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ORIGINAL ARTICLE

Self-Face Recognition Begins to Share Active Region in Right Inferior Parietal Lobule with Proprioceptive Illusion During Adolescence

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Abstract

We recently reported that right-side dominance of the inferior parietal lobule (IPL) in self-body recognition (proprioceptive illusion) task emerges during adolescence in typical human development. Here, we extend this finding by demonstrating that functional lateralization to the right IPL also develops during adolescence in another self-body (specifically a self-face) recognition task. We collected functional magnetic resonance imaging (fMRI) data from 60 right-handed healthy children (8–11 years), adolescents (12–15 years), and adults (18–23 years; 20 per group) while they judged whether a presented face was their own (Self) or that of somebody else (Other). We also analyzed fMRI data collected while they performed proprioceptive illusion task. All participants performed self-face recognition with high accuracy. Among brain regions where self-face-related activity (Self vs. Other) developed, only right IPL activity developed predominantly for self-face processing, with no substantial involvement in other-face processing. Adult-like right-dominant use of IPL emerged during adolescence, but was not yet present in childhood. Adult-like common activation between the tasks also emerged during adolescence. Adolescents showing stronger right-lateralized IPL activity during illusion also showed this during self-face recognition. Our results suggest the importance of the right IPL in neuronal processing of information associated with one's own body in typically developing humans.

Key words: functional magnetic resonance imaging, human development, proprioceptive illusion, right hemispheric dominance, self-face recognition

Introduction

The human right cerebral cortex has traditionally been considered the “non-dominant” hemisphere; yet, a growing body of evidence indicates that it is deeply involved in bodily recognition (Feinberg et al. 1990; Berlucchi and Aglioti 1997; Berti et al. 2005; Naito et al. 2005, 2016; Desmurget et al. 2009; Cignetti et al. 2014; Moro et al. 2016). Despite accumulating evidence for this role in the adult brain, little is known about when and how the brain develops such functional lateralization to the right hemisphere during typical development.

Within the right hemisphere, the inferior frontoparietal network seems to play particularly important roles in the recognition of one’s own body (Feinberg et al. 1990; Berti et al. 2005; Desmurget et al. 2009; Amemiya and Naito 2016; Naito et al. 2016). Recently, using a proprioceptive illusion task (see below), we demonstrated that adult-like right-hemispheric dominant use of the inferior parietal lobule (IPL) in this self-body recognition task (Naito et al. 2005) emerges during adolescence in the typically developing human brain (Naito et al. 2017). Since, the IPL is an important node in the inferior frontoparietal network of the adult brain (Desmurget et al. 2009; Naito et al. 2016), our developmental finding raises the possibility that the right IPL (most likely in concert with the right inferior frontal cortices) implements functions related to self-body recognition during human development. In the present study, we further demonstrate that such right-hemispheric lateralization also develops during adolescence in another type of self-body recognition task, that is, a self-face recognition task.

One’s own face represents one of the most distinctive and unique features of one’s own physical appearance and, as such, it symbolizes oneself (at least bodily self) to an even greater extent than might be expected. Thus, visual self-face recognition directly contributes to recognition (awareness) of the bodily self as distinct from others (Gallup 1982, 1998; Brooks-Gunn and Lewis 1984; Lewis et al. 1989; Gallup et al. 2014). In this sense, a task that requires recognition of one’s own face as distinct from those of others (self-face recognition) can also be considered a self-body recognition task. A series of neuroimaging studies in adults have repeatedly shown that the right inferior frontoparietal cortices and bilateral regions of the inferior occipitotemporal cortices are activated during self-face recognition tasks. Importantly, these activations are irrespective of familiarity with the others’ faces presented as controls (Uddin et al. 2005; Sugiura et al. 2006, 2008; Kaplan et al. 2008; Morita et al. 2008, 2014, 2017; Scheepers et al. 2013; Hu et al. 2016). In addition, many previous studies have highlighted the importance of the right cerebral hemisphere in self-face recognition based on developmental and clinical evidence (Feinberg and Shapiro 1982; Spangenberg et al. 1998; Feinberg 2000; Breen et al. 2001; Keenan et al. 2001; Feinberg and Keenan 2005; Uddin et al. 2006; Morin 2011; Yun et al. 2014).

In the present study, we measured blood oxygenation level-dependent signals with functional magnetic resonance imaging (fMRI) in 60 right-handed healthy children (aged 8–11 years), adolescents (aged 12–15 years), and young adults (aged 18–23 years; 20 per group) during a self-face recognition task. We presented visual images of the participant’s own face (Self) and those of others (Others) and asked the participants to judge whether the face they saw was their own or someone else’s. Thus, by identifying brain regions that are significantly more activated when the participants view their own faces than when they view faces of others, we can identify brain activity associated with self-face recognition (recognition of one’s own face as distinct from those of others). In this study, we first identify self-face-related activity (Self vs. Others) in the whole brain in each group and demonstrate developmental change of self-face-related activity and emergence of its right-side dominant activity.

The proprioceptive illusion and self-face recognition share some commonalities, including that the brain processes sensory information associated with one’s own body, although the brain must process muscle spindle kinesthetic signals derived from one’s own limb during the proprioceptive illusion (Goodwin et al. 1972; Roll and Vedel 1982; Naito et al. 2016) and visual information about one’s own face during self-face recognition (Morita et al. 2017). Indeed, we have shown in the adult brain that both self-face recognition and the proprioceptive illusion commonly activate the IPL and inferior frontal cortices, which are likely connected by the inferior branch of the superior longitudinal fasciculus tract (SLF III; Thiebaut de Schotten et al. 2012) in a right-dominant manner (Morita et al. 2017). This indicates that the self-face recognition and the proprioceptive illusion both require components of neuronal processing lateralized to the right inferior frontoparietal cortices in the adult brain. In the present study, we further examined the developmental course by which the adult-like common use of these cortices is achieved.

As described, if emergence of right-lateralized IPL activity is generally important in the development of self-body recognition, we should observe commonalities between self-face recognition and the proprioceptive illusion in the development of right-side dominant use of the IPL. Subsequently, we expect right-side dominance of IPL activity emerges during adolescence in self-face recognition, as we observed with the proprioceptive illusion (Naito et al. 2017). If this is the case, another important question is how right-side dominance develops in self-face recognition. In the case of the proprioceptive illusion, we have shown that the IPL is recruited bilaterally during childhood and its right-side dominance progresses during adolescence along with age-dependent suppression of left IPL activity (Naito et al. 2017). This means that the right IPL is already involved in proprioceptive illusion during childhood but its right-side dominance emerges during adolescence. Thus, it is important to know whether this type of developmental change (from bilateral to right-lateralized) is also observable in self-face recognition. To address this issue, we carefully examined the developmental changes in the right and left IPL activity in self-face recognition.

After this careful investigation, we further tested whether self-face recognition begins to share the right IPL region active during the proprioceptive illusion in adolescence or even before (during childhood). Here, we also investigated whether the right IPL region activated in both of these tasks shows right-lateralized brain activity and whether the degree of right-lateralization of IPL activity in self-face recognition is associated with that in the proprioceptive illusion.

In the present study, we also conducted fMRI while the same participants performed a proprioceptive illusion task (Naito et al. 2017). In this task, the blindfolded participants experienced a proprioceptive illusion of flexion of the right stationary wrist, which is elicited by muscle spindle afferent input recruited during tendon vibration of the relaxed wrist extensor muscles. We used cytoarchitectonic probability maps and a tract probability map for the SLF III of the human brain to anatomically identify activated brain regions, and for the anatomical definition of region-of-interest (ROI).

Materials and Methods

Participants

We recruited 20 healthy right-handed children (CH; mean age: 9.6 ± 0.9 years; range: 8 years 7 months–11 years 3 months), 20 adolescents (ADO; mean age: 13.3 ± 0.7 years; range: 12 years 8 months–15 years 0 months), and 20 young adults (AD; mean age: 20.9 ± 1.4 years; range: 18 years 10 months–23 years 7 months). In each group, there were 10 male and 10 female participants. All participants performed both a self-face recognition task and a proprioceptive illusion task (Naito et al. 2017). We confirmed handedness with the Edinburgh Handedness Inventory (Oldfield 1971) and ensured that no participants had a history of neurological or psychiatric disorder based on self-report and the reports from their legal guardians.

The study protocol was approved by the ethics committees of the University of Fukui and the National Institute of Information and Communications Technology. We explained the details of the study to participants before the start of the experiment, after which participants provided written informed consent. In the case of the children and adolescents, we also obtained written informed consent from their legal guardians. The study was carried out following the principles and guidelines of the Declaration of Helsinki (1975).

Materials

Before the fMRI experiment, using a digital camera (FinePix F600EXR, Fujifilm Corporation), we photographed each participant (without glasses) in front of a black background, with all participants wearing the same black t-shirt. We took 15 pictures of the face of each participant with no emotional expressions (see e.g., Supplementary Fig. 1). These pictures were used in the Self trials (see below). We also took similar pictures of another 18 people who did not participate in the fMRI experiment, and these were used in the Others trials. Pictures of Others were taken in 6 age-matched persons (3 males and 3 females) for each group (CH, ADO, and AD). Before the experiment, we confirmed that these people were unfamiliar to all participants. Face images obtained from participants and unfamiliar people were cropped to the same size and converted to gray scale (Fig. 1).

Self-Face Recognition Task

Before the fMRI experiment, participants experienced a self-face recognition task outside the scanner to familiarize them with the task before they entered the MR room. When the participants were lying in the MRI scanner, their heads were immobilized using sponge cushions and their ears were plugged. We asked the participants to relax their entire body without producing unnecessary movements and to not think about anything that was not relevant to the task.

We presented face images to the participants, who viewed them via a mirror placed in front of their eyes. To control visual presentation, we used Presentation software (Neurobehavioral systems Inc.). Participants completed 2 experimental runs, each of which lasted for 3 min 20 s. In each run, participants completed 15 Self trials (presentation of each self-face image) and 15 Others trials (presentation of images of others' faces). Each run also included 6 null events (see below). To prepare the 15 images of others' faces, we randomly selected 5 face images from each of 3 sex- and age-matched people who were unfamiliar to the participant. The order of Self and Others trials and the timing of null events was predetermined within a run in order to maximize the efficiency of detecting activity difference between Self and Others trials, and of estimating brain activity in each Self and Others trial (Dale 1999; Friston et al. 1999; see details in Morita et al. 2008). We prepared 2 sets of experimental runs, which were used consistently across participants.

In a Self or Others trial, we first presented a face image at the center of the screen for 2.5 s (Fig. 1). This was immediately followed by presentation of a selection screen for 2.5 s (selection period), during which participants reported whether the face they saw was their own or that of another person. This procedure is typical of self-face recognition tasks, and we have used the same task in our previous study (Morita et al. 2017). After the selection period, we presented the next face image. Thus, the inter-trial interval was 5 s. In a null event, we simply presented a gray screen for 5 s. No face image was presented and no particular response was required, and thus this period can be considered a baseline period in a run. Each run also

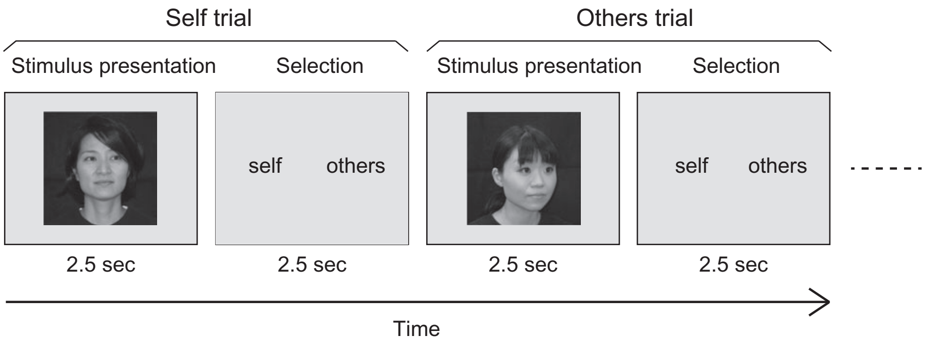


Figure 1. Example stimuli from the self-face recognition task. In each trial, either a self-face (Self) or the face of an unfamiliar person (Others) was presented for 2.5 s. Participants were asked to judge whether the face they saw was their own or anothers' by pressing 1 of 2 buttons, using their right index or middle finger during the selection period.

included a 10 s period before the start of the first trial and another 10 s period after the end of the last trial.

On the selection screen, Japanese text for "self" and "others" appeared, as 2 labels side by side, in light gray (Fig. 1). The location (i.e., right or left) of the 2 words was counterbalanced across participants. The participants were instructed to judge whether the face stimulus was their own or others-face by pressing 1 of 2 buttons using their right index or middle finger. Thus, the task required the participants to pay equal attention to the appearance of self-face images and others-face images. We used an MRI-compatible 2-button response device (Current Designs Inc.). The participants always pressed the left button with their index finger and the right button with their middle finger. The button to be pressed was counterbalanced across participants, with half pressing the left button for "self," while the remaining half pressed the right button for "self." We also instructed the participants that they could make a second response within the selection period if they made an incorrect response. The number of second responses was very small (0.17 out of a total of 60 trials [0.28%] on average across participants).

Figure 1 shows an example of the task. Here, when the face was the participant's own, she pressed the left button using the right index finger, while when it was another's face, she pressed the right button using the right middle finger. To indicate the selection she made, the color of the selected item changed to dark gray when the assigned button was pressed (not shown in figure).

The participants were instructed not to press any buttons when the face stimulus appeared, but to press the button when the selection screen appeared (selection period). Thus, in the present study, we could not evaluate reaction times. However, by adopting this experimental design, we expected to reduce body motions often accompanied when faster reactions are required, especially in children. Furthermore, we could temporally dissociate the cognitive neuronal processes underlying self-face recognition from those associated with the motor component (button press), which is suitable for a rapid event-related paradigm, wherein efficiency is highly dependent upon the temporal pattern of stimulus presentation (Dale 1999; Friston et al. 1999). We recorded the button press using Presentation software.

We first calculated the correct response rate by pooling data obtained for both Self and Others trials. This was done for each participant in each group. In the statistical evaluation, we used one-sample *t*-tests after arcsine transformation of percent values. We tested whether the correct rate in each group was significantly different from chance (50%; two-tailed). We also calculated the correct rate in Self and Others trials separately for each participant in each group. For statistical evaluation, after arcsine transformation of percent values, we performed two-way analysis of variance (ANOVA) including one between-subject factor (group [3]: CH, ADO, and AD) and one within-subject factor (trial [2]: Self and Others). For further statistical evaluation of between-group differences, we used Bonferroni's correction for multiple comparisons.

Proprioceptive Illusion Task

All participants also performed a proprioceptive illusion task during the fMRI experiment (Naito et al. 2017), with the order of the 2 tasks counterbalanced across participants. Details of this task have been described elsewhere (Naito et al. 2017). Each participant completed one experimental run of this task (3 min 25 s), which comprised 6 tendon-vibration epochs, each of which lasted for 15 s. The tendon-vibration epochs were separated by 15 s baseline periods.

During each tendon-vibration epoch (Tendon), we vibrated the tendon of the extensor carpi ulnaris muscle of the right wrist at 110 Hz, which elicited an illusory flexion of the stationary right hand (Naito et al. 2016). This illusion is elicited because the tendon vibration excites the muscle spindle afferent fibers (Goodwin et al. 1972; Roll and Vedel 1982), and the brain receives and processes the proprioceptive (kinesthetic) inputs. The tendon vibration excites not only the muscle spindle receptors but also the cutaneous vibro-tactile receptors. Thus, to evaluate the effect in the brain that is purely associated with the proprioceptive processing of muscle spindle afferent inputs, we vibrated the skin surface over a nearby bone (i.e., the processus styloideus ulnae of the hand just beside the tendon) using the same stimulus during the baseline periods (Bone). Validity of this control has been discussed elsewhere (Naito et al. 2017). The run also included a 15 s period before the start of the first epoch and another 15 s period after the end of the last epoch. We performed the bone-vibration during these periods so that the stimulus was applied during all baseline periods. By examining the increase in brain activity during the tendon-vibration epochs (Tendon) compared with the activity during the baseline periods (Bone) and then eliminating the effect of cutaneous vibro-tactile processing, we were able to identify brain activity (illusion-related activity) that is purely associated with the proprioceptive processing of muscle spindle afferent inputs that essentially contributes the generation of somatic sensation (kinesthetic illusion) of the right wrist flexion.

fMRI Data Acquisition

Methods of fMRI data acquisition were identical to those in our previous proprioceptive illusion study (Naito et al. 2017). In the self-face recognition task, functional images were acquired using T2*-weighted gradient echo-planar imaging (EPI) sequences obtained using a 3-Tesla MRI machine (Discovery MR750; GE Healthcare; Milwaukee, WI) and a 32-channel array coil. We collected 80 volumes per run (slice number = 40; slice thickness = 3.5 mm; inter-slice thickness = 0.5 mm; repetition time [TR] = 2500 ms; echo time [TE] = 30 ms; flip angle = 83 degrees; field of view [FOV] = 192 × 192 mm; voxel size [x, y, z] = 3 × 3 × 4 mm).

Imaging Data Analysis

Pre-Processing

We conducted the same pre-processing procedure used in our previous proprioceptive illusion study (Naito et al. 2017). To eliminate the effects of unsteady magnetization in the self-face recognition task, we discarded the first 4 EPI images in each fMRI run before the first trial started. Imaging data were analyzed using SPM 8 (The Wellcome Department of Cognitive Neurology, London, UK) implemented in Matlab (Mathworks, Sherborn, MA).

Initially, EPI images were realigned to the first image and then to the mean image. We first calculated mean displacement of each image from the first image for each run with each participant. All participants had less than 3 mm of cut-off maximum motion in every plane (*x*, *y*, and *z*) during each run, and thus we excluded no data from the following analyses. When we calculated the mean across 2 runs for each participant, and computed the average displacement across participants in each group, we found in the CH group that the average displacements were 0.07 mm (range: 0.02–0.21 mm), 0.13 mm (0.02–0.34 mm), and 0.3 mm (0.08–0.78 mm) in the *x*-, *y*-, and *z*-axes, respectively.

In the ADO group, these values were 0.06 mm (0.02–0.28 mm), 0.12 mm (0.02–0.31 mm), and 0.13 mm (0.05–0.37 mm). In the AD group, they were 0.04 mm (0.01–0.09 mm), 0.06 mm (0.01–0.19 mm), and 0.08 mm (0.04–0.17 mm).

The average displacement in the AD group was significantly smaller than that in the CH group in every axes direction (corrected $P < 0.05$) and that in the ADO group was significantly smaller than that in the CH group only for the z-axis direction (corrected $P < 0.05$). However, even though we found significant group differences, all of the participants showed substantially smaller displacement than the cut-off criteria. Thus, we think that the group difference is such a small displacement that it is not meaningful.

The realigned images were normalized to the Montreal Neurological Institute (MNI) space (Evans et al. 1994). By comparing functional activation foci in children and adults within a common stereotaxic space, Kang et al. (2003) provided an empirical validation of normalization for analysis of fMRI data obtained from school-aged children. Finally, the spatially normalized functional images were filtered using a Gaussian kernel with a full-width-at-half-maximum (FWHM) of 4 mm along the x-, y-, and z-axes.

Analysis of Self-Face-Related Activity in Each Group

After pre-processing, we first evaluated self-face-related activity with a general linear model (GLM; Friston et al. 1995; Worsley and Friston 1995) for each participant. The design matrix contained 2 trial-related regressors for Self and Others trials, as well as a regressor for button pressing, each of which was convolved with a canonical hemodynamic response function. To correct for residual motion-related variance after realignment, the 6 realignment parameters were also included in the design matrix as regressors of no interest.

We first generated a contrast image to examine brain regions that show self-face-related activity (Self vs. Others) in each participant (single-subject analyses). In this contrast, the effect of motor preparation should be eliminated because the participants had to consistently prepare the button press for both Self and Others trials. In addition to this contrast image, we also generated an image to examine brain regions that have increased brain activity compared with baseline in Self trials (Self > baseline) and Others trials (Others > baseline; Supplementary Fig. 2). The contrast images from all participants were entered into a second-level random effects group analysis (Holmes and Friston 1998). One-sample *t*-tests were conducted for Self versus Others, Self > baseline and Others > baseline in each group separately.

In the second-level analysis, we first generated a voxel-cluster image with a cluster-defining height threshold of $P < 0.001$ uncorrected in each group. For statistical inference, we used an extent threshold of $P < 0.05$ at the cluster level after correction for multiple comparisons with the family-wise error rate (FWE) in the whole brain. We consistently used this conservative threshold in the subsequent fMRI analyses in the present study, except for a conjunction analysis (see below). To identify self-face-related activity (Self vs. Others), we used the image Self > baseline (uncorrected height threshold of $P < 0.05$) as an inclusive mask. Using this mask image at the liberal threshold, we ensured that observed self-face-related activation is true activation rather than pseudo-activation caused merely by deactivation in the Others trials.

To identify anatomical regions of activation, we referred to the cytoarchitectonic probability maps in the MNI standard brain of the SPM anatomy toolbox v1.8 (Eickhoff et al. 2005).

Analysis of Illusion-Related Activity in Each Group

After pre-processing, we also identified illusion-related activity with a general linear model for each participant. The design matrix contained a boxcar function for the tendon-vibration (illusion) epoch, which was convolved with a canonical hemodynamic response function. To correct for residual motion-related variance after realignment, the 6 realignment parameters were also included in the design matrix as regressors of no interest. We constructed a contrast image to examine brain regions showing illusion-related activity (Tendon vs. Bone [baseline]). Details of this analysis have been reported elsewhere (Naito et al. 2017). In the present study, we used this individual image in the analyses of common brain activations across the tasks.

Comparisons of Self-Face-Related Activity Between Groups

To examine brain regions that show the developmental changes in self-face-related activity, we conducted comparisons between the groups. We first compared self-face-related activity in the AD group with that in the CH group by examining (Self_{AD} vs. $\text{Others}_{\text{AD}}$) versus ($\text{Self}_{\text{CH}}$ vs. $\text{Others}_{\text{CH}}$). In this comparison, we used the image Self_{AD} (Self > baseline, uncorrected height threshold of $P < 0.05$ in the AD group) as an inclusive mask. Using this masking procedure, we ensured that any self-face-related activation that we observed to be greater in the AD group was true activation rather than pseudo-activation caused merely by self-face-related deactivation in the CH group. We also performed 5 other possible comparisons between any 2 given groups. In these group comparisons, we used the same FWE-corrected extent threshold of $P < 0.05$ in the entire brain for a voxel-cluster image generated with a cluster-defining height threshold of $P < 0.001$ uncorrected in each comparison.

Among brain regions that showed significantly greater self-face-related activity in the AD group compared with the CH group (Fig. 3A), we confirmed the presence of activity in the right IPL, posterior part of inferior frontal gyrus (IFG) (area 44) and inferior temporal gyrus (ITG), and in the left inferior occipital gyrus (IOG) as reported in a previous meta-analysis of adult data (Hu et al. 2016). This indicated the essential importance of these regions in various self-face recognition tasks. Subsequently, we focused on these regions and examined the development of self-face-related activity in these regions from childhood to adulthood by carefully checking the activity changes in Self and Others trials separately (Fig. 3B). The meta-analysis (Hu et al. 2016) provided MNI coordinates of activation peaks for each region ([x, y, z] = [57, −23, 38] for the right IPL (area PFt), [50, 8, 26] for the right area 44, [48, −58, −12] for the right ITG, and [−46, −61, −14] for the left IOG). We extracted parameter estimates from a sphere 8 mm in radius around each peak in each participant. This was completed separately for Self and Others trials. We then calculated the average parameter estimates across participants in each group. This approach (extracting data from independently defined brain regions) may allow us to avoid the double dipping problem (Kriegeskorte et al. 2009).

In this analysis, we found a specific result in the right IPL. In this region, activity did not increase in the Others trials throughout the entire developmental course (Fig. 3B), while activity in other brain regions did increase in Others trials. To statistically evaluate whether there was no significant increase in right IPL activity in Others trials throughout the developmental course, we performed a one-sample *t*-test by pooling right IPL activity data (parameter estimate) obtained from all participants across groups ($df = 59$). We tested whether activity increase (or decrease) was significantly different from zero (two-tailed). The same t-test was also performed for the other 3 brain regions. Eventually, we corrected P-values for the 4 comparisons (4 brain regions; see above) using Bonferroni correction.

These analyses revealed that right IPL activity did not increase in Others trials in any group, while activity gradually increased from childhood to adulthood in Self trials. Subsequently, we searched for brain regions across the entire brain in which activity increased in Self trials from childhood to adulthood but which showed absolutely no increase in Others trials throughout this developmental course. We examined the contrast of Self $_{AD}$ versus Self $_{CH}$ with an exclusive mask. We used an image of brain regions where activity increased in Others trials (Others$_{AD}$ + Others$_{ADO}$ + Others$_{CH}$; uncorrected height threshold of $P < 0.05$). Thus, using this exclusive mask, we could detect brain regions where activity increased in Self trials from childhood to adulthood by excluding brain regions where activity increases in Others trials in either group. In this analysis, we used the same FWE-corrected extent threshold of $P < 0.05$ across the entire brain for a voxel-cluster image generated with a cluster-defining height threshold of $P < 0.001$ uncorrected.

Evaluation of Hemispheric Dominance of Self-Face-Related Activity in Each Group (Flip Analysis)

We examined hemispheric dominance in self-face-related activity by adopting an approach employed by Shulman et al. (2010), and used the same analysis methods performed in our previous proprioceptive illusion study (Naito et al. 2017). In this analysis, during pre-processing, the original EPI images obtained from each participant were first flipped across the midline to generate left-right reversed images (flipped EPI images). These flipped images were then realigned and normalized to MNI space (Evans et al. 1994). Thus, the right hemisphere was transformed in the best-fitting manner to the left hemisphere and vice versa. Finally, the normalized images were spatially smoothed using a 4-mm FWHM isotropic Gaussian kernel.

For each participant, in addition to the original GLM built for the analysis of the original EPI images (see above), we also constructed a second GLM for the flipped EPI images. We generated 2 contrast images showing self-face-related activity (Self vs. Others) obtained from the original GLM and from the second (flipped) GLM. In the second-level group analysis, we performed a paired t-test using these images from all participants, and for each group. This analysis allowed us to perform voxel-wise comparisons between the original and flipped images in MNI space, which enabled us to perform a direct comparison between left- and right-hemispheric activation patterns in a more anatomically precise manner.

In this analysis, we also used the same FWE-corrected extent threshold of $P < 0.05$ across the entire brain for a voxel-cluster image generated with a cluster-defining height threshold of $P < 0.001$ uncorrected in each group. Here, we used the self-face-related activity image obtained from the original image (height threshold of $P < 0.05$ uncorrected) as an inclusive mask. Using this mask image, we ensured that observed lateralized activation is true activation (Self > Others) rather than pseudo-activation caused merely by self-face-related deactivation (Others > Self) in the corresponding brain regions of the opposite hemisphere.

Among brain regions showing significant right-sided dominance in the AD group (Fig. 4A), the right IPL, area 44, anterior IFG, and ITG have also been reported in the meta-analysis of adult data (Hu et al. 2016). This also indicates the essential importance of these regions in various self-face recognition tasks. Thus, we focused on these regions and examined how right-lateralized self-face-related activity develops in these regions from childhood to adulthood. We carefully investigated self-face-related activity obtained from these regions and from corresponding regions in the left hemisphere (Fig. 4B). The previously published meta-analysis (Hu et al. 2016) provided MNI coordinates of activation peaks for each region ($[x, y, z] = [57, −23, 38]$ for the right IPL (area PFt), $[50, 8, 26]$ for the right area 44, $[46, 37, 9]$ for the right anterior IFG, and $[48, −58, −12]$ for the right ITG). As for the right hemisphere, we extracted parameter estimates from a sphere 8 mm in radius around each peak in the original contrast (Self vs. Others) image. By adopting this approach, we avoided the double dipping problem. As for the left hemisphere, data were extracted from corresponding regions in the flipped (left-right reversed) contrast images for each region in each participant, and we calculated the average parameter estimate across participants in each group.

Common Brain Activation Between Self-Face Recognition and Proprioceptive Illusion

To test when self-face recognition begins to share the same active region in the right IPL as the proprioceptive illusion, we performed a conjunction analysis (Price and Friston 1997). This analysis allows us to identify brain regions commonly activated in both of the 2 tasks. Even though each task placed different demands on different sensory modalities, we were able to conduct this analysis, as demands on different sensory modalities do not necessarily have to be matched in conjunction analysis (Price and Friston 1997).

Two contrast images (Self vs. Others and Tendon vs. Bone) were obtained from each participant and used in the second-level group analyses. We generated a voxel-cluster image with a cluster-defining height threshold of $P < 0.001$ uncorrected. For statistical evaluation, we used a FWE-corrected extent threshold of $P < 0.05$. In this evaluation, we used a ROI approach (small volume correction) because we had an *a priori* anatomical hypothesis regarding the brain regions likely to be connected by the right SLF III. In our previous study of adults, we used data obtained from almost the same participants (Morita et al. 2017) and found that the inferior frontoparietal cortices that are likely connected by the SLF III in the right hemisphere are commonly activated both in self-face recognition and in proprioceptive illusion tasks. To define the ROI, we used a 50% probability map for the SLF III in the right hemisphere obtained from 47 adult individuals (aged 22–71 years; Parlatini et al. 2017). Detailed information about this map has been reported elsewhere (Morita et al. 2017). Even though this map is obtained from the adult brain, we used this map in MNI space to indicate putative right SLF III regions in the adolescent brain, as an equivalent adolescent map is not currently available.

To further examine whether the right IPL region commonly activated in both tasks corresponds to a region showing consistently right-lateralized self-face-related activity and right-lateralized illusion-related activity in adolescents, we performed a Boolean intersection analysis. We depicted a simple overlapping region (with no statistical evaluation) between significant right-lateralized self-face-related activity (Fig. 4A) and significant right-lateralized illusion-related activity (please see Fig. 2A in Naito et al. 2017) in the ADO group (Fig. 5A, right panel). To determine the significant right-lateralized illusion-related activity, we also used an extent threshold of $P < 0.05$ FWE corrected

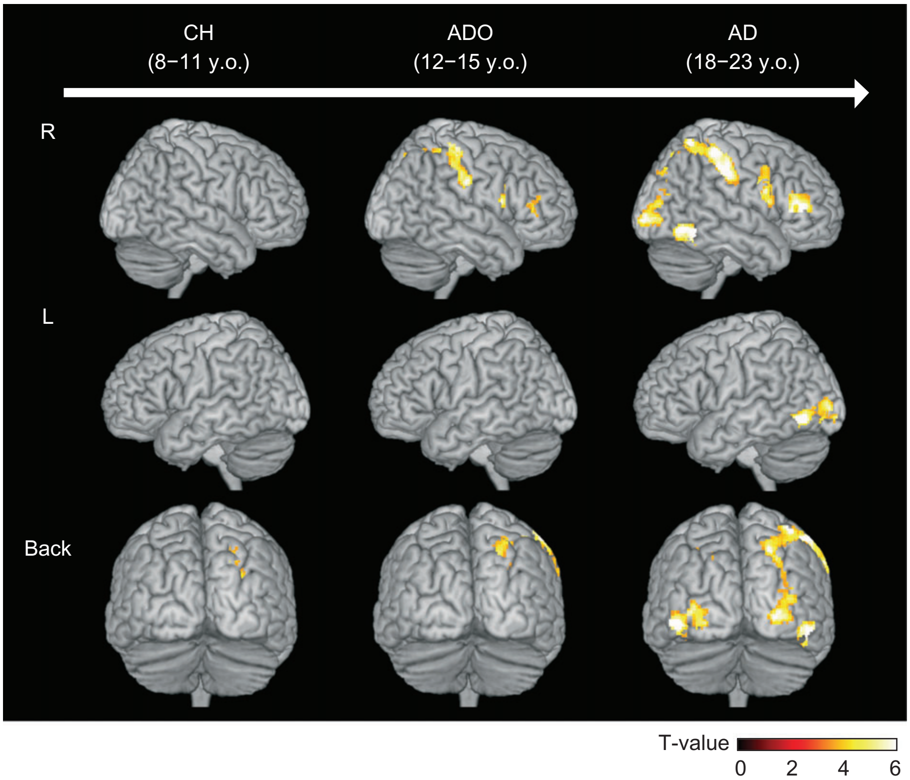


Figure 2. Brain regions that showed self-face-related activity (Self vs. Others) in each group. In each panel, brain activations are rendered onto the MNI standard brain. Adult-like self-face-related activity emerged in the right inferior frontoparietal cortices during adolescence. The left inferior frontoparietal cortices were consistently silent across all groups. The color bar at the bottom right indicates t-values. R, right hemisphere; L, left hemisphere; Back, back view; CH, children; ADO, adolescents; AD, adults; MNI, Montreal Neurological Institute.

across the entire brain for a cluster image generated with a cluster-defining height threshold of $P < 0.001$ uncorrected in the flip analysis (see above).

Finally, we examined whether the degree of right-lateralization of IPL activity in self-face recognition is associated with that in the proprioceptive illusion in adolescents. To define the search volume, we used adult data to avoid the double dipping problem. In the adult brain (Morita et al. 2017), the IPL region showing right-lateralized self-face-related activity (peak coordinates: 54, −24, 44) overlapped with the region showing right-lateralized illusion-related activity (54, −24, 38). The mean coordinates between these 2 peaks are (54, −24, 41). Therefore, we extracted parameter estimates from a sphere 8 mm in radius around this peak and also from that around the corresponding peak in the left IPL. Next, we subtracted the left IPL value from the right IPL value to evaluate the degree of right-lateralization of IPL activity. This was done for each participant in the ADO and CH groups, and for self-face recognition and for proprioceptive illusion separately. Finally, we examined positive correlations of the degree of right lateralization of IPL activity between self-face recognition and proprioceptive illusion in the ADO and CH groups separately.

Results

Behavioral Results

All participants performed the self-face recognition task with high accuracy. Overall, the mean (±standard deviation) correct response rates were 99.6 ± 0.9%, 99.7 ± 0.7%, and 97.7 ± 3.3% in the AD, ADO, and CH groups, respectively. A one-sample t-test revealed that the correct rates were significantly higher than chance level (50%) in all groups ($t = 53.5$, 60.2, and 24.3 for the AD, ADO, and CH groups, respectively; $df = 19$; $P < 0.001$ in all groups).

When we analyzed the correct rate in Self and Others trials separately, we found slightly higher erroneous responses in the CH group, especially in the Others trial. The mean correct rates in Self trials were 99.8 ± 0.8%, 99.7 ± 1.0%, and 98.8 ± 2.2% in the AD, ADO, and CH groups, respectively. Likewise, the mean correct rates in the Others trials were 99.3 ± 1.7%, 99.7 ± 1.0%, and 96.5 ± 5.5%, respectively. Two-way ANOVA showed a significant main effect of group ($F[2, 57] = 6.36$, $P < 0.01$). Further analyses using Bonferroni's correction for multiple comparisons revealed that the correct rate in the CH group was significantly lower than those in the other 2 groups ($P < 0.05$). The relatively larger number of erroneous responses in the CH group especially in the Others trials might contribute to the lower correct rate in this group. The ANOVA also showed a significant main effect of trial ($F[1, 57] = 4.49$, $P < 0.05$). This means that the correct rate in Self trials (percentage of "self" responses to self-face) was higher than that in Others trials (percentage of "others" responses to others' faces).

Self-Face-Related Activity in Each Group (Self vs. Others)

Patterns of self-face-related activity were different across groups, though some similarities were also observed between groups (Fig. 2). Activation peaks for each active-voxel cluster in each group are presented in Table 1.

Table 1 Significant self-face-related activity (Self vs. Others) in each group

Clusters	Size	x	y	z	t-value	Area
Children						
Right hemisphere						
Superior occipital cluster	169	28	−64	28	7.36	SOG
Adolescents						
Right hemisphere						
Anterior IFG cluster	135	42	36	4	5.53	IFG
		46	42	16	4.10	MFG
Area 44 cluster	163	54	10	14	6.10	Area 44
		38	6	16	6.07	Insula
		42	2	24	4.09	IFG
IPL cluster	373	58	−20	30	6.29	Area PFt
PPL cluster	538	30	−50	52	6.02	Area 7PC
		32	−46	42	5.96	SPL
		26	−58	54	5.91	Area 7A
		36	−44	52	5.55	Area 2
		22	−68	46	5.06	SOG
Adults						
Right hemisphere						
Anterior IFG cluster	477	42	36	8	9.68	IFG
		52	30	6	6.38	Area 45
Area 44 cluster	467	44	2	28	8.98	Precentral gyrus
		52	8	24	7.66	Area 44
		54	8	42	4.30	Area 6
Parieto-occipital cluster	1690	38	−56	64	9.44	Area 7A
		52	−26	42	7.62	Area PFt
		48	−36	56	7.01	Area 2
		60	−24	38	6.71	Area PF
		24	−62	48	6.36	Angular gyrus
		28	−76	42	5.35	SOG
		38	−50	54	5.03	Area hIP3
		40	−76	20	4.32	Area PGp
		34	−76	32	4.05	Middle occipital gyrus
Occipital cluster	349	26	−96	−2	6.47	Area 17
		34	−80	−2	5.52	Middle occipital gyrus
		30	−76	18	3.75	SOG
ITG cluster	436	48	−58	−8	8.52	ITG
Left hemisphere						
Parietal cluster	118	−18	−60	46	4.76	Area 7A
		−26	−50	48	4.49	IPL
Occipital cluster	232	−36	−92	2	5.64	Middle occipital gyrus
		−30	−84	−4	5.01	Area hOC4
IOG cluster	403	−46	−70	−8	7.98	IOG
		−48	−80	2	3.98	Middle occipital gyrus

Height threshold, $P < 0.001$ uncorrected; extent threshold, $P < 0.05$, FWE-corrected across the entire brain. Size = number of active voxels. For anatomical identification of peaks, we only considered cytoarchitectonic areas available in the anatomy toolbox that had a greater than 30% probability. The cytoarchitectonic area with the highest probability was reported for each peak. When cytoarchitectonic areas with more than 30% probability were not available to determine a peak, we simply provided the anatomical location of the peak. In each cluster, we report peaks that were more than 8 mm apart from each other in order of larger t-values. Abbreviations: IFG, inferior frontal gyrus; MFG, middle frontal gyrus; IPL, inferior parietal lobule; PPL, posterior parietal lobule; SPL, superior parietal lobule; SOG, superior occipital gyrus; ITG, Inferior temporal gyrus; IOG, inferior occipital gyrus.

In the AD group, self-face-related activity was identified in the inferior frontoparietal regions of the right hemisphere, and in the bilateral posterior parietal and inferior occipitotemporal cortices (Fig. 2 and Table 1). We also found activity in the right superior and middle occipital regions, which connected between the right posterior parietal and inferior occipital activations. These results are generally consistent with those reported in previous studies (Sugiura et al. 2005, 2006, 2008; Uddin et al. 2005; Kaplan et al. 2008; Morita et al. 2008, 2014; Scheepers et al. 2013; Hu et al. 2016). The right inferior frontoparietal regions corresponded well with cortical regions that are likely connected by the SLF III (see Fig. 4A). In contrast, inferior frontoparietal activity was not identified in the left hemisphere (Fig. 2).

In the ADO group, we also found self-face-related activity in similar regions of the right inferior frontoparietal, posterior parietal, and superior occipital cortices in which we identified self-face-related activity in the AD group (Fig. 2 and Table 1). As in the AD group, no left inferior frontoparietal activity was observed. However, unlike the AD group, right middle occipital and bilateral inferior occipitotemporal activity was not observed in this group.

In the CH group, we observed self-face-related activity only in the right superior occipital gyrus (SOG). Thus, the right SOG

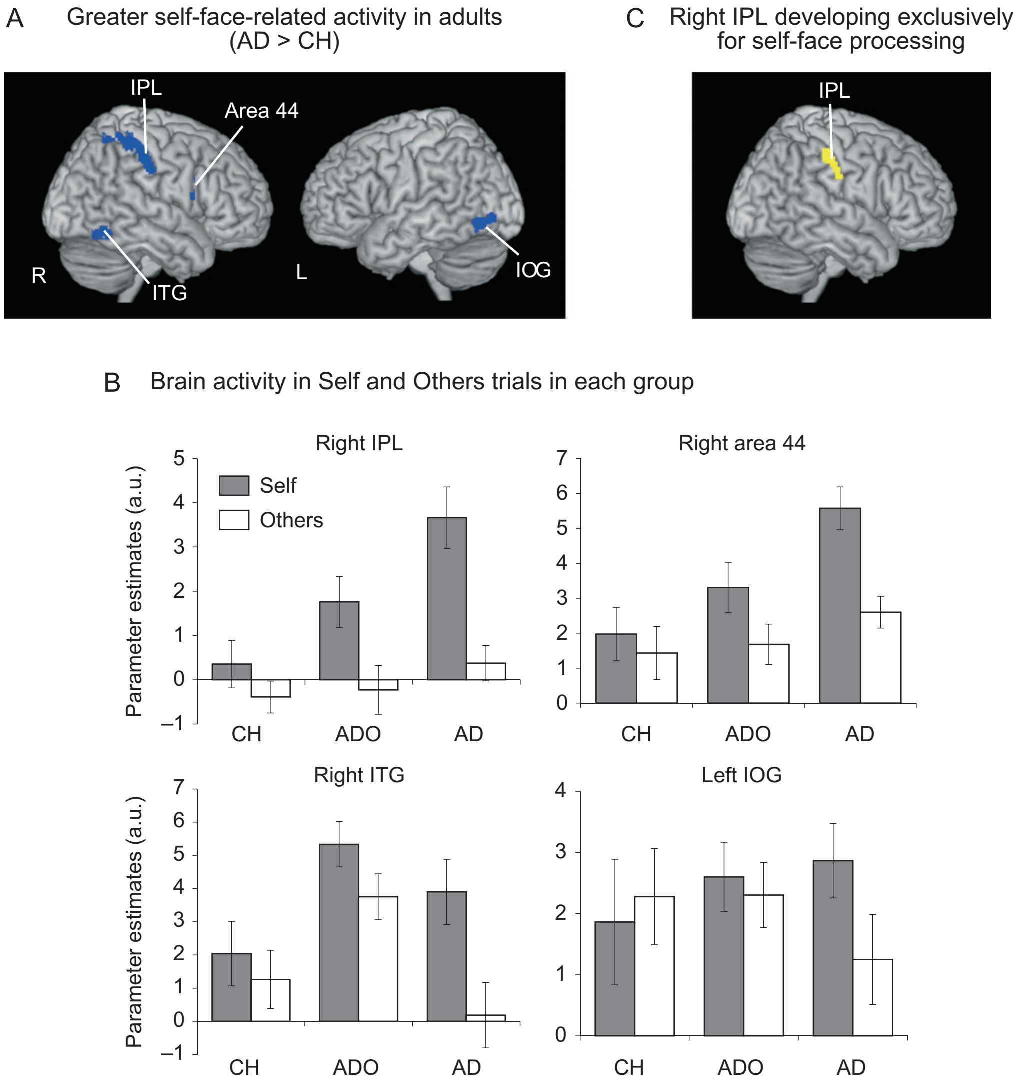


Figure 3. (*A*) Brain regions (blue) that showed significantly greater self-face-related activity in adults compared with children identified by the contrast [(Self $_{\mathrm{AD}}$ vs. Others $_{\mathrm{AD}}$) vs. (Self $_{\mathrm{CH}}$ vs. Others $_{\mathrm{CH}}$)]. (*B*) Developmental changes in brain activity in Self (gray bars) and Others (white bars) trials in the right IPL, area 44, and ITG, and left ITG (see panel *A*). Among these regions, only the right IPL developed exclusively for self-face processing, without being substantially involved in processing of others' faces. The vertical axis in each panel indicates values for parameter estimates (a.u.). Lines on each bar indicate the standard error of the mean across participants. (*C*) The right IPL (area PFt, yellow) showed significantly greater activity in Self trials in adults compared with children, while there was no increase in activity in Others trial throughout the developmental course. R, right hemisphere; L, left hemisphere; a.u., arbitrary unit; IPL, inferior parietal lobule; ITG, inferior temporal gyrus; IOG, inferior occipital gyrus; CH, children; ADO, adolescents; AD, adults.

appeared to consistently showed self-face-related activity across all groups (Fig. 2). However, no adult-like robust activity was observed in the right inferior frontoparietal and bilateral inferior occipitotemporal cortices in this group.

The different patterns of self-face-related activity across groups may indicate that brain networks associated with self-face recognition develop from childhood to adulthood especially in the right hemisphere.

Development of Self-Face-Related Activity and Specificity of the Right IPL

To confirm developmental changes in self-face-related activity from childhood to adulthood, we compared self-face-related activity between groups. When we compared activity in the adults with that in the children (AD > CH), we observed significantly greater activity in the IPL (cytoarchitectonic areas 2 and PFt), posterior parietal lobule (PPL: a peak in area 7A), posterior part of the IFG (area 44), and the ITG of the right hemisphere (Fig. 3A). We also found greater activity in the left IOG. Activation peaks for each active-voxel cluster are presented in Table 2. Among these brain regions, activity in the right IPL, area 44, and ITG, and in the left IOG were also reported in a previous meta-analysis of adult data (Hu et al. 2016). This indicated the essential importance of these regions in various self-face recognition tasks. We could not find any significant differences between any 2 given groups in any of the other 5 possible combinations.

We further investigated the development of self-face-related activity from childhood to adulthood in all 4 regions (right IPL [area PFt], area 44, and ITG and left IOG; see above) where adults showed significantly greater self-face-related activity than children (Fig. 3A). Here, we examined developmental changes in brain activity in Self and Others trials separately (Fig. 3B). The most notable difference in brain activity between Self and Others

Table 2 Group difference in self-face-related activity (Adults vs. Children)

Clusters	Size	x	y	z	t-value	Area
Right hemisphere						
Area 44 cluster	153	46	6	28	4.83	Area 44
IPL cluster	419	46	−38	56	5.31	Area 2
		60	−22	38	5.01	Area PFt
		58	−28	52	4.34	IPL
PPL cluster	110	34	−56	56	3.88	Area 7A
ITG cluster	151	48	−56	−12	5.15	ITG
Left hemisphere						
IOG cluster	278	−44	−72	−8	5.77	IOG
		−40	−80	−2	4.29	MOG

See footnote in Table 1. IPL, inferior parietal lobule; PPL, posterior parietal lobule; ITG, inferior temporal gyrus; IOG, inferior occipital gyrus; MOG, middle occipital gyrus.

trials was observed in the right IPL. In this region, brain activity remarkably increased from childhood to adulthood in Self trials, while activity never increased in Others trials throughout the developmental course (Fig. 3*B*). A one-sample *t*-test against zero confirmed no significant increase (or decrease) in brain activity in Others trials ($t = -0.31$, $df = 59$, n.s.).

Gradual increases in activity from childhood to adulthood in Self trials were also clearly observed in the right area 44 (Fig. 3*B*). However, unlike the right IPL, activity also increased in Others trial in this region, which was confirmed by a one-sample t-test ($t = 5.39$, $df = 59$, $P < 0.001$ with Bonferroni correction). Moreover, the right ITG and the left IOG regions showed other developmental changes. In these regions, apparent age-dependent activity increases in Self trials were not observed. In addition, activity increased almost equally in both Self and Others trials in the CH and ADO groups. This general trend of increased activity in Others trials in these regions was confirmed by one-sample *t*-test (right ITG: $t = 3.31$, $df = 59$, $P < 0.01$ corrected; left IOG: $t = 4.86$, $df = 59$, $P < 0.001$ corrected). In contrast, brain activity was reduced in Others trials in adults (Fig. 3*B*). It seemed that this reduction in activity in Others trials contributed to self-face-related activity (Self vs. Others) in these regions in the AD group (Fig. 2).

Hence, among brain regions that showed significant developmental changes of self-face-related activity from childhood to adulthood (Fig. 3*A*), the right IPL is the only region that seems to develop predominantly for self-face processing without being substantially involved in the processing of others' faces (Fig. 3*B*).

An additional analysis fully supported this claim. When we sought brain regions that showed increased activity in Self trials from childhood to adulthood with no increase in activity in Others trials, the only region we identified was the right IPL (peak in MNI coordinates: $x, y, z = 60, -22, 40$ in area PFt; voxel size = 152; Fig. 3*C*). Thus, it is likely that across the whole brain, only the right IPL develops predominantly for self-face processing.

Development of Right-Lateralized Self-Face-Related Activity

When we examined lateralized self-face-related activity in the AD group, we observed dominance of right-sided activity in the IPL and inferior frontal cortices (area 44 and anterior IFG), which are likely connected by the SLF III (Fig. 4*A*). We also found right-lateralized activity in the PPL and ITG outside SLF III regions. These right-lateralized activities were observed even though the participants pressed the response button with their right hands to indicate their judgment of the faces. Activation peaks for each active-voxel cluster are presented in Table 3. The right IPL, area 44, anterior IFG, and ITG were also previously reported in the meta-analysis of adult data (Hu et al. 2016). Therefore, our results suggest that these regions that are important in various self-face recognition tasks show right-side dominant activity in the adult brain. In the ADO group, we also found highly similar patterns of right-side dominant activity in the IPL and inferior frontal cortices, in addition to the PPL and SOG (Fig. 4*A* and Table 3). However, there was no right-side dominant ITG activity in this group. Importantly, the right IPL regions that showed right-lateralized self-face-related activity in adults and adolescents (Fig. 4*A*) overlapped with the region that developed predominantly for self-face processing (Fig. 3*C*).

In contrast, in the CH group, no right-lateralized activity was identified (Fig. 4*A*). Hence, adult-like right-dominant recruitment of the IPL for self-face recognition appeared to emerge during adolescence, but is not yet present in childhood, as we observed for the proprioceptive illusion (Naito et al. 2017). Finally, no regions showed left-side dominance of self-face-related activity in any groups.

To investigate how right-lateralized self-face-related activity in the IPL develops in relation to activity in the left hemisphere, we examined developmental changes in self-face-related activity obtained from the right IPL region (Fig. 4*A*) and from the corresponding left region. We found that activity gradually increased from childhood to adulthood in the right hemisphere (Fig. 4*B*). In contrast, in the corresponding left hemisphere region, no conspicuous activity increases were observed in any of the groups (Fig. 4*B*). This was consistent with the finding that the left IPL did not show significant self-face-related activity in any groups (Fig. 2). In addition, we did not find any robust decrease in activity in the ADO group, which was different from the result obtained in the proprioceptive illusion (Naito et al. 2017; see also Supplementary Fig. 3).

Viewed collectively, right-side dominance of self-face-related activity in the IPL appeared to emerge during adolescence, most likely due to gradual development of right-side activity from childhood to adulthood. Together with the finding that the right IPL develops predominantly for self-face processing (Fig. 3*B*,*C*), it is likely that neuronal processing for self-face in the IPL develops in a right-dominant manner.

Area 44 and anterior IFG regions showed similar patterns of developmental change as in the IPL region (gradual increase in right-side activity from childhood to adulthood with no conspicuous increase in left-side activity; Fig. 4*B*). In addition, the ITG region also showed a gradual increase in right-side activity from childhood to adulthood (Fig. 4*B*). However, unlike other brain regions, its left corresponding region also showed an increase of self-face-related activity in the adult brain (see also Fig. 2).

Overlapping Activation in the Right IPL Between Self-Face Recognition and Proprioceptive Illusions Emerges During Adolescence

Finally, we examined when self-face recognition begins to share an active region in the right IPL with the proprioceptive illusion. The conjunction analysis revealed that the rostral part of the right IPL (PFt and PF) was commonly activated both in the self-face recognition and in the proprioceptive illusion in the ADO group (Fig. 5*A*, left panel, and Table 4). This was the largest active-voxel cluster across the whole brain and was the only

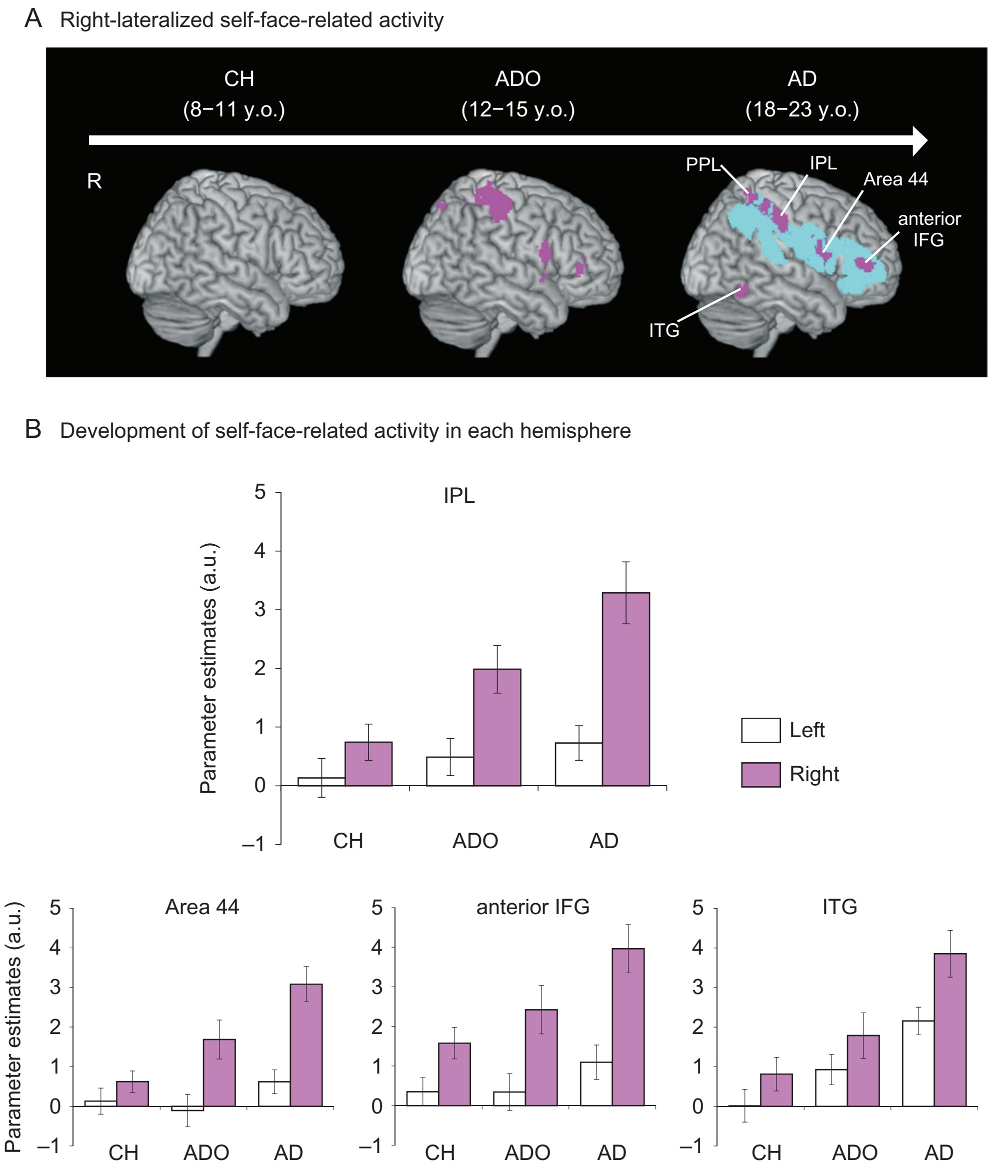


Figure 4. (*A*) Brain regions (pink) that showed right-lateralized self-face-related activity identified by the flip analysis in each group. In each panel, brain activations are rendered onto the MNI standard brain. In the adult brain, activations are also superimposed onto the 50% probability map of cortical regions likely connected by the right SLF III (cyan, see Parlatini et al. 2017). (*B*) Developmental changes in self-face-related activity in the IPL, area 44, anterior IFG, and ITG (see panel *A*) of the right hemisphere (pink bars) and in their corresponding regions in the left hemisphere (white bars). The vertical axis in each panel indicates values for parameter estimates (a.u.). Lines on each bar indicate the standard error of the mean across participants. Adult-like right-side dominant self-face-related activity in the IPL emerged during adolescence (panel *A*), most likely due to gradual development of its right-side activity from childhood to adulthood (panel *B*). R, right hemisphere; a.u., arbitrary unit; IPL, inferior parietal lobule; IFG, inferior frontal gyrus; ITG, inferior temporal gyrus; CH, children; ADO, adolescents; AD, adults; SLF, superior longitudinal fasciculus tract; MNI, Montreal Neurological Institute.

significant cluster among our ROIs (i.e., cortical regions likely connected by the right SLF III). We found no common brain regions in either the whole brain or our ROI in the CH group. Thus, self-face recognition began to share an active region in the right IPL with proprioceptive illusion during adolescence.

The right IPL region corresponded with the region (area PFt) at which we observed overlap between right-lateralized self-face-related activity during self-face recognition (peak coordinates: x, y, z = 52, −30, 48) and right-lateralized illusion-related activity during the proprioceptive illusion (58, −28, 44) in adolescents (Fig. 5A, right panel). Furthermore, this region corresponded to the right IPL region (area PFt) in which activity develops predominantly for self-face processing (Fig. 3C).

In the development of such right-lateralized IPL activity, we found a close relationship between self-face recognition and the proprioceptive illusion during adolescence. The degree of right-lateralization of self-face-related IPL activity significantly correlated with that of illusion-related IPL activity in the ADO group (r = 0.546, df = 20, $P < 0.01$ one-tailed, Fig. 5B). This means that, during adolescence, participants who recruited the IPL in a more right-side dominant manner for the proprioceptive illusion also recruited it in such a manner for self-face recognition. We also found a moderate correlation in the CH group, although this did not reach significance (r = 0.316, df = 20, $P < 0.1$ one-tailed, Fig. 5B).

Taken all together, the results indicate that the self-face recognition starts to share the right IPL region active during proprioceptive

Table 3 Right-lateralized self-face-related activity in adolescents and adults

	Adolescents							Adults					
	Size	x	y	z	t-value	Area		Size	x	y	z	t-value	Area
Anterior IFG cluster	185	42	38	2	6.20	IFG	Anterior IFG cluster	266	40	38	6	6.25	IFG
									46	46	4	4.65	MFG
Area 44 cluster	344	54	10	16	6.65	Area 44	Area 44 cluster	254	50	6	24	6.37	Area 44
		48	8	6	4.85	Insula							
IPL cluster	793	50	−22	60	7.07	Area 1	Anterior IPL cluster	247	54	−24	44	5.76	Area PFt
		52	−30	48	6.24	Area PFt			60	−28	52	3.80	SMG
		36	−40	50	5.51	Area 2			50	−18	32	3.53	Area PFop
							Posterior IPL cluster	126	44	−38	52	5.19	Area hIP2
									42	−24	40	3.79	Area 2
PPL cluster	260	28	−62	38	5.30	SOG	PPL cluster	98	34	−46	64	3.98	Area 2
		24	−70	52	4.50	Area 7P			42	−48	60	3.96	Area 7PC
		26	−52	50	3.72	Area 7PC							
							ITG cluster	130	48	−52	−14	5.57	ITG

See footnote to Table 1. No regions showed right-lateralized self-face-related activity in the children. IFG, inferior frontal gyrus; MFG, middle frontal gyrus; IPL, inferior parietal lobule; SMG, supramarginal gyrus; PPL, posterior parietal lobule; SOG; superior occipital gyrus; ITG, Inferior temporal gyrus.

illusion in adolescence by associating its right-lateralized style of recruitment with that of the proprioceptive illusion.

Discussion

In the present study, we examined when and how brain networks associated with self-face recognition develop in the typically developing human brain. We showed that, among brain regions implicated in these processes, only the right IPL developed predominantly for self-face processing without being substantially involved in the processing of others' faces throughout the developmental course. Adult-like right-dominance of the IPL for self-face recognition emerged during adolescence, as we observed for the proprioceptive illusion in our previous study (Naito et al. 2017). Furthermore, self-face recognition began to share an active region in the right IPL with the proprioceptive illusion during adolescence, whereby the same right-lateralized style of recruitment was induced as that during the proprioceptive illusion. Hence, in addition to our previous study (Naito et al. 2017), the present study further demonstrates the importance of the right IPL in the development of self-body recognition.

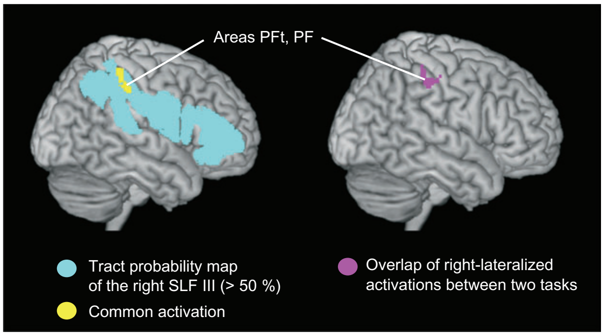
Right IPL

Our result that the right IPL develops predominantly for self-face processing (Fig. 3) was also supported when we examined brain activity in Self and Others trials separately (Supplementary Fig. 2). Thus, within the domain of face recognition, the right IPL seems to develop for self-face processing. The importance of the right IPL in self-face processing is consistent with the previous reports in adults. The right IPL is one of the brain regions showing stronger activity during self-face processing than during processing of others' faces (Uddin et al. 2005), and temporary lesioning of the right IPL using repetitive transcranial magnetic stimulation disrupts self-face recognition (Uddin et al. 2006). The specificity for self-face processing of the right IPL might contribute to the feeling of recognition that "the face I see is my own." This claim seems to be consistent with clinical finding that the right IPL (area PF) plays crucial roles in the sense of body ownership (Feinberg et al. 1990). General importance of the human IPL (intraparietal cortex and supramarginal gyrus) for the sense of body ownership has been consistently reported in neuroimaging studies where the ownership is directly assessed by experimentally manipulating it in multisensory integration tasks (Ehrsson et al. 2004; Gentile et al. 2013; Guterstam et al. 2013; Limanowski and Blankenburg 2016; Grivaz et al. 2017).

Adult-like right-dominance of the IPL also emerged during adolescence for self-face recognition (Fig. 4A), similar to the developmental pattern seen for the proprioceptive illusion (Naito et al. 2017). Importantly, right-lateralization of self-face-related activity progressed due to a gradual increase in right IPL activity from childhood to adulthood (Fig. 4B). This was distinct from the proprioceptive illusion, in which the IPL is activated bilaterally during childhood and right-side dominance progresses during adolescence along with age-dependent suppression of left IPL activity in this period (Naito et al. 2017; see also Supplementary Fig. 3). Thus, the development of functional lateralization of the right IPL in self-face recognition did not follow the same pattern as that observed in the illusion (from bilateral to right-lateralized).

Self-face recognition began to share an active region in the rostral part of the right IPL (areas PFt and PF) with the proprioceptive illusion during adolescence (Fig. 5A), by associating its right-lateralized style of recruitment with that of the proprioceptive illusion (Fig. 5B). This common IPL region was already recruited for the proprioceptive illusion during childhood (Naito et al. 2017) and overlapped with the region that develops predominantly for self-face processing (Fig. 3C). Hence, during adolescence, the brain appears to promote the development of neuronal processes in the IPL for self-face processing in a right-side dominant manner by utilizing components of higher-order neuronal processing implemented in the right IPL region that have already been used for the proprioceptive processing since childhood (Naito et al. 2017 and see below).

Further investigations are needed to elucidate the exact roles of the right IPL. However, it is highly unlikely that self-face-related activity in the right IPL is merely due to familiarity of one's own face, even though we only used unfamiliar faces in Others trials as controls. First, self-face-related activity in the right IPL has been consistently reported across many studies regardless of whether the study used familiar or unfamiliar faces of others (Hu et al. 2016). Second, the right IPL has never been considered to be a key brain structure in the series of studies that have addressed the effect of familiarity of faces (Shah et al. 2001; Kosaka et al. 2003; Sugiura et al. 2005; Gobbini and Haxby 2006, A Common right IPL activity in adolescents



B Correlation in right-lateralized IPL activity between tasks

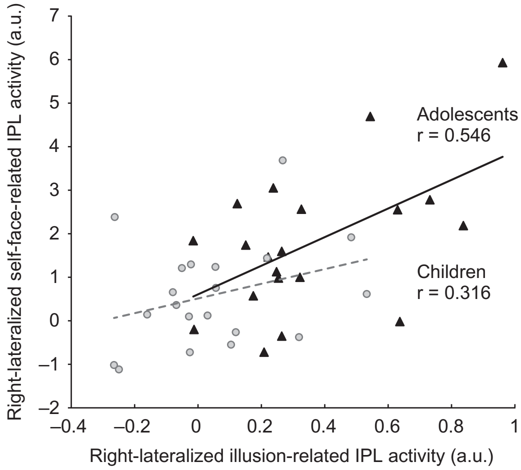


Figure 5. (*A*) Right IPL region (areas PFt and PF) commonly activated during both self-face recognition and the proprioceptive illusion in adolescents (yellow, left panel). Cyan sections indicate cortical regions likely connected by the right SLF III in the adult brain (putative SLF III regions in adolescents). Right IPL region where right-lateralized self-face-related and right-lateralized illusion-related activity overlapped in adolescents (pink section in right panel). These results were from the Boolean intersection analysis with no statistical evaluation (see Methods). However, this overlapping region corresponded well with the common IPL region (see left panel). (*B*) Correlation between the degree of right-lateralization of self-face-related IPL activity and that of illusion-related IPL activity in adolescents (triangle dots) and children (circle dots). The horizontal axis indicates values for differences in parameter estimates between the right and the left IPLs (right–left) for illusion-related activity and the vertical axis indicates the same for self-face-related activity (a.u.). Solid and dashed lines indicate regression lines that fitted to the adolescent and child data, respectively. A significant positive correlation was observed in adolescents. IPL, inferior parietal lobule; r, correlation coefficient; a.u., arbitrary unit; SLF, superior longitudinal fasciculus tract.

Table 4 Brain areas commonly activated during self-face recognition and proprioceptive illusion in adolescents

	Size	x	y	z	t-value	Area
Right IPL cluster	75	52	−36	56	4.43	Area PFt
		58	−30	44	4.10	Area PF

Height threshold, $P < 0.001$ uncorrected; extent threshold, $P < 0.05$, FWE-corrected in the ROI of cortical regions likely connected by the right SLF III. For the rest, see footnote in Table 2. IPL, inferior parietal lobule; SLF, superior longitudinal fasciculus tract

2007). Likewise, it is unlikely that the right IPL region is merely associated with attention, as this region does not seem to be a main locus of the goal-directed and/or stimulus-driven attention (Corbetta and Shulman 2002; Corbetta et al. 2008).

The IPL could be considered a higher-order multisensory brain region, because cells in homologous regions in monkeys are involved in multisensory (visuo-somatic) processing pertaining to one's own body (face, arms, and hands; Hyvarinen 1982; Graziano et al. 2004; Ishida et al. 2010; Murata et al. 2016). In humans, it has been repeatedly shown that the IPL (supramarginal gyrus) is one of the regions for multisensory (visuo-somatic) processing of one's own body parts (Gentile et al. 2011, 2013; Guterstam et al. 2013; Limanowski and Blankenburg 2016; Grivaz et al. 2017). As for the right hemisphere, it is shown that the human IPL is activated right-side dominantly during multisensory (visuo-somatic) processing for self-face recognition (Apps et al. 2015; Bufalari et al. 2015) and for one's own right-hand posture (Hagura et al. 2009). Thus, such a multisensory region in the right cerebral hemisphere is capable of higher-order neuronal processing of kinesthetic signals derived from one's own hand (proprioceptive illusion) and of visual information about one's own face (self-face recognition). The right IPL has also been shown to be a representative region, which strongly responds to visual images of one's own (headless) body than those of others' bodies (Hodzic, Kaas et al. 2009). Hence, the right IPL seems to be involved in higher-order multisensory processing of information pertaining to one's own body, regardless of the body parts, suggesting that the region contributes to the formation of multisensory representations of one's own body in the mature human brain.

The lack of self-face-related right IPL activity in children (Figs 2 and 3B) indicates that their self-face recognition does not substantially use a body representation with multisensory capability. We speculate that self-face recognition in children does not yet resemble that of adults and is more visually dependent (see Fig. 2).

After birth, we have rich visuo-proprioceptive experiences of our hand (limb) movements. In contrast, such multisensory experience is poorer for one's own face because we cannot directly see our own faces without a mirror or reflective surface. Thus, multisensory representation of one's own hand (limb) must develop earlier than that of one's own face. This appears to be consistent with our finding that the right IPL is already used for recognition of one's own hand posture (position) during childhood (Naito et al. 2017), while the brain begins to recruit this lobule for self-face processing later during adolescence. From a slightly different perspective, these results also seem to suggest that proprioceptive processing that exclusively pertains to one's own body parts may primarily contribute to the development of a central representation of one's own body, which is later shared by self-face recognition leading to recognition of the (bodily) self as distinct from others (Gallup 1982; Brooks-Gunn and Lewis 1984). This suggests that the development of self-recognition has its roots in somatic recognition of one's own body (see more in Morita et al. 2017).

Right-Hemispheric Dominance in Self-Face Recognition

Despite the right-side dominance of self-face-related activity in the ADO and AD groups, no regions showed left-side dominance of self-face-related activity in any of the groups (Fig. 4A). This indicates right-hemispheric dominance in self-face recognition, as suggested previously (Devue and Brédart 2011; Hu et al. 2016), and its general importance in self-face recognition is corroborated by clinical findings. For example, patients with right hemisphere damage are unable to identify their own faces when they are reflected in a mirror (Feinberg and Shapiro 1982; Spangenberg et al. 1998; Feinberg 2000; Breen et al. 2001; Feinberg and Keenan 2005). Intracarotid injection of amytal to the right hemisphere also lowers the rate of self-attribution when participants view self-other morphing faces (Keenan et al. 2001). Moreover, as we reported in our illusion study (Naito et al. 2017), right-hemispheric dominance for visual search functions also becomes apparent during adolescence (Everts et al. 2009). Thus, accumulating evidence implies that dominant use of the right cerebral cortex for certain brain functions emerge during adolescence. This developmental period seems to be substantially later than that when left-lateralized language (production) function becomes observable (Szaflarski et al. 2006, Holland et al. 2007). Hence, functional lateralization to the right cerebral cortex seems to develop slowly, as if the human brain preserves the right “non-dominant” hemisphere as a spare for the left “dominant” hemisphere to subserve the function of the left hemisphere in case the left hemisphere malfunctions (e.g., Hertz-Pannier et al. 2002; Yuan et al. 2006).

Right Inferior Frontal Cortices and the SLF III Network

The right inferior frontal cortices (area 44 and anterior IFG) also showed right-lateralized self-face-related activity in the ADO and AD groups (Figs 2 and 4A). It is noteworthy that the present right area 44 activity is located in close proximity to the ventral premotor region, which is an important constituent of brain networks associated with the sense of body ownership (Ehrsson et al. 2004; Gentile et al. 2013; Limanowski and Blankenburg 2016; Grivaz et al. 2017). The right inferior frontal cortices most likely belong to the inferior frontoparietal SLF III network (Fig. 4A) with strong connections to the right IPL (Matsumoto et al. 2012). These results suggest the particular importance of the inferior frontoparietal SLF III network for self-face recognition within the right hemisphere. Right dominant involvement of the SLF III network in self-face recognition was also supported by our evaluation of the lateralization index (LI) for the present self-face-related activity (Supplementary Fig. 4). In this analysis, we also confirmed that adult-like right-side dominant use of this network emerges during adolescence, as seen in Figure 4A.

The dominant use of the right-hemispheric SLF III network for self-face recognition might be associated with its anatomical features. It has repeatedly been shown in human adults that the volume of the right SLF III is greater than that of the left SLF III (Thiebaut de Schotten et al. 2011; Hecht et al. 2015; Budisavljevic et al. 2017). This indicates higher-capacity information processing in the right SLF III, which seems to be suitable for efficient processing of complex multisensory information pertaining to one’s own various body parts, including the face. In addition, the importance of this network in self-face recognition is also suggested by findings from a chimpanzee study, in which richer SLF III termination in right areas 44 and 45 was associated with higher self-face recognition ability (Hecht et al. 2017).

Even though the IPL and the inferior frontal cortices likely belong to the SLF III network, their roles and development seem to be different. First, unlike the right IPL, the right area 44 increased its activity not only in Self trials but also in Others trials, especially in the AD group (Fig. 3B), which was also supported by our supplementary analysis (Supplementary Fig. 2). Thus, the right area 44 appears to develop for self-face processing, but this region also participates in the processing of others’ faces, similar to a mirror neuron system, especially in the adult brain (Buccino et al. 2001; Carr et al. 2003), though self-face processing is still dominant in this region (Morita et al. 2008). Such shared coding of the self and others in area 44 (ventral premotor region) is consistent with the findings from an fMRI-adaptation study (Brozzoli et al. 2013). Second, in the adult brain, we previously reported that self-face recognition and the proprioceptive illusion both activate not only the IPL but also the inferior frontal cortices (Morita et al. 2017). In contrast, in the present study, we found such shared activation only in the right IPL during adolescence (Fig. 5A). We speculate that this discrepancy might be due to differences in regional maturation within the SLF III network, as gray matter maturation of the inferior frontal cortices seems to be slower than that of the parietal cortices (Gogtay et al. 2004) and structural maturation of the right SLF is very slow and continues into adulthood (Giorgio et al. 2008).

Inferior Occipitotemporal Cortices

In adults, we found significant self-face-related activity in broader regions of the bilateral inferior occipitotemporal cortices, but this activity was not observed in children and adolescents (Fig. 2). This was because these cortices were almost equally activated during both self-face processing and processing of others’ faces in the latter 2 groups (see Supplementary Fig. 2). Slightly different developmental patterns were observed in posterior-medial regions (peak coordinates; x, y, z = −36, −92, 2, and 34, −80, −2) and anterior-lateral regions (see below for peak coordinates). In the anterior-lateral regions, adult brains were characterized by reduced responses to others’ faces (Fig. 3B). Indeed, an additional analysis revealed that responses to others’ faces in these regions were significantly smaller in adults than in children and adolescents, and that these were the only regions that showed such developmental changes across the whole brain (Supplementary Fig. 5). Thus, self-face-related activity in these regions of the adult brain (Fig. 2) was most likely due to adult-specific reduction of brain activity for the processing of others’ faces. In contrast, self-face-related activity in posterior-medial regions of the adult brain seemed to be caused by a relative augmentation of activity for self-face processing (not shown in figure).

Importantly, the anterior-lateral regions corresponded with regions in the right ITG (48, −56, −12) and left IOG (−44, −72, −8) in which we found significant developmental changes of self-face-related activity from childhood to adulthood (Fig. 3A and B). Viewed collectively, it seems that these extrastriate regions develop into regions that predominantly process self-face information in the adult brain. Since similar regions in the adult brain seem to show greater responses to visual images of one’s own body than to those of others’ bodies (Sugiura et al. 2006; Hodzic, Kaas et al. 2009; Hodzic, Muckli et al. 2009), these extrastriate regions might be areas that predominantly participate in visual processing of one’s own body parts in the adult brain. These regions seem to be located apart from well-known areas that selectively respond to visual stimuli of (others’) faces or body parts, such as the fusiform face area (FFA; Kanwisher et al. 1997; Kanwisher and Yovel 2006), the occipital face area (OFA; Rotshtein et al. 2005; Pitcher et al. 2011), and the extrastriate body area (EBA; Downing et al. 2001). Further studies are needed to determine the existence of such extrastriate areas that are specialized for self-face processing; however, the predominant self-face processing in the adult extrastriate regions (Fig. 3B) might indicate a particular importance of self-face, which may lead to the recognition (awareness) of the bodily self (see references in introduction).

The emergence of such brain regions during adulthood indicates slow maturation of self-face processing in human extrastriate areas. In the development of central visual processing of others' faces (Grill-Spector et al. 2008; Scherf et al. 2011), it is shown that the FFA starts to exhibit selective responses to (others') faces during adolescence (Scherf et al. 2007). Thus, the emergence of self-face predominant areas during adulthood implies the possibility that central visual processing of one's own face matures more slowly than that of others' faces. As described above, this may be because we have less experience seeing our own faces than we do seeing others' faces.

Finally, the right ITG region (Fig. 3A) corresponded well with the region in which right-lateralized self-face-related activity emerges during adulthood (Fig. 4A). Thus, right-lateralization of this extrastriate area likely emerges even after right-lateralization of the SLF III network (Fig. 4A).

Overall, in the development of self-face recognition, the notion that 2-year-old children can already recognize their own faces is widely accepted (Amsterdam 1972). To date, several basic and clinical studies on this topic have been conducted in the field of neuroimaging (Uddin et al. 2008; Kita et al. 2011; Quevedo et al. 2016; Stapel et al. 2017). However, to the best of our knowledge, the study presented here is the first fMRI study clearly demonstrating that neuronal processes for self-face recognition develop slowly and change drastically from childhood to adulthood in typically developing humans.

Supplementary Material

Supplementary material is available at *Cerebral Cortex* online.

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