Behavioral/Cognitive

Typical and Atypical Development of Functional Connectivity in the Face Network

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Extensive studies have demonstrated that face recognition performance does not reach adult levels until adolescence. However, there is no consensus on whether such prolonged improvement stems from development of general cognitive factors or face-specific mechanisms. Here, we used behavioral experiments and functional magnetic resonance imaging (fMRI) to evaluate these two hypotheses. With a large cohort of children ($n = 379$), we found that the ability of face-specific recognition in humans increased with age throughout childhood and into late adolescence in both face memory and face perception. Neurally, to circumvent the potential problem of age differences in task performance, attention, or cognitive strategies in task-state fMRI studies, we measured the resting-state functional connectivity (RSFC) between the occipital face area (OFA) and fusiform face area (FFA) in human brain and found that the OFA-FFA RSFC increased until 11–13 years of age. Moreover, the OFA-FFA RSFC was selectively impaired in adults with developmental prosopagnosia (DP). In contrast, no age-related changes or differences between DP and normal adults were observed for RSFCs in the object system. Finally, the OFA-FFA RSFC matured earlier than face selectivity in either the OFA or FFA. These results suggest the critical role of the OFA-FFA RSFC in the development of face recognition. Together, our findings support the hypothesis that prolonged development of face recognition is face specific, not domain general.

Key words: **development; developmental prosopagnosia; face recognition; fusiform face area; occipital face area; resting-state functional connectivity**

Significance Statement

There is long-standing debate on whether the prolonged age-related improvement in face recognition performance stems from development of general cognitive factors or face-specific mechanisms. Here, we provide novel evidence for protracted development of face-specific mechanisms. Specifically, the resting-state functional connectivity (RSFC) between the fusiform face area and occipital face area, two core brain areas in the face network, increased until 11–13 years of age and was selectively impaired in adults with developmental prosopagnosia. These results suggested the importance of the face network RSFC in the development of face recognition. Our study invites a broader investigation of whether the development of other cognitive abilities is similarly guided by the development of connectivity within the corresponding neural networks.

Introduction

One striking aspect of the development of face recognition is that adult-like face recognition processes are present at 3–4 years of age (Pellicano and Rhodes, 2003; Pellicano et al., 2006; de Heering et al., 2007), yet not until adolescence does performance on face recognition tasks approach adult levels (Lawrence et al., 2008; Germine et al., 2011). Why does face recognition performance reach adult levels so late? One hypothesis is that face-specific processing matures no later than 4 years and the later improvements in task performance reflect the development of general cognitive factors (de Heering et al., 2007; McKone et al., 2012). Alternatively, it may be that face recognition itself continues to develop late via changes of face-specific mechanisms (Carey and Diamond, 1977; Mondloch et al., 2002).

Evidence from neuroimaging studies appears to support the face-specific development hypothesis by showing late development of the face-selective regions, including the fusiform face area (FFA) (Kanwisher et al., 1997) and the occipital face area (OFA) (Gauthier et al., 2000). Specifically, many functional mag-

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netic resonance imaging (fMRI) studies have observed an increase in the size or face selectivity of the FFA and OFA with age that extends into adolescence (Golarai et al., 2007; Scherf et al., 2007; Peelen et al., 2009; Golarai et al., 2010; Joseph et al., 2011; Haist et al., 2013) and the task-state functional connectivity among face-selective regions continues to increase with age after childhood (Kadosh et al., 2011; Joseph et al., 2012). However, researchers disagree on the interpretation of these fMRI results. One major concern is that age-related changes in task-state fMRI measures may be accounted for by age differences in task performance, attention, or cognitive strategies (Church et al., 2010).

To overcome these potential problems in task-state fMRI studies, we used resting-state functional connectivity (RSFC), which measures correlation of spontaneous blood oxygen level dependent (BOLD) fluctuations between brain regions (Biswal et al., 1995). The RSFC is believed to reflect functional coupling and communication between regions and is constrained by anatomical connectivity (for reviews, see Fox and Raichle, 2007; van den Heuvel and Hulshoff Pol, 2010; Buckner et al., 2013). In particular, we chose the RSFC between the FFA and OFA as a neural marker for the development of face-specific recognition for the following reasons. First, the connectivity between the OFA and FFA has demonstrated the largest change during development in task-state studies (Kadosh et al., 2011; Joseph et al., 2012; He et al., 2015). Second, the magnitude of the OFA-FFA RSFC is associated with face-specific recognition ability across individuals (Zhu et al., 2011). Third, RSFC has been proven to be a sensitive index of brain maturation (Dosenbach et al., 2010). Finally, any age-related changes in RSFC are unlikely to result from task-related differences between age groups (e.g., task performance, attention, cognitive strategies).

Here, we tested the aforementioned two alternative hypotheses about the development of face recognition with behavioral and fMRI data. In Study 1, we depicted the developmental trajectory of face-specific recognition ability with a face memory task and a face discrimination task, contrasting faces with nonface objects, in a large population of participants from 6 to 19 years of age ($n = 379$). In Study 2, we examined the development of the OFA-FFA RSFC in another group of typically developing children from 7 to 13 years of age ($n = 25$). Next, we determined whether the OFA-FFA RSFC is impaired in adults suffering from the atypical development of face-specific recognition (i.e., developmental prosopagnosia; DP) (Behrmann and Avidan, 2005; Duchaine and Nakayama, 2006). Finally, we compared the developmental trajectory of the OFA-FFA RSFC with that of face selectivity in the OFA and FFA. If the late development of both face-specific recognition ability and its specialized neural underpinnings was observed, the face-specific development hypothesis would be supported. Alternatively, if neither face-specific recognition ability nor the OFA-FFA RSFC increases after 6 years of age, the general cognitive development hypothesis would be supported.

Materials and Methods

Study 1

Participants

Table 1 summarizes the number of participants and their demographic information in each study. In Study 1, 379 participants from 6 to 19 years of age (M = 12.6, SD = 2.6, 206 females) were recruited from elementary, middle, and high schools in Beijing, China. Figure 1*B* shows the number of participants at each age. All participants had normal or corrected-to-normal vision, with no history of neurological or psychiatric diseases. A subset of the participants were those from an ongoing project on the heritability of face recognition and part of the data have been reported previously (Zhu et al., 2010). In this study, we used this dataset to examine the development of face-specific recognition ability. Our investigation protocol was approved by the Institutional Review Board (IRB) of Beijing Normal University (BNU). Before testing, we obtained written informed consent from all participants and/or their parents.

Table 1. The number of participants and demographic information in each study

Study	*n*	Age range (y)	Sex
Study 1			
Old/new recognition task	379	6–19	206F/173M
Discrimination task	376	6–19	203F/173M
Study 2			
Children			
fMRI	23	7–13	13F/10M
Whole-part task	22	7–13	12F/10M
Adults			
fMRI and whole-part task	16	18–23	11F/5M
Face/object identification task	15	18–23	10F/5M
DP			
fMRI	16	18–20	7F/9M
Behavioral tasks	17	18–20	7F/10M

Experimental procedure

All participants completed an old/new recognition task and 376 of them also completed a discrimination task. In the old/new recognition task (Wang et al., 2012), 40 face images and 40 flower images were used (Fig. 1*A*). The face stimuli were gray-scale pictures of adult Chinese faces, with external contour (an approximately oval shape with hair on the top and sides) removed. Flower images were gray-scale pictures of common flowers with leaves and background removed. There were two blocks in this task: a face block and a flower block, which were counterbalanced across participants. Each block consisted of one study segment and one test segment. In the study segment, 20 images of 1 object category were shown for 1 s per image with an interstimulus interval (ISI) of 0.5 s and these studied images were shown twice. In the test segment, 10 studied images were shown twice, randomly intermixed with 20 new images from the same category. On presentation of each image, participants were instructed to indicate whether the image had been shown in the study segment. It has been proposed that, to avoid the restriction of range problem in development studies (for a review, see McKone et al., 2012), a valid comparison of development slopes between different stimulus categories requires that behavioral performance is matched between stimulus categories at certain age group and does not show floor or ceiling effects (McKone et al., 2012; Weigelt et al., 2014). Therefore, we selected face and flower stimuli to match performance between stimulus categories in the oldest group tested (age: 16–19 years; $n = 45$) and to avoid the ceiling effect. Note that all experiment procedures were identical across different age groups.

In the discrimination task, 40 face images and 30 3D asymmetrical assemblages of cubes images were used (see Fig. 1*E*). The face images were frontal-view and three-quarter-view faces, and the cube stimuli were generated based on the classic mental rotation task (Shepard and Metzler, 1971). There were two blocks in this task: a face block and a cube block, which were counterbalanced across participants. Each trial started with a blank screen for 0.5 s, followed by the first stimulus presented at the center of the screen. After an ISI of 0.5 s, the second stimulus appeared for the same duration as the first one, with the viewpoint being changed. To match behavioral performance in the youngest group tested (age: 6–9 years; $n = 42$), face stimuli were presented for 0.2 s and cube stimuli were presented for 0.7 s. Participants were instructed to indicate as quickly as possible whether the second stimulus was the first one rotated or another stimulus. Each block consisted of 40 trials.

Study 2

Participants

Twenty-five children (7–13 years, M = 10.4, SD = 1.8, 13 females) and 16 adults (18–23 years, M = 20.3, SD = 1.5, 11 females) with normal face

recognition ability and 17 adults with DP (18–20 years, M = 19.1, SD = 0.8, 7 females) participated in the study. All participants were right handed and had normal or corrected-to-normal visual acuity. None of them had any history of neurological or psychiatric diseases. One child participant of Study 2 also took part in Study 1. Our investigation protocol was approved by the IRB of BNU. Before testing, we obtained written informed consent from all participants and/or their parents.

Selection of DP subjects

Seventeen subjects with DP were selected from 1512 college students (61% females) from BNU and the Chinese Academy of Sciences, China. Based on the standard procedure suggested by previous studies (Behrmann and Avidan, 2005; Duchaine and Nakayama, 2005), we used both self-report questionnaires on face recognition ability (stage 1: screening) and the famous face task (stage 2: selection) to identify DP subjects from the population.

Stage 1: screening. College students were asked to complete a one-item question and a 14-item questionnaire in class. The one-item question asked the students to evaluate their face recognition ability relative to their peers on a five-point Likert scale ranging from "extremely superior" to "extremely inferior." The 14-item questionnaire was a Chinese version of Kennerknecht et al.'s (2007) self-reported questionnaire for diagnosing prosopagnosia, which asked the frequency of encountering difficulties in face recognition in daily life. The frequency was evaluated in a five-point Likert scale ranging from "never" to "always." Reliability analysis based on the current dataset suggested that the questionnaire had adequate level of reliability (Cronbach's $\alpha = 0.79$). Twenty-six students who rated their face recognition ability as "extremely inferior" in the first questionnaire were selected directly as DP candidates. In addition, 24 students who meet two criteria simultaneously were selected as DP candidates as well, including: (1) those who rated face recognition ability as "inferior" in the first questionnaire and (2) those who scored 1.65 SD below the participant population mean in the second questionnaire. Therefore, 50 of 1512 university students were selected as the DP candidates (18–22 years, 37 females) based on self-report.

Stage 2: selection. To identify DP subjects from the DP candidates, we used a paper-based famous face test. There were 30 faces of Chinese celebrities (politician, movie stars, pop singers, and athletes) with external contours removed and participants were instructed to name the celebrities one by one. If participants could not recall the name, they were asked to provide information that could identify the celebrities successfully. A total number of 94 college students from BNU (18–22 years, 45 females) with normal face recognition ability were tested to construct the norm for the famous face test. Nineteen of the 50 DP candidates whose score was 3 SDs below the mean of the controls in the famous face test (mean = 0.89, SD = 0.12) were identified as persons suffering a severe deficit in face recognition (i.e., DP). Seventeen agreed to participate in the study.

fMRI scanning

For the normal adults and the DP subjects, each participant completed a resting-state run and two localizer runs. In the resting-state run lasting 10 min 30 s, participants were instructed to lie still, keep their eyes closed, and think of whatever they would like in the scanner without performing any tasks. Importantly, the resting-state run was conducted before the localizer runs to eliminate the possibility that participants might imagine any stimulus seen in the localizer run.

During the localizer run, 15 s blocks (20 stimuli per block) of faces, objects, scenes, or scrambled objects were presented. Each image was presented for 300 ms, followed by a 450 ms ISI. Each run contained 21 blocks (four blocks of each stimulus category and five blocks of fixation only), totaling 5 min and 15 s. During the scan, participants performed a 1-back task (i.e., pressing a button when 2 consecutive images were identical). To make the scan comfortable to child participants, we slightly modified the scanning procedure by splitting a standard localizer run for adults into two shorter runs. During the localizer run for children, each image was presented for 600 ms, followed by a 400 ms ISI. In each block, 15 exemplars of each category stimuli were presented. Each run contained 11 blocks (2 blocks of each stimulus category and 3 blocks of fixation), totaling 2 min and 45 s. Despite these differences, the total duration for stimulus presentation was approximately the same between adults and children.

fMRI data acquisition

Scanning was performed on a 3T Siemens Trio scanner at the BNU Imaging Center for Brain Research, Beijing, China. Functional images were acquired using a standard 12-channel head matrix coil and a gradient-echo echoplanar imaging sequence [25 slices, repetition time (TR) = 1.5 s, echo time (TE) = 30 ms, flip angel = 90°, voxel size = 3.1 × 3.1 × 4.0 mm, matrix = 64 × 64, 0.8 mm interslice gap]. Slices were oriented parallel to each participant's temporal cortex covering the whole brain. In addition, MPRAGE, an inversion prepared gradient echo sequence (256 slices, TR/TE/inversion time = 2.53 s/3.44 ms/1 s, flip angle = 7°, voxel size = 1 × 1 × 1 mm), was used to acquire 3D structural images.

fMRI data analysis

Data preprocessing. Functional data were analyzed with the Freesurfer functional analysis stream (Cortech) (Dale et al., 1999; Fischl et al., 1999), the fROI (http://froi.sourceforge.net), and in-house Matlab code. The preprocessing consisted of motion correction, intensity normalization, and spatial smoothing (Gaussian kernel, 5 mm full width at half maximum). Then, voxel time courses for each participant were fitted by a general linear model, with each condition modeled by a boxcar regressor matching its time course that was then convolved with a gamma function (delta = 2.25, tau = 1.25). In addition, six motion correction parameters and slow signal drifts (linear and quadratic) were also removed from the functional data.

ROI selection and measurement of selectivity. To define the OFA and FFA in each hemisphere for each participant, we first localized the peak voxels that responded more strongly to faces than objects and scenes in the fusiform gyrus and in the inferior occipital cortex ([2 * faces − (objects + scenes)], $p < 10^{-4}$, uncorrected). Then, a set of 27 contiguous significantly activated voxels (Zhu et al., 2011; Davies-Thompson and Andrews, 2012; Stanley et al., 2013) centered at the peak voxels were defined as the FFA and OFA, respectively. The reason to limit the number of voxels in an ROI rather than to select all voxels within a face-selective cluster is to keep the signal-to-noise ratio consistent across ROIs when averaging all voxels within an ROI. Two object-selective regions, the lateral occipital sulcus (LO) and the posterior fusiform gyrus (pFs) (Grill-Spector et al., 1999), were defined in the same way with the contrast of [2 * objects − (faces + scenes)]. In addition, because the left and right hemisphere showed a similar pattern, the data from both hemispheres were collapsed to increase statistical power.

The category selectivity of each ROI was calculated as the average of the *t*-scores of all voxels within an ROI with certain contrast (face selectivity: faces vs scenes and objects; object selectivity: object vs faces and scenes) based on data from all the localizer runs. Note that the selectivity of an ROI was calculated from the same set of data that were used to define the ROI; however, this bias was unlikely to affect the comparison of selectivity between groups because the selectivity indices of all groups were calculated in the same way.

Participants exclusion. Participants whose absolute head motion was >3° in rotation or 3.0 mm in translation throughout the fMRI scan were excluded from further analyses. As a result, two children who had excessive head motion were excluded. In addition, one DP who did not show the left FFA was excluded from further analysis. The ROIs were successfully localized in the remaining participants.

Resting-state correlation. In addition to the aforementioned standard preprocessing of fMRI data, several additional preprocessing steps were used to reduce spurious variance unlikely to reflect neural activity in resting-state data. These steps included using a temporal band-pass filter (0.01–0.08 Hz) to reduce low-frequency drifts and high-frequency noise, regressing out the six head realignment parameters obtained from rigid-body head motion correction and regressing out the mean time course of whole-brain BOLD fluctuations.

After the preprocessing, a continuous time course for each ROI consisting of 420 data points was extracted by averaging the time courses of

all voxels in an ROI for each participant. Correlation coefficients (r) between the extracted time courses of the ROIs were calculated and transformed to Gaussian-distributed z-scores via Fisher's transformation to improve normality and these z-scores were then used as measures of RSFC for further analyses. Moreover, because the interregional distance between two ROIs may partly account for the variances in RSFC, we also calculated the distances between the peak voxels of each ROI in the native volume space of each participant.

Control analyses were performed to examine whether the RSFC results were confounded by head micromovements (Van Dijk et al., 2012; Power et al., 2012; Power et al., 2015), signal/noise ratio over time (tSNR; McKone et al., 2012), or global signal regression (Murphy et al., 2009; e.g., Fox et al., 2009; Saad et al., 2012; Gotts et al., 2013). We calculated the mean framewise displacement (FD), which is the relative displacement of each brain volume compared with the previous volume, in the resting-state run as well as the localizer runs for each participant per Van Dijk et al. (2012). The mean FD magnitudes in the resting-state run for normal adults, children, and DP subjects were 0.025 ± 0.011 mm, 0.035 ± 0.026 mm, and 0.025 ± 0.006 mm, and the mean FD magnitudes in the localizer runs were 0.022 ± 0.008 mm, 0.029 ± 0.006 mm, and 0.025 ± 0.005 mm, respectively. We also computed the tSNR of each ROI for children and adults. Then, we recomputed the correlation between RSFC and age with FD and tSNR controlled out respectively. In addition, we recomputed the RSFC using data preprocessed without global signal regression.

Behavioral experiments

To characterize the impairment of face recognition in the DP subjects, we compared their performance in two behavioral tasks with normal adults. The first task is a face and object identification task, measuring participants' ability in recognizing familiar faces and objects (Grill-Spector et al., 2004; see Fig. 3*A*). In the face identification task, there were 60 trials, with 30 exemplars of the target face (i.e., the Chinese movie star Chiu-Wai Leung) and 30 exemplars of other famous faces. In each trial, a face image was presented for 33 ms and immediately followed by a mask. The mask remained on the screen until the participants responded. Participants performed a two-alternative forced-choice task to report whether the image was the target face or other faces. In the object identification task, three object categories were tested in separate blocks: (1) chrysanthemum versus other flowers, (2) jeep versus other cars, and (3) pigeon versus other birds. There were 20 trials for each object category, with 10 exemplars of the target object and 10 exemplars from the same category. In each trial, an object image was presented for 50 ms and other parameters were identical to those in the face identification task. Participants were asked to report whether the image was the target object or other objects. The order of the face and object identification tasks was counterbalanced across participants. One normal adult who did not accomplish this task was removed from further analysis.

Another task is the whole-part task, which is used to measure holistic processing of faces (Tanaka and Farah, 1993; see Fig. 3*B*). The task contained a learning phase and a testing phase. In the learning phase, participants were instructed to memorize three faces and their associated names. Each face–name pair was shown for 5 s with an ISI of 1 s. Only when the participants could correctly identify all face–name pairs were they allowed to enter the testing phase. In each trial of the testing phase, a question on a target face part (e.g., "Which is Xiao Zhang's nose?") was presented, followed by two pictures presented on the left and right sides of the screen. The display remained on the screen until the participants responded. There were two conditions, each consisting of 36 trials. For the part condition, the display contained two isolated features (e.g., two noses): one was from the target face (e.g., Xiao Zhang's face) and the other was from one of the other studied faces. For the whole condition, the display contained two whole faces, with the target and a foil face differing only with respect to the target part. Stimuli were matched between the two conditions such that each part (e.g., Xiao Zhang's nose) tested in the whole condition was also tested in the part condition. Trials from the whole and part conditions were randomly intermixed. In addition to normal adults and the DP subjects, the child participants were also tested with the whole-part task. One child who did not accomplish this task was removed from further analysis.

Results

Face-specific recognition improves with age

In Study 1, we investigated whether face-specific recognition ability increased from ages 6–19 with two tasks. In the memory task, participants performed an old/new recognition task on faces and flowers (Wang et al., 2012; Fig. 1*A*). In the perception task, a successive same–different matching task was used on faces and assemblages of cubes presented in different views (Shepard and Metzler, 1971; Fig. 1*E*). Table 2 shows the mean accuracy, SD, and reliability of the two tasks.

We found that participants' accuracy of differentiating previously presented faces from novel faces was positively correlated with age (Pearson $r = 0.36$, $p < 0.001$; Spearman $\rho = 0.33$, $p < 0.001$), with older participants performing better (Fig. 1*B*). In contrast, no significant correlation was observed between flower memory performance and age (Pearson $r = 0.06$, $p = 0.21$; Spearman $\rho = 0.01$, $p = 0.86$; Fig. 1*C*). To isolate face-specific memory, we regressed out the variance of flower memory from that of face memory and found that the residual (i.e., face-specific memory) was still positively correlated with age (Pearson $r = 0.36$, $p < 0.001$; Spearman $\rho = 0.34$, $p < 0.001$; Fig. 1*D*). Moreover, the effect size (Cohen's $d = 1.57$) indicated a large increase in face-specific memory from early childhood (6–8 years, $n = 20$) to early adulthood (18–19 years, $n = 20$). Because the old/new memory task may be influenced by response bias, we also used A-prime as the dependent measure (Wang et al., 2012) and similar results were obtained. A-prime for faces was positively correlated with age (Pearson $r = 0.30$, $p < 0.001$; Spearman $\rho = 0.33$, $p < 0.001$). In contrast, no significant correlation was observed between A-prime for flower and age (Pearson $r = 0.09$, $p = 0.09$; Spearman $\rho = 0.025$, $p = 0.63$). In addition, the residual of the variance of A-prime for face regressing out that for flower (i.e., face-specific memory) was still positively correlated with age (Pearson $r = 0.28$, $p < 0.001$; Spearman $\rho = 0.33$, $p < 0.001$).

Similarly, accuracy in discriminating successively presented faces with minimum memory demands was also positively correlated with age (Pearson $r = 0.41$, $p < 0.001$; Spearman $\rho = 0.39$, $p < 0.001$; Fig. 1*F*). Although the correlation between the accuracy in discriminating cubes and age was also significant (Pearson $r = 0.21$, $p < 0.001$; Spearman $\rho = 0.19$, $p < 0.001$; Fig. 1*G*; Nishimura et al., 2015), the magnitude of this correlation was significantly smaller than that for faces (Steiger's $Z = 3.28$, $p < 0.01$). Further, face-specific discrimination ability (i.e., the residual of the variance of face discrimination regressing out that of cube discrimination) was also positively correlated with age (Pearson $r = 0.37$, $p < 0.001$; Spearman $\rho = 0.36$, $p < 0.001$; Fig. 1*H*). In addition, the effect size (Cohen's $d = 1.54$) indicated large increases of face-specific perception from early childhood (6–8 years, $n = 20$) to early adulthood (18–19 years, $n = 20$).

The observed age-related improvements in face-specific recognition ability were not likely subject to the restriction of range problem (McKone et al., 2012) because the overall performance was approximately matched either at the oldest (age: 16–19; $n = 45$; old/new task accuracy: faces = 0.80 ± 0.09, flowers = 0.82 ± 0.08; $t_{(44)} = 1.21$, $p = 0.24$) or the youngest participants tested (age: 6–9; $n = 42$; discrimination task accuracy: faces = 0.61 ± 0.11, cubes = 0.59 ± 0.10; $t_{(41)} = 1.02$, $p = 0.31$) depending on the nature of the tasks, and these means did not approach ceiling or floor. Neither was the correlation driven by outliers. For the memory task, we removed all the participants who responded below or near chance level (accuracy <0.60) in both the face and flower conditions and the same results were obtained ($n = 374$).

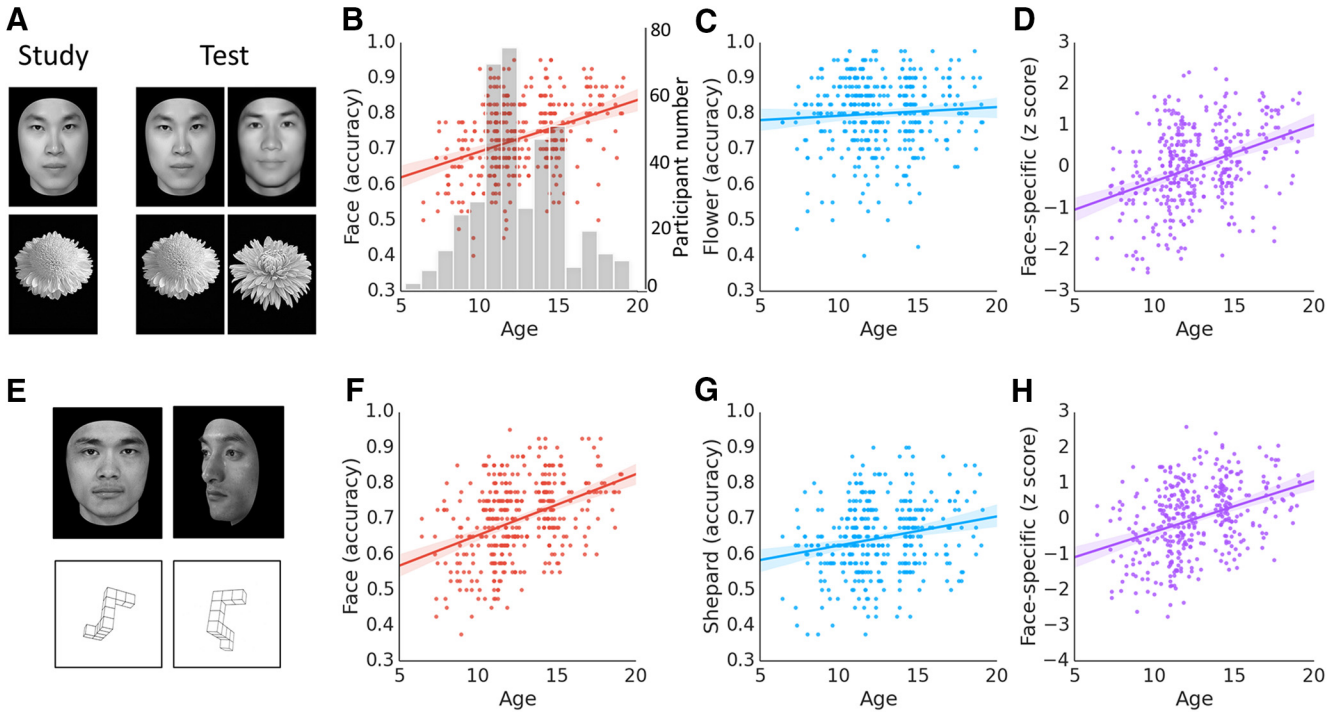

Figure 1. Behavioral development of face-specific recognition ability. ***A***, Example stimuli and trial types in the old/new recognition task. In the study segment, participants studied a series of images of either faces or flowers. In the test segment, the studied images were shown with new images from the same category intermixed. Participants were asked to indicate which of the images had been shown in the study segment. ***B***, Scatter plot showing correlation between age and face memory and a histogram showing the number of participants at each age. ***C***, Scatter plot showing correlation between age and object memory. ***D***, Scatter plot showing correlation between age and face-specific memory (regressing out the variance of flower memory from that of face memory). ***E***, Example stimuli and trial types in the discrimination task. In each trial, a frontal-view image and a three-quarter-view image of either a face or a 3D asymmetrical assemblage of cubes were presented successively. Participants were asked to indicate whether the second image was of the same face/cubes as the first. ***F–H***, Scatter plots showing the correlation between age and face discrimination (***F***), object discrimination (***G***), and face-specific discrimination (regressing out the variance of object discrimination from that of face discrimination) (***H***).

Table 2. Means, SDs, and reliability estimates for each measure in Study 1

Task, trial type, and measure	Mean (SD)	Reliability
Old/new memory task		
Face	0.73 (0.11)	0.58
Flower	0.80 (0.10)	0.62
Face-specific memory		0.52
Discrimination task		
Face	0.70 (0.11)	0.58
Cube	0.65 (0.10)	0.45
Face-specific discrimination		0.56

That is, participants' accuracy of face memory was positively correlated with age (Pearson $r = 0.35$, $p < 0.001$; Spearman $\rho = 0.32$, $p < 0.001$), whereas no significant correlation was observed between flower memory and age (Pearson $r = 0.03$, $p = 0.62$; Spearman $\rho = -0.01$, $p = 0.79$). Further, the residual of the variance of face memory regressing out that of flower was also positively correlated with age (Pearson $r = 0.36$, $p < 0.001$; Spearman $\rho = 0.33$, $p < 0.001$). Similarly, for the perception task, we removed all the participants who responded below or near chance level (accuracy <0.60) in both the face and cube conditions and the same results were obtained ($n = 349$). That is, accuracy in discriminating faces was positively correlated with age (Pearson $r = 0.36$, $p < 0.001$; Spearman $\rho = 0.34$, $p < 0.001$). Although the correlation between the accuracy in discriminating cubes and age was also significant (Pearson $r = 0.15$, $p = 0.005$; Spearman $\rho = 0.13$, $p = 0.02$), the magnitude of this correlation was significantly smaller than that for faces (Steiger's $Z = 3.00$, $p < 0.01$). Further, the residual of the variance of face discrimination regressing out that of cube discrimination was also positively correlated with age (Pearson $r = 0.36$, $p < 0.001$; Spearman $\rho = 0.33$, $p < 0.001$). In addition, we computed two robust measures of correlation between performance and age, the percentage-bend correlation and skipped-correlation, which are less sensitive to outliers than the classic Pearson's and Spearman's correlations (Pernet et al., 2012). The results remained unchanged; that is, both face memory (Fig. 1*B*, 20% percentage-bend correlation: $r = 0.34$, $p < 0.001$; skipped correlation: $r = 0.36$, $p < 0.001$) and face discrimination performance (Fig. 1*F*, 20% percentage-bend correlation: $r = 0.39$, $p < 0.001$; skipped correlation: $r = 0.41$, $p < 0.001$) increased with age. In addition, face-specific memory (Fig. 1*D*, 20% percentage-bend correlation: $r = 0.34$, $p < 0.001$; skipped correlation: $r = 0.39$, $p < 0.001$) and face-specific discrimination (Fig. 1*H*, 20% percentage-bend correlation: $r = 0.36$, $p < 0.001$; skipped correlation: $r = 0.37$, $p < 0.001$) also correlated with age.

By showing different development slopes between face and object conditions and matching performance across conditions at one end of the age range to avoid the restriction of range problem, the results of Study 1 convincingly supported face-specific development throughout childhood and into late adolescence in both face perception and memory. One possible source of such face-specific recognition improvements is the development of specialized neural underpinnings of face recognition, which was examined in Study 2.

OFA-FFA RSFC increases with age

We acquired resting-state fMRI data from another group of children ($n = 25$, age 7–13 years) to depict the development of RSFC between the OFA and FFA. The OFA and FFA were localized in

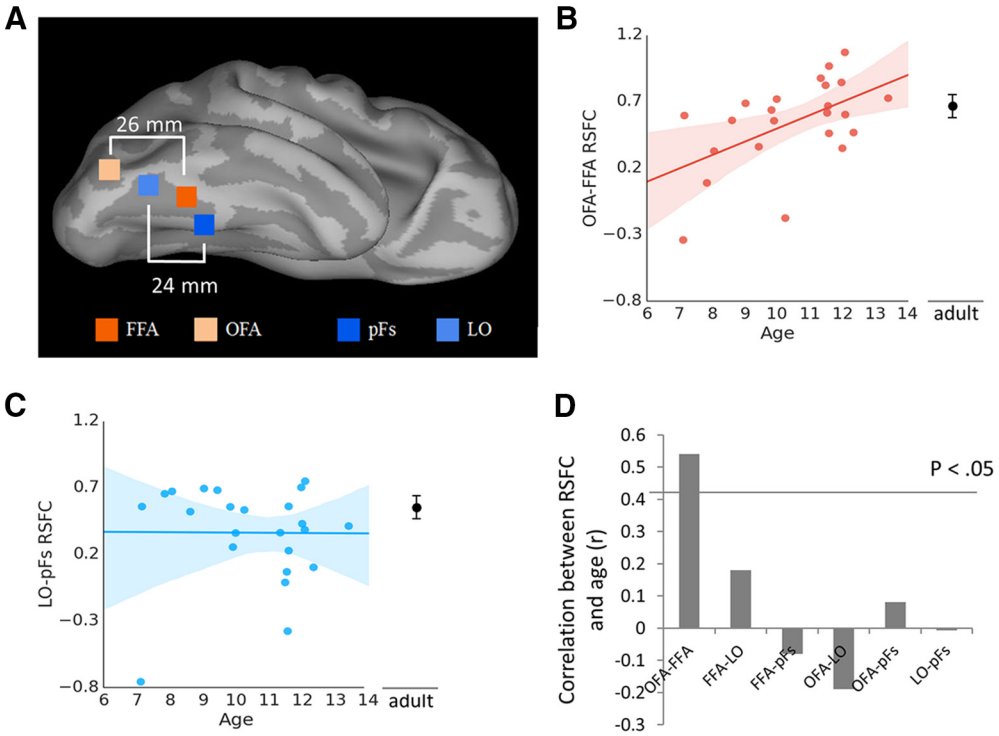

Figure 2. Development of RSFC in the ventral visual pathway. ***A***, Face- and object-selective regions centered at averaged Talairach coordinates across child participants. The face-selective regions OFA and FFA ($p < 10^{-4}$, uncorrected, red) and the object-selective regions LO and pFs ($p < 10^{-4}$, uncorrected, green) are shown on an inflated right hemisphere of MNI standard template. Sulci are shown in dark gray and gyri in light gray. ***B***, Scatter plots of the correlation between OFA-FFA RSFC and age. ***C***, Scatter plots of the correlation between LO-pFs RSFC and age. ***D***, Magnitude of Pearson's correlation coefficients between RSFCs in the ventral pathway and age.

Table 3. Talairach coordinates of the ROIs averaged across participants (mean ± SD)

		Children			Adults			DPs		
ROI	Hemisphere	*x*	*y*	*z*	*x*	*y*	*z*	*x*	*y*	*z*
FFA	Right	43 ± 4	−52 ± 7	−15 ± 3	40 ± 4	−59 ± 7	−13 ± 5	43 ± 4	−55 ± 7	−14 ± 4
	Left	−42 ± 5	−53 ± 8	−15 ± 6	−40 ± 2	−56 ± 4	−15 ± 4	−41 ± 5	−59 ± 9	−15 ± 2
OFA	Right	42 ± 6	−76 ± 8	−5 ± 4	37 ± 6	−82 ± 4	−4 ± 4	39 ± 4	−80 ± 8	−4 ± 5
	Left	−40 ± 8	−80 ± 7	−6 ± 5	−36 ± 6	−84 ± 7	−5 ± 4	−38 ± 7	−84 ± 7	−5 ± 5
LO	Right	46 ± 6	−63 ± 8	−7 ± 5	47 ± 5	−71 ± 7	−2 ± 5	39 ± 9	−82 ± 6	−8 ± 7
	Left	−45 ± 5	−68 ± 8	−6 ± 5	−45 ± 6	−74 ± 10	−3 ± 5	−36 ± 6	−83 ± 8	−8 ± 7
pFs	Right	33 ± 4	−45 ± 7	−16 ± 3	28 ± 3	−54 ± 6	−12 ± 4	33 ± 4	−45 ± 9	−16 ± 4
	Left	−33 ± 3	−50 ± 7	−15 ± 4	−31 ± 3	−50 ± 9	−14 ± 4	−31 ± 5	−48 ± 9	−16 ± 6

the occipital-temporal cortex of the participants (Golarai et al., 2007; Scherf et al., 2007; Fig. 2*A*; for Talairach coordinates, see Table 3), except that two children were excluded for excessive head motion. We found that children's OFA-FFA RSFC was positively correlated with age (Pearson's $r = 0.54$, $p = 0.009$; Spearman's $\rho = 0.45$, $p = 0.03$; Fig. 2*B*), with the spontaneous neural activity being more synchronized between the OFA and FFA in older children. Two robust correlation analyses (Pernet et al., 2012) showed that the age-related increase of OFA-FFA RSFC was unlikely caused by outliers (20% percentage-bend correlation: $r = 0.49$, $p = 0.02$, skipped correlation: $r = 0.535$, $p < 0.01$). In addition, the age-related increase of OFA-FFA RSFC cannot be explained by the anatomical distance between the OFA and FFA: after controlling for the variance in interregional distance, the correlation between OFA-FFA RSFC and age remained (partial correlation $r = 0.43$, $p = 0.045$). Further, we divided child participants into two subgroups based on a visual inspection of the scatter plot in Figure 2*B*, which suggested that the magnitude of children's OFA-FFA RSFC appears to reach adult levels at ~11–13 years of age. Indeed, OFA-FFA RSFC in adults was significantly stronger than that of children aged 7–10 ($n = 11$, mean = 8.8, SD = 1.1; $t_{(25)} = 2.49$, $p = 0.02$), but not stronger than that of children aged 11–13 ($n = 12$, mean = 11.9, SD = 0.6; $t_{(26)} = 0.15$, $p = 0.88$; Fig. 3*D*).

Are the age-related increases of RSFC restricted to the face system or do they reflect a general increase in the connectivity between the face-selective regions and other brain regions? To test these possibilities, we localized two object-selective regions in the same group of children: the LO and the pFs (Fig. 2*A*; for Talairach coordinates see Table 3). We found that the LO-pFs RSFC did not increase with age among our child participants (Pearson's $r = -0.007$, $p = 0.97$; Spearman's $\rho = -0.12$, $p = 0.60$; Fig. 2*C*) and the magnitude of correlation between LO-pFs RSFC and age was lower than that between OFA-FFA RSFC and age (Steiger's $Z = 2.16$, $p < 0.05$), indicating specific development of the OFA-FFA RSFC. In addition, the anatomy between OFA-FFA connectivity and LO-pFs connectivity was closely matched: the LO is adjacent to the OFA and the pFs lies next to the FFA (Fig. 2*A*); the LO-pFs distance (23.52 ± 1.21 mm) was comparable to that of the OFA-FFA distance (26.12 ± 1.02 mm).

Therefore, the LO-pFs RSFC can also serve as a control to rule out the confounding factor of interregional distance. Moreover, the RSFC between face-selective regions (OFA or FFA) and object-selective regions (LO or pFs) remained unchanged from ages 7–13 years (correlation between age and OFA-LO RSFC: $r = -0.19$, $p = 0.39$; OFA-pFs RSFC: $r = 0.08$, $p = 0.74$; FFA-LO RSFC: $r = 0.18$, $p = 0.40$; FFA-pFs RSFC: $r = -0.08$, $p = 0.74$; Fig. 2*D*). Therefore, the age-related increase of the OFA-FFA RSFC may reflect an integration process specifically between face-selective regions in forming the face network during childhood.

However, one may argue that the observed age-related increases of OFA-FFA RSFC can be accounted for by age-related differences in tSNR (McKone et al., 2012), whole-brain BOLD fluctuations (Gotts et al., 2013), head motion (Power et al., 2015), or other age-dependent factors (Cole et al., 2010). A series of control analyses were performed to ensure that the age-related increase of OFA-FFA RSFC was not caused by these confounding factors. First, the confounding effect of tSNR may arise from the use of adult-sized head coils on children (McKone et al., 2012). We compared tSNR in the resting-state run of each ROI between children and adults (Table 4). Children and adults showed comparable tSNR in all 4 ROIs (FFA: $t_{(37)} = 1.05$, $p = 0.30$; OFA: $t_{(37)} = 1.18$, $p = 0.25$; pFs: $t_{(37)} = 0.58$, $p = 0.57$; LO: $t_{(37)} = 0.66$, $p = 0.51$). Further, we recalculated the correlation between the OFA-FFA RSFC and age after controlling for the tSNRs in both the OFA and FFA and found that children's OFA-FFA RSFC increased with age (partial correlation $r = 0.48$, $p = 0.03$). In contrast, the LO-pFs RSFC did not increase with age after controlling out the tSNR of both the LO and pFs (partial correlation $r = 0.03$, $p = 0.89$). Therefore, the age-related increase of OFA-FFA RSFC was unlikely to be caused by the confounding effects of tSNR.

To investigate whether our results were confounded by head micromovements (Van Dijk et al., 2012; Power et al., 2012; Power et al., 2015), we calculated the mean FD for each participant (Van Dijk et al., 2012). We found that FD values did not differ between children and normal adults (children aged 7–10 vs adults: $t_{(25)} = 1.67$, $p = 0.11$; children aged 11–13 vs adults: $t_{(26)} < 1$), nor between children aged 7–10 and those aged 11–13 ($t_{(21)} = 1.08$, $p = 0.30$). Further, we recalculated the correlation between the RSFC and age after controlling for the FD, and the results remained unchanged. That is, children's OFA-FFA RSFC was positively correlated with age (partial correlation $r = 0.48$, $p = 0.02$), whereas LO-pFs RSFC did not increase with age (partial correlation $r = -0.28$, $p = 0.21$). Therefore, our results could not be accounted for by head micromovements.

In light of recent debate on global signal regression (Murphy et al., 2009; Fox et al., 2009; Saad et al., 2012; Gotts et al., 2013), we recomputed the RSFC using data preprocessed without global signal regression and obtained highly similar results. That is, children's OFA-FFA RSFC was positively correlated with age (Pearson's $r = 0.62$, $p = 0.002$; Spearman's $\rho = 0.63$, $p < 0.001$), whereas LO-pFs RSFC did not increase with age (Pearson's $r = 0.03$, $p > 0.05$; Spearman's $\rho = -0.04$, $p > 0.05$). Therefore, our results could not be ascribed to global signal regression; rather, the age-related increase of OFA-FFA RSFC may reflect the development of intrinsic properties of the face network.

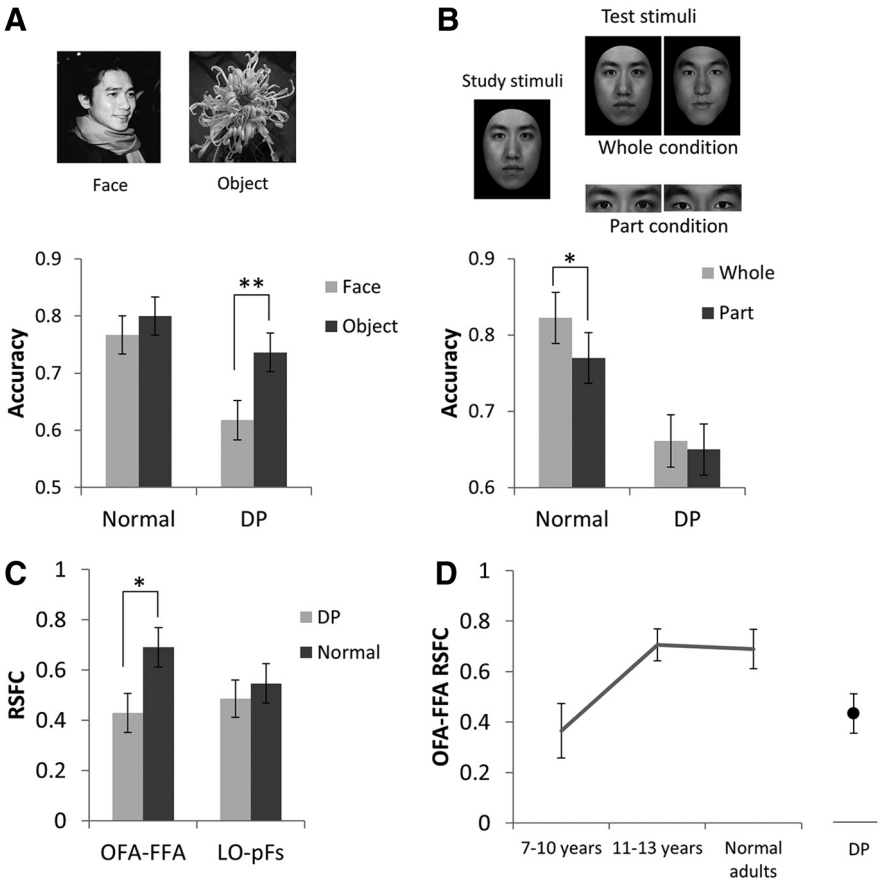

Figure 3. Deficits in behavioral performance and disruption of RSFC in DP. ***A***, Top, Example stimuli and trial types in the identification task on faces and objects. Participants reported the prespecified targets at the subordinate level: Chiu-Wai Leung (a famous Chinese movie star), chrysanthemum, pigeon, and jeep. Bottom, Accuracies of normal adults and DP subjects in the face- and object-identification tasks. ***B***, Top, Example stimuli and trial types in the whole-part task. Participants identified a face part of one individual (nose, mouth, or eyes) presented either in the context of the whole face or in isolation (part). Bottom, Accuracies of normal adults and DP subjects in the whole-part task. ***C***, Magnitude of OFA-FFA RSFC and LO-pFs RSFC in normal adults and DP subjects. ***D***, Magnitude of OFA-FFA RSFC in the DP subjects, children 7–10 years of age, children 11–13 years of age, and normal adults. Error bars indicate SEM. $^*p < 0.05$; $^{**}p < 0.001$.

Table 4. tSNR at each ROI for children and normal adults (mean ± SD)

	FFA	OFA	pFs	LO
Children	275.19 ± 78.37	284.68 ± 70.55	325.29 ± 71.45	246.76 ± 71.01
Adults	318.67 ± 175.09	329.55 ± 162.21	350.00 ± 186.13	268.00 ± 128.05

OFA-FFA RSFC is selectively disrupted in DP

Is OFA-FFA RSFC selectively disrupted in individuals suffering atypical development of face-specific recognition ability? To address this question, we tested a group of adult DP participants ($n = 17$), as well as age-matched normal adults ($n = 16$). DP subjects were selected according to standard procedures used in previous studies (Behrmann and Avidan, 2005; Duchaine and

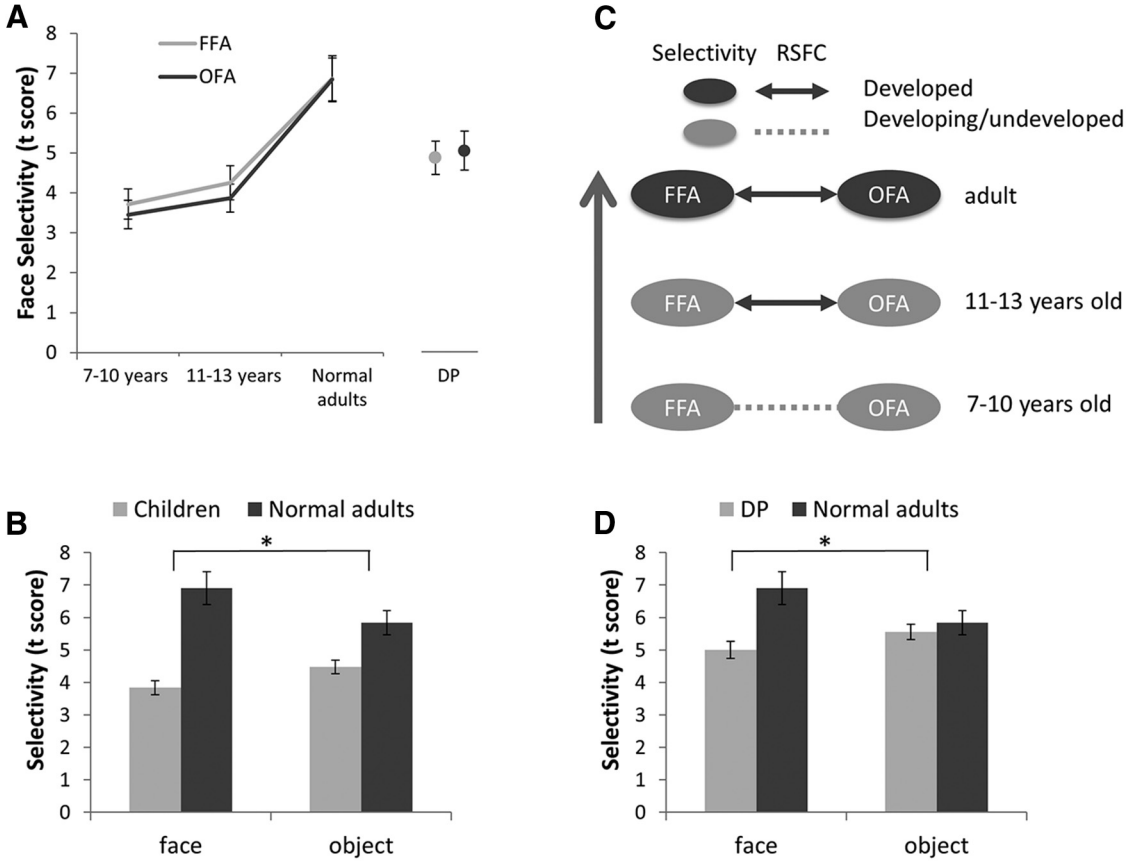

Figure 4. Different developmental trajectories of functional connectivity and face selectivity in the face system. ***A***, Face selectivity in the OFA and FFA in children 7–10 years of age, children 11–13 years of age, normal adults, and DP subjects. ***B***, Magnitude of face selectivity and object selectivity in children and normal adults. The OFA and FFA were averaged for face selectivity and the LO and pFs were averaged for object selectivity. ***C***, Schematic summary showed that the development the OFA-FFA RSFC preceded the development of face selectivity. For children 7–10 years of age, both the RSFC and face selectivity were developing. For children 11–13 years of age, the RSFC was comparable to adult levels, whereas face selectivity was still developing. ***D***, Magnitude of face selectivity and object selectivity in the DP subjects and normal adults. Error bars indicate SEM. *$p < 0.05$.

Nakayama, 2005), which are described in detail in the Materials and Methods. In particular, 50 individuals who reported severe deficits in face recognition in their daily activities were selected from 1512 college students as DP candidates. These DP candidates were then instructed to name Chinese celebrities based on photographs of their faces. The 19 candidates who scored 3 SDs below the mean of the normal controls were identified as DP subjects and 17 of them agreed to participate in the study.

Behaviorally, the DP subjects exhibited selective impairment in face recognition. As expected, in an identification task (Grill-Spector et al., 2004; Fig. 3*A*, top), the DP subjects were poorer at identifying familiar faces than at identifying three categories of familiar objects (i.e., birds, flowers, and cars; $t_{(16)} = 5.76$, $p < 0.001$), whereas normal controls showed equal performance ($t_{(14)} = 1.44$, $p = 0.17$; Fig. 3*A*, bottom). The selective deficit in face identification of the DP subjects was confirmed by a significant two-way interaction of stimulus category (faces vs objects) and participant group (DP vs normal control) ($F_{(1,30)} = 7.62$, $p = 0.01$). Further, the DP subjects were tested with a whole-part task (Tanaka and Farah, 1993; Pellicano and Rhodes, 2003; Fig. 3*B*, top). The whole-part effect (i.e., better recognition of a face part when in the context of the whole face than in isolation) was only observed in normal controls ($t_{(15)} = 2.23$, $p = 0.04$), but not in the DP subjects ($t_{(16)} = 0.42$, $p = 0.68$; Fig. 3*B*, bottom). This indicates that the deficits of DP may result from an inability to process faces as integrated wholes. In addition, child participants were also tested with the whole-part task. Neither the 7–10-year-old ($t_{(10)} = 0.91$, $p = 0.39$) nor the 11–13-year-old children ($t_{(12)} = 0.27$, $p = 0.79$) showed a significant whole-part effect. Moreover, the accuracies in both the part and whole conditions of the DP subjects were comparable to those of children 11–13 years of age (whole: $t_{(27)} = 0.93$, $p = 0.36$, part: $t_{(27)} = 0.97$, $p = 0.34$), but worse than normal adults (whole: $t_{(31)} = 3.32$, $p = 0.002$; part: $t_{(31)} = 2.49$, $p = 0.02$). These results suggest that the behavioral performance of the DP subjects in our whole-part task was comparable to that of children 11–13 years of age.

Next, we investigated whether OFA-FFA RSFC was selectively disrupted in the DP subjects. Consistent with previous findings (Avidan and Behrmann, 2009; Furl et al., 2011), the regions of interest (OFA, FFA, LO, and pFs) were successfully localized in most DP subjects and normal controls (for Talairach coordinates, see Table 3) except for one DP participant who did not show the left FFA and was excluded from further analysis. Critically, OFA-FFA RSFC in the DP subjects was significantly weaker than that of normal controls ($t_{(30)} = 2.37$, $p = 0.03$; Cohen's $d = 0.87$; Fig. 3*C*). In contrast, no significant difference in LO-pFs RSFC was observed between the DP subjects and normal controls ($t < 1$), indicating that the disruption of the RSFC in DP may be specific to the face system. In addition, there was no significant difference in FD values between normal adults and DP subjects ($t < 1$) and an analysis of covariance with FD as a covariate showed a significant group difference of OFA-FFA RSFC between the DP subjects and normal controls ($F_{(1,29)} = 5.65$, $p = 0.02$),

indicating that the group difference of OFA-FFA RSFC was not accounted for by head micromovements.

To further quantify the severity of the OFA-FFA RSFC disruption in DP, we compared OFA-FFA RSFC in the DP subjects with that of typically developing children (Fig. 3*D*). The comparison between the DP subjects and children showed that OFA-FFA RSFC in the DP subjects was comparable to that of children 7–10 years of age ($t_{(25)} = 0.49, p = 0.63$), but significantly weaker than that of children 11–13 years of age ($t_{(26)} = 2.63, p = 0.01$). That is, the DP subjects were at the same level of development as the children 7–10 years of age in terms of their OFA-FFA RSFC.

Next, we investigated whether the DP subjects demonstrated atypical RSFC-behavior relationship compared with typical adults. A study on the behavioral relevance of OFA-FFA RSFC in normal adults has revealed that its strength is positively correlated with face-specific identification and the whole-part effect (Zhu et al., 2011). In the DP subjects, we did not observe significant correlation between the OFA-FFA RSFC and behavioral performance in recognizing faces (face identification: $r = -0.32$, $p = 0.22$; whole-part effect: $r = -0.36$, $p = 0.17$). Similarly, the OFA-FFA was not associated with the whole-part effect for children ($r = -0.20$, $p = 0.39$). This result fits nicely with a recent study showing that, although there is positive correlation between behavioral performance in face recognition and white-matter connection local to the FFA in typical adults, this correlation is absent in DP subjects (Gomez et al., 2015).

We found that the development of OFA-FFA RSFC in the DP subjects was selectively disrupted, with its strength comparable to that of children 7–10 years of age. These results suggest that the impairment of face-specific recognition in DP may be caused by the arrested development of OFA-FFA RSFC. Next, we compared the developmental trajectory of OFA-FFA RSFC with that of the face selectivity in the OFA and FFA.

OFA-FFA RSFC develops earlier than face selectivity in the OFA and FFA

Previous studies have shown that the selectivity of face-selective regions increases with age (Scherf et al., 2007; Golarai et al., 2007; Golarai et al., 2010). Here, we compared the developmental trajectories of the RSFC and face selectivity. Three age groups of normal participants showed significant differences in face selectivity in the FFA ($F_{(2,38)} = 12.50, p < 0.001$) and OFA ($F_{(2,38)} = 18.64, p < 0.001$). *Post hoc* comparisons by Tukey's HSD test showed that (Fig. 4*A*) no significant difference existed between children 7–10 years of age and those 11–13 years of age in face selectivity (FFA: $p = 0.76$; OFA: $p = 0.82$); however, both groups showed significantly lower face selectivity than normal adults in the FFA (children aged 7–10 vs normal adults: $p < 0.001$; children aged 11–13 vs normal adults: $p = 0.001$) and OFA (children aged 7–10 vs normal adults: $p < 0.001$; children aged 11–13 vs normal adults: $p < 0.001$). Again, the increase in face selectivity of the FFA and OFA during development was unlikely to be accounted for by confounding factors such as head motion or tSNR. A significant two-way interaction ($F_{(1,37)} = 8.11, p = 0.007$) of group (children vs adults) and category of selectivity (faces vs objects: OFA and FFA were averaged for face selectivity and LO and pFs were averaged for object selectivity) indicated that the increase in face selectivity with age (Cohen's $d = 0.57$) is larger than that for object selectivity (Cohen's $d = 0.43$; Fig. 4*B*).

Although both OFA-FFA RSFC and face selectivity of each region increased with age, the developmental trajectories of these two measures were not at the same pace (Figs. 3*D*, 4*A*, and schematic summary in Fig. 4*C*). Critically, children 11–13 years of age showed adult levels of OFA-FFA RSFC, but not adult levels of face selectivity. That is, in the face-processing system, the interregional functional connectivity appears to mature earlier than the face selectivity of each component region.

The result that OFA-FFA RSFC matured earlier than face selectivity raised the intriguing possibility that the development of OFA-FFA RSFC may guide the development of face selectivity in the OFA and FFA. Consistent with this idea, given the deficit in OFA-FFA RSFC in the DP subjects, we expected a deficit of face selectivity in the DP subjects as well. Indeed, we found that face selectivity of both the FFA and OFA in the DP subjects was significantly weaker than in normal adults (FFA: $t_{(30)} = 2.96, p = 0.006$; OFA: $t_{(30)} = 2.61, p = 0.014$; Fig. 4*A*). Finally, the deficits in selectivity were restricted to the face-processing system because there was no significant difference in object selectivity between the DP subjects and normal adults in either the LO ($t_{(30)} = 0.45, p = 0.66$) or the pFs ($t_{(30)} = 0.69, p = 0.50$). This was further confirmed by a significant two-way interaction of group (DP vs normal adults) and category of selectivity (face vs object; $F_{(1,30)} = 5.57, p = 0.025$; Fig. 4*D*).

Discussion

In this study, we investigated whether the prolonged age-related improvement in face recognition performance reflected development of face-specific mechanisms or general cognitive factors. Behaviorally, we found that the face-specific recognition ability increased with age throughout childhood and into late adolescence. This is consistent with previous studies showing the prolonged domain-specific development of face recognition (Carey and Diamond, 1977; Lawrence et al., 2008; Germine et al., 2011; de Heering et al., 2012; Weigelt et al., 2014). Neurally, we found that the OFA-FFA RSFC increased until 11–13 years of age in typically developing children. Further, the OFA-FFA RSFC was disrupted in the DP subjects suffering from atypical developmental of face-specific recognition ability. In contrast, no age-related changes and no differences between DP and normal adults were observed for the RSFCs among object-selective regions. Finally, face selectivity in the OFA and FFA matured later than OFA-FFA RSFC did. Together, these findings demonstrated the prolonged development of both the ability to recognize faces and its specialized neural underpinnings and indicated that impaired face-specific recognition in DP may be ascribed to arrested development of the OFA-FFA RSFC. Therefore, our results support the hypothesis that the prolonged development of face recognition performance is face specific, not domain general.

A number of confounding factors of RSFC have been proposed in recent studies, such as head motion (Power et al., 2015), cardiac and respiratory noise (Shmueli et al., 2007; Birn et al., 2008; Chang and Glover, 2009), tSNR (McKone et al., 2012), and wakefulness state (Picchioni et al., 2013; Tagliazucchi and Laufs, 2014). We have conducted a series of control analyses to show that our findings could not be ascribed to confounding factors including head motion, global signal regression, tSNR, or interregional distance, thus providing convincing evidence for domain-specific development of the OFA-FFA RSFC. Future studies collecting the independent sleep, cardiac, and respiration measures will address the impacts of these confounding factors on RSFC more directly and more rigidly (Jo et al., 2010; Tagliazucchi and Laufs, 2014).

Our study underlines the pivotal role of OFA-FFA RSFC in the development of face recognition. Current neuroimaging studies

have conceptualized the face network as consisting of multiple anatomically discrete regions, with each performing different functions of face processing (Haxby et al., 2000). Synchronized spontaneous neural activity among these regions may facilitate signal propagation among them and enable them to work in concert for successful face recognition. Indeed, OFA-FFA RSFC can predict an individual's performance on face-processing tasks (Zhu et al., 2011), indicating the behavioral significance of OFA-FFA RSFC in face recognition. A recent study showed that white-matter connections adjacent to the FFA were consistently correlated with behavioral performance of face processing (Gomez et al., 2015). Extending these findings to development, the current study, for the first time, showed prolonged development of OFA-FFA RSFC until late childhood, which may drive the prolonged development of face-specific recognition ability. Consistently, late development of effective connectivity between the OFA and FFA during task state has been reported (Kadosh et al., 2011), whereas our study circumvented the problem that age-related changes in task-state measures may be accounted for by age differences in task performance, attention, or cognitive strategies (Church et al., 2010). Therefore, our study provides novel evidence for the face-specific development hypothesis (Carey and Diamond, 1977; Mondloch et al., 2002). Moreover, different functions being supported by different regions in face network suggests that disconnection may be a mechanism underlying prosopagnosia (Fox et al., 2008). Indeed, results from acquired prosopagnosia have indicated that interaction between the OFA and FFA is necessary for successful face identification (Rossion, 2008). Developmentally, our study showed that disrupted OFA-FFA RSFC accompanies poor face recognition in DP (see also Avidan et al., 2014). Although the result of normal children demonstrated prolonged development of the RSFC specific to the face network, the selective impairment in the RSFC of the face network in the DP subjects indicated interruption of normal developmental processes specific to faces. Therefore, the results of normal children and DP subjects provide complimentary and converging evidence for domain-specific development of the face network. Interestingly, extensive training of face discrimination in DP leads to an increased FC between the OFA and FFA during face viewing that accompanies improvements on face recognition (DeGutis et al., 2007). Together, these findings suggest the crucial role of typical development of OFA-FFA RSFC in the normal development of face recognition abilities.

Further, we found that OFA-FFA RSFC reached adult levels earlier than face selectivity in the OFA and FFA and face recognition performance. The prolonged development of face selectivity after late childhood observed here is consistent with previous studies showing an age-related increase in the selectivity of the FFA and OFA extending through childhood and into adolescence when the ROIs are defined either with fixed size (Golarai et al., 2007; Scherf et al., 2007; Peelen et al., 2009) or individually in size (Golarai et al., 2010). Together with the findings of the age-related increase in size of the FFA and OFA (Golarai et al., 2007; Scherf et al., 2007; Peelen et al., 2009; Golarai et al., 2010; Joseph et al., 2011; Haist et al., 2013), it seems that the development of face-selective regions manifests as an increase both in size and in face selectivity. The different paces in maturation suggest that the connectivity among face-selective regions may drive the development of regional selectivity and behavioral performance. It has been proposed that domain specificity in a cortical region is constrained by its pattern of connectivity with a network of regions processing the same domain (Mahon and Caramazza, 2011). Consistent with this, several studies in adults have shown that functional activity in face-selective regions can be predicted by its structural connectivity (Turk-Browne et al., 2010; Saygin et al., 2012). Extending these ideas to development, the interactive specialized framework proposes that, during development, the specialization of a region is shaped by the context of its connection patterns (Johnson, 2011). Specifically, at an early age, the functionality of cortical regions is poorly specified; therefore, they may be activated by a wide range of tasks even unrelated to faces. During development, strengthening of functional connectivity among face-selective regions may promote the propagation of neural information among these regions and tune up the functionality of these regions so that their activities become more selective to faces. Subsequently, the development of face selectivity in the OFA and FFA drives the later maturation of face-specific recognition. A recent development study shows that the age-related increase in FFA size is associated with age-related differences in its structural connectivity (Scherf et al., 2014). Taking this one step further, our results showed that the refinement of functional connectivity preceded the maturation of functional specialization of the face network, suggesting the possibility that the latter is perhaps the consequence of the former. In contrast, OFA-FFA RSFC was impaired in the DP subjects and, accordingly, they often show deficits in functional specialization in face-selective regions (Furl et al., 2011).

Why is the development of face-specific recognition and its specialized neural underpinnings prolonged compared with that of general object recognition? This may reflect the combined impact of both visual experience and genetic contributions. The role of visual experiences in sharpening face recognition ability has been revealed by studies of own-race bias (Meissner and Brigham, 2001); that is, individuals' recognition performance is tuned toward the faces of their own races. Similarly, extroverts are better at face recognition than introverts (Li et al., 2010), and individuals suffering DP often report avoidance and difficulties in social interactions (Yardley et al., 2008), suggesting a close link between face recognition ability and visual experience in social interaction. The increasing visual exposure to faces through childhood may gradually shape face recognition ability during development. On the flip-side of visual experiences, recent studies have shown the genetic contribution to face-specific recognition, providing evidence for "specialist genes" that specifically modulate face recognition (Wilmer et al., 2010; Zhu et al., 2010).

In sum, our study demonstrated prolonged development of face-specific recognition ability and its specialized neural underpinnings, which has profound implications. First, it will be interesting to see whether the prolonged development of other cognitive abilities, such as spatial navigation (Pine et al., 2002) and number sense (Halberda et al., 2012), is domain specific or domain general. Second, is the development of these cognitive abilities similarly guided by the development of connectivity within corresponding neural networks (Koyama et al., 2011; Vogel et al., 2013)? Third, atypical patterns of RSFC are often observed in neurodevelopmental disorders, including ADHD (Konrad and Eickhoff, 2010) and autism (Philip et al., 2012). The description of the development trajectory of the RSFC specific for these neurodevelopmental disorders and effective training methods to modulate their plasticity will be helpful for the diagnosis and treatment of the disorders. Finally, future studies on children DP subjects are needed to test the intriguing hypothesis of a sensitive period for the development of face-specific RSFC around the ages of 11–13 years; that is, the arrested development of face-specific RSFC during this age may result in impaired face recognition in DP.

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