > Scrambled across children and adults: one peak approximating the reported adult region responsive to letter strings in inferior temporal/fusiform gyrus (−52, −52, −12) and bilateral peaks approximating the reported face-selective region in the mid-fusiform gyrus (44, −48, −20; −40, −48, −20), proximal to coordinates from studies of adults reported in Dehaene and Cohen (2007) and Downing et al. (2006), respectively. With these peaks as the starting point, we used the contrast All Whole Stimuli > Scrambled to identify the 10 strongest peak voxels (rather than using just a single peak voxel) within a search area (sphere, 10-mm radius) for each individual. These peak voxels for the All > Scrambled contrast defined the ROIs. Once these ROIs were defined for each subject, we tested for category-related responses: the mean contrast-weighted beta values for each category > scrambled were extracted from the ROI voxels for each subject. We then performed planned contrasts to test for differences among these categories in children and adults. Note that the ROI contrasts are orthogonal to their voxel selection criterion (Friston et al. 2006).

Correlations with Behavior
Correlation analyses between brain activity and behavior were conducted between the mean ROI values for each category described in the preceding paragraph and the mean accuracy measures from the behavioral tasks described in the following section. The analyses were corrected for multiple comparisons using false discovery rate (FDR) correction.

Medial-to-Lateral ROI Analysis
To visualize the medial-to-lateral organization of activation, which has been reported as an important parameter separating face and letter-string responses (Allison et al. 1994; Puce et al. 1996), a sliding-window ROI analysis was also conducted using the ROI method described above but with a smaller search area (8-mm sphere). The strongest 10 voxels from the contrast All Whole Stimuli > Scrambled were selected as the ROI and tested for category-related activity. The ROI was moved along the x-axis at constant y-coordinate (−48) and z-coordinate (−16), generating a series of 14 mean amplitudes across the x-axis to characterize the medial-to-lateral response profile of the mid-

fusiform/inferior temporal region. The *y*- and *z*-coordinates were set based on the mean coordinates, in voxel units, of the centers of the ROI analyses described above.

Behavioral Measures

A few days after the fMRI scanning session, children returned to the laboratory for a behavioral testing session. During this session, we tested children's recognition abilities for faces and shoes using the same stimuli from the fMRI session. We also tested their letter- and number-naming ability for the alphabetic and numerical characters tested in the fMRI study. Four children declined participation in the behavioral tasks. To compensate for dropout, one additional child was recruited for only this component of the study (female, age = 4.75 years). The behavioral data were examined for outliers who performed 2 SDs from the mean score for each test. There were no outliers in the behavioral data.

Recognition Test

Children were tested in a delayed-match-to-sample task on a touch screen computer in which a sample stimulus was presented for 1-s, then a 3-s delay ensued, and then 2 choices appeared (the match and a distractor). Children were instructed to select the choice that matched the sample stimulus. Sixteen trials for each category were presented. Children were rewarded for each correct response with a sticker and audio–visual computer feedback. The stimuli were the same photographs of faces and shoes that were presented in the fMRI experiment.

Symbol Naming

Children were shown 16 flashcards of alphanumeric characters and asked to orally name them. Half of the cards were letters and half were numbers. For numbers, half were single digit and half were double digit. Within these constraints, each flashcard was randomly selected from the cache of letters A to Z and numbers 1 to 26 without repetition. The stimuli were printouts of the stimuli from the fMRI experiment.

Parental Report

Children's parents were asked to rate their child's reading and writing abilities on a scale of 0–3. On this scale, a score of 0 indicated no reading/writing ability whatsoever, 1 indicated they could read/write letters and/or their own name, 2 indicated reading/writing some real words, and 3 indicated reading/writing correct sentences. Reading and writing ability were evaluated with separate scores.

Results

Category-Selective Activity in Occipitotemporal Cortex

Our experimental conditions consisted of faces, letters, numbers, shoes, and their scrambled counterparts. We conducted a series of analyses for category-specific activity that was restricted to the map of object-selective occipitotemporal cortex (defined as occipitotemporal regions that responded more strongly to whole stimuli than scrambled stimuli in the statistical contrast All > Scrambled).

Children and adults exhibited a common pattern of face-selectivity in the right mid-fusiform gyrus at a locus consistent with previously reported face-selective sites in adults (Fig. 2). The common pattern emerged both as a main effect of Face > All Categories (Shoes, Letters, and Numbers) in the Group-level ANOVA (Fig. 2a) and in the individually defined ROI analysis as a significantly greater response for faces compared with nonface categories in children and adults (Fig. 2b; children: $F_{1,14} = 4.29$; Adults: $F_{1,13} = 16.10$; overall: $F_{1,27} = 16.48$, $P < 0.001$; no Group interaction, $P = 0.24$). Face-selectivity in the right fusiform ROI remained significant across both groups when faces were compared only with shoes, the most perceptually complex of the nonface categories ($F_{1,27} = 13.12$, $P < 0.005$; no

Group interaction, $P = 0.69$). The center of the ROI in both children and adults (x, y, z: 44, –48, –20) was 7 mm from the face-selective ROI reported in Downing et al. (2006).

There was no correlation between children's motion estimates and the BOLD responses to faces, shoes, or symbols in this ROI (translation: P's = 0.99, 0.31, 0.53; rotation: P's = 0.63, 0.46, 0.48, respectively). Thus, it is unlikely that our results can be explained by motion artifacts in children.

The same region of the fusiform gyrus in the left hemisphere did not emerge as face-selective in the Group-level ANOVA, and there was a Group × Category interaction in the left for the individually defined ROI analysis ($F_{3,81} = 3.87$, $P < 0.05$). Only adults showed a face-selective effect in the left mid-fusiform gyrus (Adults > Children × Faces > All: $F_{1,27} = 7.50$, $P < 0.01$).

In terms of the brain response to symbols, children exhibited a different pattern of activity than adults in a left fusiform/inferior temporal region. In the Group-level ANOVA, although there was a main effect of Letters > Faces across both groups in the left fusiform/inferior temporal region (peak [x, y, z]: –44, –64, –8; 31 voxel extent), there was also a Group × Category interaction wherein children showed greater activity than adults for symbols compared with nonsymbols in the left lateral mid-fusiform/inferior temporal gyrus (Fig. 3b). The precise pattern of activity in this region is shown by the results of our individually defined ROI analysis (Fig. 3a). There was a main effect of letters compared with the other categories ($F_{1,27} = 9.93$, $P < 0.005$) but, whereas adults activated this region more strongly to letters than numbers ($P < 0.01$), children showed equivalent responses to letters and numbers ($P = 0.48$). Yet, children activated this region more strongly to symbols (letters and numbers together) than faces and shoes ($F_{1,27} = 4.16$, $P < 0.05$). Thus, a left hemisphere region of occipitotemporal cortex that exhibits letter-selectivity in adults exhibits a bias for symbol processing (for both letters and numbers) in children (Maurer et al. 2005). The center of this ROI in both children and adults (x, y, z: –52, –52, –12) was 8 mm from the letter-selective region reported by Polk et al. (2002) and 10 mm from the visual word form area reported by Dehaene and Cohen (2007). Children's motion estimates did not correlate with the BOLD responses to symbols, faces, or shoes from the individually defined ROI analysis (translation: $P = 0.94$, 0.20, 0.98; rotation: $P = 0.99$, 0.20, 0.64, respectively).

To visualize the dissociation between symbols and faces in children and adults, we performed a medial-to-lateral ROI analysis across the inferior temporal and fusiform gyri for these categories (Fig. 4). The medial-to-lateral pattern of responses to faces and letters reflects a comparable dissociation between these categories across the left and right hemispheres in adults and children (Fig. 4a). When letters are compared with numbers (Fig. 4b), however, there is a difference in the pattern of category-related activity between the 2 groups: children generate similar neural responses to letters and numbers in a left hemisphere occipitotemporal region that responds more strongly to letters than numbers in adults.

It is unlikely that superficial differences between children and adults (e.g., generic differences in foveation patterns between groups) can explain the observed pattern of results. The similarity between children and adults in the loci of face- and symbol-related activity and between our results and those of previous fMRI studies that used explicit recognition tasks (e.g., Polk et al. 2002; Golarai et al. 2007) indicates that the picture-viewing paradigm (with an incidental detection task) is
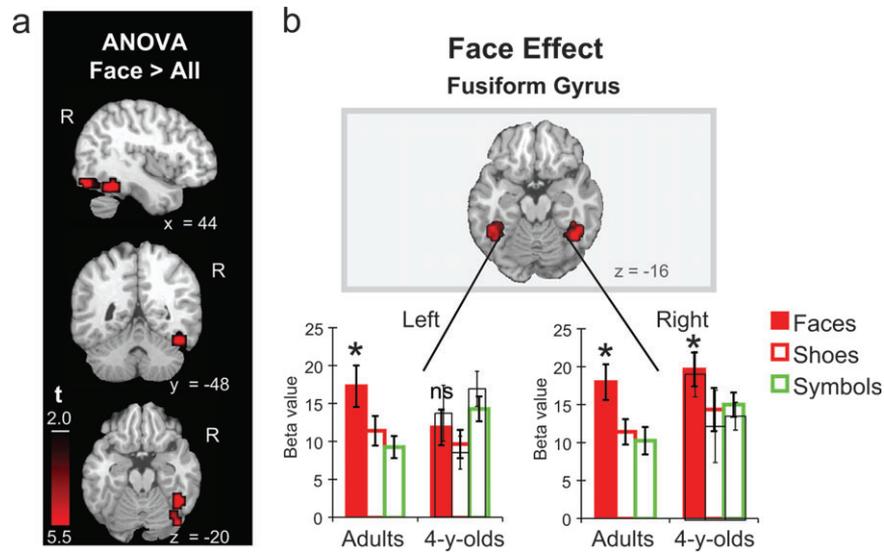
Figure 2. The right fusiform face effect. The right fusiform gyrus face effect for adults and children was evident in (a) a main effect of Faces > All Categories (shoes, letters, and numbers) in an ANOVA ($P < 0.05$, corrected) and (b) an ROI analysis in which voxels were selected based on their average response across all categories (faces, shoes, letters, and numbers) > scrambled. The center of this ROI in both children and adults (x, y, z: 44, −48, −20) was within 7 mm of the face-selective ROI reported in Downing et al. (2006). The light gray bars within the data from 4-year-olds represent children with motion estimates equal to those of adults (these data are equivalent to the full 4-year-old sample).
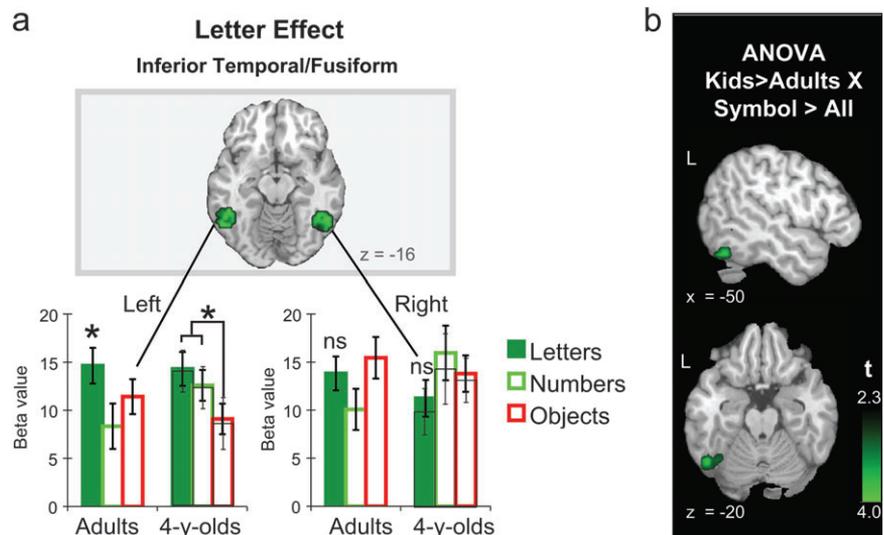
Figure 3. The left inferior temporal/lateral fusiform letter effect. In an ROI analysis (a), the left lateral fusiform gyrus, overlapping the inferior temporal gyrus, responded most strongly to letters in adults. However, in children it did not distinguish between letters and numbers but rather responded to both letters and numbers more strongly than nonsymbolic Objects (faces and shoes). The ROIs were defined as in Figure 2. In a second analysis, this effect was also evident as an interaction in an ANOVA (b) wherein children showed greater activity than adults to Symbols (letters and numbers) than nonsymbols (faces and shoes; $P < 0.05$, corrected). The light gray bars within the data from 4-year-olds represent children with motion estimates equal to those of adults (these data are equivalent to the data from the full 4-year-old sample).

a valid method for measuring visual responses in children. Additionally, as described below, children's BOLD responses from our fMRI task correlated with their performance on explicit recognition tasks with the same stimuli. These findings indicate that children's BOLD responses were related to the stimuli in our fMRI task.

Behavioral Correlations with Category-Selective Activity

What cognitive changes might be linked to children's developing category-specific brain responses to faces and letters? In a separate session following the fMRI scan, the same children were tested on a matching task in which they were shown an

image (e.g., a face) and then, after a 3-s delay, attempted to choose the same image from 2 options. The stimuli in this task were the exact stimuli from the fMRI session. Children performed significantly above chance across the 16 trials of this task (Table 1).

Our main finding is that children's accuracy on the face-matching task was not correlated with an increase in the neural response to faces in the right mid-fusiform face-selective ROI as might be expected ($r = -0.04$, $n = 12$, $P = 0.90$). Instead, accuracy on the face-matching task correlated with a decrease in the response to shoes in the face-selective ROI ($r = -0.65$, $n = 12$, $P = 0.02$; FDR corrected $\alpha = 0.02$; Fig. 5a). This finding
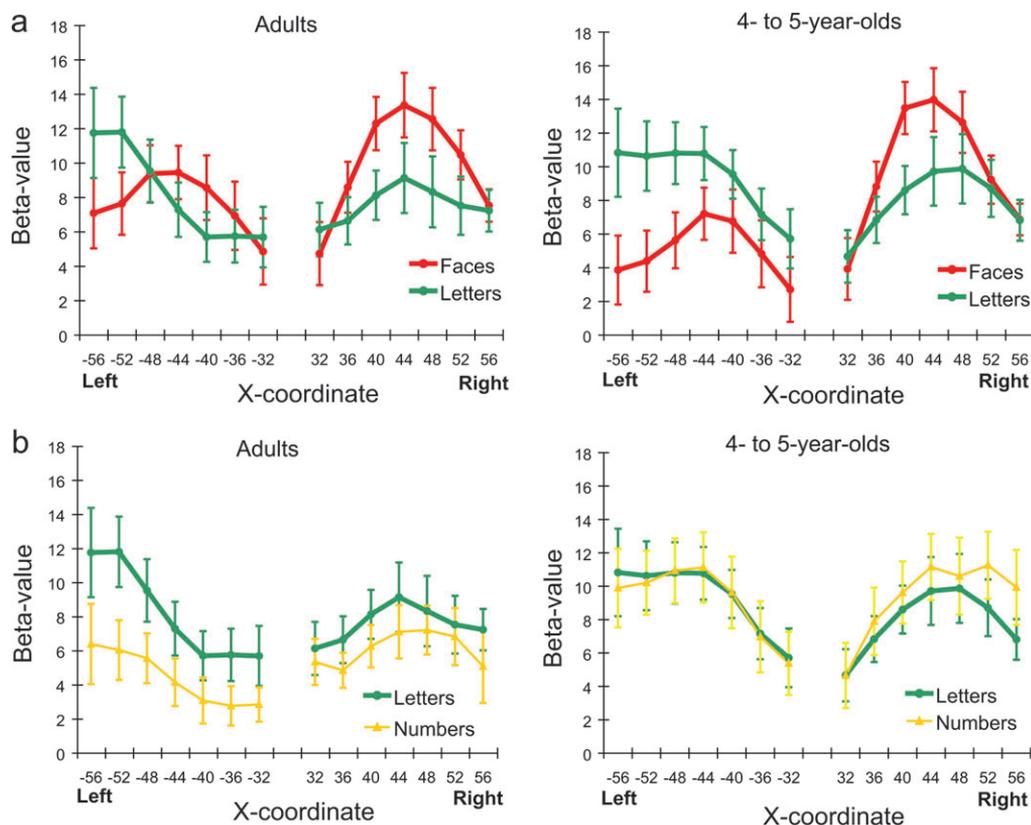
Figure 4. A left-to-right, medial-to-lateral analysis of the inferior temporal and fusiform gyri for face, letter, and number effects. While keeping the y- and z-coordinates constant (−48 and −16, respectively), we averaged over consecutive ROIs along the x-axis. This analysis revealed (a) a left-to-right, medial-to-lateral dissociation between letters (at left lateral points) and faces (at right medial points) for children and adults, and (b) divergent responses to numbers between adults and children wherein adults showed a greater response to letters than numbers at left lateral points but children evoked equivalent responses to letters and numbers at these loci.

Table 1

Children's performance on the face and shoe identification tasks (chance = 50%), the symbol-naming task (a conservative estimate of chance = 4%), and the results of parents' reports of reading and writing ability (scale of 0–3)

|	Mean	σ	Versus chance {t,p}
Face recognition	78.6%	14.99	6.60, $P < 0.001$
Shoe recognition	88.7%	8.87	15.09, $P < 0.001$
Symbol naming	73.2%	26.87	9.63, $P < 0.001$
Parent report reading	0.92	0.79	NA
Parent report writing	1.08	0.67	NA

Note: N/A, not applicable.

suggests that as children in this age range become more proficient at recognizing faces, the mid-fusiform face-selective region reduces its response to other visual classes (as opposed to increasing its response to faces). However, there was no relationship between accuracy on face matching and activity related to symbols in this region ($r = 0.01$, $P = 0.98$), indicating that performance on face matching is not uniformly anticorrelated with all nonpreferred categories in 4-year-olds.

We also examined the relationship between children's performance on an alphanumeric naming task and activity in the left occipitotemporal letter-selective region. According to parental reports, none of the children tested in this study could read. Only 2 of the children could read a small set of words and the remaining children could, at best, read or write individual

letters and/or their own name. We tested children on an alphanumeric naming task in the laboratory that required children to orally state the names of letters and numbers presented on flashcards. We tested children with the same letters and numbers from the fMRI study and children performed significantly above chance in both categories (Table 1).

Children's performance on the symbol-naming task did not exhibit a positive relationship with symbol-related activity in the left fusiform/inferior temporal ROI ($r = 0.25$, $P = 0.43$). Instead, scores on the symbol-naming task were negatively correlated with face-related activity in that region (symbols: $r = -0.78$, $P < 0.005$; FDR corrected $\alpha = 0.02$; letter-naming alone: $r = -0.82$, $n = 12$, $P < 0.001$, number-naming alone: $r = -0.60$, $n = 12$, $P < 0.05$). Figure 5b presents the correlation between performance on the symbol-naming task and the BOLD response to symbols versus faces in the Symbol ROI. The same negative relationship between performance and the nonpreferred category BOLD response that emerged in the face-selective region also emerged in this symbol-selective region: children's improvement in category identification was correlated with a decrease in the brain response to a nonpreferred category (in this case, faces) rather than an increase in the response to the preferred category (symbols). However, there was no relationship between symbol-naming accuracy and the response to shoes in this region ($r = -0.01$, $P = 0.98$), indicating that the negative relationship between accuracy and the BOLD response to nonpreferred categories is not universal among these categories in children.
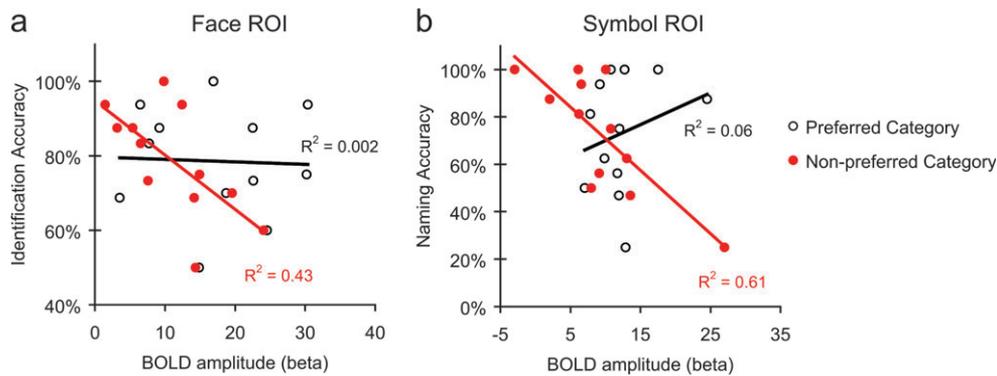
Figure 5. Negative correlations between behavioral performance and BOLD response to the nonpreferred category, suggesting a pruning effect. In the ROI that showed the face effect (a: ROI from Fig. 2), children's accuracy on a face identification task was correlated with a decrease in activity to the nonpreferred category (shoes) rather than an increase in activity to the preferred category (faces). Chance on the face identification task was 50%. The same pattern was observed for symbols (b: ROI from Fig. 3) wherein children's performance on a letter and Arabic numeral naming task improved with decreases in the response to the nonpreferred category (faces), not increases in the preferred category response (symbols). A conservative estimate of chance on the symbol-naming task is 4%, assuming that children restricted their responses to the stimuli they viewed in the fMRI session (the letters A–Z on the letter flashcards and to the numbers 1–26 on the number flashcards).

The general pattern these data suggest is that brain regions that will eventually become selective for a particular category already produce a relatively strong response to their preferred category in early childhood, but they gradually decrease their responses to the nonpreferred categories as knowledge is acquired.

Discussion

Although the brain expresses greater plasticity during development than in adulthood, certain features of adult brain organization have already taken form by 4 years of age (Cantlon et al. 2006; Polk et al. 2007; Grill-Spector et al. 2008; Mahon et al. 2009). The dissociation between faces and symbols in occipitotemporal cortex, evident in 4-year-olds and adults, is one example of this phenomenon. The biased activity to faces in the right mid-fusiform gyrus, overlapping regions previously reported as face-selective in older children and adults (Grill-Spector et al. 2008), represents an early-developing visual specialization in occipitotemporal cortex.

A second early-developing specialization suggested by our data is that symbols elicit greater responses than faces in the left lateral fusiform/inferior temporal gyrus. The fact that this region already prefers symbols over nonsymbols in 4-year-olds is surprising and suggests 2 nonexclusive interpretations: either this region has an early bias to represent the visual features of symbols (e.g., simple geometry, high spatial frequencies) or a bias rapidly develops after minimal exposure to symbols (Szwed et al. 2009; M Szwed, S Dehaene, A Kleinschmidt, E Eger, R Valabregue, A Amadon, L Cohen, unpublished data). The former interpretation is made plausible by evidence that reading exhibits a remarkably consistent pattern of brain organization across cultures. In particular, selective activation to written words is systematically observed in the left lateral occipitotemporal sulcus, within ±5 mm, in all cultures, whether they rely on alphabetic or logographic systems (Cohen et al. 2000; Jobard et al. 2003; Bolger et al. 2005). Such findings have led to the "cultural recycling" hypothesis which proposes that although culturally recent cognitive abilities can partially adapt cortical regions to their processing needs, they are also constrained by the inherent processing biases of cortical

regions passed down by evolution (Dehaene and Cohen 2007). Our data from children support this hypothesis by demonstrating early-developing symbol-selectivity in left inferior temporal cortex prior to reading proficiency. Further support for this hypothesis, however, will require scanning children at an even earlier age, prior to any strong symbol exposure. Other constraints may also contribute to the selectivity of this cortical location for visual word recognition, including a preference for high-resolution foveal inputs (Hasson et al. 2002) and a pattern of direct projections to the left-hemispheric spoken language network (Epelbaum et al. 2008).

Despite the fact that adult category-selective brain regions show similar types of category biases in early childhood, there are undoubtedly developmental changes in the structure and function of those regions. For example, Golarai et al. (2007) reported that the spatial extent of activation in face-selective fusiform regions expands with increased memory for faces between 7 years of age and adulthood. The degree to which face-selective cortex expands over the course of early childhood (i.e., 0–7 years) remains in question. Our data do not address that dimension of developmental change. However, our data do suggest that one catalyst of those functional changes could be a decreasing representation of nonpreferred (i.e., nonface) entities in face-selective regions.

Developmental change is also evident in children's occipitotemporal responses to symbols. The majority of children tested in this study could not read or write yet, but they could identify many letters and numbers in a naming test. At this developmental stage, children elicited equal responses to digits and letters in a region of high-level visual cortex that, in adulthood, ultimately responds more strongly to words, letters, and letter strings than digits (Polk et al. 2002). This occipitotemporal region evidently requires more than a brief exposure to written symbols in order to respond selectively to those symbols important for reading words. Reading experience is likely critical for shaping letter-selective processing over development (Polk and Farah 1998; Schlaggar and McCandliss 2007). This interpretation is consistent with event-related potential studies reporting no distinction in the N170 response to letters compared with pseudosymbols in children, with a progressive differentiation in the response

over the course of literacy acquisition (Maurer et al. 2005, 2006).

Many questions remain about exactly how the development of category-specialization unfolds. One aspect of this process, evident in our results, is that neural responses in category-selective regions to nonpreferred categories need to be pruned away. Our results indicate that children's increasing skill in face and symbol recognition is accompanied by decreased responses to nonpreferred stimuli (pruning) as opposed to an increased response to the preferred category. The notion that learning proceeds by "selection," "attrition," or a "use it or lose it" principle has long been proposed at the theoretical level (Changeux and Danchin 1976; Changeux 1985; Changeux and Dehaene 1989; Bourgeois and Rakic 1993; Purves et al. 1996; Dehaene-Lambertz and Dehaene 1997) and has received empirical support in domains such as bird song acquisition or speech perception that exhibit perceptual narrowing over development (Werker and Lalonde 1988; Kuhl et al. 1992). Our data suggest a similar selectionist principle in the development of category-selective occipitotemporal cortex in human children.

It should be noted that our data are not inconsistent with a moderate form of the constructivist view (Sirois et al. 2008), which posits a selection process via lateral inhibition following category learning (for evidence of this phenomenon in adults, see Allison et al. 2002; Pelphrey et al. 2003). Under that hypothesis, however, one might expect preferred and nonpreferred category-related responses in occipitotemporal cortex to become increasingly anticorrelated over development. Although this pattern did not emerge in our data, longitudinal fMRI data on children's category-related visual responses at different points in their acquisition of category knowledge will help to further adjudicate among these hypotheses. Such data could reveal developmental periods during which representations are being constructed (with increasing responses to preferred categories) as well as periods during which a selection mechanism is engaged (with decreasing responses to the nonpreferred category). The degree to which selection or construction is observed at a given point in early childhood likely will depend on children's experience with the specific categories examined. At a single point in development, some categories could exhibit a pattern of increasing responses to preferred stimuli while other categories exhibit decreasing responses to nonpreferred stimuli. Such a proposal is consistent with our data and with previously reported studies of ventral temporal activation in older children (Golarai et al. 2007; Scherf et al. 2007; Grill-Spector et al. 2008; Libertus et al. 2009).

A tentative biological mechanism for the reduction in high-level visual activity to nonpreferred categories over development may be the known reduction in synaptic density between 2 and 11 years of age (Huttenlocher et al. 1982; Chugani et al. 1987; Huttenlocher and Dabholkar 1997; Giedd et al. 1999; Shaw et al. 2008). Synaptic density in visual areas steadily increases between birth and 1–2 years of age, reaches levels that are approximately 50–60% higher than adult levels, and then gradually decreases over the next several years. Some evidence indicates that vascular density parallels synaptic density in primary visual areas and thus blood supply might be related, at least in sensory areas, to neural plasticity and synapse formation/elimination (Duvernoy et al. 1981;

Logothetis and Wandell 2004). Yet, whether or not those observations relate to our observed correlation between BOLD signal decrease and performance increase in preschool children, our data seem more consistent with a selectionist view of category development in 4-year-old children than a constructivist proposal.

Notes

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