

“What” Precedes “Which”: Developmental Neural Tuning in Face- and Place-Related Cortex

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Although category-specific activation for faces in the ventral visual pathway appears adult-like in adolescence, recognition abilities for individual faces are still immature. We investigated how the ability to represent “individual” faces and houses develops at the neural level. Category-selective regions of interest (ROIs) for faces in the fusiform gyrus (FG) and for places in the parahippocampal place area (PPA) were identified individually in children, adolescents, and adults. Then, using an functional magnetic resonance imaging adaptation paradigm, we measured category selectivity and individual-level adaptation for faces and houses in each ROI. Only adults exhibited both category selectivity and individual-level adaptation bilaterally for faces in the FG and for houses in the PPA. Adolescents showed category selectivity bilaterally for faces in the FG and houses in the PPA. Despite this profile of category selectivity, adolescents only exhibited individual-level adaptation for houses bilaterally in the PPA and for faces in the “left” FG. Children only showed category-selective responses for houses in the PPA, and they failed to exhibit category-selective responses for faces in the FG and individual-level adaptation effects anywhere in the brain. These results indicate that category-level neural tuning develops prior to individual-level neural tuning and that face-related cortex is disproportionately slower in this developmental transition than is place-related cortex.

Keywords: adolescent, fMRI, fusiform gyrus, parahippocampal gyrus, visual processing

Introduction

The computational and representational demands of face processing make it one of the most taxing visual challenges confronting observers. Unlike other objects, which are often recognized at the basic category level (e.g. guitar vs. spoon), faces are typically distinguished at the individual level. For example, when we see a face of Barack Obama, the typical response is one of identification (i.e., that is Barack Obama not Denzel Washington) rather than one of categorization (i.e., that is a face not a house). Furthermore, faces are remarkably perceptually homogenous (all faces have 2 eyes, a nose, and a mouth in the same spatial arrangement) compared with other classes of objects, such as musical instruments or kitchen utensils. This perceptual homogeneity requires that observers are sensitive not only to differences in facial features but also to differences in the subtle metric spacing among the features (Maurer et al. 2002). In addition, multiple kinds of information, such as gender, age, emotional state, mate potential, social status, trustworthiness, intentions, and “person knowledge,” are seamlessly extracted from the input, even as faces change

dynamically as a function of facial expression and speech production and vary across many transformations (i.e., changes in lighting, viewpoint, and context). Notwithstanding this complexity, adults execute these processes accurately and rapidly multiple times every day, revealing accurate recognition of thousands of individual faces (Landauer 1986).

The perceptual challenges and added representational demand of face processing may contribute to the fact that it has an extended and prolonged developmental trajectory. The ability to encode and recognize unfamiliar faces (Ellis et al. 1973; Carey and Diamond 1977; Carey et al. 1980; Diamond and Carey 1986; Itier and Taylor 2004; Mondloch et al. 2004) and facial expressions (Herba and Phillips 2004) continues to improve well into adolescence. Consistent with this, recent neuroimaging studies report a protracted developmental course for the emergence of face-related activation in the developing brain, particularly in the fusiform face area (FFA: Passarotti et al. 2003; Gathers et al. 2004; Aylward et al. 2005; Golarai et al. 2007, 2010; Scherf et al. 2007; Peelen et al. 2009; Pelphrey et al. 2009; Joseph et al. 2010). In one recent study, we tested children (5–8), adolescents (11–14), and adults (20–23) as they viewed naturalistic movies of unfamiliar faces, buildings and navigation scenes, and objects (Scherf et al. 2007). Whereas object- and place-related cortex reflected adult-like category selectivity even in children, there were clear developmental differences in face-selective cortex. Although 80% of the individual children exhibited some face selectivity in the fusiform gyrus (FG), as a group, children failed to show consistent face-selective activation in the FFA, occipital face area (OFA), and superior temporal sulcus (see also Golarai et al. 2007). Interestingly, adolescents showed adult-like face-selective activation, except that it was more asymmetrical than the bilateral adult pattern. These results indicate that although category-selective activation for places and objects is well established even in childhood, comparable activation for faces continues to develop into early adulthood.

Note that this study, as well as every other previous study investigating the development of face-related cortex (Passarotti et al. 2003; Gathers et al. 2004; Aylward et al. 2005; Golarai et al. 2007, 2010; Scherf et al. 2007; Peelen et al. 2009; Pelphrey et al. 2009; Joseph et al. 2010), investigated the emergence of “category specificity” (e.g., faces vs. objects) in the functional organization of the ventral visual pathway. In other words, a consensus is emerging to suggest that the neural basis of the ability to represent “basic” level information is relatively delayed for faces compared with other visual classes. This is especially relevant since most objects are recognized at the basic level of abstraction (e.g., dog vs. chair) and can be distinguished by unique features or configurations of features

(Rosch 1978; Tanaka and Taylor 1991). The basic level is “privileged” in recognition because the combination of features that identifies a basic-level category is distinct and informative, allowing for fast and efficient recognition. However, all objects (and particularly faces) can be recognized at increasingly more “subordinate” levels (e.g., Asian vs. Caucasian faces) and ultimately at the “individual” level (e.g., Barack’s face vs. Denzel’s face), where all exemplars share similar parts in a similar basic configuration but differ in the spatial relations within this basic configuration. At this last level, sensitivity to subtle differences in the metric variations of the configural information is critical for discriminating between individuals (Diamond and Carey 1986). Faces are the paradigmatic example of visual stimuli that must be recognized at this individual level, which may contribute to the fact that face processing behavior has an extended and prolonged developmental trajectory (Ellis et al. 1973; Carey and Diamond 1977; Carey et al. 1980; Diamond and Carey 1986; Mondloch et al. 2004).

The central goal of this paper was to address a previously unanswered question about developmental changes in the neural basis of this individual level processing; namely, how does the developing brain become functionally organized to represent individual faces and houses? To our knowledge, there are no studies evaluating how the ability to represent “individual exemplars” within an object category develops at the neural level for any visual class represented in the ventral visual pathway. This is particularly important to understand given that individual identification is an especially critical component of face processing and, in adults, is subserved, in part, by the FFA (Sergent et al. 1992; Haxby et al. 1994; Gauthier et al. 2000; Nestor et al. 2008) but also by more anterior parts of inferotemporal cortex (Sugiura et al. 2001; Kriegeskorte et al. 2007; Rajimehr et al. 2009). Also, as mentioned previously, despite the emergence of category selectivity for faces in adolescent ventral visual cortex, individual face recognition abilities continue to improve through adolescence, which may be due to the increasing effectiveness of configural encoding (Ellis et al. 1973; Carey and Diamond 1977; Carey et al. 1980; Diamond and Carey 1986; Mondloch et al. 2004). One clear prediction, then, is that, developmentally, category-level neural tuning for faces in the FG may be mostly mature by adolescence (“what”: face vs. object) but that the precision of the neural computation for representing individual faces (i.e., “which”: individual face) for identification may still be insufficient to support adult-like recognition behavior.

In other words, given that a subset of children, adolescents and adults can be identified who show regions of “equally selective” face-related activation in the FG (albeit in different locations and sizes than is observed in adults), are these regions computing similar kinds of representations and are they tuned to the same degree of specificity at both the category (i.e., what) and exemplar (i.e., which) levels?

To address this question, we evaluated developmental changes in neural tuning for individual exemplars in the ventral visual cortex and, specifically, assessed whether there is a differential trajectory for tuning in face- versus place-related cortex. We employed an functional magnetic resonance imaging (fMRI)-adaptation (fMRI-a) paradigm (Grill-Spector and Malach 2001) to perform a fine-grained analysis of the functional properties of face- and place-selective cortex from childhood to early adulthood (ages 6–23 years). fMRI-a para-

digms provide a powerful method for evaluating subvoxel level functional organization and have revealed a wealth of knowledge about the nature of adult representations for faces and other visual objects (Grill-Spector et al. 1999; Avidan et al. 2002; Avidan et al. 2005; Andrews and Ewbank 2004; Winston et al. 2004; Rotshtein et al. 2005; Mazard et al. 2006; Ewbank and Andrews 2008) that could not otherwise be evaluated with more traditional (blocked or event-related) fMRI paradigms. The fMRI-a paradigm involves presenting repeated stimuli and nonrepeated stimuli. In our case, this involved presenting a picture of the same face or house in identical blocks and pictures of different faces/houses in different blocks. In specific regions of cortex (e.g., FG), the identical blocks generally lead to a reduction in the fMRI signal compared with the different blocks. This pattern of results is taken to reflect that the underlying neural representation in such a region is sensitive to the stimulus properties that change across the different and identical blocks (e.g., identity; Grill-Spector et al. 2006). If such a pattern is not observed, the results indicate that the region is invariant to the changing stimulus properties.

In adults, the FFA exhibits adaptation to identical compared with different faces (Avidan et al. 2002; Rotshtein et al. 2005), whereas the parahippocampal place area (PPA) exhibits the same pattern, albeit slightly weaker, for identical versus different houses (Avidan et al. 2002). Both regions also exhibit adaptation to other object classes but to a lesser extent than for their “preferred” class. Together with neuroimaging studies of category selectivity in the ventral visual pathway (i.e., Hasson et al. 2004; Avidan et al. 2005), these results indicate that, in adults, populations of neurons in the FFA and PPA are tuned both at a categorical level for their preferred stimulus class (e.g., faces more than objects or houses in the FFA) and also at a stimulus-specific level (e.g., individual faces elicit different patterns of activation across the FFA).

In this paper, we evaluated the developmental emergence of both levels of neural tuning within functionally defined face-selective (in the fusiform gyri) and place-selective (in the PPA) regions of interest (ROIs) in children, adolescents, and adults (see Fig. 1). We did not expect to observe individual-level neural tuning in the face-selective ROIs in children, given the relatively poor behavioral performance on individual face recognition tasks in this age range (Carey and Diamond 1977; Carey et al. 1980; Diamond and Carey 1986; Mondloch et al. 2004). However, based on findings that children show adult-like processing of upright houses (Carey and Diamond 1977), we predicted that children might show individual-level neural tuning for houses in the house-selective ROIs. In adolescents, we expected to observe category-level neural tuning for houses in the PPA and for faces in the FG. However, based on findings of ongoing improvements in individual face recognition in adolescence (Carey et al. 1980; Diamond et al. 1983; Flin 1985; McGivern et al. 2002), we also predicted that the precision of the neural representations in the FG for “individual faces” may still be developing in adolescence, in which case, we would observe less individual-level neural tuning in the FG in adolescents than in adults.

This pattern of results would provide evidence that the representational capacity of the FG to encode individual faces and the PPA to encode individual houses is increasingly refined into early adulthood even though many of the functional characteristics of these regions have matured earlier in

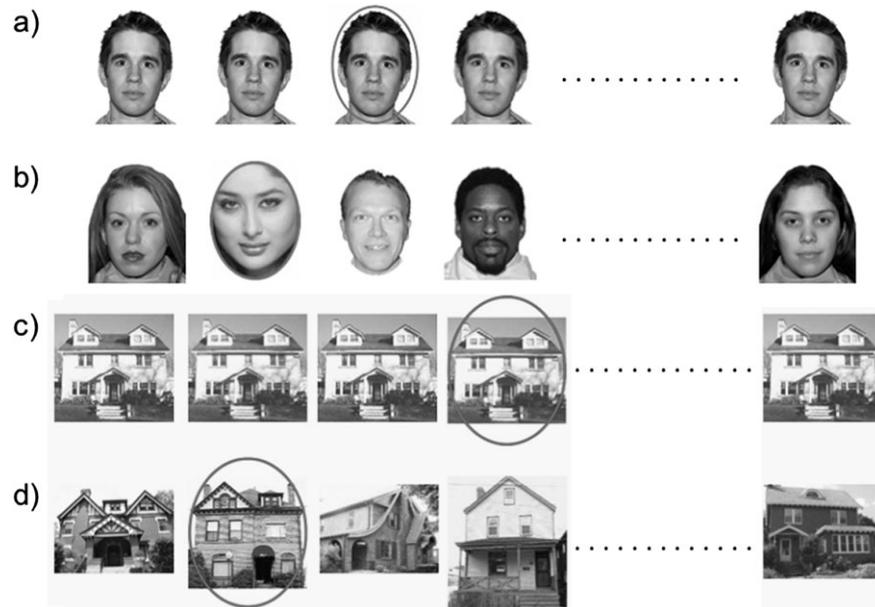


Figure 1. Examples of stimuli in the face and house adaptation experiment. In separate blocks, participants viewed consecutive images of identical faces (a), different faces (b), identical houses (c), and different houses (d). To maximize our ability to discern adaptation effects, we chose to repeat the exact same image of a particular face/house in the identical blocks and to maximize differences between faces/houses during different blocks (i.e., differences in size, gender, expression, hair style, race, facial hair, number of windows, color, overall shape). Participants indicated, via a button press, when a red circle encompassed the entire stimulus.

adolescence (e.g., location, magnitude of face selectivity: Golarai et al. 2007; Scherf et al. 2007). It would also provide novel evidence that, developmentally, category-level neural tuning precedes and may even be a prerequisite for individual-level neural tuning throughout the ventral visual pathway. Such findings would represent an important step in understanding how multiple mechanisms contribute to the functional maturation of a cortical region and shed light on age-related and experience-dependent optimization of the representational ability within the ventral visual pathway. Furthermore, our results could uncover a potential neural mechanism for existing psychological models of conceptual development that argue for a developmental hierarchy in the formation of conceptual categories from basic to more subordinate levels of categorization (e.g., Mervis and Crisafi 1982; Quinn 2004; Quinn and Tanaka 2007).

Materials and Methods

Participants

Participants included 13 children (age: 6–10 years; $M = 7$, standard deviation [SD] = 1; 9 males), 13 adolescents (age: 11–14 years; $M = 13$, SD = 1; 8 males), and 13 adults (age: 20–23 years; $M = 22$, SD = 1; 4 males). Only participants who completed both the localizer and adaptation tasks in their entirety, with minimal motion (no more than 2.6 mm or 87% of a voxel in either task), were included in the analyses. As a result, an additional 6 children, 2 adolescents, and 1 adult were excluded from the analyses due to excessive head motion in one or both tasks. All participants were healthy with no history of neurological or psychiatric disorders in themselves or in their first-degree relatives, as determined in an interview with participants or participant's parents. All were right-handed and had normal or corrected vision. Participants and/or their legal guardians provided informed consent prior to participating in the study. All the experimental procedures complied with the Code of Ethics of the World Medical Association (1964 Declaration of Helsinki) and the standards of the University of Pittsburgh and Carnegie Mellon University Internal Review Boards.

General Procedure and Imaging Parameters

Immediately prior to the scanning session, all participants were trained to lie still for 15 min in a mock scanner that simulated the noise and confinement of an actual MR scanner. During the scanning session, the stimuli were displayed on a rear-projection screen located inside the MR scanner. Echo-planar imaging blood oxygen level-dependent (BOLD) images were acquired in 35 anterior commissure - posterior commissure (AC-PC) aligned slices on a Siemens 3-T Allegra scanner, covering most of the brain and all the occipital and temporal lobes (time repetition = 3000 ms; time echo = 35 ms; 64×64 , 3-mm slice thickness, 3.203×3.203 mm in-plane resolution). Anatomical images were acquired using a 3D magnetization prepared rapid gradient echo pulse sequence with one hundred and ninety-two 1-mm, T_1 -weighted, straight sagittal slices. The data were analyzed using Brain Voyager QX (Brain Innovation). Preprocessing of functional images included 3D-motion correction, filtering out of low frequencies, and resampling the voxels to 1 mm^3 . Children exhibited more motion compared with adolescents and adults in the localizer task but only in the Z -translation dimension ($F_{2,39} = 4.3$, $P < 0.025$), which did not affect age group differences in the location of either the face- or place-related ROIs (see Z coordinate for all ROIs in Table 1). Importantly, there were no age group differences in any of the 6 motion dimensions in the adaptation task. Therefore, any age-related differences in the magnitude of the category-selective adaptation responses cannot be explained by motion differences across the age groups.

The time series images for each brain volume in each participant were analyzed for stimulus category and/or experimental condition differences in a fixed-factor general linear model (GLM). The GLM was computed on the z -normalized raw signal in each voxel. Each of the categories/conditions was defined as a separate predictor and was modeled with a box-car function, which was shifted 6 s in the localizer task and convolved with a canonical hemodynamic response in the adaptation task, to accommodate the delay in the BOLD response. The time series images were then spatially normalized into Talairach space, an approach that has been validated in previous studies (Burgund et al. 2002), prior to being analyzed for age group differences.

In all functional tasks, the average percent signal change across 7 volumes (21 s) from the onset of the stimulus block was extracted for each condition from individually defined ROIs. Importantly, the baseline for this computation was the volume immediately preceding the onset of the task block. This approach is analogous to the averaging

Table 1

ROIs identified in movie localizer task for subsequent analyses of age-related differences in face and house adaptation responses

		Fusiform face activation					Parahippocampal place activation				
		<i>N</i>	<i>x</i>	<i>y</i>	<i>z</i>	Voxels	<i>N</i>	<i>x</i>	<i>y</i>	<i>z</i>	Voxels
Adults	Right	13	43 (2)	-47 (9)	-20 (6)	2342 (1759)	13	30 (2)	-43 (9)	-13 (5)	1485 (1375)
	Left	12	-40 (3)	-48 (8)	-20 (5)	1365 (1189)	12	-26 (2)	-47 (7)	-11 (5)	1557 (1545)
Adolescents	Right	12	39 (4)	-41 (9)	-18 (4)	2556 (1422)	11	27* (2)	-46 (7)	-10 (5)	1708 (1406)
	Left	11	-39 (3)	-51 (11)	-18 (6)	1807 (1521)	11	-25 (5)	-48 (7)	-11 (5)	1585 (1240)
Children	Right	11	36** (8)	-44 (8)	-16 (6)	914* (697)	11	26* (3)	-46 (10)	-12 (6)	1794 (2623)
	Left	11	-35** (3)	-55 (10)	-20 (4)	468* (324)	10	-25 (2)	-43 (8)	-13 (5)	1887 (2427)

Note: Cells contain mean (SD) values. The ROIs were “individually defined” from the GLM analyses of each individual participant’s movie localizer data (thresholded at FDR of $q < 0.10$ for each contrast in each participant). *N* represents the number of individuals contributing data to the cell means. *x*, *y*, and *z* represent the Talairach coordinates of the mean peak activation for the region. The number of voxels is reported in $1 \times 1 \times 1$ mm voxels. One-way ANOVAs with age group as a between-subjects factor were computed on each value. Bonferroni corrected post hoc comparisons indicate that when the ROIs were defined at the individual level, children exhibited smaller and more medial face-related activation in the right and left fusiform and children’s and adolescents’ right parahippocampal place activation was slightly more medial than the adults’. ** $P < 0.01$, * $P < 0.05$.

performed in event-related potential (ERP) analyses. Although the task blocks were shorter than the time course of a complete BOLD response, the averaged 7-volume time course allowed us to model the full BOLD response after adjusting for the delay in hemodynamic response function. This averaged time course was used to compute the magnitude of category selectivity and the magnitude of individual-level adaptation in the adaptation task. Variance was equal across age groups for all measures, as determined by Levene’s Tests for Equality of Variances ($F < 1$), unless specified otherwise.

Movie Localizer Task

To localize independently regions in the ventral visual pathway that are category selective for faces and places in each individual subject, each participant freely viewed a silent, fluid concatenation of short movie vignettes, containing scenes of people and faces, buildings, navigation through open fields, or miscellaneous common objects (Hasson et al. 2004) prior to the adaptation task. The vignettes were organized into 32 randomized 15-s blocks containing stimuli from a single category. Importantly, each category block preceded each other category block with equal probability, such that the 8 face blocks were preceded by 2 buildings blocks, 2 navigation blocks, 2 object blocks, and 2 face blocks. The task began with a 29-s blank screen followed by a 9-s block of abstract pattern stimuli and ended with a 21-s blank screen. This passive viewing task using rich visual inputs has been used successfully to map face- and place-selective activation in individual children as young as 5 years of age (face selectivity and place selectivity can be identified in approximately 85% of individual children: Scherf et al. 2007).

There has not been a consistent way of defining category selectivity in the developmental literature, and, in the adult literature, category selectivity is usually defined by the following contrasts; FFA: faces-objects, and PPA: places-objects. However, a consensus is beginning to emerge in the developmental literature to employ a weighted contrast in which each visual category is contrasted with all others (e.g., Scherf et al. 2007; Joseph et al. 2010). As in previous studies using this movie task, we defined face-selective ROIs by the weighted contrast [$3 \times$ (faces) - (objects + buildings + navigation)], and place-selective ROIs were defined as [(buildings + navigation) - $2 \times$ (faces)] because scenes of buildings and navigation both drive PPA activation (Hasson et al. 2004; Avidan et al. 2005; Scherf et al. 2007, 2010; Humphreys et al. 2008). This approach is particularly useful for 2 reasons. First, these definitions significantly minimize commonalities in the neural representation across visual categories, including the low-level, 2D nature, semantic (i.e., that they are namable), and featural goodness of the stimuli. Also, defining the contrasts this way allowed us to directly compare findings of developmental differences in category selectivity with this previous body of work (Note: we did not define a selectivity index as in previous studies, that is, Grill-Spector et al. 2006: [preferred - nonpreferred]/[preferred + nonpreferred]; because negative values are often observed in fMRI data, which can inflate the magnitude of selectivity [see Simmons et al. 2007]).

In each participant, each contrast was computed on the *z*-transformed raw signal and was corrected for multiple comparisons using the false discovery rate procedure (Genovese et al. 2002) with $q < 0.10$. The face-related ROIs included the set of contiguous face-selective voxels “anywhere” in the FG (as determined by the maximal *x*, *y*, and *z* coordinates of BA 37 in the Talairach atlas). The place-related ROI included the contiguous place-selective voxels in the parahippocampal gyrus (as determined by the maximal *x*, *y*, and *z* coordinates of BAs 34, 35, and 36 in the Talairach atlas). These ROIs were defined independently in each hemisphere in each individual. The variability in the presence of these individually defined ROIs from the movie localizer task led to slightly different numbers of participants contributing to the analyses in each age group (see Table 1). However, this approach allowed for the investigation of age group differences in the “maximally” category-selective regions for each participant at each developmental stage. Such an approach provides the means for conducting cross-age comparisons of neural representation under optimal conditions as selectivity is defined separately for each individual. Also, it is important to note that this method allowed the ROIs to be identified a priori and independently of the adaptation task, which prevents any selection bias in the analysis of the magnitude of adaptation response within these regions (see Baker et al. 2007; Kriegeskorte et al. 2009, 2010). The ROIs were quantified in terms of the total number of active voxels (size) and the coordinates of the centroid of activation.

The magnitude of selectivity, size, and location of the ROIs were compared for age group differences. The magnitude of selectivity in each of these ROIs was computed for each participant separately using the mean percent signal change across all the voxels in the ROI. In other words, once the significant voxels were identified in the GLM and subsequent weighted contrast, all the voxels in the ROI were used to compute the magnitude of selectivity; there were no additional constraints applied to select the voxels within the ROI that would then contribute to the computation of the magnitude of selectivity.

The baseline volume for the percent signal change computation in the movie localizer task was the final volume of the previous stimulus block since there were no intervening fixation blocks. However, each category block preceded each other category block with equal probability. This means that for each stimulus category, there were 2 baseline volumes from each of the other categories from which the percent signal change was computed. For each of the 7 volumes following the onset of a category block, the percent signal change was computed as follows: [(volume of interest value - baseline volume value)/baseline volume value]. These values were averaged across the 7 volumes and across the 8 category-specific task blocks for each of the 4 stimulus categories and then entered into the weighted contrast formula to develop a single value of category selectivity for each ROI in each participant. Note that when percent signal change values are positive using this baseline procedure, the category of interest elicits greater percent signal change than all other categories (Because of a concern that our weighted contrast could misrepresent the selectivity of an ROI, we evaluated how often there were “violations

of selectivity” such that the category of interest did not elicit the highest percent signal change within the ROI. For example, in the right FG face-selective ROIs, faces did not always elicit the highest overall percent signal change prior to being submitted to the weighted contrast in all participants. Approximately, 16% of adults and adolescents and 36% of children exhibited this pattern of results in the right FG. Also, individuals for whom faces do not elicit the highest percent signal change in the right FG show the “smallest” face selectivity within an age group and actually “reduce” the mean selectivity of the group; therefore, the inclusion of these individuals potentially “underestimates” the magnitude of selectivity in each age group. However, as we described previously, once the ROIs were identified by the GLM and weighted contrast on the normalized raw signal, we used all the voxels within the ROI to determine the magnitude of selectivity, even when the category of interest did not elicit the highest average percent signal change across the 7 volumes. These results in the right FG suggest that such violations of selectivity are more prevalent in children, and these individuals contribute lower values of selectivity to the group mean [despite the comparable mean face selectivity values across groups]. Also, because the percent signal change is computed across 7 volumes, not at the peak of the hemodynamic response function, the overall mean percent signal change could be negative for a condition, despite a positive response at the peak of the hemodynamic response function. Therefore, we did include negative percent signal change values in the computation of the magnitude of selectivity since we took all the voxels in an ROI to compute selectivity. Finally, what is most important about our definition of selectivity is reflected in the computation of a “difference” score. As a result, the absolute sign of the average percent signal change is not as relevant as is the relative difference in percent signal change across conditions within an individual. These selectivity values were then compared for age group differences in separate one-way analyses of variance (ANOVAs) for each region in each hemisphere.

Prior to being compared for age group differences, the size of each ROI for each participant was submitted to a square root transformation to normalize variance across the age groups. Previous studies have verified the feasibility of making direct statistical comparisons in hemodynamic response time courses between children and adults (Kang et al. 2003) (In a separate analysis, we also defined the ROIs based on the adult group activation for face-selective FG and place-selective PPA activation in the localizer task. However, the variance in the percent signal change across conditions in the adaptation task within these 2 regions was unequal across the 3 age groups and could not be equalized with a transformation, preventing any direct comparison across the age groups. This, in itself, is an interesting finding and confirms the results of previous studies reporting large differences in activation patterns across the age groups, particularly in the FG [Aylward et al. 2005; Golarai et al. 2007; Scherf et al. 2007].).

Face and House Adaptation Task

The adaptation task was modeled after that used by Avidan et al. (2005) in which blocks of 12 different stimuli (faces or houses) or of 12 presentations of the same identical stimulus were interleaved with blocks of fixation (see Fig. 1). There were 6 blocks of each stimulus condition, the order of which was randomized for each participant. The stimulus blocks lasted 12 s, and the interleaving fixation blocks were 6 s. Within a stimulus block, each item was presented for 800 ms followed by 200 ms of fixation. The task began with a 21-s block of fixation, followed by a block of abstract pattern stimuli, which was excluded from the statistical analyses, and ended with a 15-s block of fixation.

We specifically chose to use a blocked stimulus presentation to maximize 1) the signal-to-noise ratio, particularly in children and 2) the opportunity to observe differences in the mean percent signal change when comparing different and identical stimuli. Blocked designs have the advantage of prolonged repetition that increases the magnitude of the adaptation effect. Previous work has shown that the magnitude of adaptation increases with an increasing number of image repetitions (Grill-Spector and Malach 2001; Sayres and Grill-Spector 2006) and is very small with only one repetition (Grill-Spector and Malach 2001). Also, the magnitude of the adaptation effect is maximal when there are

no intervening stimuli between repeats (Henson et al. 2004; Sayres and Grill-Spector 2006) and under conditions when comparing multiple presentations of the “same identical stimulus” versus sequential presentations of different stimuli in other blocks (Konen and Kastner 2008). Therefore, an event-related design in which different and identical trials were randomized would have significantly reduced the magnitude of the adaptation effect, even in adults, and may have precluded our ability to observe any adaptation in the adolescents and children. Similarly, presenting images of the same object identity under different viewing conditions (e.g., viewpoint) can reduce or eliminate the magnitude of the adaptation effect in adults (Grill-Spector and Malach 2001; Epstein et al. 2003; Park and Chun 2009) and could have limited the ability to observe individual level adaptation effects in the children and adolescents. Finally, fMRI-a studies have shown that the PPA is not view invariant in adults (Epstein et al. 2003; Park and Chun 2009), which limits the options for presenting different images of the same house. As a result, to maximize our ability to discern adaptation effects, especially in the children, we chose to repeat the exact same image of a particular face/house in the identical blocks and to maximize differences between faces/houses during different blocks (i.e., differences in size, gender, expression, hair style, race, facial hair, number of windows, color, overall shape) (Note that this blocked fMRI-a paradigm in which the exact same image is repeated in the identity blocks is widely used in the adult literature [e.g., Andrews and Ewbank 2004; Avidan et al. 2005; Ewbank et al. 2005; Mazard et al. 2006; Ewbank and Andrews 2008; Cohen Kadosh et al. 2009; Davies-Thompson et al. 2009; Rhodes et al. 2009; Andrews, Clarke, et al. 2010; Andrews, Davies-Thompson, et al. 2010].).

To minimize the potential confound between attentional differences during different and identical blocks (greater attention in different than identical blocks) (Kanwisher and Yovel 2006), we engaged attention across all blocks by instructing participants to indicate, via button press on a customized glove button box, whenever a red circle was present in the display (2 trials per block). Importantly, the red circle encompassed the entire stimulus with the result that attending to the location of the red circle enhanced perception of the stimulus itself. Data from one child and one adult were excluded from the behavioral analysis of these data because they misplaced their fingers on the response glove, and the data were not recorded.

The face stimuli included a total of 78 (39 males and 39 females) color images of adult faces, which were compiled from multiple sources. Thirty-six of the faces were selected from the NimStim Face Stimulus Set (Tottenham et al. 2009), and an additional 21 images of foreign celebrities who are largely unknown in the United States were selected from a database of faces used in previous neuroimaging studies of face adaptation in typical adults (Avidan and Behrmann 2008). The proportion of faces by sex and race was similar in both the different and identical blocks of trials, such that male faces were presented 50% of the time and Caucasian faces roughly 70% of the time with the remaining 30% a combination of African American and Asian faces. The house stimuli included 78 color images of houses downloaded from the Internet. In order to maximize responsiveness in the FG and PPA during the “different” condition, both the face and house stimuli were selected to be highly heterogeneous.

ROI Analyses

The z -normalized average percent signal for the 4 stimulus conditions (same and different faces and houses) was extracted from within each participant’s independently defined right and left face-selective FG and place-selective PPA ROIs. The baseline volume for the percent signal change computation in the adaptation task was the final volume of the fixation block immediately preceding a task block. For each of the 7 volumes following the onset of a task block, the percent signal change was computed as follows: [(volume of interest value - baseline volume value)/baseline volume value]. These values were averaged across the 7 volumes and across the 6 task-specific blocks for each of the 4 conditions (different and identical faces and houses). These scores were submitted to repeated-measures ANOVAs to evaluate age group differences in patterns of both category-level selectivity and individual-level adaptation across these ROIs. Although the ROIs were independently defined based on their category selectivity in the movie localizer

task, we also wanted to verify that these same regions were also category selective as defined in the adaptation task with less rich stimuli. Category selectivity in the adaptation task was determined by a main effect of stimulus class in each ROI (e.g., faces > houses), and individual-level adaptation was defined by an interaction between stimulus class and condition in each ROI (e.g., in the FG: faces different > face identical; houses different = houses identical).

Whole Brain Voxelwise Analysis

To include every individual in the analysis and evaluate the possibility that adaptation effects occur in regions other than the a priori-defined regions we selected, face and house adaptation effects were also investigated throughout the whole brain on a voxelwise basis for each age group. The time series images from all participants in each age group were submitted to separate mixed-effects GLMs in which the stimulus category and condition effects were fixed factors and participant was a random factor. Category-level specificity effects were evaluated in every voxel in separate face > house and house > face contrasts. Individual-level face and house adaptation effects were also computed in each voxel in separate contrasts. Face adaptation was defined as (faces different-faces identical), and house adaptation was defined as (houses different-houses identical). These contrasts were corrected for multiple comparisons using a Monte Carlo simulation (This is a standard cluster correcting strategy in analyses of fMRI data. It incorporates the observation that neighboring voxels often activate in clusters and is based on Monte Carlo simulations calculating the likelihood to obtain different cluster sizes [Forman et al. 1995]. The Monte Carlo simulation is performed by iterating [1000 times] the processes of image generation, gaussian filtering, image scaling and thresholding, and clustering. This simulation results in a table of cluster size "frequencies," that is, it records how many clusters were found with 1, 2, 3 ... contiguous voxels in the generated "noise-only" volumes. The table is interpolated to estimate the cluster-level thresholds event at the anatomical resolution. For each iteration, after gaussian filtering, the image is scaled with respect to the sample mean and sample SD. Then, the image is thresholded such that, approximately the theoretical number of "false" positive voxels are activated in each random map. Based on the clustering, a tabulation of cluster size frequencies is, finally, reported with an estimate of the overall significance level achieved for the various combinations of the current voxel-level probability threshold and all the cluster size thresholds within the spanned interval. The minimum cluster size for the user-specified confidence level [alpha] is reported according to the original table [in voxels] and the interpolated table [in mm].), which required 302 contiguous voxels with a t -value ≥ 3.00 to achieve $P < 0.025$ significance. Only significant nonoverlapping voxels from the face and house adaptation contrasts within each age group were considered to reflect individual-level adaptation that was specific to one or the other stimulus category.

Results

Localizer Task: Identifying Face- and Place-Selective ROIs

Monkey neurophysiology and human neuroimaging studies indicate that stimulus-specific adaptation occurs maximally in visually excited neurons (Sobotka and Ringo 1994) and in cortical regions that are strongly biased for a preferred object category (Avidan et al. 2002). To independently identify regions in which both category- and exemplar-level adaptation effects might be revealed, an independent localizer task was initially used to demarcate regions of face-selective activation in the FG and place-selective activation in the parahippocampal gyrus in each individual participant separately in each hemisphere. This task has been used previously to localize face- and place-selective activation in the ventral visual pathway in individual children and adolescents (Scherf et al. 2007). Table 1 shows the number of participants with identifiable category-selective

activation, the mean location of the centroid of the ROI, and the size (in $1 \times 1 \times 1$ mm voxels) for each age group and ROI. Figure 2 provides a visual representation of the variability in size, location, number of participants who showed face- and place-selective ROIs, and the magnitude of category selectivity in each of these ROIs across the age groups.

Separate one-way ANOVAs with age group as a between-subjects factor indicated that children exhibited smaller face-selective ROIs in the right ($F_{2,33} = 5.7, P < 0.01$) and left ($F_{2,31} = 5.8, P < 0.01$) FG than did adolescents or adults, which is consistent with previous findings (Golarai et al. 2007, 2010; Scherf et al. 2007; Peelen et al. 2009; Joseph et al. 2010). Children also exhibited more medial (as measured by the Talairach x coordinate) face-selective activation in the right ($F_{2,33} = 5.6, P < 0.01$) and left ($F_{2,31} = 7.4, P < 0.005$) FG than the adults and adolescents, who were not different from each other (We are confident that the more medial face-selective activation in the children [generated from the localizer task] is not due to a selective error in the alignment procedures for the children. The procedures for reconstructing the structural images and coregistering the functional and structural images were identical across all age groups. We were particularly vigilant about fine-tuning the coregistration in the children to ensure that the functional and structural data were aligned. In some cases, individuals from each age group were positioned in the head coil in a tilted fashion, which impacts the position of both the functional and structural images. This is evident as soon as the structural images are reconstructed. In severe cases, we eliminated such participants from the study, as was the case for 2 children. In all but these severe cases, the tilt can be adjusted by rotating the structural image in 3D around any or all the primary axes [x, y, z] during the normalization using the Talairach procedure. Once the functional images are normalized to Talairach coordinates as well, the functional and structural images are in the same straight, normalized space. We visually inspected the normalization and coregistration results for each participant to ensure accurate alignment.). Despite the differences in size and location, the magnitude of face selectivity (measured as the difference in percent signal change to faces compared with other visual classes) was not different across the age groups in either the right ($F_{2,33} = 0.1, P = \text{n.s.}$) or the left ($F_{2,31} = 0.2, P = \text{n.s.}$) FG ROIs (see Fig. 2*d*). The groups also did not differ in the size or the magnitude of place selectivity within the place-related ROIs in the parahippocampal gyrus (see Table 1 and Fig. 2*b*), but children's and adolescents' right PPA activation was slightly more medial than that of the adults' ($F_{2,33} = 5.2, P < 0.025$).

Adaptation Task

Behavioral Performance

Participants were instructed to indicate, via button press on a customized glove button box, whenever a red circle appeared in the display (recall that the circle surrounded the stimulus in its entirety). All 3 groups were highly accurate at detecting the presence of the red circles (>97%), attesting to their high level of task completion, although children were slightly less accurate and slower to respond (see Table 2). A repeated-measures ANOVA with stimulus class (faces and houses) and condition (different and identical) as within-subject factors and age group as a between-subjects factor revealed a main effect

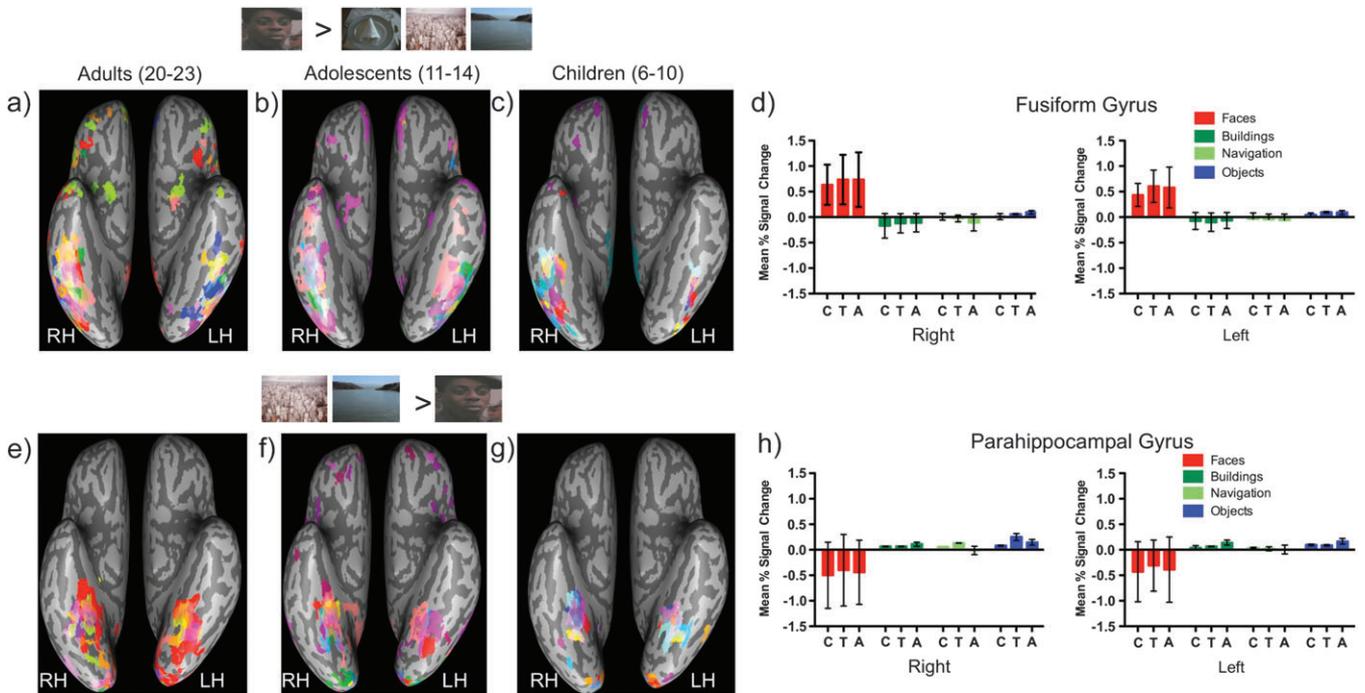


Figure 2. Size, location, and magnitude of category selectivity of individually defined face (*a-d*)- and place-selective (*e-h*) ROIs from the independent movie localizer task within each age group. Each participant within each age group is represented “in a unique color,” which is consistent across both the face- and place-selective maps. All the contrasts were mapped onto the same representative inflated brain. Selectivity was defined as the mean percent signal change from the defining contrast. For example, the selectivity in the FG was defined as [(3 × face activation) – (object + buildings + places activation)]. In *d* and *h*, the percent signal change for each visual category is plotted separately for children (C), adolescents (T), and adults (A) in each ROI and each hemisphere. Children (*c*) exhibited significantly smaller and more medial face-selective ROIs in the right and left fusiform gyri compared with both adolescents (*b*) and adults (*a*); however, they exhibited comparable face selectivity in both the right and left fusiform gyri (*d*). None of the groups differed in the size or the selectivity of the place-selective ROIs in the parahippocampal gyrus (*h*); however, adults (*e*) exhibited slightly more lateral ROIs on average than did the adolescents (*f*) and children (*g*).

Table 2

Behavioral performance during adaptation task in scanner

		Faces		Houses	
		Different	Identical	Different	Identical
Adults	Accuracy	0.99 (0.01)	1.00 (0.00)	1.00 (0.01)	0.99 (0.02)
	RT	449 (66)	450 (64)	449 (59)	455 (63)
Adolescents	Accuracy	0.98 (0.02)	0.99 (0.02)	0.99 (0.02)	0.99 (0.01)
	RT	508 (58)	484 (49)	479 (57)	477 (32)
Children	Accuracy	0.98 (0.02)	0.98 (0.03)	0.97 (0.03)	0.98 (0.02)
	RT	573 (51)	576 (52)	562 (59)	557 (58)

Note: Cells contain mean (SD) values. Accuracy is measured as proportion correct, and RT is measured in milliseconds.

of age group in accuracy ($F_{1,34} = 4.6, P < 0.025$). Bonferroni corrected post hoc comparisons indicated that children ($M = 97.6\%$, $SD = 1.9$) were slightly less accurate than adults ($M = 99.4\%$, $SD = 1.5$) ($P = 0.015$), who were as accurate as adolescents ($M = 99.0\%$, $SD = 1.3$). There were neither main effects of stimulus class or condition nor interactions between these factors and age group (all $P > 0.10$).

There was also a main effect of age group in reaction time (RT) ($F_{1,34} = 16.1, P < 0.001$). Children were slower than both adolescents and adults ($P < 0.001$), who responded equally fast. There was a main effect of stimulus category ($F_{1,34} = 5.0, P < 0.05$): across all age groups, participants were 10 ms slower on average to identify circles in the faces than houses blocks. There was no main effect of condition or interaction with age group. Together, these results suggest that all age groups were

performing at ceiling for all conditions, even though the children were a bit less accurate and slower than were the adults (Importantly, neither accuracy nor RT correlated with any measure of category-selective adaptation or of activation in any of the ROIs, once age was controlled for [all $P > 0.10$], suggesting that the ability to detect circles surrounding the stimuli did not affect activation levels or the magnitude of adaptation within these ROIs.).

FG and PPA ROI Analyses: Age Group Differences

Investigating category selectivity and individual-level adaptation responses in these “independently defined ROIs” provides the means for conducting cross-age comparisons of neural representation under optimal conditions, as selectivity is defined separately for each individual (the magnitude of which was not different for any of the ROIs across the age groups when defined this way). Critically, this method allowed the ROIs to be identified a priori and independently of the adaptation task, which prevents any selection bias in the analysis of the magnitude of adaptation response within these regions (Baker et al. 2007; Kriegeskorte et al. 2009). This method also precluded the possibility that a lack of individual level adaptation was the result of a lack of response because the ROIs were clearly defined based on a pattern of significant category selective responses in the localizer task.

There were significant developmental changes in both levels of neural tuning in the FG (Fig. 3*a-f*) and PPA (Fig. 3*g-l*). Age group differences in patterns of adaptation within these independently defined ROIs were evaluated by submitting

the average percent signal change scores (averaged across 7 volumes and across all the voxels in the ROI) to a repeated-measures ANOVA with age group as a between-subjects factor and region (FG, PPA), hemisphere (right, left), stimulus category (face, house), and condition (identical, different) as within-subjects factors. Significant category-level effects were reflected in an interaction between region and stimulus category, with stronger activation to the preferred category in the appropriate region (e.g., stronger activation for faces compared with houses in the FG). Significant individual-level adaptation effects were reflected in interactions between region, stimulus category, and condition (e.g., in the FG, stronger activation to different compared with identical faces but not to different compared with identical houses).

In the omnibus ANOVA, the region \times stimulus \times condition \times age group interaction ($F_{2,29} = 3.3$, $P = 0.051$) superseded main effects of region ($P < 0.001$) and stimulus ($P < 0.05$) and several other interactions (see Supplementary Table 1). This 4-way interaction reflects age-related differences in both category selectivity and individual-level adaptation across the FG and PPA. To understand the nature of this interaction, subsequent analyses were conducted within each age group to evaluate region, stimulus, and condition effects and interactions (An alternative approach to conducting the follow-up analyses would have been to evaluate between-group differences within each ROI. However, if we do the analysis this way, different individuals across the age groups contribute to the results differently across each ROI. For example, some participants

contribute 3 ROIs but others may contribute just one, leaving this analysis horribly unbalanced. This is because not all individuals had definable ROIs in each region. When we do the analyses within group, only individuals who have all 4 definable ROIs are ultimately included in the omnibus ANOVA for each age group. As a result, we are much more confident in our ability to compare category specificity and individual-level adaptation profiles across stimulus classes and ROIs within each age group.) We report the highest order interaction in each analysis (i.e., the interaction among the most variables). The details of the lower order interactions and main effects are all described in Supplementary Table 1.

Adults. Within the adult group, there were category-level effects in both the FG and PPA (region \times stimulus, $F_{1,12} = 28.4$, $P < 0.001$), with faces eliciting more activation than houses bilaterally in the FG and houses more than faces bilaterally in the PPA. There was a differential pattern of individual-level adaptation in the FG and PPA (region \times stimulus \times condition, $P < 0.01$) that superseded a main effect of condition ($P < 0.001$). Separate analyses within each region revealed that in the FG, adults exhibited selective individual-level adaptation to faces bilaterally (stimulus \times condition, $F_{1,12} = 7.1$, $P < 0.025$) (Fig. 3*a,b*). Post hoc analyses revealed that adults exhibited adaptation to faces (different > identical) but not to houses (different = identical) in both the right and left FG.

In the PPA, although there were main effects of stimulus ($P < 0.001$) and condition ($P < 0.05$), reflecting stronger

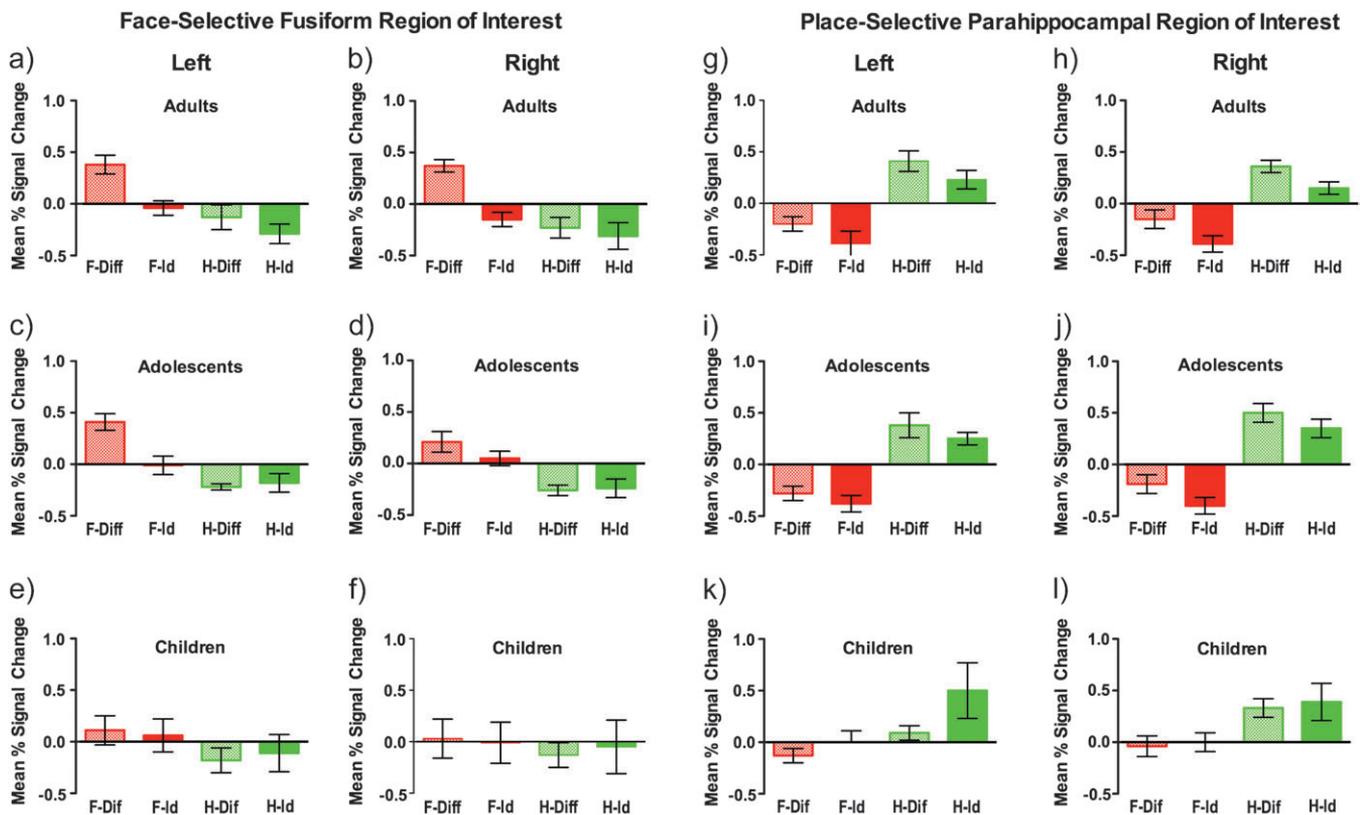


Figure 3. Age group differences in category and individual-level adaptation. Mean BOLD responses to face (red) and house (green) stimuli in each condition in the individually defined FFA (*a-f*) and PPA (*g-l*) ROIs plotted as a function of age and hemisphere. Only adults exhibited face-selective adaptation bilaterally in the FFA (*a-b*). However, adolescents exhibited face-selective adaptation in the left (*c*) but not the right (*d*) FFA. Children did not exhibit any face-selective adaptation in the FFA (*e-f*). Although all age groups showed significantly stronger activation to houses than faces bilaterally in the PPA, none of the age groups exhibited selective adaptation to houses in the individually defined PPA (*g-l*).

responses to houses than faces and to different than identical items, there was no stimulus \times condition interaction indicating a lack of “house-specific” individual-level adaptation bilaterally in the PPA (Fig. 3*g,b*). In other words, the PPA did evince adaptation to both visual classes equally in both hemispheres.

In sum, in the adaptation task, adults exhibited both category-level selectivity for faces in the FG and for houses in the PPA, as well as individual-level adaptation for faces in the FG. They also exhibited adaptation in the PPA, but it was not specific to houses. This replicates previous findings that individual-level adaptation is notoriously weaker for houses in the PPA than for faces in the anterior FG (Avidan et al. 2005).

Adolescents. Within the adolescent group, as in the adult group, there were category-level effects in both the FG and PPA (region \times stimulus, $F_{1,11} = 83.1$, $P < 0.001$), indicating stronger responses for faces in the FG and for houses in the PPA (Fig. 3*c,d,i*, and *j*). Unlike with the adults, there was no “differential” pattern of individual-level adaptation in the FG and PPA (no region \times stimulus \times condition interaction). However, there was a main effect of condition ($P < 0.025$) such that different items elicited more activation than did identical items in both the FG and PPA. Also, there was a stimulus \times condition interaction ($P < 0.05$). Turkey HSD post hoc comparisons revealed that across both ROIs, there was significant adaptation to faces (different $>$ identical), $P < 0.01$, but this effect only showed a trend toward significance for houses, $P < 0.10$. Exploratory analyses within each ROI revealed that in the FG, there was a main effect of stimulus category, $F_{1,11} = 17.4$, $P < 0.005$, with faces eliciting more activation than houses as well as a nearly significant main effect of condition, $F_{1,11} = 4.5$, $P = 0.058$, with different items eliciting more activation than identical items. There was only a trend for the stimulus \times condition interaction, $F_{1,11} = 3.3$, $P = 0.098$. Post hoc comparisons failed to reveal significant adaptation (different $>$ identical) for either faces or houses (Note that this result collapses across the ROIs in both hemispheres since the highest order interaction within the omnibus ANOVA did not include hemisphere as a significant variable.). In the PPA, there was a main effect of stimulus, $F_{1,11} = 35.1$, $P < 0.001$, indicating a stronger response to houses compared with faces, and only a weak trend for a main effect of condition, $F_{1,11} = 3.5$, $P = 0.087$, indicating that different items tended to elicit more activation than identical items (see Fig. 3*c,d*).

In sum, in the adaptation task, adolescents exhibited category-level selectivity for faces in the FG and for houses in the PPA and significant category general adaptation in both the FG and PPA. In other words, the individual-level adaptation in both of these ROIs was not specific to faces or houses and may simply reflect a sensitivity to the image-specific qualities of the stimuli.

Children. As with the adults and adolescents, among children, there was a significant region \times stimulus interaction, $F_{1,10} = 8.5$, $P < 0.025$, (see Fig. 3*e,f,k*, and *l*), indicating category-level differences by region. Subsequent analyses within each region revealed that this interaction was driven by category-level selectivity for houses bilaterally in the PPA ($P < 0.01$) but not for faces in the FG, which replicates our previous findings (Scherf et al. 2007). Children failed to exhibit either a main effect of condition or an interaction between stimulus \times condition (see Supplementary Table 1) indicating no individual-level adaptation for faces in the FG or for houses in the PPA.

In sum, although both the right and left PPA and FG ROIs were category selective as defined in the localizer task, children only exhibited category-level selectivity for houses in the PPA but not for faces in the FG in response to the stimuli in the adaptation task. Additionally, children failed to exhibit either category specific or category general adaptation in either the FG or PPA.

FG and PPA ROI Analyses: Adolescents versus Adults Given that the children do not exhibit category-level selectivity for faces in the FG in response to the stimuli in the adaptation task, we conducted a secondary analysis to evaluate the significance of age group differences just between adolescents and adults in the existence of both category selectivity and individual-level adaptation, particularly for faces in the FG. A repeated-measures ANOVA with age group (adolescent, adult) as the between-subjects factor and region (FG, PPA), hemisphere (right, left), stimulus category (face, house), and condition (identical, different) as within-subjects factors revealed a significant region \times hemisphere \times stimulus \times condition \times age group interaction, $F_{1,20} = 4.5$, $P < 0.05$ (for complete set of results, see Supplementary Table 2). Not only does the interaction survive significance in this analysis without the children, it reveals important hemispheric differences between adolescents and adults in individual-level adaptation. This 5-way interaction reflects differences between adolescents and adults in both category selectivity and individual-level adaptation across the FG and PPA. To understand the nature of this interaction, subsequent analyses were conducted within both age groups to evaluate region, hemisphere, stimulus, and condition effects and interactions. As before, only the highest order interaction is specified. Details of all other interactions and main effects can be found in Supplementary Table 2.

Adults. Adults exhibited individual-level adaptation to faces but not houses in the FG (region \times stimulus \times condition, $F_{1,11} = 7.9$, $P < 0.025$), which was bilateral (did not interact with hemisphere). In other words, post hoc comparisons revealed that in both the right and left FG, only faces elicited a greater response to different compared with identical items (see Supplementary Table 2). In the PPA, adults exhibited a main effect of stimulus class (houses $>$ faces) and of condition (different $>$ identical); however, there was no stimulus \times condition interaction, indicating that the adaptation was not specific to houses in the PPA and may reflect more general adaptation to the physical characteristics of the stimuli across both visual categories.

Adolescents. In contrast with the adults, adolescents exhibited differential individual-level adaptation across the hemispheres in the FG (hemisphere \times stimulus \times condition, $F_{1,10} = 5.5$, $P < 0.05$). In the right FG, there was more activation to faces than houses, $F_{1,10} = 12.4$, $P < 0.005$, but no main effect of condition, $F_{1,10} = 1.2$, $P = \text{n.s.}$ or stimulus \times condition interaction, $F_{1,10} = 1.6$, $P = \text{n.s.}$, indicating no individual-level adaptation for either faces or houses (different = identical, see Fig. 3*d*). In contrast, in the left FFA (Fig. 3*c*), there was significant individual-level adaptation for faces (different $>$ identical) but not houses (stimulus \times condition, $F_{1,10} = 6.8$, $P < 0.05$). In the PPA, like the adults, there was no house-specific individual-level adaptation in either the right or left PPA (i.e., no stimulus \times condition interaction, see Fig. 3*i,j*). In sum, adolescents exhibit category-level selectivity for faces in the FG and for houses in the PPA

bilaterally in both the localizer and adaptation tasks; however, unlike adults, they only exhibit individual-level adaptation for faces in the left FG.

Finally, to evaluate the relation between the functional characteristics of the independently defined ROIs and the magnitude of the individual-level adaptation effects, an adaptation index was regressed on the size of each ROI (as determined from the movie localizer task) separately. The individual-level adaptation index was computed in each region as the difference of the individual-level adaptation effects across stimulus categories (corrected for negative numbers, Simmons et al. 2007). For example, for face adaptation, the index was computed as [(faces different - faces identical) - (houses different - houses identical)]. Interestingly, the size of the ROI strongly predicted the magnitude of the individual-level adaptation effect for faces across individuals but only in the right FG, $F_{1,34} = 10.1$, $P < 0.005$ (Fig. 4a). The relation between the size of the ROI and the face-selective adaptation was present in the children, $F_{1,9} = 6.7$, $P < 0.05$ and adults, $F_{1,11} = 8.4$, $P < 0.025$, but not in the adolescents, $F_{1,10} = 0.2$, $P = n.s.$ There were no significant relations between the magnitude of individual-level adaptation and size of the ROI or the magnitude of category selectivity in any other region (Fig. 4).

Whole Brain Voxelwise Analyses of Adaptation Effects

To include every individual in the analysis (not only those who exhibited a definable ROI in the localizer task) and evaluate the possibility that category-level selectivity and individual-level adaptation effects occur in regions other than the a priori defined regions we selected, adaptation effects were investi-

gated throughout the whole brain on a voxelwise basis for each age group. Category-level selectivity in the adaptation task (Fig. 5a-c) for faces (red) was defined as faces > houses collapsed across condition (different, identical) and for houses (green) as houses > faces. Individual-level adaptation (Fig. 5d-f) was computed as different > identical items for faces (red) and houses (green). Only voxels that exhibited significant adaptation for one visual category (nonoverlapping with the other category) were considered to reflect category-specific individual-level adaptation.

Category-level selectivity in the adaptation task. All 3 age groups demonstrated category-level specificity for faces in the right FG (see Fig. 5a-c). This replicates our previous findings in adults and adolescents (Scherf et al. 2007). Unlike in our previous findings and in the ROI-based analyses, as a group children showed selectivity for faces in the FG; however, the group defined face-selective ROI was 58% the size of the adult region. The FG face selectivity that was identifiable in children as a group may be related to the use of a larger sample than in previous studies and the use of a somewhat more lenient contrast (faces > houses). Similarly, all 3 age groups exhibited category-level selectivity for houses bilaterally in the PPA (children's right PPA activation is more ventral and not visible on the inflated brain). These early developing category-specific effects in the PPA are also consistent with our previous findings (Scherf et al. 2007). These results indicate that similar regions of category-selective activation were elicited by both the movie localizer and adaptation tasks in all 3 age groups, particularly in the right hemisphere.

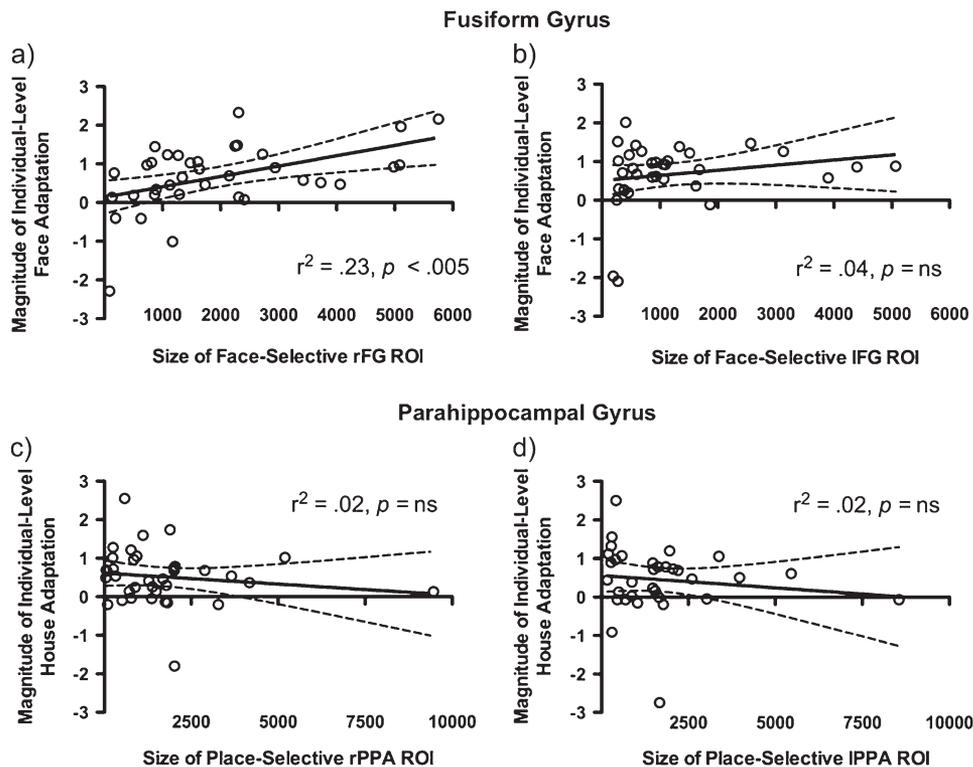
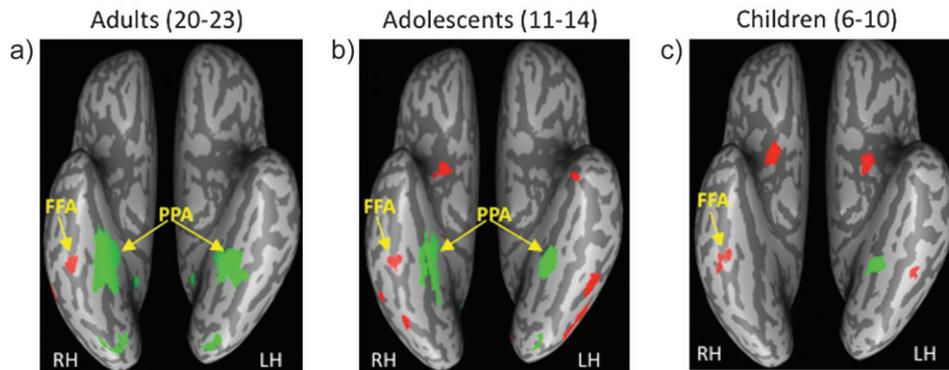


Figure 4. Relation between size of category-selective ROI and magnitude of individual-level adaptation effect in the right (a) and left (b) fusiform gyri and right (c) and left (d) parahippocampal gyri. Interestingly, only in the right FG (a) did the size of the ROI strongly predict the magnitude of the individual-level adaptation effect for faces across individuals. The individual-level adaptation index was computed as the difference of the individual-level adaptation effects across stimulus categories. For example, for face adaptation, the index was computed as [(faces different - faces identical) - (houses different - houses identical)].

Category Level Selectivity



Individual-Level Adaptation

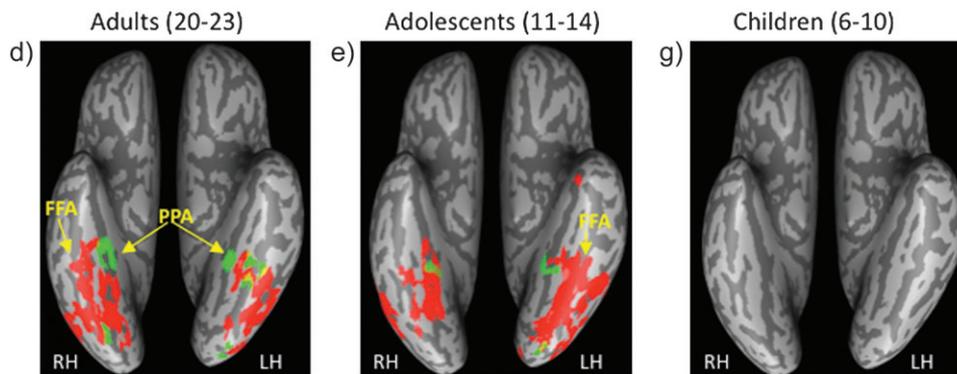


Figure 5. Results of whole brain voxelwise analysis evaluating category-level specificity (a–c) and individual-level adaptation effects (d–f) within each age group in the adaptation task. Category-level adaptation for faces (red) was defined as faces > houses collapsed across condition (different, identical) and for houses (green) as houses > faces. Individual-level adaptation was computed as different > identical for faces (red) and houses (green) in separate contrasts. Each contrast was thresholded at a corrected $P < 0.025$. All 3 age groups exhibited some category-level adaptation for faces in the right FG and for houses bilaterally in the PPA (children’s right PPA activation more ventral). Adults were the only group to exhibit selective individual-level adaptation for faces in the right FG (nonoverlapping with adaptation for individual houses), which was centered on the classic FFA region and for houses bilaterally in the PPA. Both adults and adolescents exhibited individual-level adaptation for faces in the medial occipitotemporal gyrus. However, adolescents only exhibited individual-level adaptation for faces in the FG and for houses in the PPA in the left hemisphere. Children failed to exhibit individual-level adaptation in any region.

Individual-level adaptation. As was revealed in the ROI analyses, adults exhibited individual-level adaptation for faces bilaterally within the classic FFA region (Fig. 5d) but also throughout the extent of the FG and in the right medial occipitotemporal gyrus. In contrast with the ROI analyses, adults also exhibited individual-level adaptation for houses bilaterally in the PPA. The ROI analyses reported above only indicated significant category-level selectivity in the PPA for houses but not significant house-specific individual-level adaptation. The different findings from these 2 analyses appear to derive from the large number of voxels in the PPA ROI that exhibit individual-level adaptation for houses and for faces (see Fig. 5d), prohibiting the ability to observe significant “house-selective” individual-level adaptation. The whole brain analyses reveal that only a small anterior portion of the larger PPA ROI exhibits selective individual-level adaptation for houses.

Consistent with the ROI analyses, adolescents exhibited individual-level adaptation for faces throughout the extent of the left FG (Fig. 5e) but also in posterior regions of the right FG. Like adults, adolescents also exhibited individual-level adaptation for faces in the right medial occipitotemporal gyrus and for houses bilaterally in the PPA. However, the ROIs reflecting individual-level adaptation for houses were much smaller in adolescents than in adults. Finally, as in the ROI analysis, the children did not exhibit individual-level adaptation effects for faces or houses anywhere in the brain (Fig. 5f). To evaluate whether the lack of individual-level adaptation effects in children is related to a more general insensitivity to repetition per se, a secondary whole brain analysis contrasting different versus identical items (collapsed across visual category) was conducted. In fact, children exhibited individual-level adaptation bilaterally in the FG (left: $-29, -48, -12$; right: $30, -34, -16$).

This suggests that children do exhibit repetition suppression in the BOLD response in the ventral visual pathway; however, it is not category selective for either faces or houses.

Finally, none of the groups exhibited more activation to different compared with identical items in either the face or house condition in regions specifically related to attention (e.g., superior parietal lobule or intraparietal sulcus). Together with the behavioral results (i.e., no task block differences in accuracy or RT across or within any age group), this finding supports the notion that the different blocks of trials were not inherently more attentionally engaging than were the identical blocks.

Discussion

This is the first study to investigate developmental changes in the specificity of face and house representations in the ventral visual pathway at a subvoxel resolution. It is also the first study to investigate age-related increases in both “category-level selectivity” as well as in “individual-level adaptation.” In analyses based on independently defined face-selective FG and place-selective PPA ROIs and in whole brain voxelwise analyses, these results replicate previous findings that, in adults, populations of neurons in the FG and PPA are tuned both at a categorical level for their preferred stimulus class but also at a stimulus-specific or individual level to support more fine-grained individual discrimination. More importantly, our findings provide novel evidence that, developmentally, category-level neural tuning precedes individual-level neural tuning throughout the ventral visual pathway: across all 3 age groups, stimulus-specific neural tuning (i.e., individual-level adaptation) for faces and/or houses was present only if category-level selectivity for these stimulus classes was already established.

The convergence of several findings led us to this interpretation. First, within the individually defined ROIs from the localizer task, children do not show either category-selective activation or adaptation to individual faces in the adaptation task. Importantly, they do show category-level selectivity for houses in the individually defined PPA in the adaptation experiment but fail to show adaptation to individual houses. This pattern of results rules out a general difficulty in eliciting category-selective activation to the static stimuli in the adaptation paradigm in the children. Second, the within group whole brain analyses of the adaptation data, which have more subjects and therefore more power, revealed that children did, in fact, exhibit category-selective responses for faces in the right and left FG and for houses in the right and left PPA (Fig. 5*a*) but still failed to exhibit individual-level adaptation responses, which was not due to a general insensitivity to repetition per se. Third, and more importantly, the adolescents all showed category selectivity for faces in the right and left FG and for houses in the right and left PPA in the adaptation task. However, the ROI analyses revealed that, despite the pervasive category-selective activation in the ventral visual pathway, adolescents only exhibited individual level adaptation to faces in the left FG. Finally, the whole brain analyses, which include more subjects and thus more power, revealed that, consistent with the ROI analyses, adolescents exhibited individual-level adaptation for faces throughout the extent of the left FG (Fig. 5*e*) but also in posterior regions of the right FG and for houses bilaterally in the PPA. Importantly, the ROIs reflecting individual-level adaptation for houses were much smaller in

adolescents than in adults. This pattern of results across age groups and types of analyses led us to the conclusion that the neural development of “what” precedes that for “which”.

Although speculative, this interpretation of our findings suggests that category-level neural tuning may be “necessary” to develop neural representations that are fine-grained enough to encode stimulus-specific information. However, category-level specificity may not be “sufficient” for individual-level neural tuning since adolescents and children both exhibited category-selective activation for faces and houses (as defined in the movie localizer task) in the absence of significant stimulus-specific adaptation. Finally, this developmental transition from category-level to individual-level neural tuning is disproportionately slowed for face- versus place-related cortex.

Developmental Changes in Neural Tuning

Developmental Changes in FG

Despite our ability to define equally selective face ROIs in the FG across the 3 age groups in the localizer task, only adults exhibited both category-selective responses to faces as well as face-specific individual-level adaptation in these same ROIs. Both the ROI and voxelwise analyses indicated that only adults exhibit a selective attenuation of the BOLD signal for identical compared with different faces “bilaterally” in the FG, which was localized near the classic FFA region. This finding reflects the specificity of the neural representations for faces in this region in adults.

Although adolescents exhibited bilateral category-selective responses for faces in the FG, they only exhibited individual-level adaptation for faces in the left FG, which was only evident in the analyses that excluded children. One possible explanation for the left/right difference in the adolescents is that there are hemispheric asymmetries in the kinds of information encoded by the fusiform gyri and that only left hemisphere computations are sufficiently mature in adolescence. Indeed, there is growing consensus that the right fusiform is more specialized for holistic processing, whereby the spatial metric of individual faces is encoded (Rossion et al. 2000; Meng et al. 2008; Yovel et al. 2008; Schlitz et al. 2010). In contrast, the left fusiform appears to be more implicated in part-based processing. One interpretation of our results is that adolescents are actually using more part-based representations, computed in the left FG, to process face identity, which leads to the significant face-selective adaptation there. This interpretation is consistent with findings from several groups that have argued that the ability to recognize individual faces continues to improve as children develop visuo-perceptual expertise in recognizing faces on the basis of subtle metric variations between their constituent features, also called configural processing (Carey et al. 1980; Diamond and Carey 1986; Mondloch et al. 2004; Sangrigoli and de Schonen 2004). Neuroimaging studies with adults have also shown that both the FFA and the OFA are involved in recognizing individual faces (Gauthier et al. 2000) and that expertise for classes of perceptually homogenous novel objects and objects of expertise produces increased activation in the classically defined FFA region (Gauthier et al. 1999). This transition in the development of face representations in the FG may be related to the acquisition of expertise for individual face recognition and the subsequent fine-tuning of large populations of neurons to subserve a more holistic or configural kind

of face processing. A direct test of this possibility will involve contrasting adaptation profiles in response to faces that differ in features or in spatial configurations among the features.

Finally, despite the comparable selectivity for faces and places in the ROIs generated from the localizer task, children failed to evince category-selective responses to faces in these same ROIs during the adaptation task. It was quite unexpected to find that the face-selective FG ROIs defined in the localizer task were not selective for faces in the adaptation task in the children. However, recent evidence indicates that even in adults, dynamic stimuli, like those used in the movie localizer task, evoke much stronger responses from face-selective regions than do static stimuli (Schultz and Pilz 2009). Our findings extend these results to suggest a similar pattern in children. However, it is important to note that several previous studies investigating developmental changes in the topography of the ventral visual pathway also used static stimuli and detected face- and place-selective activation in individual children with a larger proportion of children exhibiting place-compared with face-selective ROIs (Golarai et al. 2007, Golarai et al. 2010). It is possible that the locus of the individually definable face-selective ROIs in the 2 tasks may be slightly different because of the stimuli differences (dynamic vs. static) but also because of the nature of the contrasts to define selectivity (faces-multiple object categories vs. faces-houses). Also, both adults and adolescents did evince face selective responses in the localizer-defined ROIs during the adaptation task despite the differences in the dynamic nature of the stimuli. Together, this pattern of results converges with our previous findings of late developing face-related regions within the ventral temporal region.

One possibility is that children might show individual level adaptation effects using dynamic stimuli, like those in the localizer task. This is an interesting, but unprecedented, approach even in adults making it difficult to predict whether and/or how adaptation effects for dynamic faces could be measured. There are 3 reasons why we argue that driving the face-selective regions with more activation via dynamic stimuli may not have induced the face-specific adaptation that we see in adults bilaterally and in the adolescents in the left FG. First, to our knowledge, there is no evidence that adaptation responses are driven more strongly by dynamic stimuli. Second, the whole brain analyses of the adult and adolescent adaptation effects revealed ROIs in the FG and PPA that overlapped with the individually defined ROIs from the movie localizer task, indicating that both tasks elicited activation in similar regions across individual adults and adolescents. Third, neither the children nor the adolescents exhibited weaker overall signal within the localizer-defined ROIs during the adaptation task. This indicates that the localizer-defined ROIs were activated to a similar extent across the age groups in the adaptation task but were qualitatively different in their response profile (Another approach to evaluate category selectivity in individual children would have been to define the ROIs using the adaptation data. Given the strong concerns about overestimating the magnitude of effect sizes within ROIs that are not defined independently [e.g., Kriegeskorte et al. 2009, 2010], we did not use this approach as our primary method of analysis. However, we do include this as a secondary analysis with a figure of these results in the Supplementary Information. We caution readers about this nonindependence when evaluating these results. Within these internally defined ROIs, we were able to demonstrate

category selectivity for both the FG and PPA bilaterally in the children; however, we still do not observe individual-level adaptation in any of the ROIs in the children. In the future, it will be useful to include 2 runs of the adaptation task and use one of the runs to define the ROIs and the other to investigate the magnitude of the category-selective and individual-level adaptation effects.).

Children also failed to exhibit individual-level adaptation for faces in either the right or left FG, although we did observe such category specificity when the ROIs were defined within the adaptation task (see Supplementary Fig. 2). This result was evident in both the whole brain and ROI analyses. One potential explanation for the lack of individual level adaptation to faces is that the neural basis of category-based representations are still developing at this time and may be a precursor for the emergence of neural tuning to individual exemplars. This could be manifest in the smaller and more variable face-selective ROIs defined from the localizer task. ROIs were smaller and more variable in location in the children, which may have contributed to the absence of individual-level adaptation. The linear relation between the size of the ROI (as defined in the localizer task) and the magnitude of the individual-level adaptation to faces in the right FG supports this notion. The absence of adaptation in children may be a result of an insufficient number of face-selective neurons to represent the level of detail required for individual face recognition that drives this face-selective adaptation response.

Importantly, the lack of individual-level neural tuning in children converges with several behavioral studies suggesting that individual face recognition skills are immature even in early adolescence (Ellis et al. 1973; Carey and Diamond 1977; Carey et al. 1980; Diamond and Carey 1986; Mondloch et al. 2002, 2004; Itier and Taylor 2004). Unfortunately, we did not employ a behavioral measure that could be used to evaluate potential developmental changes in the correspondence between the magnitude of adaptation and performance on individual face and house recognition tasks. Future studies employing specific tests of fine-grained face and house identity processing that have previously discriminated children's, adolescents', and adults' face-processing behavior (Mondloch et al. 2002, Mondloch et al. 2004) may be predictive of age-related changes in the magnitude of the face-selective individual-level adaptation response in the FG.

Also, future studies incorporating task demands to attend explicitly to face and house identity during localizer and adaptation tasks are clearly necessary. In the current study, the behavioral task (detecting red circles) was orthogonal to the nature of the stimuli. Also, we specifically choose to maximize our ability to discern adaptation effects by repeating the exact same image of a particular face/house in the identical blocks and to maximize differences between faces/houses during different blocks. Identity-specific processing may modulate age-related differences, but whether such identity task demands would enhance or minimize age group differences cannot be predicted. The adult literature is quite inconsistent as to whether changes in the physical characteristics of the image or in the identity of the face in the image (which inherently incorporates changes in the physical characteristics of the image) actually produce comparable or differential releases from adaptation in the fMRI BOLD signal in the FFA (e.g., Rotshtein et al. 2005; Xu et al. 2009).

These results may seem at odds with earlier studies reporting early maturity in individual face recognition behavior (for review, see Crookes and McKone 2009) and in the neural differentiation of responses to familiar and unfamiliar faces even in young infants (e.g., de Haan and Nelson 1997, 1999). For example, in the infant studies, researchers measured ERPs as infants passively view images of their own mother's face, a stranger face, as well as of a favorite and a novel toy. They reported a larger amplitude negative central (Nc) component for the mother's face than a stranger's face but also for familiar compared with novel toys (although the spatial distribution of this effect differs for faces compared with toys). These results would seem to suggest that there is neural specialization for individual face recognition (at least of an infant's own mother's face) at a much younger age than early adolescence as we have reported. However, several pieces of evidence convince us that these previous results may not contradict our current pattern of results. First, the increase in amplitude of the Nc is not category specific (as are the adolescent and adult adaptation effects in the FFA and PPA). The Nc has been interpreted to reflect more general processes in either the infant's allocation of attention or their attribution of emotional salience to stimuli (for review, see de Haan et al. 2003). Second, the modulation of the Nc by face familiarity is only observed when the mother's and stranger's faces are very perceptually distinct (de Haan and Nelson 1997). In other words, there is no differentiation in the Nc when infants are presented with 2 perceptually similar faces, even if one of them is the infant's own mother. More recent evidence suggests that even adolescents have difficulty discriminating perceptually similar faces (Golarai et al. 2010). These findings suggest that there is enormous developmental change in both discrimination/recognition behavior of individual faces and in the neural basis of this ability. In fact, age-related changes in the Nc have been documented in at least 2 studies for faces but not objects (Carver et al. 2003) or monkey faces (Scott et al. 2006), from infancy to the preschool years. It is also an open question whether the Nc or other components such as the N290 or positive slow wave reflect developmental precursors of any of the adult face-related components (see de Haan et al. 2003). Finally, the few studies investigating developmental changes in face-related ERP components in older children and adolescents (e.g., N170) support the notion that the neural substrates for face perception and recognition processes mature through adolescence (Itier and Taylor 2004). Future studies of face identity recognition that test infants, children, adolescents, and adults under similar methodological and viewing conditions (with both highly and less familiar and perceptually similar faces) are clearly needed to understand any potential continuity, or lack thereof, between the infant ERP and child and adolescent fMRI results investigating the neural basis of the ability to represent individual faces.

Developmental Change in PPA

As in the FG, our results indicate that the cortical representations in the PPA become more fine-tuned across development but at a faster rate than do the in the FG. The ROI analyses indicated that none of the age groups exhibited significant individual-level adaptation for houses, despite the fact that they all exhibited category selectivity for houses bilaterally in the PPA in both the localizer and adaptation tasks. However, the whole brain voxelwise analyses showed that both adults and adolescents demonstrated attenuated BOLD signal to individual

compared with different houses bilaterally in the PPA. Although children exhibited strong house-selective activation bilaterally in the PPA in the adaptation task, they failed to exhibit individual-level adaptation for houses in any region.

The discrepancy in the ROI and whole brain analyses among the adolescents and adults may be related to a difference in the size of the neural regions tuned at the category and individual levels in the PPA. The place-selective ROIs (defined in both the localizer task and in the houses > faces contrast in the adaptation task) are significantly larger compared with the size of the regions that show category-specific individual-level adaptation for houses (as revealed in the whole brain analysis in Fig. 5). Only a subset of anterior voxels in this larger house-selective ROI selectively encodes the uniqueness of a house in both adolescents and adults. Importantly, this subset of voxels is much smaller in adolescents than in adults and is nonexistent in children. This larger portion of house-selective activation in the posterior portion of the PPA that does not exhibit individual-level adaptation for houses may be more involved in encoding places in context (Aminoff et al. 2007) rather than in encoding the uniqueness of a specific place. The transition from adolescence to adulthood is marked by an increase in the size of the anterior region of the PPA that selectively encodes the uniqueness of places.

The lack of individual-level adaptation for houses in the PPA for children was somewhat unexpected given the (albeit limited) evidence of adult-like house recognition in children (Carey and Diamond 1977). Interestingly, fMRI studies with adults reveal that the PPA encodes a spatial scene as a unified object, separate from its component parts, with particular emphasis on the geometric structure of the entire space (for review, see Epstein 2008). Although it is still unclear, even in adults, how this spatial layout is encoded at the neural level in terms of visual features and or shapes in the PPA (Epstein 2008), the PPA seems to integrate this information to encode a global representation of the spatial scene. The lack of category-selective individual-level adaptation for houses in the PPA in children may have been related to limitations in the ability to integrate the component parts of a spatial scene into a global geometric shape. This interpretation is consistent with perceptual organization studies showing that the ability to perceptually group spatially disparate elements for the purpose of perceiving a global shape continues to develop into early adulthood (Scherf et al. 2008).

Alternative Explanations

We interpret the developmental differences in individual-level adaptation to reflect an emerging narrowing in the neural tuning of populations of face-selective neurons in the FG and of place-selective neurons in the PPA to represent individual exemplars in increasingly fine-grained detail. However, these differences may also be related to group differences in visual scanning of faces and houses. Although we did not collect eye-tracking data and cannot rule out this possibility completely, the existing, although limited, literature suggests that children and adults may not be so different in their visual scan paths of faces. For example, by 2 months of age infants' visual scanning focuses on the internal features of faces (Maurer and Salapatek 1976), and, by 5 years old, children are similar to adults in their use of outer features to recognize unfamiliar faces (Want et al. 2003). To our knowledge, nothing is known about developmental differences or commonalities in visual scan paths of

houses or even common objects. Future studies investigating children's and adolescents' visual scan paths of faces and houses relative to adults' during fMRI-a tasks will help evaluate this alternative explanation more clearly.

A second alternative explanation is that participants exhibited an own-age bias in face processing that affected the level of encoding for individual faces. Since we only used adult face stimuli, the bilaterally individual-level adaptation for faces may reflect efficient encoding of individual faces in the adults but not the children or adolescents. We think this explanation is unlikely for 3 reasons. First, although some evidence suggests that adults exhibit better recognition memory for unfamiliar faces that are within their peer age group (Fulton and Bartlett 1991; Wright and Stroud 2002), the evidence for an own-age bias in recognition memory for children and adolescents is quite mixed (see Chung 1997; Anastasi and Rhodes 2005). Second, in recent fMRI experiments, typically developing children and adolescents exhibit similar extent of face-selective activation in the FG when viewing faces of familiar and unfamiliar adults and peers (Pierce and Redcay 2008; Golarai et al. 2010). Finally, it is difficult to extend the hypothesis of an own-age bias to explain the developmental differences in individual-level adaptation for houses as well. However, additional fMRI-a studies contrasting individual-level adaptation responses to faces of adults and age-matched peers are required to adequately evaluate this alternative hypothesis.

Importantly, the developmental differences in both the FG and PPA are not likely to be attributed to differences in attention or in overall BOLD response. All age groups were at ceiling in the behavioral task across the conditions for both face and house stimuli, indicating that all 3 groups maintained equal vigilance across conditions. Also, the whole brain analyses contrasting different and identical stimuli failed to reveal attenuated activation to the identical items in attention networks in any age group. Finally, previous studies investigating object-selective adaptation effects in adults have shown that explicit modulation of attention does not reduce the magnitude of adaptation effects in a blocked fMRI-a design (Konen and Kastner 2008). It is also critical to note that the localizer task of this experiment the individually defined ROIs were equally category selective and active (see Fig. 3) across the 3 age groups; however, only children failed to exhibit category-selective individual-level adaptation responses across all the ROIs. Children did exhibit an individual-level adaptation effect bilaterally in the FG, but it was not specific to faces or houses, indicating that they are capable of exhibiting repetition suppression to identical stimuli, just not in a category-selective way. Also, in the ROI analyses of the adaptation task, comparable BOLD signals in all 4 regions (right and left FG and PPA) were evident in all age groups (no main effect of age). These findings rule out the explanation that weaker or nonexistent BOLD signal in some age groups, and the children in particular, leads to smaller magnitude adaptation responses (Avidan et al. 2002).

Category-Level Neural Tuning Precedes Individual-Level Tuning

Our novel developmental results indicate that 1) category-level neural tuning precedes and may be a prerequisite for individual-level neural tuning throughout the ventral visual

pathway, 2) category-level neural tuning may be necessary but not sufficient for individual-level neural tuning, and 3) face-related cortex is disproportionately slower in this developmental transition of neural tuning than is place-related cortex.

These developmental results reflect more broadly on psychological models of the organization of conceptual knowledge, categorization, and visuo-perceptual expertise and are most consistent with findings of a basic-level advantage in categorization and the slow acquisition of expert individual-level recognition. The basic-level advantage in categorization reflects the finding that of all the categories to which a particular object can belong (e.g., animal, dog, pug), most objects are recognized at the basic level of abstraction (e.g., dog vs. chair) and can be distinguished by unique features or configurations of features (Rosch 1978; Tanaka and Taylor 1991). However, all objects can be recognized at increasingly more subordinate levels and ultimately at the individual level, where all exemplars share similar parts in a similar basic configuration but differ in the spatial relations within this basic configuration. Expertise with any particular object class is indicated by the ability to recognize objects equally fast at the individual level (e.g., Joey's face), where featural differences are less diagnostic than configural properties for recognition, and at the basic level, where featural differences are very discriminating (Gauthier et al. 1999).

Although the overwhelming evidence supporting these models of the organization of conceptual knowledge has been generated in adults, several studies have provided behavioral evidence that the conceptualization of categories develops ontogenetically in a similar way from basic to more subordinate levels of categorization (e.g., Mervis and Crisafi 1982; Quinn 2004; Quinn and Tanaka 2007). Our results provide the first evidence of developmental changes in neural tuning that support these models of conceptual development and the organization of conceptual knowledge. More specifically, we found that there is a developmental hierarchy in the neural tuning of populations of neurons in the ventral visual pathway, such that category-level selectivity emerges before and may be required for the development of stimulus-specific neural tuning. Furthermore, our results indicate that there are different developmental trajectories that characterize the transition from category-level to individual- or exemplar-level neural tuning across stimulus classes, with face-related cortex proceeding much more slowly than place-related cortex. One possibility for this delay in face-related cortex is that the mature profile of shape tuning for faces is narrower than is the tuning profile for other general object categories (Gilaie-Dotan and Malach 2007), which may result from years of experience acquiring visuo-perceptual expertise at encoding and discriminating subtle featural and configural differences between faces.

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Supplementary Material

Supplementary material can be found at: <http://www.cercor.oxfordjournals.org/>

Notes

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