Homogenization of face neural representation during development

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ABSTRACT

Extensive studies have demonstrated that face processing ability develops gradually during development until adolescence. However, the underlying mechanism is unclear. One hypothesis is that children and adults represent faces in qualitatively different fashions with different group templates. An alternative hypothesis emphasizes the development as a quantitative change with a decrease of variation in representations. To test these hypotheses, we used between-participant correlation to measure activation pattern similarity both within and between late-childhood children and adults. We found that activation patterns for faces in the fusiform face area and occipital face area were less similar within the children group than within the adults group, indicating children had a greater variation in representing faces. Interestingly, the activation pattern similarity of children to their own group template was not significantly larger than that to adults' template, suggesting children and adults shared a template in representing faces. Further, the decrease in representation variance was likely a general principle in the ventral visual cortex, as a similar result was observed in a scene-selective region when perceiving scenes. Taken together, our study provides evidence that development of object representation may result from a homogenization process that shifts from greater variance in late-childhood to homogeneity in adults.

1. Introduction

Face contains an array of biological, social and emotional information critical for interpersonal communication and social interaction. Although adults are experts in face recognition, previous studies have shown that face recognition performance does not reach adult level until adolescence (Carey and Diamond, 1977; Lawrence et al., 2008; Germine et al., 2011; Song et al., 2015). For example, Lawrence et al. (2008) tested children aged from 6 to 16 years old and found that the ability in recognizing unfamiliar faces increased as a function of age. These findings highlight that face processing goes through a prolonged development process from children to adults. However, the mechanism underlying this prolonged development process is less clear.

One hypothesis is that the development of face processing ability is a process of qualitative transformation on representation (Carey and Diamond, 1994; Hills, 2018; Hills and Lewis, 2018). That is, children and adults have different typical representation patterns (Fig. 1A, left). Supporting behavioral evidence comes from the fact that children rely heavily on the face parts or featural information to process faces, qualitatively different from adults who mainly use holistic and configural information (Carey and Diamond, 1994; Mondloch et al., 2002, 2003; Karayanidis et al., 2009). Because featural and configural/holistic information engage distinctive mechanisms (Bombari et al., 2009; Liu et al., 2010; Zhang et al., 2012), it is likely that children and adults use qualitatively different mechanisms in processing faces.

An alternative hypothesis is that the development is a homogenization process from greater representation variation in children to a template representation shared by adults and children (Durston et al., 2006; Mckone et al., 2012) (Fig. 1B, left). This hypothesis argues that children have already established the ability to process faces in a holistic and configural manner, but their performance is constrained by the underdevelopment of general cognitive factors or face processing strategies (de Heering et al., 2007; Mckone et al., 2012). Such constraints likely lead to greater variation in representing faces among children, and with the maturation of the abilities and strategies, the representation for faces in children likely converges to a template representation in adults.

These two hypotheses are not mutually exclusive, as development might be associated with both qualitative transformation and quantitative homogenization of face representation. However, these two hypotheses are difficult to be decoupled with behavioral studies because both lead to poor behavioral performance of children in face recognition. Here, to characterize the development of face neural representation, we combined the fMRI and behavioral experiments in children aged 9–14 years old and adults. In the fMRI experiment, participants viewed movie clips of faces, scenes and objects. We measured the neural representation by multivariate activation patterns, and used a between-participant correlation method to measures the representation similarity across participants (Between-Participant Pattern Similarity, BP-PS) (Tian et al., 2020). The two hypotheses made distinct predictions on pattern similarity. That is, if we observe that the representation for faces in children is more similar to the typical representation of their own group than that of the adults, the hypothesis of representation transformation during development is supported (Fig. 1A, right). In contrast, the hypothesis of representation homogenization predicts that both children and adults share the same representation template, but children show a greater within-group variance in representation as compared to adults (Fig. 1B, right). Because both behavior performance of face recognition (e.g., Lawrence et al., 2008; Germine et al., 2011; Song et al., 2015) and neural activation in the face-selective regions (e.g., Cohen Kadosh et al., 2013a, 2013b; Golarai et al., 2007, 2009; Scherf et al., 2007, 2011, 2014; Song et al., 2015; Wang et al., 2018) show age-related changes after late childhood and extending into adolescence, we compared children in late childhood (9–14 years old) with adults to explore the mechanism underlying the prolonged development of the face processing.

2. Materials and methods

2.1. Participants

A total of 122 children (63 females; 9–14 years old, mean age = 11.26 years, SD = 0.82 years) participated in the study. The adult participants were from a dataset of an ongoing project investigating the relation among brain, behaviors, environments, and gene (e.g., Zhen et al., 2015, 2017; Kong et al., 2016; Wang et al., 2016). There were 287 adults in the dataset. Because the large difference in the amount of participants in the two groups may have an impact on the statistical results, we randomly selected half of the adult participants by using the MATLAB function of 'randperm'. That is, we included 144 adults (73 females; mean age = 19.00 years, SD = 1.04 years) in the study. All the participants had normal or corrected-to-normal vision, and no history of psychiatric or neurophysiological disorders. We obtained written informed consent from all participants and/or their parents prior to the study, which was approved by the Institutional Review Board of Beijing Normal University.

2.2. Behavioral test

We used a face-inversion effect (FIE) task (Yin, 1969) to measure the participant's face processing ability. The FIE was a computer-based task, and included twenty-five face images (Zhu et al., 2011). All the face images were gray-scale adult Chinese faces with the external contours
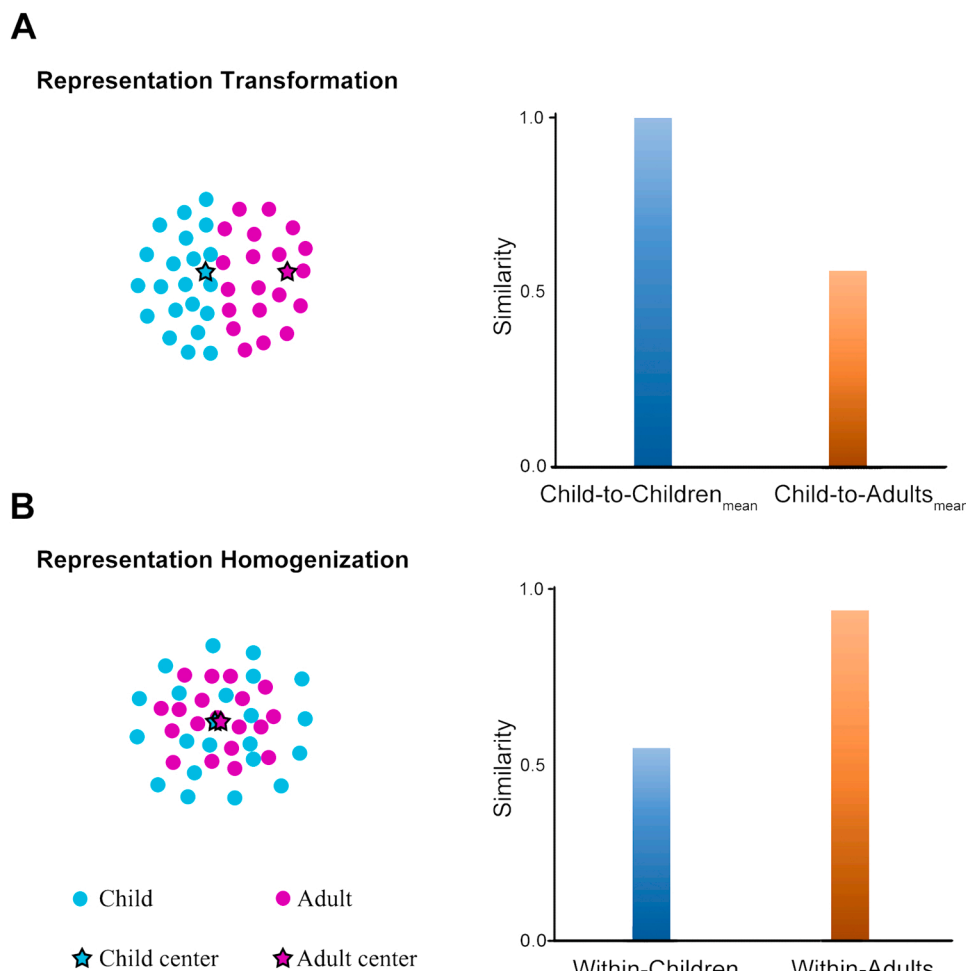

Fig. 1. Schematic illustration of the two hypotheses on the mechanisms underlying the development of face representation. (A) Representation transformation hypothesis. Children and adults have two distinct templates in representing faces. Each dot corresponds to an individual's representation in a representation space, and distance among the dots indicates similarity of representation between individuals. Stars indicate the template of each group, which is the average of the group's representations. Adults are in pink, and children in cyan. The distance (similarity) of each cyan dot to the cyan star (the template of children's representation) is closer than that to the pink star (the template of adults). (B) Representation homogenization hypothesis. Children and adults share the same template, but children show greater variance in representing faces among each other.

(e.g., hair) removed, which were selected from an in-house database of adult Chinese faces. During the task, pairs of face images were presented sequentially, either both upright or both inverted, with upright- and inverted-face trials randomly interleaved. The participants were instructed to indicate as quickly as possible whether the two sequentially presented stimuli were identical. Specifically, each trial started with a blank screen for 1 s, followed by the first face image presented at the center of the screen for 0.5 s. Then, with an inter-stimulus interval (ISI) of 0.5 s, the second image was presented until a same or different response was made. There were 50 trials for each condition, and half of the face pairs were identical and the other from different individuals. For each participant, the accuracy was calculated as the average proportion of hits and correct rejections for the upright and inverted condition, respectively. To achieve the upright-specific FIE, we regressed out the accuracy of inverted condition from that of upright condition and used the residual FIE for the following analyzes.

2.3. FMRI scanning

Each participant completed a dynamic functional scan, which contained four visual categories (faces, scenes, objects, and scrambled objects). The stimuli were presented in movie clips, which were randomly drawn from a pool of 60 clips of Pitcher et al. (for more details on the stimuli, see Pitcher et al., 2011). Stimuli were presented using the Psychtoolbox 2.5.4.

The functional scan was acquired using a blocked-design with three functional runs. Each run consisted of two block sets, intermixed with three 18-s fixation blocks at the beginning, middle and end of the run. Thus, it lasted 198 s in total. Each block set consisted of two blocks of the four visual categories, with each stimulus category presented in an 18-s block that contained six 3 s movie clips. The order of stimulus category blocks in each run was palindromic and randomized across runs. During scanning, participants were instructed to passively view the movie clips (Huang et al., 2014; Zhen et al., 2015, 2017). FMRI data acquisition and
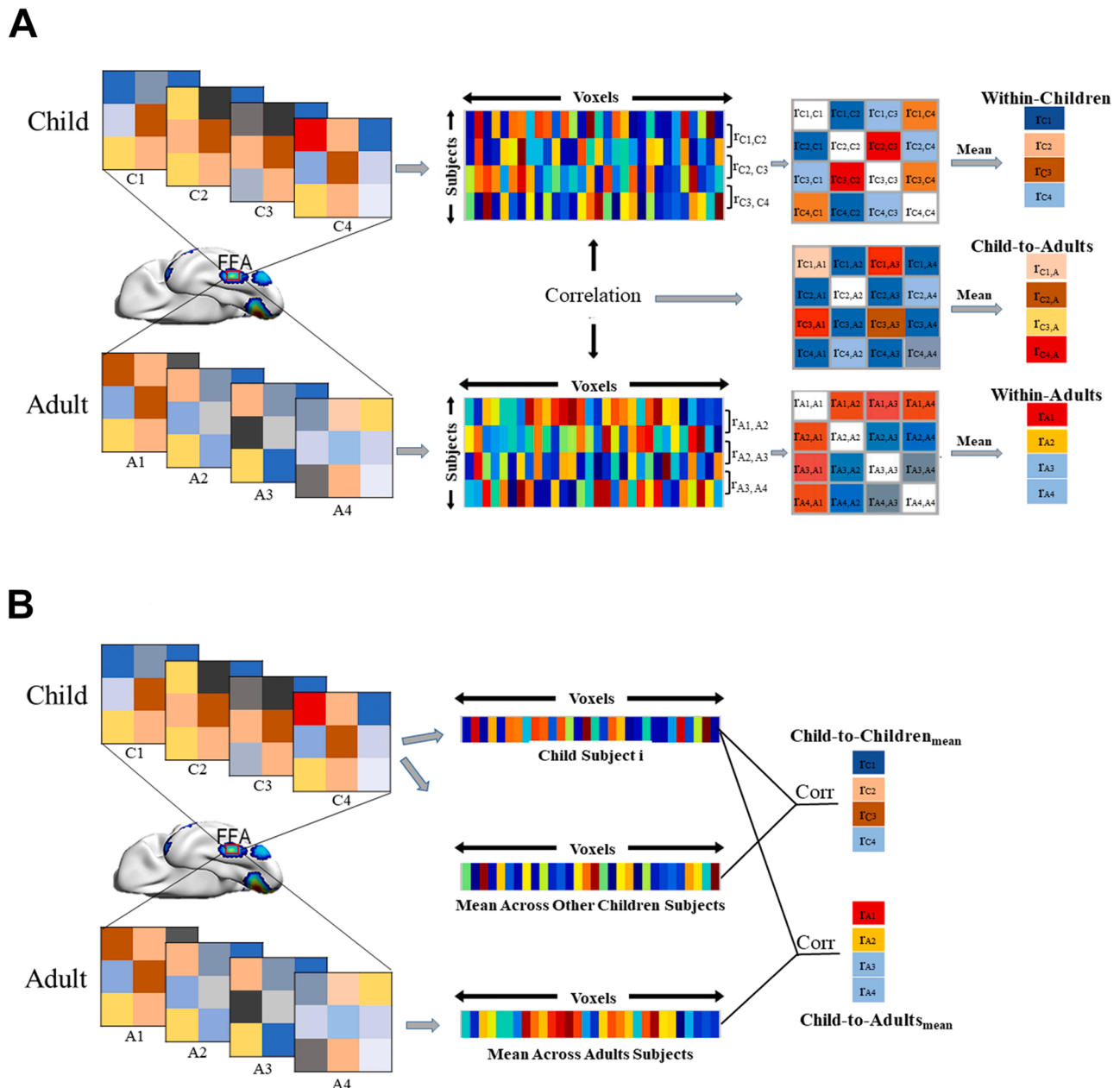

Fig. 2. Flowcharts of the methods to calculate the Between-Participant Pattern Similarity (BP-PS) values. (A) The method to calculate the Child-to-Adults, Within-Children, and Within-Adults BP-PS values. (B) The method to calculate the Child-to-Children$_{mean}$ and Child-to-Adults$_{mean}$ BP-PS values.

Image pre-processing and statistical analysis see Supplementary methods 1.1 and 1.2.

2.4. Definition of the face- and scene-selective masks

In order to define the category-selective masks, we obtained probabilistic activation maps (PAM) for face and scene processing with all our participants (Zhen et al., 2015, 2017). The contrast of faces > (scenes + objects) was used to obtain the PAM for faces, and the contrast of scenes > (faces + objects) was used to obtain the PAM for scenes. The category-selective masks were created by keeping the voxels with activation probability higher than 0.2 in the PAMs. The face-selective mask was further anatomically restricted within the right occipitotemporal cortex and the left fusiform gyrus and occipital cortex; the scene-selective mask was restricted within bilateral occipitotemporal cortex (Supplementary Fig. 1).

2.5. Between-participant correlation analyses on activation patterns

To evaluate the development of representation in face-selective regions, we employed a between-participant correlation method to measure the similarity of multi-voxel activation pattern across participants (BP-PS) with task fMRI (Tian et al., 2020) (Fig. 2). Specifically, we used a searchlight method (Kriegeskorte et al., 2006) to perform the BP-PS analysis within the face-selective mask. For each voxel, we first formed an activation spatial pattern by extracting the contrast values (faces vs. (scenes + objects)) from a cubic region containing 125 surrounding voxels ($5 \times 5 \times 5$) for each participant (Xue et al., 2013; Choo and Walther, 2016). Then, we calculated the Pearson correlations on activation spatial patterns between each participant and the rest participants. Then, for each participant, the r values with all other participants were averaged to obtain the BP-PS value (Fig. 2A). Finally, these similarity scores were then transformed to z scores via Fisher's z transformation.

Based on the between-participant correlation analyses on activation patterns, we calculated the BP-PS value of each child to that of adults by averaging his/her r values with all adults (Child-to-Adults BP-PS value). Similarly, two within-group BP-PS values, coined as Within-Children and Within-Adults BP-PS, were calculated as the average representation similarity of one participant with all the rest members of his/her group (Fig. 2A). Unlike the Child-to-Adults BP-PS values that measure between-group similarity, the within-group BP-PS values reflect how close a participant's representation is to other members of his/her own group.

Finally, to assess whether the template of the child group was qualitatively different from that of the adult group, we calculated the representation similarity between each child with the typical representation of their own group (Child-to-Children$_{mean}$) and with that of the adults' (Child-to-Adults$_{mean}$), respectively for each ROI. Specifically, we used the activations of all the selected voxels in each ROI as the representation patterns to calculate the representation similarity of each child with the averaging pattern of the children group (Child-to-Children$_{mean}$) and adult group (Child-to-Adults$_{mean}$). The typical representation was calculated by averaging the representation patterns of all participants in each group (Fig. 2B). Note that in this analysis, to avoid the inflation when calculating correlation, the typical representation was constructed without the participant whose Child-to-Children$_{mean}$ value was calculated (i.e., leave one out).

2.6. Permutation test

Statistical significance of the groups differences was evaluated using a permutation analysis that randomly shuffling the group labels for 5000 times to generate a null distribution of the group differences in BP-PS value. This procedure was performed for each searchlight cube. And then the results were corrected for multiple comparisons by controlling the false discovery rate (FDR, q = 0.05).

2.7. Control analyses

To rule out the influence of confounding factors on the results, we did the following control analyses. First, in our analyzes, all children's brains were registered to the MNI template based on adult brains, which might induce registration bias (Cantlon et al., 2006). To avoid this bias, we normalized the fMRI images to an unbiased study-specific template without transforming data to MNI space (Dong et al., 2020, see Supplementary methods 1.3 for details), and re-calculated the BP-PS values using the activation data pre-processed with the study-specific template.

Second, to examine whether the results were face-specific or explained by general factors such as attention or the eye movements, we examined two regions as control. One was a scene-selective region, the right parahippocampal place area (PPA, Epstein, 2008), which was identified based on the PAM for scenes. We included the 200 voxels with top activation probability in the PPA to do this analysis to control possible influence of voxel number. The other region was the primary visual cortex (V1), defined from the anatomic label of Brodmann 17 area by using the WFU PickAtlas (http://fmri.wfubmc.edu/software/PickAtlas) (Maldjian et al., 2003), with a volume of 275 voxels. In addition, we also examined the non-preferred condition (i.e., object condition) in the ROIs of FFA/OFA.

Finally, to exclude the effect of head motion, we performed an analysis by controlling for framewise displacement (FD) of each participant, which calculated the relative displacement of each brain volume compared with the previous volume (Power et al., 2012).

2.8. Participant exclusion

For the MRI data, participants whose absolute head motion > 3° in rotation or 3.0 mm in translation throughout the course of the scan were excluded from further analyzes. As a result, seven children who met this criterion were excluded. In addition, we also calculated FD of head motion, and another four children were also excluded with FD greater than 2 * SD of the group mean (mean FD = 0.11 mm, SD = 0.06 mm). No adults were excluded. Therefore, the fMRI analyses included 111 children (62 females; mean age = 11.23 years, SD = 0.75 years) and 144 adults (73 females; mean age = 19.00 years, SD = 1.04 years). For the behavior task, thirty children and sixteen adults who did not finish the behavior task were removed from further behavior analyses. Besides, the outliers were identified as three standard deviation (SD) away from the mean accuracy, and one child and one adult were excluded with this method. Therefore, the behavior test included 80 children (43 females; mean age = 11.28 years, SD = 0.73 years) and 127 adults (64 females; mean age = 18.99 years, SD = 1.07 years).

3. Results

3.1. Children's neural representation for faces was still under development

We measured the activation pattern of children and adult groups when they perceived the face stimuli during fMRI scan. First, we examined how similar the face activation pattern of children was to that of adults. To do this, we conducted a voxel-wise searchlight analysis within a face-selective mask (Supplementary Fig. 1A). In the searchlight analysis, we calculated the similarity of each child's activation pattern to those of all adults (i.e., the Child-to-Adults BP-PS value) and the similarity of each adult's pattern to the other adults' (i.e., the Within-Adults BP-PS value) in a cube of $5 \times 5 \times 5$ voxels surrounding each voxel, and then compared the difference between the Child-to-Adults and Within-Adults values using a permutation test. As shown in Fig. 3A, in the face-selective mask, we found three clusters that showed a significantly lower Child-to-Adults than Within-Adults BP-PS values in
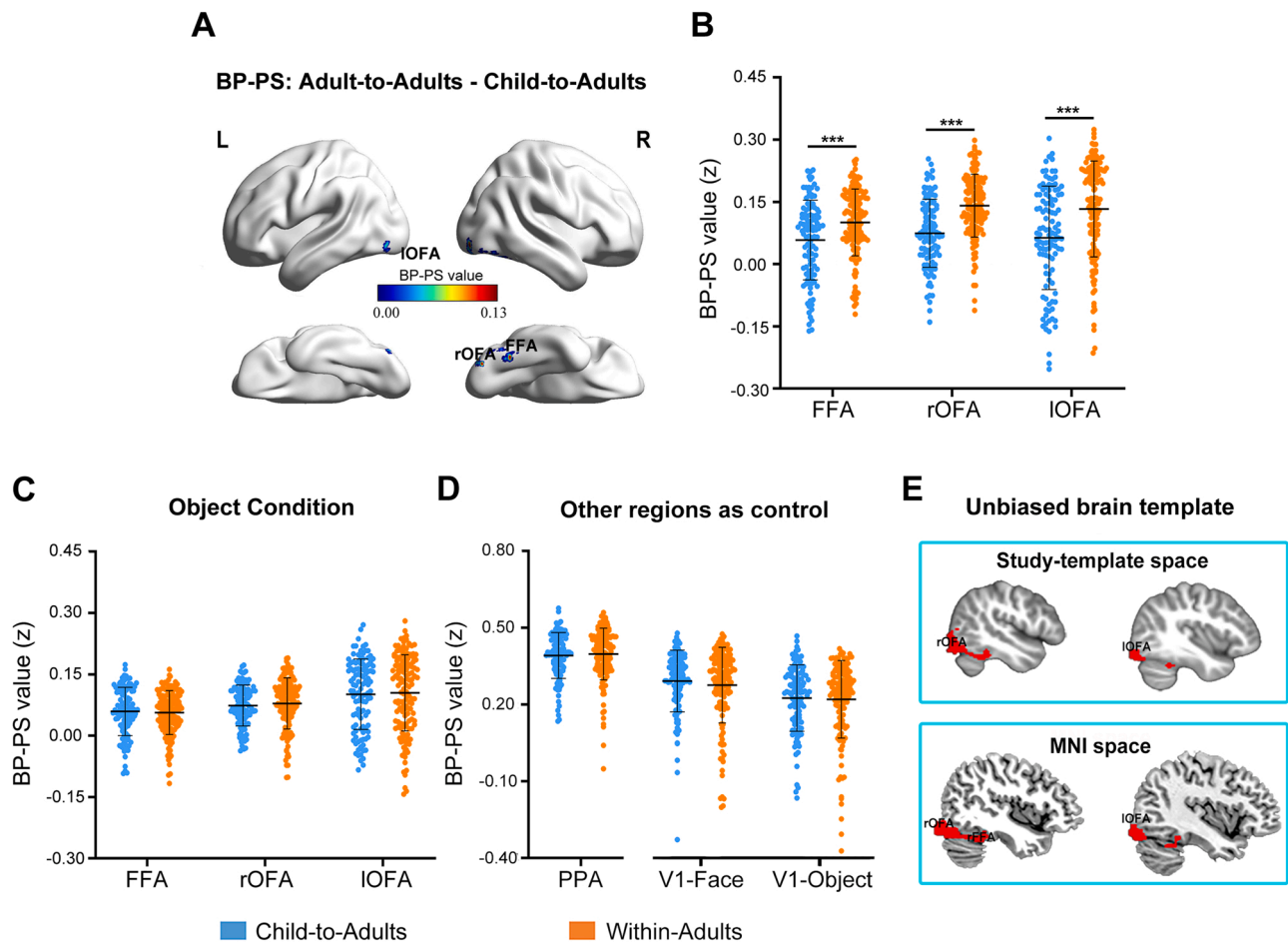
Fig. 3. Children's neural representation for faces was still under development. (A) The right FFA and bilateral OFA showed significantly lower Child-to-Adults than Within-Adults BP-PS values in response to faces. The values on the brain map reflected the differences between the Child-to-Adults and Within-Adults on the BP-PS value. FFA: fusiform face area, OFA: occipital face area. (B) The magnitude of the BP-PS values extracted from the clusters in the right FFA and bilateral OFA. This is shown only for illustration purposes. Error bars indicate standard errors of the mean. ***p < 0.001. (C) The magnitude of BP-PS values of the right FFA and bilateral OFA in the object condition. (D) The magnitude of BP-PS values of the PPA in the scene condition (Left); The magnitude of BP-PS values of the V1 in the face condition (Middle) and object condition (Right). PPA: parahippocampal place area. (E) Clusters that showed significantly lower Child-to-Adults than Within-Adults BP-PS values in response to faces (p < 0.01, uncorrected) using the unbiased study-specific template. The results were shown in the study-specific template space (top) and then registered to MNI space for illustration purposes (bottom).

response to faces, one in the right fusiform face area (rFFA, 108 voxels; MNI coordinates: 42, − 60, − 22), which extended to the right occipital face area (rOFA, 333 voxels; MNI coordinates: 46, − 84, − 16), and the last one in the left occipital face area (lOFA, 129 voxels; MNI coordinates: − 48, − 84, − 8, FDR corrected, q = 0.05, voxel size > 50, Fig. 3A, B). Note that the three clusters also located within the FFA and OFA defined from a face-selective PAM with another dataset (Zhen et al., 2015). That is, children's rFFA and bilateral OFA failed to show 'adult-like' activation pattern when viewing faces, suggesting that their representation for faces was still under development. There were no clusters that showed higher Child-to-Adults than Within-Adults BP-PS values after multiple comparison correction.

A series of control analyses were performed to exclude possible confounding factors that may explain this result. First, to examine whether our results might be accounted for by some general factors such as attention and eye movements, we calculated the Child-to-Adults and Within-Adults BP-PS values in object condition for the clusters that showed under-development of face representations (i.e., the rFFA and bilateral OFA, Fig. 3A). We found that the group differences in the BP-PS values of FFA/OFA were only observed in the face condition, but not in the object condition (all ts < 1, Fig. 3C, Table S1). Moreover, we examined a scene-selective region, the parahippocampal place area (PPA), and the primary visual cortex (V1) as control regions, and found

that there was no group difference in the BP-PS values either in the PPA when perceiving scenes (t < 1, Fig. 3D, Table S2) or in V1 when perceiving faces or objects (all ts < 1, Fig. 3D, Table S2). These results suggested that the group difference in the BP-PS values was specific to face-selective regions when perceiving faces and could not be accounted for by some general factors such as attention and eye movements.

Second, our finding was unlikely to be explained by the registered bias optimized for the adult brain (Cantlon et al., 2006). We registered the fMRI data of each participant to a study-specific template and re-performed the voxel-wise analysis in Fig. 3A (see Supplementary methods 1.3). In the face-selective mask, we found the clusters of rFFA and bilateral OFA that showed significantly lower Child-to-Adults than Within-Adults BP-PS values in response to faces (p < 0.01, uncorrected, Fig. 3E), consistent with the result obtained in the Fig. 3A.

Finally, our results could not be explained by different head motion between children and adults. After controlling for the framewise displacement (FD) of head motion, the group differences in the BP-PS values in the FFA/OFA were still obtained in the rFFA (t(253) = 2.26, p = 0.024, Cohen's d = 0.29) and bilateral OFA (right: t(253) = 5.02, p < 0.001, Cohen's d = 0.63; left: t(253) = 3.23, p = 0.001, Cohen's d = 0.41, Supplementary Fig. 2A).

In short, the representation for faces in children's FFA and OFA was still under development. Next, we asked how the representation of FFA

and OFA evolved into more 'adult-like' representation during development. The significant clusters that showed the under-development of face representations (the rFFA and bilateral OFA, Fig. 3A) were used as the regions of interest (ROIs) for the following analyzes. Univariate analysis indicated that the children also showed under-development of univariate face activation in these ROIs (rFFA: t(253) = 3.68, p < 0.001, Cohen's d = 0.47; rOFA: t(253) = 1.82, p = 0.069, Cohen's d = 0.23; lOFA: t(253) = 3.11, p = 0.002, Cohen's d = 0.39), consistent with previous findings (e.g., Golarai et al., 2007, 2009; Scherf et al., 2007, 2011, 2014; Song et al., 2015).

3.2. Representation for faces developed through homogenization

To explore how the face representation developed in the ROIs, we first tested the representation transformation hypothesis that children and adults have different typical representations. If this was the case, we expected that the representation similarity of each child with their group's typical representation would be greater than that with the adult group's typical representation. Therefore, we used the activations of all the selected voxels in each ROI as the representation patterns to calculate the representation similarity of each child with the averaging pattern of the children group (Child-to-Children$_{mean}$) and adult group (Child-to-Adults$_{mean}$). However, we failed to find evidence supporting

this hypothesis, as the Child-to-Children$_{mean}$ BP-PS value was not significantly larger than the Child-to-Adults$_{mean}$ BP-PS value in the rFFA (t(110) = − 1.02, p = 0.31, Cohen's d = 0.097) or bilateral OFA (right: t (110) = 0.24, p = 0.81, Cohen's d = 0.023; left: t(110) = 0.33, p = 0.74, Cohen's d = 0.031)) (Fig. 4A). Further, the typical representation (i.e. averaging pattern) of the children was highly similar to that of the adults in both the rFFA (r = 0.85) and bilateral OFA (right: r = 0.87; left: r = 0.82). In short, despite a lower performance in recognizing faces, the face representation in children's FFA and OFA seemed not qualitatively different from that in adults'.

An alternative hypothesis is the representation homogenization hypothesis that both children and adults share the same representation template, but children show a greater within-group variance in representation. To test this hypothesis, for each voxel in the ROIs, we calculated the representation similarity of each participant with all the rest members of his/her own group, which were the within-children and within-adults BP-PS values, and averaged across the voxels in each ROI. The result found that the within-children BP-PS was significantly lower than the within-adults BP-PS in both the rFFA (t(253) = − 6.49, p < 0.001, Cohen's d = 0.82) and bilateral OFA (rOFA: t(253) = − 12.13, p < 0.001, Cohen's d = 1.53; lOFA: t(253) = − 8.41, p < 0.001, Cohen's d = 1.06) (Fig. 4B), suggesting greater within-group variance in children.
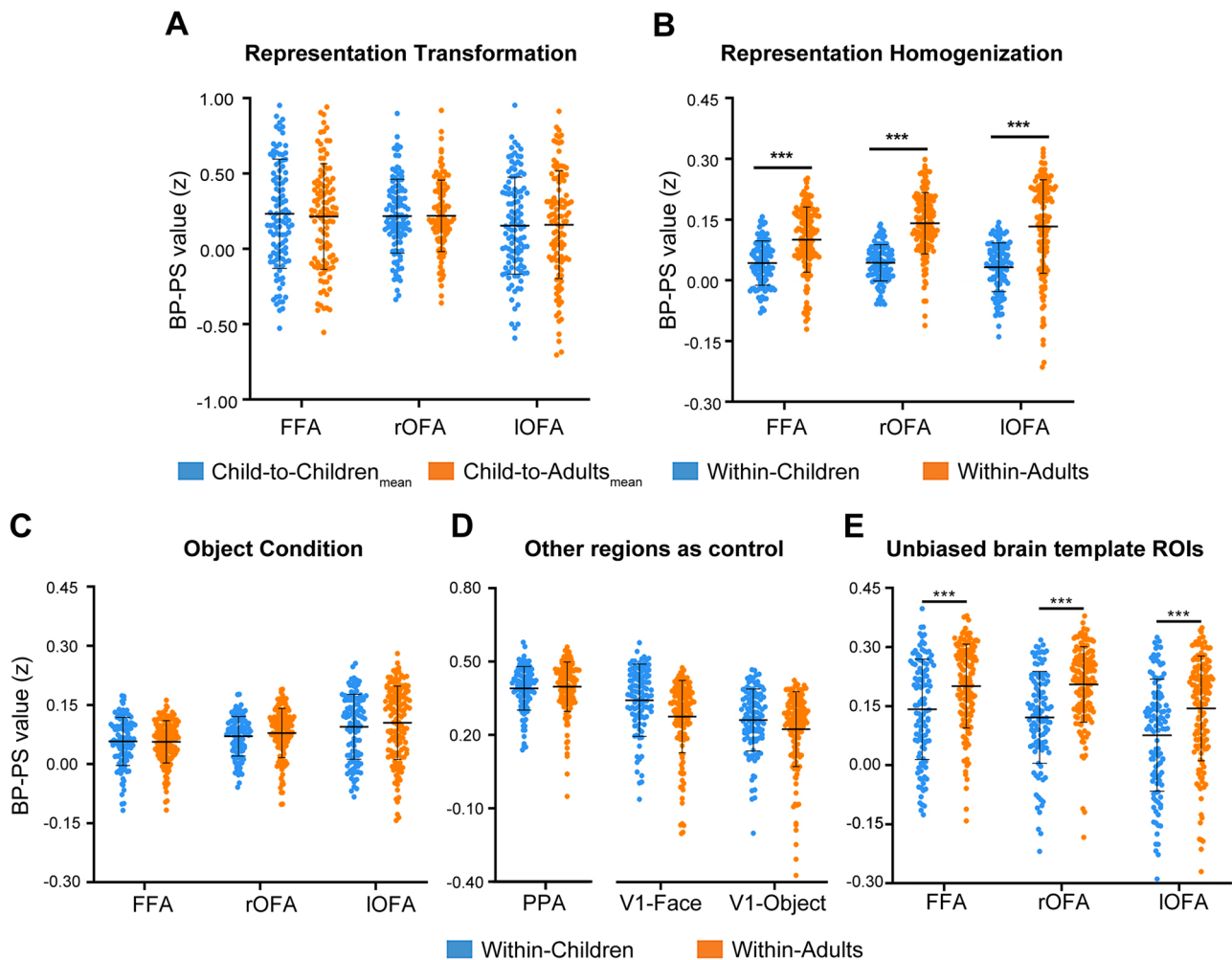

Fig. 4. Representation for faces developed through homogenization. (A) Representation transformation hypothesis: no significant difference was found between Child-to-Children$_{mean}$ and Child-to-Adults$_{mean}$ BP-PS values in the right FFA and bilateral OFA. (B) Representation homogenization hypothesis: Within-Children BP-PS values were significantly lower than the Within-Adults values in the right FFA and bilateral OFA. Error bars indicate standard errors of the mean. (C) Within-group BP-PS values of the right FFA and bilateral OFA in the object condition. (D) Within-group BP-PS values of the PPA in the scene condition (Left); within-group BP-PS values of the V1 in the face condition (Middle) and object condition (Right). (E) Within-group BP-PS values in the ROIs obtained from unbiased study-specific template. ***p < 0.001.

Besides, the lower within-group similarity in children than adults was not observed in the object condition in the FFA/OFA or in the PPA and V1 (Fig. 4C, D, Tables S1 and S2). Neither could this result be explained by registration bias: using the clusters obtained from the unbiased study-specific template (Fig. 3E), we also found lower within-group similarity in children than adults (rFFA: t(253) = 4.04, p < 0.001, Cohen's $d = 0.51$; rOFA: t(253) = 6.30, p < 0.001, Cohen's $d = 0.80$; lOFA: t(253) = 3.93, p < 0.001, Cohen's $d = 0.50$, Fig. 4E). Additionally, the result could not be explained by confounding factors such as head motion (after controlling for head motion, rFFA: t(253) = 4.90, p < 0.001, Cohen's $d = 0.62$; rOFA: t(253) = 9.74, p < 0.001, Cohen's $d = 1.23$; lOFA: t(253) = 6.98, p < 0.001, Cohen's $d = 0.88$, Supplementary Fig. 2B), voxel selection procedure of the ROI analysis (see Supplementary analysis 1 and Supplementary Fig. 3), different age ranges between the child and adult groups (see Supplementary analysis 2, Supplementary Fig. 4 and Table S3), or the size difference of face-selective regions between groups (see Supplementary analysis 3). Finally, our results showed good reproducibility across the adult samples (see Supplementary analysis 4 and Supplementary Fig. 5).

3.3. Homogenization of scene representation during development

Is the observed representation homogenization process specific to the face processing system? Or does it reflect a general principle of how the neural representation developed in the ventral visual cortex? To expand the finding to other object systems, we conducted the same voxel-wise searchlight analyses within the scene-selective mask (Supplementary Fig. 1B) when perceiving scenes as for faces. In general, we observed the same pattern of representation development for scenes. First, within the scene-selective mask we found only one cluster in the right retrosplenial cortex (RSC, 30 voxels; MNI coordinates: 14, − 58, 14; FDR corrected, q = 0.05) showed a significantly lower Child-to-Adults BP-PS value in response to scenes (Fig. 5A) than the Within-Adults BP-PS value, suggesting that children were still under development in representing scenes in the RSC. Second, the similarity of scene representation in children to their own template (i.e., Child-to-Children$_{mean}$) was not significantly larger than that to adults' template (i.e.,

Child-to-Adults$_{mean}$) (t(110) = 1.81, p = 0.076, Cohen's $d = 0.17$, Fig. 5B), suggesting that children and adults shared the same template in representing scenes in the RSC. Finally, the similarity of scene representation within children (Within-Children BP-PS) was significantly lower than that within adults (Within-Adults BP-PS) (t(253) = − 8.20, p < 0.001, Cohen's $d = 1.04$, Fig. 5C), suggesting that the representation for scenes in the RSC also developed through the decrease of within-group variation in representation.

3.4. Association between typicality of face neural representation and face recognition performance

Does the greater variance in neural representation account for children's lower performance in face recognition? To explore the association, we tested the correlation between the typicality of face representation (i.e., representation similarity of an individual to adults) in the ROIs defined from significant clusters in Fig. 3A and the behavioral signature of face recognition, where children were less affected by the face inversion effect (upright-specific FIE, t(205) = 3.87, p < 0.001, Cohen's $d = 0.55$, Fig. 6A, B). We found that greater representation similarity of an individual to adults (i.e., the BP-PS value of each individual to adults) was associated with better performance in the face inversion task after controlling for age and head motion, in both the rFFA (r = 0.191, p = 0.006, Fig. 6C; adults: r = 0.203, p = 0.022; children: r = 0.176, p = 0.119) and rOFA (r = 0.140, p = 0.045, Fig. 6D; adults: r = 0.155, p = 0.082; children, r = 0.116, p = 0.304), but not the lOFA (r = 0.083, p = 0.237). Further control analyses showed that this correlation could not be explained by template registration bias (FFA: r = 0.196, p = 0.005; rOFA: r = 0.168, p = 0.016, Supplementary Fig. 6). In contrast, performance in the face inversion task was not correlated with the BP-PS value in the RSC when perceiving scenes (r = 0.063, p = 0.368, Fig. 6E), suggesting that the correlations with the face recognition performance was specific to the typicality of face neural representation. In short, it is likely that the development of face recognition ability may be accompanied with the increase of typicality in neural face representation.
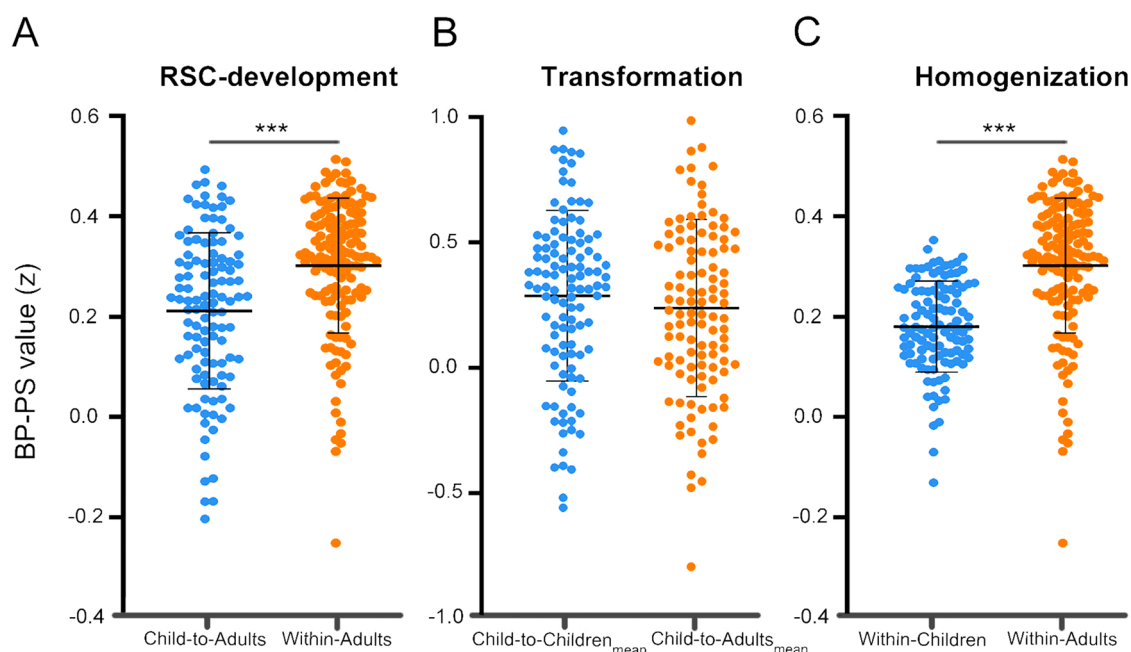

Fig. 5. Homogenization of scene representation during development. (A) Child-to-Adults BP-PS values were significantly lower than Within-Adults values in the right RSC. (B) Representation transformation hypothesis: no significant difference was found between Child-to-Children$_{mean}$ and Child-to-Adults$_{mean}$ BP-PS values in the RSC. (C) Representation homogenization hypothesis: Within-Children BP-PS values were significantly lower than Within-Adults values in the RSC. Error bars indicate standard errors of the mean. ***p < 0.001.
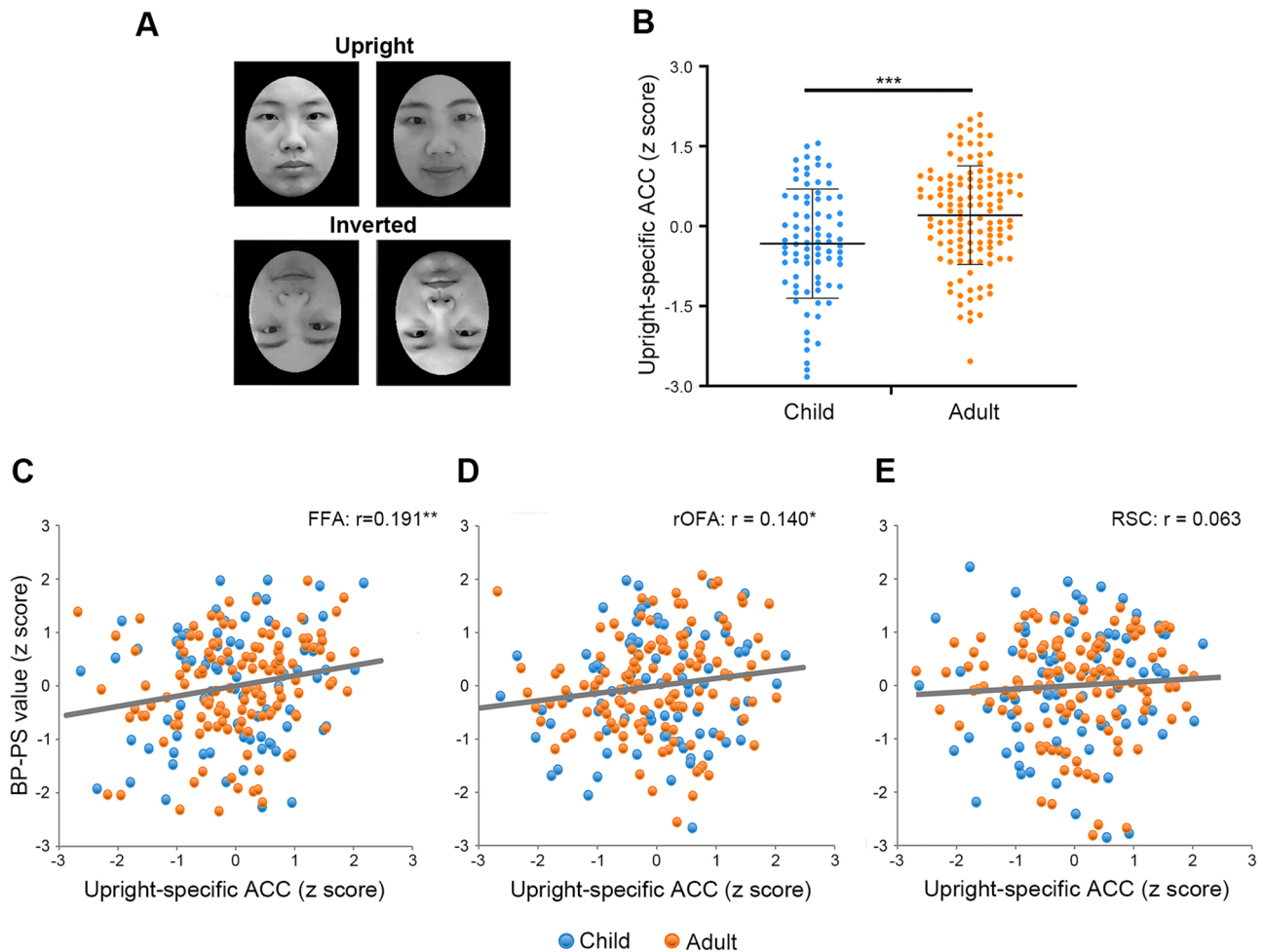
Fig. 6. Association between typicality of face neural representation and face recognition. (A) Stimulus exemplars in the face-inversion task. Note that the faces shown here are not the faces used in the experiment. The volunteers with these faces have provided written consent for publication. Participants performed a successive same-different matching task on upright or inverted faces. (B) Accuracies in matching upright faces after regressing out accuracies of inverted faces for children and adults. (C)–(E) Scatterplots showing the correlations between the upright-specific accuracy (regressing out age) and the typicality of representation (i.e., representation similarity of an individual to adults, regressing out head motion and age) (C) in the significant clusters of the right FFA, (D) in the significant clusters of the right OFA, (E) and in the RSC when perceiving scenes. Error bars indicate standard errors of the mean. *p < 0.05; **p < 0.01; ***p < 0.001.

4. Discussion

In the current study, we used the between-participant correlation method on pattern similarity to explore the mechanisms underlying the development of face representation in the ventral visual cortex. We found that the activation patterns in the face-selective regions were less similar within the children group than within the adults group when perceiving faces. Interestingly, the activation pattern similarity of children to their own group template was not significantly larger than the similarity of children to adults' template. These results together suggest that late-childhood children might share the same template with adults, but with a greater variation in representing faces. Further, the decrease in variation during development was also observed in a scene-selective region when perceiving scenes, implying that it was likely a general principle in the ventral visual cortex. Therefore, our results support the hypothesis proposing the development as a homogenization process from greater variation in representation in late-childhood children to a template shared by adults and late-childhood children.

First, we found that the activation patterns of late-childhood children' face-selective regions in response to faces showed greater variation than adults. This finding is in line with prior research that has shown a more variable brain response to faces and scenes in children (e. g., Passarotti et al., 2003; Golarai et al., 2007; Scherf et al., 2007;

Moraczewski et al., 2018). Besides, previous studies have found that typical adults usually show higher neural similarity, while individuals with brain immaturity, aging, and psychiatric disorders are accompanied by higher neural variability (lower similarity) (Hasson et al., 2009; Cantlon and Li, 2013; Campbell et al., 2015; Hahamy et al., 2015; Wild et al., 2017). It may be the accumulation of largely shared experience and adoption of similar effective strategies in typical development process that lead to the higher neural similarity in typical adult group. Golarai et al. (2017) have shown an "own-age bias" for face activation patterns, with higher decoding accuracy of activation patterns to adult faces than child faces in adult participants, but not in children. In our study, we used only child faces as stimuli. If adult faces were used, given that adults typically share more experience with peer faces than child faces, it can be speculated that adults would show a similar own-age bias (i.e., greater within-group representation similarity for adult faces than child faces), and the observed difference in within-group similarity between adults and children in the present finding would be more significant. Future studies using adult faces are needed to test this hypothesis.

The greater variation of children's activation pattern, on one hand, suggests that at this development stage (9–14 years old), children have a less stable and more flexible face representation than adult. Interestingly, a body of neural studies have shown adult-like category-level neural response around 11–12 years of age, but not in the identity-level

neural tuning (Scherf et al., 2011; Cohen Kadosh et al., 2013b). These findings suggest the possibility of a coarse acquisition of face processing in childhood and a prolonged fine-tuning of expertise to subserve more refined processing (Grill-Spector et al., 2008; Scherf et al., 2010). On the other hand, greater variance in representation also suggests stronger neural plasticity in children's brain (Mueller et al., 2013; Kaufmann et al., 2017; Cao et al., 2018). For example, prior evidence suggests that the childhood is one of the most dynamic phases in cognitive development paralleled by the brain development, such as the rapid expansion of cortical volume, and the reorganization of brain structure and function (Casey et al., 2005; Paus, 2005; Foulkes and Blakemore, 2018). Therefore, cognitive training in children is more likely to speed up the development of the brain, including making a more 'adult-like' activation pattern and increasing the specialization of the brain networks (Rueda et al., 2005; Jolles and Crone, 2012; Zatorre et al., 2012).

Second, although late-childhood children's face representation had a greater variation, it likely shared the same template with adults, supporting the hypothesis of the development as a quantitative change process from great variation in representation in late-childhood children to a template shared by adults and children. This observation is consistent with previous behavioral studies that adolescence have already established an adult's manner to process faces (e.g., processing faces in holistic manner) (de Heering et al., 2007; Mckone et al., 2012), but they may adopt various and ineffective strategies to process faces, which leads to poor performance in face perception. Notably, both the FFA and OFA showed similar representation homogenization with development in our study. Previous studies have suggested that the FFA is involved in holistic processing of faces and the OFA is likely to process local face features (Yovel and Kanwisher, 2005; Liu et al., 2010; Zhang et al., 2012). This result implies that both local and holistic face processing may develop through the homogenization process during development. It is therefore proposed that with development, more consistent and effective processing strategies are adopted across children (Passarotti et al., 2003), leading to improved performance in face recognition. Supporting this conjecture, we found the increase in representation typicality during development was correlated with the improvement of behavioral performance in face perception. In addition, we found that on average, the adults showed higher within-group similarity than children, while some adult individuals showed particularly low within-group similarity, even lower than the lowest values in children. These results suggest an interesting possibility that as a whole group, adults tend to be more homogenous in representing faces than children, which correspond to the typical individuals in adults; while for the atypical individuals in adults, their deviations from other group members become more pronounced with development.

Third, the decrease in representation variation during development was likely a general principle in the ventral visual cortex, as a similar result was observed in a scene-selective region when children perceiving scenes. The finding that the ventral visual cortex achieved the functional reorganization from heterogeneity to a more regularized and homogenous pattern supports the functional specialization hypothesis that the development is a process shifting from a distributed pattern of activation to a more sparse coding scheme (Johnson, 2001, 2011; Moses et al., 2002).

Finally, the BP-PS method we employed is the key to examine the development of representation in this study. There are two advantages of this method. (1) It can quantify the development of representation by calculating similarity of the neural activation patterns between individuals to characterize the variance of the individual's brain development; (2) it can differentiate within-group variance and between-group variance and examine differences in representation variances between groups. Thus, our method can be extended to studies on developmental disorders, such as developmental prosopagnosia and autism spectrum disorders, and the understanding of their development trajectory in representation may shed light on their etiology.

The test-retest reliability of task-based fMRI measures has recently been questioned (Elliott et al., 2020), and the critique has focused on univariate measures (i.e., average activation within individual regions). However, in contrast to univariate measures, it is proposed that multivariate measures can exhibit high reliability by exploiting the high dimensionality in fMRI data (Elliott, et al., 2020; Kragel et al., 2021). For example, the activation pattern of face (vs. shape) processing from HCP data had excellent reliability (Kragel et al., 2021). Hence, our study, which measured multivariate activation pattern of face processing in a large sample of participants, is expected to have sufficient reliability. In addition, our findings also showed good reproducibility across different adult samples.

In sum, in this study we found that the representation of face-selective brain regions reached the adult-level representation by reducing variation in representation among late-childhood children. However, the age range of the child participants in the study is from 9 to 14 years old, so our results more reflected the development of face processing from late childhood and adolescence to adults. For children in early childhood (aged 5–8 years old), previous studies have shown that they do not evince consistent adult-like face activation (e.g., Scherf et al., 2007). Thus, it is possible that at an earlier stage from early to late childhood, face processing might follow the development path as suggested by the representation transformation hypothesis, with young children using a different face processing template from that of older children and adults. Future studies are needed to address this possibility with children at younger age. In addition, our study focused on the development of the representation at the perceptual stage, and previous studies on development prosopagnosia suggest that the mnemonic stage of face processing is also critical (Duchaine et al., 2003; Klargaard et al., 2016). Future studies need to examine the development of the representation at the mnemonic stage with proper experimental paradigms.

Data Availability Statement

The data in our study comes from an ongoing project (Gene Environment Brain & Behavior).

The data is available upon request. The Data-Sharing and Usage Agreement will be signed between the user and provider (Gene Environment Brain & Behavior Project, directed by Dr. Jia Liu) of data. In particular, the user should agree to the following terms, including using the database only for academic research, protecting the participants' information, not release data to a third party without approval, and so on.

The data sharing is in compliance with the standards of the Institutional Review Board of Beijing Normal University and funding agreement.

The data is still accumulating and the means of data sharing in public repositories have not been fully discussed yet. Thus, I am not uploading our data, but we agree that eventually the data shall be put in public repositories.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the

online version at doi:10.1016/j.dcn.2021.101040.

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