

FAST-TRACK REPORT

Visual category-selectivity for faces, places and objects emerges along different developmental trajectories

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Abstract

The organization of category-selective regions in ventral visual cortex is well characterized in human adults. We investigated a crucial, previously unaddressed, question about how this organization emerges developmentally. We contrasted the developmental trajectories for face-, object-, and place-selective activation in the ventral visual cortex in children, adolescents, and adults. Although children demonstrated adult-like organization in object- and place-related cortex, as a group they failed to show consistent face-selective activation in classical face regions. The lack of a consistent neural signature for faces was attributable to (1) reduced face-selectivity and extent of activation within the regions that will become the FFA, OFA, and STS in adults, and (2) smaller volumes and considerable variability in the locus of face-selective activation in individual children. In contrast, adolescents showed an adult-like pattern of face-selective activation, although it was more right-lateralized. These findings reveal critical age-related differences in the emergence of category-specific functional organization in the visual cortex and support a model of brain development in which specialization emerges from interactions between experience-dependent learning and the maturing brain.

Introduction

The functional topography of the ventral visual cortex in adults reflects an organized category-selective map with particular stimulus classes eliciting robust and distinct patterns of cortical activation (Downing, Chan, Peelen, Dodds & Kanwisher, 2006; Grill-Spector & Malach, 2004). Converging neuropsychological and neuroimaging studies indicate that faces consistently engage a lateral portion of the posterior fusiform gyrus ('fusiform face area' [FFA]; Kanwisher, McDermott & Chun, 1997), a lateral region in the inferior occipital cortex ('occipital face area' [OFA]; Gauthier, Tarr, Moylan, Skudlarski, Gore & Anderson, 2000), and the superior temporal sulcus (STS; Hoffman & Haxby, 2000). Common objects activate more medial portions of the posterior fusiform gyrus and a region of the lateral occipital cortex separable from the face-related region (LO; Grill-Spector, Kushnir, Edelman, Avidan, Itzhak & Malach, 1999), whereas buildings and landscapes activate the collateral sulcus (CoS; Aguirre, Zarahn & D'Esposito,

1998) and the parahippocampal gyrus ('parahippocampal place area' [PPA]; Epstein & Kanwisher, 1998).

Almost nothing is known about how this functional topography in the ventral temporal lobe emerges developmentally. None of the existing developmental neuroimaging studies has mapped object- or place-specific activation in children under the age of 9. The few existing studies have focused on the development of face-related activation specifically in the fusiform gyrus. Although a PET study with infants suggested that face-related activation may be present in 2-month-old infants (Tzourio-Mazoyer, De Schonen, Crivello, Reutter, Aujard & Mazoyer, 2002), fMRI studies, which have better spatial resolution, indicate that the FFA is not adult-like even in early adolescence (Aylward, Park, Field, Parsons, Richards, Cramer & Meltzoff, 2005; Gathers, Bhatt, Corbly, Farley & Joseph, 2004; Passarotti, Paul, Bussier, Buxton, Wong & Stiles, 2003). In addition to the discrepant findings about the age at which face-related activation is present in the fusiform gyrus, there is no consensus about the mechanism of developmental change underlying this pattern of activation. Some evidence

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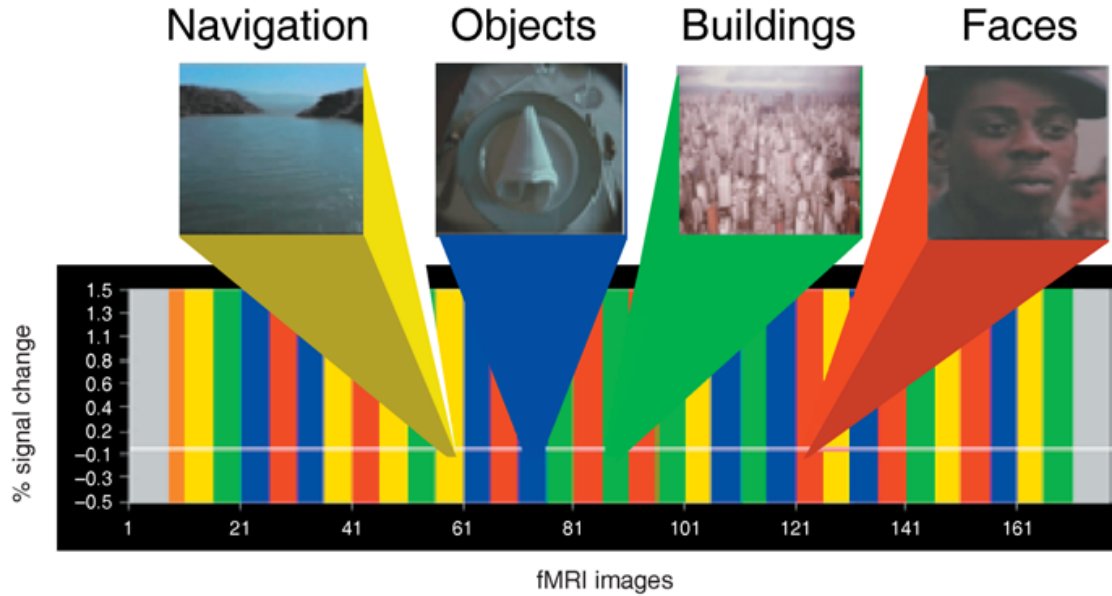


Figure 1 *Movie task. Still-frame images from real-time movie vignettes in each category of the task. The movie categories included close-up shots of novel faces in natural situations (e.g. looking at the camera while walking through a crowd), the camera panning through a building area, the camera panning through open fields, and objects being manipulated by hands (e.g. rolling dough with a rolling pin, whisking flour in a pot, picking up objects from a desk).*

suggests a shift in the locus of activation from more posterior regions, like the OFA, to the anterior fusiform (Aylward *et al.*, 2005; Gathers *et al.*, 2004), an increase in the size (Aylward *et al.*, 2005) and in the localization of FFA within the fusiform (Passarotti *et al.*, 2003), but no accounts of increasing magnitude or selectivity of activation within the FFA. Also, in the studies that have not found FFA activation in children, the authors have suggested that the failure to find such activation may be due to inter-subject variability in the locus of face-related activation, although none of them has verified this possibility. Finally, because the focus of the existing developmental work has been on face-related activation, it is not clear whether the developmental trajectory of such activation is specific to faces as a visual class or whether it is characteristic of other visual classes too.

The goal of this study was to contrast the developmental trajectories for face-, object-, and place-selective activation in the ventral visual cortex in children, adolescents, and adults. We were specifically interested in evaluating whether (1) there are similar or different developmental trajectories for emerging category-selectivity of the three visual classes, (2) emerging category-selectivity is related to changes in location, size, and/or magnitude of neural responses, and (3) inter-subject variability contributes to the ability to identify category-selective activation, especially in young children. We employed a novel task to evaluate potential developmental differences in category-selective activation. Participants viewed naturalistic,

real-time movies of unfamiliar faces, buildings, navigation through open fields, and objects in a blocked fMRI paradigm (Figure 1). This task has been used successfully to map category-selective activation in the ventral visual cortex in adult brains (Hasson, Nir, Levy, Fuhrmann & Malach, 2004, Figure 5 and online Supplementary Material) and has three clear benefits for a developmental study. First, it elicits more natural exploration of the visual environment than the static photographs used in previous developmental neuroimaging studies. Second, this task elicits greater category-specific activation in the ventral temporal lobe than more traditional tasks with static images (Avidan, Hasson, Malach & Behrmann, 2005). Third, since there are no specific task demands, developmental differences in performance are not a confound for different levels of functional activation.

In addition to providing novel insights about the emerging functional organization within the ventral visual cortex, we were also interested in using these findings to shed light, more broadly, on competing models of functional brain development. In particular, we anticipated three potential patterns of developmental change in the ventral visual cortex that could help adjudicate between several models of functional brain development. First, given the importance of object recognition, and face recognition in particular, one might expect that this category-specific organization is architecturally innate and functionally mature from an early age (Farah, Rabinowitz, Quinn & Liu, 2000). In this case, one would expect to see adult-like face-selective

activation even in very young children. Other models of functional brain development focus on changes to endogenous maturational factors, for example changes in the neurochemistry of a region that 'fossilize' patterns of local functional connectivity (Murphy, Beston, Boley & Jones, 2005). Given the close proximity of the category-selective regions in the ventral temporal lobe, this model might predict that selectivity for all three stimulus classes matures simultaneously. In this case, one might expect to see diffuse and unspecified patterns of activation that become localized and category-specific within a particular developmental window. Alternatively, since plasticity is a hallmark of brain development, several models of functional brain development argue that functional specialization is dependent on learning processes and interrelations with other brain regions (Johnson, 2001; Johnson & Munakata, 2005). Given that face and facial expression recognition skills take much longer to develop than do object or house recognition skills (Carey & Diamond, 1977; Herba & Phillips, 2004), one might expect to see different developmental trajectories for the functional specialization of face-, object-, and place-selective patterns of brain activation that coincide with the ages at which recognition skills become adult-like.

Methods

Participants

Participants included 10 children (age: 5–8 years; $M = 7.2$, $SD = 1.0$; 6 males), 10 young adolescents (age: 11–14 years; $M = 12.5$, $SD = 1.0$; 6 males), and 10 adults (age: 20–23 years; $M = 22.2$, $SD = 1.0$; 6 males). An additional seven children, four adolescents, and one adult were excluded from the analyses due to excessive head motion (three children, four adolescents, one adult), unwillingness to complete the imaging protocol (three children), or falling asleep during the task (one child). All participants had normal or corrected vision, were right-handed, and healthy with no history of neurological or psychiatric disorders in themselves or in their first-degree relatives. Prior to participating in the study, participants and/or their legal guardians provided written consent. All the experimental procedures complied with the standards of the University of Pittsburgh Internal Review Board.

Procedure

Movie task

Participants freely viewed a silent, fluid concatenation of short movie vignettes (see Figure 1), containing scenes

of people and faces, buildings, navigation through open fields, or miscellaneous common objects (Hasson *et al.*, 2004). The vignettes were organized into 32 randomized 15-second blocks containing stimuli from a single category. The task began with a 29-second blank screen followed by a 9-second block of abstract pattern stimuli and ended with a 21-second blank screen. The movie vignettes were displayed on a rear-projection screen located inside the MR scanner. Immediately prior to the scanning session, all participants were trained for 20 minutes in a mock scanner that simulated the noise and confinement of an actual MR scanner.

Data acquisition

EPI BOLD images were acquired in 35 AC-PC aligned slices on a Siemens 3T Allegra scanner, covering most of the brain and all of the occipital and temporal lobes ($TR = 3000$ ms; $TE = 35$ ms; 64×64 , 3 mm slice thickness, 3.203×3.203 mm in-plane resolution). Anatomical images were acquired using a three-dimensional volume magnetization prepared rapid gradient echo (3D-MPRAGE) pulse sequence with 192 1-mm, T1-weighted, straight sagittal slices.

Data analyses

The data were analyzed using Brain Voyager QX (Brain Innovation, Maastricht, Netherlands). Preprocessing of functional images included 3D-motion correction and filtering out low frequencies up to 10 cycles per experiment (slow drift). Participants who moved more than 2.0 mm ($\frac{2}{3}$ voxel) were not included in the analyses. Separate one-way ANOVAs on each of the six motion dimensions revealed no age group differences in movement ($F < 1$).

For each participant, the time-series images for each brain volume were analyzed for category differences in a fixed-factor GLM. Each of the categories was defined as a separate predictor and was modeled with a box-car function. The time-series images were then spatially normalized into Talairach space.

Defining category-selectivity

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, LOC: objects–scrambled objects, and PPA: places–objects. However, as in previous studies using this movie task, we adopted a more conservative definition for category-specificity, contrasting each category with respect to the others (Avidan *et al.*, 2005; Hasson *et al.*, 2004). For

example, face-selective activation was defined by the weighted contrast (faces-[objects + buildings + navigation]). Because scenes of buildings and navigation both drive PPA activation, place-selective activation was defined as ([buildings + navigation]-[faces + objects]). Defining the contrasts this way allowed us to directly compare any findings of developmental differences to an adult profile of category-selectivity that has been consistently mapped out with this task. Each contrast map for each participant was corrected for multiple comparisons using the False Discovery Rate Procedure to ensure that fewer than 10% of the significantly active voxels were false positive activations (Genovese, Lazar & Nichols, 2002).

Category-selectivity for each age group was evaluated by submitting the time-series images to a random-effects GLM in which the category was a fixed factor and participant was a random factor. The group-level contrast maps were corrected for multiple comparisons using a Monte Carlo simulation. To achieve $p < .05$ significance, the simulation required a minimum of 190 mm² contiguous voxels with a t -value ≥ 2.5 .

Evaluating age group differences in target regions of interest (ROI)

In passive viewing tasks such as the one we adopted, the adult profile of activation in five ROIs (LO, PPA, FFA, posterior STS, and OFA) has been consistently demarcated. The adults represent the mature state of functional organization in the ventral temporal lobe. We used the mature adult organization as the template for identifying immaturities within the system. Our goals for evaluating age group differences in functional activation are twofold: We are interested in understanding the functional profile of these very same regions in children and adolescents that will *ultimately become* the most optimized and functionally organized regions when these individuals become adults. To this end, we extracted the magnitude (% signal change) and the extent (proportion of active voxels) of activation for each participant in five adult-defined ROIs from the adult group map (PPA, LOC, FFA, OFA, STS) in each hemisphere¹ (see Table 1). The z -normalized average percent signal change across seven volumes from the onset of the stimulus block for each object category was extracted for each participant in each ROI. Previous studies have verified the feasibility of making direct statistical com-

¹ We also considered the possibility of identifying the ROIs based on the union or the intersection of activity from all three groups. When we performed a face contrast from a GLM including all participants, the FFA, OFA, and STS regions from this map overlapped entirely with those identified in the adult only map. Therefore, we do not believe that the results would be different if we identified the ROIs based on this analysis.

Table 1 Coordinates and size of adult-defined volumes of interest from group-level contrast maps

	Right				Left			
	x	y	z	Voxels	x	y	z	Voxels
FFA	40	-41	-21	577	-38	-44	-19	337
OFA	50	-66	-4	1410	-47	-70	6	1564
STS	53	-50	11	3367	-53	-52	14	3545
PPA	26	-43	-13	2170	-23	-43	-11	1991
LO	46	-62	-4	527	-40	-66	-7	3444

Note: All regions thresholded at $p < .05$ (corrected), except LO which was thresholded at $p < .005$ (corrected) because of the increased size of the VOI at the lower threshold.

parisons in hemodynamic response timecourses between children and adults (Kang, Burgund, Lugar, Petersen & Schlaggar, 2003). Also, the proportion of total active voxels (total number active determined by individual participant FDR value/total number of voxels in adult ROI) in each of the appropriate contrasts was computed for each participant in each ROI. Each of these measures was submitted to separate repeated-measures ANOVAs with hemisphere and category as within-subjects factors and age group as the between-subjects factor.²

Second, we were also interested in evaluating whether children and adolescents demonstrate category-selectivity in regions other than those defined by the adults, particularly for the face-related regions. When group differences were observed in the magnitude or extent of activation in the adult-defined ROIs, we investigated the functional profile of category-selective activation in *individually defined* ROIs for each participant. This second approach also allowed us to investigate the degree of inter-subject variability in category-selective activation within and between groups. First, we generated composite maps of each individual participant's category-selective activation mapped onto a single inflated brain, illustrating the relative size and extent of overlap in each participant's individually defined category-selective activation. Second, we determined the x, y, and z coordinates of the peak locus of activation for each individual in each individually defined ROI and computed the relative distance in mm from the appropriate age group mean location and from the adult group mean location for each of the x, y, and z coordinates,

² A direct group comparison (GLM) of differences in magnitude of activation at the whole brain level might identify additional mature regions where children do not show the degree of face-selectivity that adults and/or adolescents do. Candidate regions might include those identified in Table 2 that were present in the adult and adolescent group maps that were not evident in the child group maps. Although we did not include the analysis in this paper, we agree that this is a potentially informative approach to analyzing our data and acknowledge that it might help us understand how prefrontal, posterior cingulate, and anterior temporal pole regions vary with age.

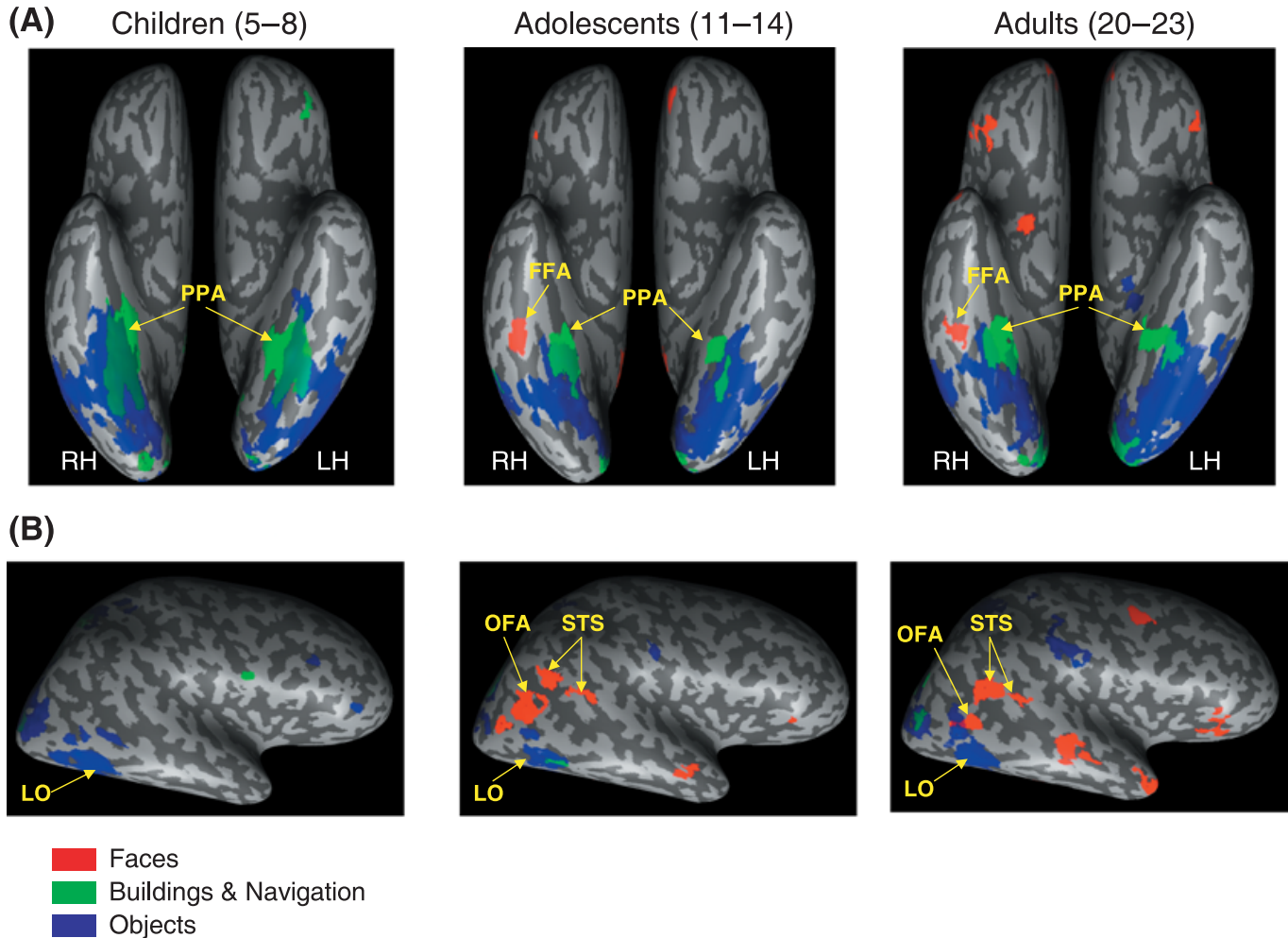


Figure 2 Ventral stream category-specific topography within each age group. Contrast maps for each object category ($p < .05$ corrected) from the group-level random-effects GLM mapped onto the ventral projection (a.) and the lateral right hemisphere (b.) of a single representative inflated brain in order to show consistency, or lack thereof, across the age groups in category-selective activation. FFA = fusiform face area, OFA = occipital face area, STS = superior temporal sulcus, LO = lateral occipital object area, PPA = parahippocampal place area.

transformed the distances into standard scores, and submitted them to separate one-way ANOVAs with age group as a factor. Third, we extracted the number of active voxels and percent signal change from each participant's individually defined ROIs and submitted these measures to separate ANOVAs with age group as a between-subjects factor.

This two-pronged approach for evaluating group differences in the functional profile of what will become the optimized adult regions and regions that children are currently using provides a comprehensive approach to understanding developmental changes in the functionality of the ventral temporal lobe. If we had adopted only one of these approaches, we might have been misled, in that using only adult-defined regions does not allow us to examine unique areas of activation that children may

be displaying. Similarly, examining only the activations offered by the children's brains does not allow a direct comparison with those anatomical regions that we know will be optimized for face recognition in adulthood.

Results

Ventral stream category-specific topography within each age group

Figure 2 shows the average face-, object-, and place-related activation maps for each age group projected onto the inflated cortical surface of a representative individual. All regions of significant activity for each contrast in each age group are reported in Table 2, but the focus of

Table 2 Regions of significant activation in the group-level contrast maps for each age group

Contrast	Children										Adolescents										Adults									
	Talairach					# Voxels	Hem	Region	BA	Talairach			# Voxels	Hem	Region	BA	Talairach			# Voxels										
	x	y	z	x	y					z	x	y					z													
Faces	Right Fusiform	36/37	42	-68	-19	296	Right	FFA	37	39	-47	-22	1054	Right	FFA	37	40	-41	-21	577										
	Right OFA	19/37	45	-74	1	2418	Right	OFA	19/37	45	-74	1	2418	Right	OFA	19/37	50	-66	-4	1410										
	Right Post. STS	21	60	-49	9	1141	Right	Post. STS	21	60	-49	9	1141	Right	Post. STS	21/22	49	-55	14	1564										
	Right Ant. Temporal Pole						Right	Ant. Temporal Pole	38	55	-4	-16	524	Right	Ant. STS	21	53	-15	-9	1220										
	Right PC						Right	PC	31	10	-59	28	3776	Right	Mid. STS	21	40	-14	-15	677										
	Left Angular Gyrus						Left	Angular Gyrus	39	-39	-70	18	351	Left	Post. STS	22	-46	-56	15	1204										
	Left IFG						Left	IFG	47	-47	17	-8	276	Left	Mid. STS	22	-57	-48	20	2362										
	Right IFG						Right	IFG	47	39	25	-9	701	Right	Ant. Temporal Pole	38	39	8	-36	2443										
	Right SFG						Right	SFG	8	5	54	44	1202	Right	PC	31	0	-54	35	345										
	Left SFG						Left	SFG	6	-6	-4	57	234	Left	Precentral Sulcus	6	40	-7	47	1194										
Places	Right SFG	10	-15	56	5	357	Right	MFG	6	21	-2	54	210	Right	MFG	8	3	47	40	5392										
	Right Precuneus	7	14	-80	38	864	Right	Precuneus	7	26	-66	46	906	Right	MFG	8	-13	42	40	808										
	Left Precuneus	7	-14	-76	51	479	Left	Precuneus	7	-11	-67	50	570	Left	Precuneus	7	27	-69	44	1893										
	Right PC	23	6	-41	25	1160	Right	PC	6	21	-2	54	210	Right	Cuneus	7/19	-14	-82	37	2158										
	Right SOG	19/39	29	-75	31	5514	Right	SOG	19/39	29	-75	31	5514	Right	MFG	8	-13	42	40	808										
	Left MOG	18/19	-22	-79	13	6728	Left	MOG	19	28	-79	8	2736	Left	Precuneus	7	27	-69	44	1893										
	Right IOG	18	21	-85	-5	1409	Right	IOG	18	-27	-85	19	2097	Right	MOG	18/19	33	-83	11	959										
	Left IOG	18	-22	-85	-3	2249	Left	IOG	18	-27	-85	19	2097	Left	MOG	19	-23	-85	7	3639										
	Right Lingual Gyrus	18	13	-86	-6	1936	Right	Lingual Gyrus	37	45	-55	-8	352	Right	Lingual Gyrus	18	8	-83	-8	3672										
	Left Lingual Gyrus	18	-19	-94	-5	812	Left	Lingual Gyrus	37	-45	-60	-5	384	Left	Lingual Gyrus	18	1	-92	-11	5544										
Right PPA	35/36	19	-30	-18	6311	Right	PPA	30	26	-40	-4	2944	Right	PPA	36	26	-43	-13	2170											
Left PPA	36/37	-28	-53	-6	6311	Left	PPA	30	-25	-48	-1	2076	Left	PPA	36	-23	-43	-11	1991											

Table 2 *Continued*

Contrast	Hem	Region	Children										Adolescents										Adults									
			Talairach					# Voxels	Hem	Region	BA	Talairach			# Voxels	Hem	Region	BA	Talairach			# Voxels										
			x	y	z	x	y					z	x	y					z													
Objects	Right	Precuneus	7	29	-53	49	418	Left	Precuneus	7	-22	-73	53	2440	Right	Precuneus	7	29	-66	50	1358											
	Left	Precuneus	7	-21	-59	43	719	Right	SPL	7/40	32	-52	51	380	Left	Precuneus	7	-8	-72	53	362											
	Left	Cuneus	19	-23	-82	37	361	Left	Cuneus	18	-14	-95	12	6799	Right	IPL	40	55	-27	26	654											
	Right	MTG	19/39	31	-70	20	994	Left	IPL	40	-54	-34	33	816	Left	IPL	40	-56	-30	38	550											
	Right	LO	18	18	-94	-5	5232	Right	LO	19/37	40	-60	-7	1565	Right	LO	19/37	43	-80	-4	5903											
	Left	LO	18/19	-23	-86	28	6264	Left	LO	19/37	-41	-57	-3	2084	Left	LO	19/37	-46	-53	-1	5098											
	Left	Lingual Gyrus	17/18	-9	-97	-15	747	Right	Lingual Gyrus	18	11	-81	-3	1546	Left	Lingual Gyrus	17/18	-4	-70	-14	5055											
	Right	Lateral Fusiform	19/37	41	-72	-12	3500	Right	Fusiform	37	22	-73	-18	2936	Right	Fusiform	37	33	-55	-13	4244											
	Left	Lateral Fusiform	37	-40	-60	-17	2906	Left	Fusiform	37	-27	-73	-14	3423	Left	Fusiform	37	-33	-69	-19	6392											
	Right	Medial Fusiform	36/37	22	-39	-14	5062																									
	Left	Medial Fusiform	36/37	-21	-79	-24	4732	Right	MOG	18/19	33	-88	2	2536	Midline	AC	32	0	-5	38	295											
								Left	Precentral Gyrus	6	-34	-5	32	197																		

Note: AC = anterior cingulate, Ant = anterior, FFA = fusiform face area, IOG = inferior occipital gyrus, IPL = inferior parietal lobule, IFG = inferior frontal gyrus, LO = lateral occipital object area, MFG = middle frontal gyrus, Mid = middle, MOG = middle occipital gyrus, MTG = middle temporal gyrus, OFA = occipital face area, PPA = parahippocampal place area, PC = posterior cingulate, Post = posterior, SFG = superior frontal gyrus, SOG = superior occipital gyrus, STG = superior temporal gyrus, STS = superior temporal sulcus.

these results will be on patterns of significant activity in the target ROIs including the FFA, OFA, STS, LO, and PPA.

Consistent with previous findings from this task, adults activated the classic FFA, OFA, and STS when viewing faces. When viewing common objects, adults activated a more medial portion of the fusiform gyrus and the ventral LO, a region that is classically identified by contrasting objects–scrambled objects. Finally, adults activated bilateral PPA when viewing scenes of buildings and navigation. Because this place-selective activation was not clearly apparent in the initially defined contrast, the contrast was redefined as ([buildings + navigation]–[faces]).³ This contrast produced robust bilateral PPA activation and was used for all subsequent analyses.

Like adults, adolescents exhibited face-related activation in the FFA, OFA, and STS regions although this was more right-lateralized than the bilateral activation observed in adults (see Table 2). Adolescents also activated the medial portion of the fusiform gyrus and the ventral LO when viewing common objects and bilateral PPA when viewing places.

Children showed adult-like activation when viewing objects and places, with object-selective activation in similar medial portions of the fusiform gyrus and the ventral LO and place-selective activation in the bilateral PPA. However, unlike adults and adolescents, as a group, children did not activate any of the classically defined face-related regions but did show a patch of face-related activation in a small more posterior, lateral portion of the right lateral fusiform (Talairach coordinates of the midpoint: 42, –68, –19). Because children as a group did not show consistent face-selective activation when it was defined relative to the other visual categories, a separate group-level map contrasting (faces–objects) was created. Even with this more lenient contrast, children failed to activate the classic face-selective regions. This contrast revealed face-related activation in a more dorsal and medial portion of the fusiform gyrus compared to the adult-defined FFA in the right (22, –40, 10; 444 voxels) and left (–17, –43, 12; 217 voxels) hemispheres, but no activation in the classical FFA, OFA, or STS regions.

Age group comparisons in category-selective activation

Place-related activation

As reflected in the average group maps in Figure 2, all three age groups activated bilateral PPA when viewing

scenes involving buildings and navigation. Results from the adult-defined ROI analyses reflect that there were no age group differences in the magnitude of activation in the PPA regions. Figure 3A shows the average percent signal change in the right and left PPA to buildings and navigation and to faces for each age group.

Magnitude of activation. In all groups, there was more activation to places than faces; there was a main effect of category, $F(1, 27) = 23.8, p < .001$. There was also a main effect of hemisphere, $F(1, 27) = 9.3, p < .005$, with more activation to both visual categories in the left hemisphere. However, there was a hemisphere \times category interaction, $F(1, 27) = 6.2, p < .05$. Tukey post-hoc comparisons revealed that there was more category-selectivity in the right compared to left hemisphere, $p < .05$. Importantly, there was no main effect of age, $F(2, 27) = 0.4, p = \text{n.s.}$, or interaction between age and hemisphere, $F(2, 27) = 0.0, p = \text{n.s.}$, or age and category, $F(2, 27) = 0.3, p = \text{n.s.}$

Extent of activation. All age groups revealed a larger proportion of significantly active voxels in the right than left adult-defined PPA; there was a main effect of hemisphere, $F(1, 27) = 15.2, p < .001$. However, there was also a hemisphere \times age group interaction, $F(2, 27) = 4.0, p < .05$. Tukey post-hoc comparisons revealed that children and adults were similarly bilateral in the extent of the PPA activation, but adolescents were more right-lateralized than both adults, $p < .05$, and children, $p = .07$. Importantly, there was no main effect of age group, $F(2, 27) = 1.3, p = \text{n.s.}$, indicating equivalent extent of activation in the PPA across the age groups.

Object-related activation

All age groups activated bilateral LO when viewing scenes involving objects (Figure 2). Results from the adult-defined ROI analyses also demonstrate consistency in LO activation both within and between the age groups. Figure 3B shows the average percent signal change in the right and left LO to common objects and to all other stimuli combined for each age group.

Magnitude of activation. There were no age group, $F(2, 27) = 0.7, p = \text{n.s.}$, or hemisphere, $F(1, 27) = 0.2, p = \text{n.s.}$, differences in the magnitude of activation in the adult-defined ventral LO regions. For all age groups, there was more activation to objects than to other classes of stimuli across both hemispheres, $F(1, 27) = 32.0, p < .001$.

Extent of activation. Analyses on the extent of activation in the adult-defined LO revealed that all age groups activated a larger proportion of significantly active voxels in the right than left adult-defined LO; there was a main effect of hemisphere, $F(1, 27) = 44.6, p < .001$. There were no differences in the size of the LO across the age groups, $F(2, 27) = 1.0, p = \text{n.s.}$

³ Other groups have reported having difficulty mapping clear PPA activation in this task (I. Dinstein, personal communication) and find this contrast acceptable and robust for identifying place-selective activation with this task (G. Avidan, personal communication).

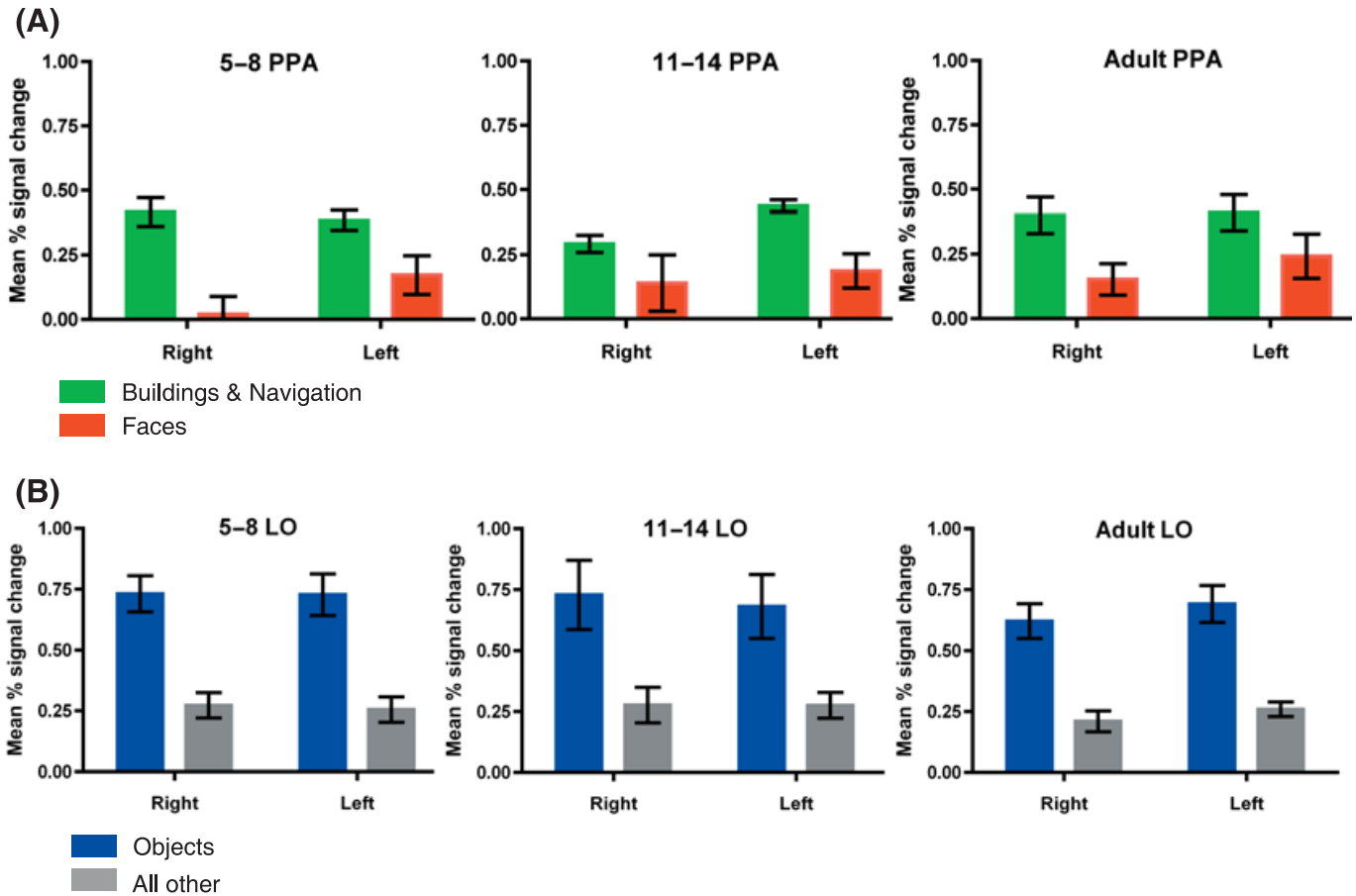


Figure 3 Age group comparisons in place- and object-selective activation. (A). Mean percent signal change for each age group in the adult-defined PPA. Across all three age groups there was more activation in the left hemisphere ($p < .005$) and more activation to buildings and navigation than to faces ($p < .001$), particularly in the right hemisphere (hemisphere \times category, $p < .05$). There were no significant differences involving age as a factor. (B). Mean percent signal change for each age group in the adult-defined LO. Across all three age groups there was more activation to objects than to the other classes of stimuli ($p < .001$). There were no significant differences involving age as a factor.

Face-related activation

Results from the adult-defined ROI analyses demonstrate that children exhibited less face-specific activation in all the face-related regions.

Magnitude of activation. Figure 4A shows the average percent signal change in the right and left FFA to faces and to all other stimuli combined for each age group. Faces elicited more activation than other stimuli for all age groups; there was a main effect of category, $F(1, 27) = 4.7$, $p < .05$, and a hemisphere \times category interaction, $F(1, 27) = 4.5$, $p < .05$. Tukey post-hoc comparisons revealed that there was more category selectivity in the right hemisphere, $p < .05$. There was no main effect of age, $F(2, 27) = 2.7$, $p = \text{n.s.}$, indicating that children did, in fact, exhibit activation in the adult-defined FFA when viewing visual stimuli. However, this activation was not face-specific as was revealed in the marginally significant age group \times

object category interaction, $F(2, 27) = 3.2$, $p = .056$. Tukey post-hoc comparisons revealed that children showed less category-specificity for faces compared to adults, $p < .05$, but not adolescents, $p = \text{n.s.}$, whereas adolescents and adults showed comparable face-specificity in the FFA.

The age group differences in the magnitude of activation in FFA were mirrored in OFA. Figure 4B shows the average percent signal change in the right and left OFA to faces and to all other stimuli combined for each age group. Faces elicited more activation than did other stimuli for all age groups; there was a main effect of category, $F(1, 27) = 19.8$, $p < .001$, and a marginally significant category \times hemisphere interaction, $F(1, 27) = 3.9$, $p = .058$. Tukey post-hoc comparisons revealed that there was more face-selectivity in the right hemisphere, $p < .05$. There was no main effect of age, $F(2, 27) = 0.6$, $p = \text{n.s.}$, but as in the FFA, there was a significant age group \times object category interaction, $F(2, 27) = 3.5$, $p < .05$.

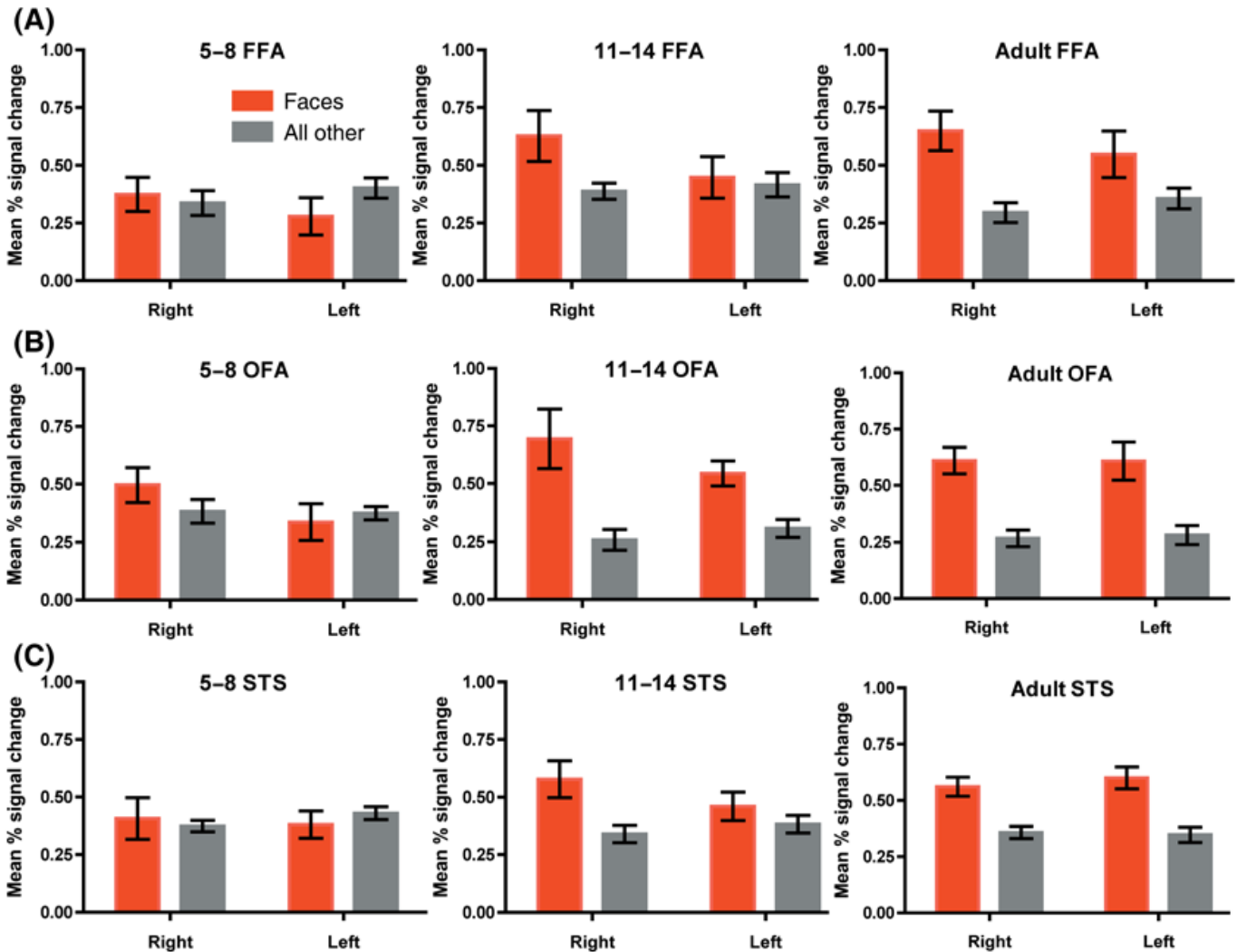


Figure 4 Age group comparisons in face-selective activation. (A). Mean percent signal change for each age group in the adult-defined FFA. Across all three age groups there was more activation to faces than to the other classes of stimuli ($p < .05$), particularly in the right hemisphere (hemisphere \times category, $p < .05$). Children showed less category-specific activation in both hemispheres compared to both adolescents and adults (age \times category, $p < .05$). (B). Mean percent signal change for each age group in the adult-defined OFA. Across all three age groups there was more activation to faces than to the other classes of stimuli ($p < .001$), particularly in the right hemisphere (hemisphere \times category, $p < .05$). Children showed less category-specific activation in both hemispheres compared to both adolescents and adults (age \times category, $p < .05$). (C). Mean percent signal change for each age group in the adult-defined STS. Across all three age groups there was more activation to faces than to the other classes of stimuli ($p < .005$), particularly in the right hemisphere (hemisphere \times category, $p < .05$). Children showed less category-specific activation in both hemispheres compared to both adolescents and adults (age \times category, $p < .05$).

Tukey post-hoc comparisons revealed that children tended to show less face-specificity than either the adults, $p = .07$, or adolescents, $p = .07$, whereas adolescents and adults showed comparable face-specificity in the OFA.

Again, there were age group differences in the magnitude of face-specific activation in the posterior STS. Figure 4C shows the average percent signal change in the right and left STS to faces and to all other stimuli combined for each age group. Faces elicited more activation than

other stimuli for all age groups; there was a main effect of category, $F(1, 27) = 8.1$, $p < .01$, and a category \times hemisphere interaction, $F(1, 27) = 5.4$, $p < .05$. Tukey post-hoc comparisons revealed that there was more face-selectivity in the right hemisphere, $p < .05$. There was no main effect of age, $F(2, 27) = 1.3$, $p = \text{n.s.}$, but there was a statistical trend for an age group \times category interaction, $F(2, 27) = 2.5$, $p = .09$. Tukey post-hoc comparisons revealed that children only tended to show less face-specificity in

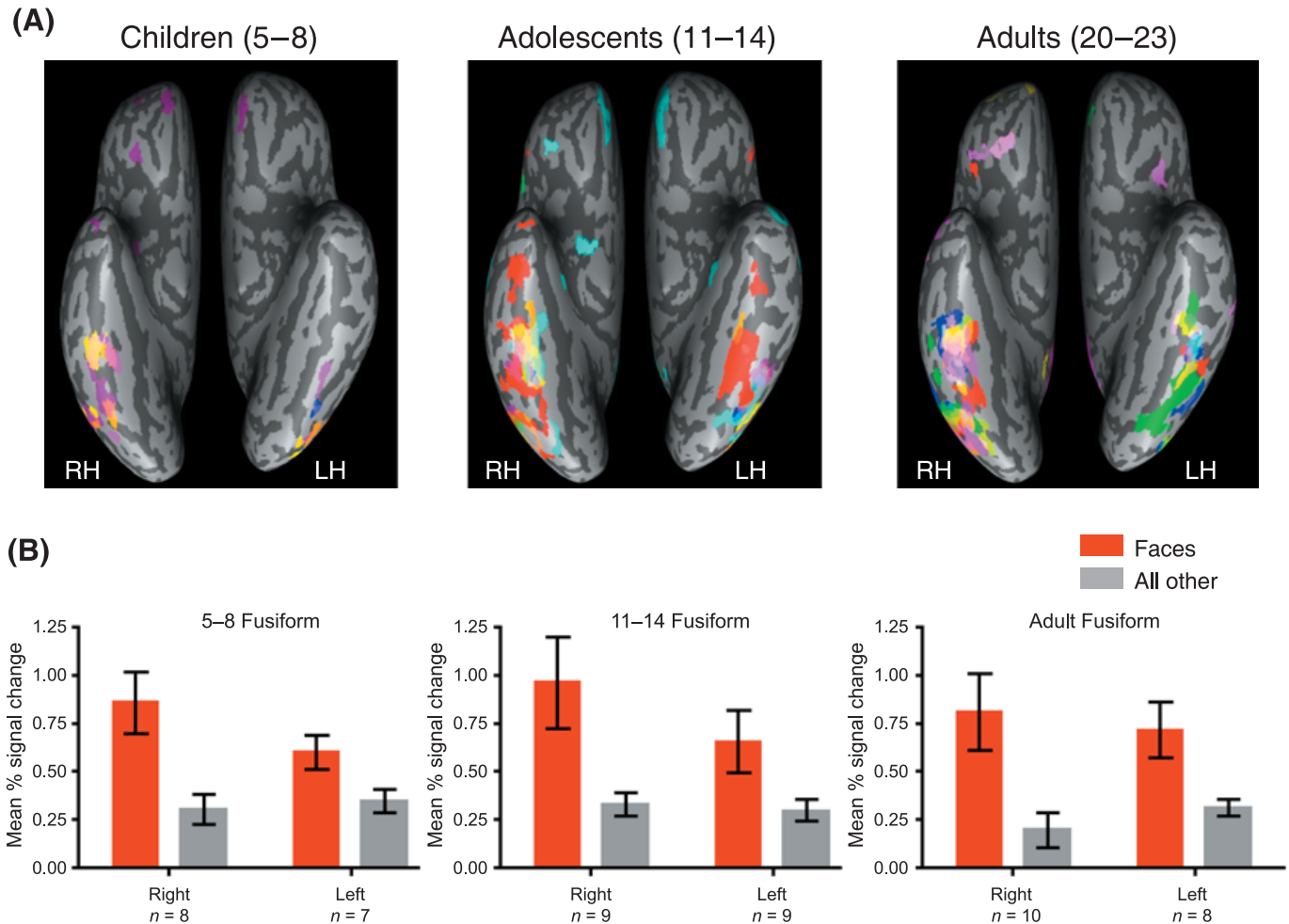


Figure 5 Inter-subject variability in size, location, and magnitude of face-selective activation in the fusiform. (A). Variability in the extent of the individually defined activation for faces for each participant within each age group. The face contrast map for each participant, represented in a unique color, was thresholded using the FDR procedure ($q < .10$) and overlaid onto a single inflated brain. Only participants who generated face-selective activation somewhere in the fusiform gyrus were included in the analyses. For example, only 8 children showed some kind of face-selective activation in the right fusiform gyrus and 7 in the left fusiform gyrus. There is much less consistent overlap among fewer individual participants in children in both the right and left fusiform face area (FFA) compared to either the adolescents or the adults. Children tended to have smaller volumes of activation than adolescents in the right and left fusiform, and more variable locations of activation than adults in the right fusiform and than adults and adolescents in the left fusiform. (B). Mean percent signal change for each age group in the individually defined fusiform ROI. Across all three age groups there was more activation to faces than to the other classes of stimuli ($p < .001$) in both hemispheres. Despite the difference in size of the fusiform activation, children showed the same degree of category-specific activation in both hemispheres as did adolescents and adults.

the STS compared to adults, $p = .08$, whereas adolescents and adults showed comparable face-specificity.

Extent of activation. A repeated-measures ANOVA with the factors of age group (children, adolescents, adults), hemisphere (right, left), and region (FFA, OFA, STS) on the extent of activation in the adult-defined regions identified a main effect of age group, $F(2, 27) = 5.6$, $p < .01$. Tukey post-hoc comparisons revealed that across all three regions children activated smaller volumes than

both the adolescents, $p < .05$, and adults, $p < .025$, and there were no differences between the two older age groups. For all age groups, participants activated larger proportions of the face-related ROIs in the right hemisphere, $F(1, 27) = 11.3$, $p < .005$, and in the FFA and OFA compared to the STS, $F(2, 54) = 6.7$, $p < .005$.

Inter-subject variability in location of face-selective activation. To understand further the age group differences in location, magnitude, and extent of activation within the

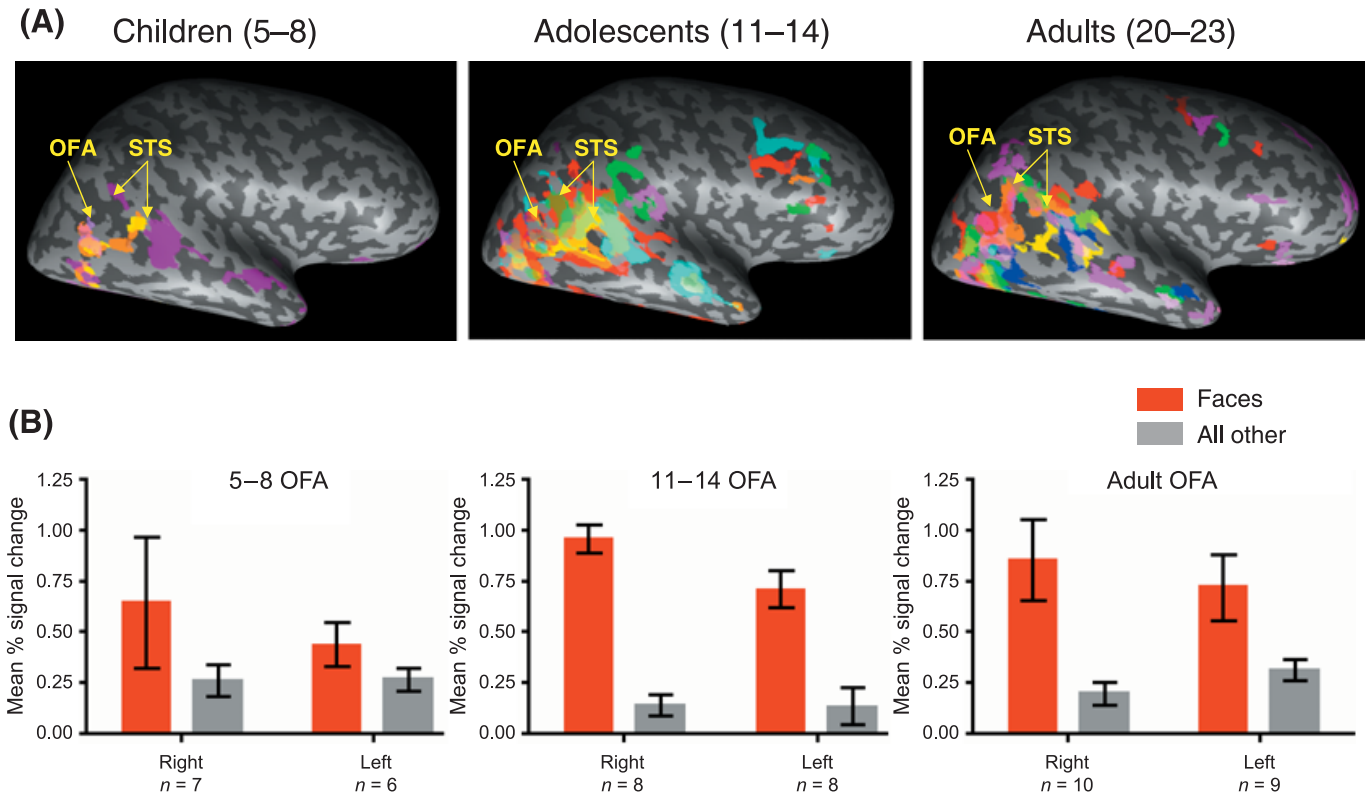


Figure 6 Inter-subject variability in size, location, and magnitude of face-selective activation in OFA and STS. (A). Variability in the extent of individually defined activation for faces for each participant within each age group. The face contrast map for each participant, represented in a unique color, was thresholded using the FDR procedure ($q < .10$) and overlaid onto a single inflated brain. Only participants who generated face-selective activation somewhere in the right occipital face area (OFA) or superior temporal sulcus (STS) were included in the analyses. There is much less consistent overlap among fewer individual participants in children in both the OFA and STS compared to either the adolescents or the adults. (B). Mean percent signal change for each age group in the individually defined OFA. Across all three age groups there was more activation to faces than to the other classes of stimuli in both hemispheres ($p < .001$). Despite the difference in size of the OFA, children showed the same degree of category-specific activation in both hemispheres as did adolescents and adults. There were too few children with active voxels in the STS to perform statistical analyses on the magnitude of activation from the individually defined ROI.

adult-defined face-related ROIs, we investigated whether and how inter-subject variability contributed to such differences. Figures 5A and 6A show the composite maps of face-related activation defined uniquely for each individual within each age group in the fusiform, OFA, and STS. The analyses on the variability in location of the individually defined FFA revealed a marginally significant main effect of age group when computed as a deviation from the adult mean location, $F(2, 26) = 3.2$, $p = .056$. Tukey post-hoc comparisons revealed that children showed larger deviations from the adult mean than did the adults, $p = .06$. There was also a significant main effect when the variability in location was computed as a deviation from the appropriate age group mean, $F(2, 26) = 3.3$, $p < .05$. Tukey post-hoc comparisons revealed that children showed more deviation from their own group peak location than adults did from their own

group peak location, $p < .05$. Similarly, there was a main effect of age group in the analysis of deviations in location of the left FFA when computed as a distance from the adult mean, $F(2, 23) = 4.2$, $p < .05$. Tukey post-hoc comparisons revealed that children were more variable than adolescents, $p < .05$, and tended to be more variable than adults, $p = .086$, in the location of the left FFA. There were no statistically reliable differences in the location of the OFA and there were too few children with STS activation to compute the analyses in STS location.

Inter-subject variability in extent of face-selective activation. Even when each region was defined individually, children tended to activate smaller portions of the right, $F(2, 26) = 3.2$, $p = .06$, and left, $F(2, 23) = 2.7$, $p = .09$, fusiform gyri and the left OFA, $F(2, 21) = 3.1$, $p = .07$. However, it was not the case that children always activated less

cortex than the adolescents or adults. When the total number of active voxels across all five individually defined ROIs (FFA, OFA, STS, PPA, LO) in both hemispheres was submitted to a one-way ANOVA with the factor of age group, there was no main effect of age group, $F(2, 29) = 1.4$, $p = \text{n.s.}$ Only the volumes of the face-related ROIs were smaller in the children.

Inter-subject variability in magnitude of face-selective activation. Despite the differences in size and location, there were no age group differences in the magnitude of activation in the individually defined fusiform and OFA regions. Figure 5B shows the average percent signal change in the right and left individually defined FFA to faces and to all other stimuli combined for each age group. Across all three age groups, individuals exhibited stronger activation to faces than to the other visual categories in both hemispheres, $F(1, 21) = 22.2$, $p < .001$. There was no main effect of age group or age group \times category interaction. Similarly, in the OFA, individuals exhibited more activation to faces than to other classes of visual stimuli in both hemispheres (see Figure 6B), $F(1, 19) = 23.5$, $p < .001$, and no main effect of age or interaction between age group \times category. Only two children exhibited significant activation in the posterior STS regions, precluding us from contrasting the size and magnitude differences in this ROI.

Discussion

The goal of this study was to contrast the developmental trajectories for face-, object-, and place-selective activation in the ventral visual cortex in children, adolescents, and adults to evaluate whether (1) there are similar or different developmental trajectories for emerging category-selectivity within the three visual classes, (2) emerging category-selectivity is related to changes in location, extent, and/or magnitude of neural responses, and (3) inter-subject variability contributes to the ability to identify category-selective activation, especially in young children.

Our results suggest that the development of category-selectivity follows different trajectories depending on the visual class. We have provided the first evidence of adult-like functional specificity for place- and object-related activation in children and adolescents. Both developmental groups exhibited bilateral PPA activation in response to scenes of buildings and navigation that was comparable to adults in location, extent, magnitude of activation, and magnitude of specificity. Similarly, when viewing scenes of objects, both developmental groups exhibited activation from a lateral portion of the occipital complex (LO), a region linked with object-selective

processing in adults. The LO activation in children and adolescents was also comparable to adults in site, extent, magnitude of activation, and magnitude of specificity. Previous studies that have not been able to map place- or object-specific activation in children (Aylward *et al.*, 2005; Gathers *et al.*, 2004) or that found prolonged development of place-selective activation (Golarai, Ghahremani, Whitfield-Gabrieli, Reiss, Eberhardt, Gabrieli & Grill-Spector, in press) used static images. Our ability to map adult-like PPA and LO activation in children and adolescents may be related to our use of rich, naturalistic stimuli that have been shown to recruit more category-selective activation compared to tasks with static images. Our results clearly reveal adult-like functional specificity for both object and place activation in the ventral temporal lobe even in early childhood.

We found pervasive age group differences, particularly from childhood to adolescence, in the development of face-selective cortex in several regions, including FFA, OFA, and STS. As a group, children do not activate any of the classic face-related regions. The only face-selective region generated by the children was located in a very ventral and posterior portion of the right fusiform. This region was different in location from the posterior occipital gyrus activation for faces in the 5–8-year-olds reported previously (Gathers *et al.*, 2004). Even when the definition of face-selectivity was redefined more leniently as faces–objects, children exhibited activation in a more dorsal and medial portion of the fusiform compared to the classical FFA location. These differences in the locus of face-selective activation are not due to either greater head motion (corrected head motion was equivalent for all three age groups) or to an inability to activate these regions in response to visual stimuli. In fact, children showed overall magnitudes of activation within the adult-defined regions that were similar to adolescents and adults.

Instead, the lack of a consistent BOLD signature for faces is attributable to (1) reduced face-selectivity and extent of activation within the regions that will become the adult FFA, OFA, and STS, and (2) the smaller volumes and considerable variability in the locus of face-selective activation in individual children. Importantly, 80% of children do exhibit adult-like magnitudes of face-selective activation in some portion of the fusiform gyrus and lateral occipital region, but this selectivity is not consistent across individuals nor is it located in the same region as that of adolescents and adults. With the onset of adolescence emerges greater consistency in the location and selectivity of face-related activation, particularly in the right hemisphere. In adulthood, face-selective activation is seen in the left hemisphere as well.

These findings are remarkably consistent with the extant, albeit limited, developmental neuroimaging experiments investigating the emergence of face-selective activation. One other study also reported adult-like magnitudes of face-selective activation in some portion of the fusiform gyrus in 85% of children and found a similar increase in the size of the right FFA through age 11 (Golarai *et al.*, in press). We have also shown that the OFA and STS increase in size as well. Two other studies have also reported a change in the locus of face-selective activation from a more posterior OFA region to the classical FFA region (Aylward *et al.*, 2005; Gathers *et al.*, 2004) and one reported increasing localization from a distributed medial and lateral portion of the fusiform in childhood to a more medial portion in adulthood (Passarotti *et al.*, 2003). Depending on the definition of face-selectivity that we used, we found evidence for a posterior–anterior shift and a ventral–lateral shift in the fusiform from childhood to adulthood. We have also shown that this lack of selectivity for faces is characteristic of other important face-related parts of cortex, including the OFA and STS. Together with these previous findings, our results suggest that there is no robust, consistent locus of face-selective activation in childhood, but such consistency emerges in early adolescence.

Our results suggest that the transition from childhood to early adolescence appears to represent an important transition in the development of face-specificity in the ventral visual cortex. This transition overlaps a great deal with that observed in behavioral performance on face processing tasks. A large literature supports the notion that the ability to encode and recognize unfamiliar faces (Carey & Diamond, 1977; Carey, Diamond & Woods, 1980; Ellis, Shepard & Bruce, 1973; Diamond & Carey, 1986; Mondloch, Dobson, Parsons & Maurer, 2004) and facial expressions (Herba & Phillips, 2004) continues to improve into late childhood. Many of these groups have argued that the ability to recognize individual faces continues to improve through late childhood due to the increasing effectiveness of configural encoding, which involves recognizing faces on the basis of subtle metric variations between their constituent features, that comes with the acquisition of expertise. Several neuroimaging studies with adults have 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 homogeneous novel objects and objects of expertise produces increased activation in the classically defined FFA region (e.g. Gauthier, Tarr, Anderson, Skudlarski & Gore, 1999). This apparent transition in the development of face-selective activation may be related to the acquisition of expertise for individual face recognition

and the subsequent fine-tuning of large populations of neurons in all three of the adult face-related regions.

Whereas changes in the FFA may reflect the development of expertise in individual face perception and recognition, developmental changes in the functioning of the posterior STS may reflect improvements in the ability to process more changeable qualities of faces. This region has been implicated in the ability to process a variety of changeable aspects of faces like eye gaze, facial expression, and lip-reading (Haxby, Hoffman & Gobbini, 2000; Gobbini & Haxby, 2007). Finally, in addition to the classic face-related areas in the ventral visual cortex, only adolescents and adults exhibited face-selective activation in a more widespread cortical network, including the anterior temporal pole, posterior cingulate gyrus, and prefrontal cortex. These other regions may be part of an extended system that supports further processing of faces, such as person identity and biographical information (Haxby *et al.*, 2000). These findings indicate that developmental changes in the neural signature for faces also involve accessing a widespread and distributed network of regions.

Our results show, for the first time, how the development of category-specificity in the ventral temporal lobe differs for different object categories. Children show mature common object- and place-selective functional organization even between the ages of 5 and 8. However, the development of face-selective functional organization is much more protracted and does not become adult-like in the right hemisphere until early adolescence and in the left hemisphere until early adulthood. This delay in the functional specialization of face-related regions is coincident with the maturation of face and emotion recognition skills and may be related to the acquisition of expertise in the ability to extract configural properties of faces. These results suggest that the transition from early childhood to adolescence represents an important period for the fine-tuning and functional organization of face-related regions in the ventral temporal lobe.

Alternatively, the developmental differences in face-related cortex may have been related to group differences in visual scanning of faces. Although we did not collect eye tracking data and cannot rule out this possibility completely, the existing, albeit 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 & Salapatek, 1976), and by 5 years old children are similar to adults in their use of outer features to recognize unfamiliar faces (Want, Pascalis, Coleman & Blades, 2003). Future studies investigating children's visual scan paths of faces relative

to adults during localizer tasks will help evaluate this alternative explanation more clearly.

Importantly, our results have profound implications for models of functional brain development. Our results do not support either the innately specified or the endogenous maturation models of functional brain development since face-related cortex is clearly not mature in young children and different visual classes follow different developmental trajectories of functional specialization within the ventral temporal lobe. Instead, our findings are consistent with predictions from the interactive specialization model of functional brain development, which argues that specialization emerges from interactions between experience-dependent learning and the maturing brain (Johnson, 2001; Johnson & Munakata, 2005). The functional specialization of face-, object-, and place-selective brain activation follows different developmental trajectories that coincide with the ages at which recognition skills become adult-like. As the ability to recognize the different classes of visual stimuli becomes mature, so does the functional specificity of the brain activation, with faces being the last stimulus class to show adult-like recognition abilities and specialization in the ventral temporal lobe.

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