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Developmental shifts in cortical loci for face and object recognition

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Abstract

Information on normal functional organization and development of the ventral processing stream in 5- to 11-year-old children is minimal. The present fMRI study identified neural correlates for face and object processing in children aged 5–8 and 9–11 years, with data from a similar adult study used for comparison. All age groups showed face-preferential activation in the ventral processing stream, but adults and children aged 9–11 years showed face-preferential loci near the classically defined fusiform face area, whereas children aged 5–8 years showed this activation in the posterior ventral processing stream. In addition, the degree of category-selectivity in other brain regions increased with age. Collectively, these developmental changes may reflect fine-tuning in visual recognition processes based on learning and experience.

Keywords

Development; Face recognition; fMRI; Ventral processing stream

INTRODUCTION

The ventral processing stream is a functional pathway in the primate brain that supports visual recognition. The functional organization of this pathway remains a controversial topic. Studies of damaged and healthy adult brains [1–4] yield two divergent hypotheses concerning the functional architecture of the ventral processing stream. One view posits that ventral processing stream organization is based on neural specializations, or modules, dedicated to the processing of particular categories [4]. An opposing view is that the ventral processing stream is characterized by overlapping regions sensitive to the recognition of multiple categories [1,3]. In support of the modular view, the fusiform face area, an anterior region of this pathway, appears to be specialized for face recognition [4]. However, in support of neural generalization, our previous adult study demonstrated that the fusiform face area was not selective for faces but exhibited a graded response in which faces produced a greater response than did objects, but objects produced a statistically greater

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response than baseline [1]. In fact, face-selective responses, those in which categories other than faces did not activate the region significantly more than baseline, were absent within this processing stream.

Further controversy focuses on whether the functional organization of the ventral processing stream is predetermined and established early [5–7] or sculpted by experience and learning over time [8,9]. Farah [5] and Gilchrist and McKone [6] propose early established (prior to age 3) face and object recognition systems whereas both Carver [10] and Passarotti *et al.* [9] suggest changing neural architecture from childhood to adulthood [9,10]. To delineate the neural correlates of face and object recognition at different developmental stages, we compared brain activation patterns of children aged 5–8 and 9–11 years, and adults who passively viewed blocks of faces, natural objects, and manufactured objects, similar to tasks implemented in previous studies [1,4]. One goal of the present study was to examine the cortical locus of face responsive regions throughout development. The classically defined fusiform face area falls in the anterior fusiform gyrus but a posterior locus is also often reported [1,4]. To isolate the fusiform face area, we defined face-preferential activation as a statistically stronger response to faces than to both object categories and to baseline but object responses were not statistically constrained relative to baseline. Our question was whether the classically defined fusiform face area (i.e. a face-preferential response in the anterior fusiform gyrus) emerges in all age groups. Based on other developmental fMRI studies of face processing [6], language [11,12], and working memory [13] that confirm similar cortical regions of activation in school-aged children and adults, it is likely that the functional organization of the ventral processing stream is stable across the ages we are studying.

Another goal was to determine whether face-preferential activation is exclusive for faces (face-selective) or whether other object categories (i.e. manufactured and natural objects) also activate face-preferential regions to a statistically significant degree relative to baseline (graded-activation). If face-preferential activation is not exclusive for faces, then it should spatially overlap more with face-graded activation than with face-selective activation, as previously reported in adults [1]. We tested the developmental stability of these functional activation profiles from 5 to 11 years of age.

A final goal was to determine whether developmental changes are unique to a particular object category (i.e. faces, natural objects, and manufactured objects). To that end, we also isolated brain regions that were selective for natural or manufactured objects and compared the degree of category-selectivity across age groups.

MATERIALS AND METHODS

Child subjects

Twenty-nine 5- to 11-year-old healthy children (18 males, 11 females, mean age 8.3 years) with no significant medical histories were compensated for participation. All volunteers had normal visual acuity, were fluent in English, and showed a right-hand preference based on the Edinburgh Handedness Survey. Receptive and expressive language skills were within normal age limits as determined by the Peabody Picture Vocabulary Test [14] and the

Expressive Vocabulary Test [15]. Three children did not complete the study. Data from six other participants were omitted due to excessive head motion. Thus, data from 20 subjects (12 males, 8 females, mean age 8.8) were submitted to further analyses. Children gave written assent and parents provided written consent in accordance with the guidelines of the University of Kentucky Institutional Review Board.

Adult subjects

Nine adults (five males, mean age 20.8 years, one left-handed) with normal or corrected-to-normal vision and no significant medical or psychological conditions participated in a previously published study [1]. The adult data were submitted to additional analyses and used to compare with the pediatric data in this study.

Pediatric design and procedure

Children completed a 9 min run consisting of eight fixation (fix) blocks interleaved with nine, 42 s, pseudo-randomly ordered task epochs: 3 each of human faces (F), natural objects (N, fruits and vegetables), and manufactured objects (M, tools and everyday objects). Within each task block, 30 randomly ordered stimuli appeared for 1000 ms each followed by a fixation cross for 400 ms. Sixty grayscale photographs scanned from a high school yearbook served as face stimuli. Grayscale photographs of 30 natural and 30 manufactured objects were obtained from Photodisc CD (Photodisc, Seattle, WA, USA) or scanned from The MacMillan Visual Dictionary [16]. During task blocks, participants viewed the face and object pictures and pushed a button each time a picture appeared. During fixation blocks, volunteers fixated a single crosshair presented for 18 s (baseline). Pictures were projected onto a screen using an LCD projector connected to a Dell Computer running E-prime 1.0 (Psychology Software, Pittsburg, PA, USA) and participants viewed the stimuli (visual angle of 6.74°) via a mirror on the head coil. Computerized training preceded the experiment to ensure subjects could perform the task.

fMRI data acquisition and analysis

A Siemens Vision 1.5 T magnet equipped with a head coil and a T2*-weighted gradient echo sequence was used for functional image collection (40 ms echo time, 64 × 64 matrix, 230 mm field of view, 46 3-mm slices with a 20% gap acquired in ascending order, 6 s repetition time). These parameters allowed whole brain coverage with 3.6 mm³ voxels.

Medx software (Sensor Systems, Sterling, VA, USA) was used for all functional imaging analyses. The 87 functional images were motion corrected using automated image registration (AIR), spatially filtered (Gaussian FWHM 6 mm³), global intensity normalized, and high pass filtered (period=120 s). Functional runs were discarded when the center of intensity of a volume was not corrected to within 0.2 mm of the first time point. Using root mean squared error (RMSE) as a measure of head motion, repeated-measures ANOVAs indicated significant interactions of head motion (before and after correction) and age (children v. adults): children had more motion before correction than adults for anterior–posterior ($F(1,27)=5.2$, $p<0.031$) and superior–inferior ($F(1,27)=5.3$, $p<0.03$) planes, but these differences did not persist after motion correction. All brains were spatially normalized to the same standardized space, as in other developmental fMRI studies [17]. Four condition

mean images for the four experimental conditions (F, M, N, fix) were computed for each subject and then spatially normalized using warp algorithms of AIR, yielding images with 2 mm³ resolution.

For each of three age groups, paired *t*-tests with subjects as a random effect yielded 12 group statistical maps which were converted into z-maps: F>M, F>N, F>fix, fix>M, fix>N, fix>F, N>M, N>F, N>fix, M>N, N>F, and N>fix. To test for specific brain activation patterns using logical combination [12], the z-maps were combined using logical operators (AND=&, OR=|, NOT=~) in the image calculator of Medx. Six logical combination masks were created: face-preferential=[(F>M)|(F>N)] & (F>fix), used to isolate the FFA; face-graded=[(F>M) & (M>fix)] | [(F>N) & (N>fix)]; face-selective=[(F>fix) & (F>M) & (F>N)] & ~(M>fix) & ~(M>N) & ~(N>fix) & ~(N>M) & ~(fix>M) & ~(fix>N); natural-selective=[(N>fix)& (N>M) & (N>F)] & ~(M>fix) & ~(M>F) & ~(F>fix) & ~(F>M) & ~(fix>M) & ~(fix>F); manufactured-selective= [(M>fix) & (M>F) & (M>N)] & ~(N>fix) & ~(N>F) & ~(F>fix) & ~(F>N) & ~(fix>N) & ~(fix>F); and conjoined=[(F>fix)&(M>fix)&(N>fix)]&~(F>M) &~(F>N) &~(M>F) &~(M>N) &~(N>F)&~(N>M). The clusters that emerged ($z>2.33$) served as regions of interest (ROIs) for further analysis. For each cluster isolated for each group ROI, the mean signal for each condition (F, M, N, fix) for each subject was submitted to a repeated measures ANOVA and *post-hoc t*-tests were performed to confirm logical combination profiles.

RESULTS

To localize the fusiform face area, we isolated face-preferential activation in all three age groups. Adults showed two bilateral foci of face-preferential activation in the ventral processing stream; one focus in the classically defined fusiform face area (anterior aspects of the fusiform gyrus in Brodmann's Area (BA) 37) and a more posterior fusiform locus in BA 18, as reported previously [1] (Fig. 1a). Children aged 9–11 years showed face-preferential activation in the right anterior fusiform gyrus (BA 37; 42, –56, –22), close to the classically defined fusiform face area (Fig. 1b). Face-preferential activity in children aged 5–8 years emerged in the right (BA 17; 28 –96 –14) and left occipital gyri (BA 18; –32, –85, –19) as shown in Fig. 1c.

As in our previous study [1], we were interested in whether face-preferential regions are better characterized by graded or selective responses to faces to assess the degree of specialization in the fusiform face area. In all three age groups, face-preferential activation (blue voxels in Fig. 1) overlapped primarily with face-graded responses (yellow voxels) and minimally with face-selective activation (red voxels). A repeated-measures ANOVA examined the effect of overlap (preferential-graded vs preferential-selective) and age on the number of voxels that overlapped throughout the brain. Extent of face-preferential and face-graded overlap (19.5% of preferential voxels were also graded voxels) was greater than extent of face-preferential and face-selective overlap (2.3%; $F(1,26)=4.6, p<.001$). Neither the age effect nor the age $\times$ overlap interaction was significant. Hence, the functional characteristics of face-preferential regions do not change after 5 years of age. Moreover, face-preferential activation, including the classically defined fusiform face area, does not reflect specialized activation for faces.

Although the ventral processing stream did not show category-selective activation, the degree of category-selectivity increased with age in other regions of the brain. Five-to eight-year-old children had no selective activation for any object category whereas children aged 9–11 years had selective activation for each category: natural objects (right inferior parietal lobe, bilateral middle frontal gyri), manufactured objects (left temporal pole, right inferior frontal gyrus), faces (left inferior frontal gyrus). Adults also showed distinct regions of category selectivity: natural objects (left superior parietal lobule, left temporal pole), manufactured objects (right calcarine sulcus, right middle occipital gyrus), and faces (left hippocampus). Although these selective brain regions were small and few, percent of face-selective voxels throughout the brain relative to the total number of voxels for face-graded, conjoined, and object-selective activation increased from 0% in children aged 5–8 years to 0.14% at 9–11 years and 0.41% in adults.

Finally, we defined conjoined activation as statistically equivalent responses to all stimulus categories in our study relative to each other, and significantly different responses for each category relative to baseline. This non-category specific activation dominated other task-relevant forms of activation for all three age groups. For adults, 84% of total activated voxels were conjoined (i.e. relative to all six profile types combined), 89% for children aged 9–11 years, and 74% for 5- to 8-year-old children. The bulk of conjoined activation fell within the ventral processing stream.

DISCUSSION

The present study contributes several new findings to our understanding of ventral processing stream development. First, only adults and children aged 9–11 years showed face-preferential responses near the classically defined fusiform face area, whereas 5- to 8-year-old children only showed face-preferential responses in the posterior ventral processing stream. These differences in cortical locus for face processing are not due to greater head motion in children because corrected head motion was equivalent for all age groups. Instead, changes in ventral processing stream locus for face processing may be due to a variety of developmental factors. Shifts in face-preferential loci may result from maturation of neural pathways and connections. For example, visual recognition may be facilitated by connections to the frontal lobe [18,19], a later developing region of cortex [20]. Hence, shifts may occur in the neural architecture of the ventral processing stream to accommodate maturation of frontal lobe connections. In addition, behavioral studies [21,22] have suggested developmental changes in cognitive mechanisms for face recognition. Interestingly, around 10 years of age, children display more adult-like strategies for face recognition [21]. Our data suggest that this change in cognitive processing may be accompanied by an anterior shift in the ventral processing stream locus for face recognition because only adults and 9-to 11-year-old children activated the anterior fusiform gyrus during face recognition, whereas younger children did not.

Second, the functional activation profiles of face responsive brain regions did not change with age. Specifically, for all age groups face-preferential activation in the ventral processing stream significantly overlapped with face-graded activation but never with face-selective activation. Although the cortical locus of face-preferential activation changed with

age, regions showing face-preferential responses did not show exclusive responses for faces. Rather, other object categories also activated these regions to a significant degree. In addition, neither fMRI signal strength nor variability changed systematically across development. Five- to 8-year-old children produced stronger fMRI signals in some regions than adults, and between-subject variability in signal strength (reflected by s.e. bars in Fig. 1d–f) was not markedly different across age.

Third, no category selective regions emerged within the ventral processing stream but they emerged in other brain regions for children aged 9–11 years and for adults. The emergence of category-selective clusters with age may be due to plasticity driven by learning and experience [8]. Moreover, other studies suggest that category-selective processing may require recruitment of cortical regions other than the ventral processing stream [19]. The present data support this by showing that much of the ventral processing stream in childhood as well as in adults was explained by conjoined and graded activity, both of which reflect non-category specific responses. An alternative explanation for the failure to find selective activation in the 5- to 8-year-old children is that the cortical locus for category-selective activation is more variable at this age and is, thus, more difficult to detect in group-averaged maps. In fact, another developmental fMRI study reports more distributed VPS processing in children than in adults [9]. However, this variability in and of itself may reflect fine-tuning of neural circuitry with development of expertise.

We [23] and others [24] have suggested that face-preferential responses in the ventral processing stream may not reflect taxonomic category distinctions per se, but instead reflect a process of differentiating members of object categories that are highly perceptually similar or similar in shape. We have further suggested that if more perceptual differentiation is required (as in face recognition), then a relatively more anterior ventral processing stream locus of activation will emerge. Hence, an anterior shift in the ventral processing stream locus for face processing with age may support more skilled perceptual differentiation of objects that are highly similar in shape [21], such as faces. This anterior shift may emerge around the time that face processing skills become more adult-like (around 10 years of age).

CONCLUSION

The details of neural circuitry related to visual processing continue to be fine-tuned throughout childhood as supported by anterior shifts in the ventral processing stream locus for face recognition across age as well as the emergence of category-selective activation with increasing age in other brain regions. Other investigations [8,9] also support this refinement of visual recognition neural pathways during development.

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Fig. 1.

Two axial slices for group-averaged activation in **(a)** adults, **(b)** children aged 9–11 years and **(c)** children aged 5–8 years (MNI z-coordinate indicated in the lower left corner of each slice). Face-preferential activation (blue); face-graded activation (yellow); face-selective activation (red). Percentage fMRI signal change as a function of age and condition (F, M, N) is shown for one selected region in each age group: **(d)** right fusiform gyrus BA (37) in adults ($F(3,26)=27.6$, $p<0.0001$, for main effect of condition); **(e)** right fusiform gyrus BA (37) region in children aged 9–11 years ($F(3,9)=13.1$, $p<0.001$); **(f)** right occipital gyrus BA (17) region in children aged 5–8 years ($F(3,5)=9.4$, $p<0.05$). Error bars indicate s.e.m.