

Effects of Age, Task Performance, and Structural Brain Development on Face Processing

Kathrin Cohen Kadosh^{1,2}, Mark H Johnson³, Frederic Dick³, Roi Cohen Kadosh² and Sarah-Jayne Blakemore¹

¹Institute of Cognitive Neuroscience, University College London, 17 Queen Square, London WC1N 3AR, UK, ²Department of Experimental Psychology, University of Oxford, South Parks Road, Oxford OX1 3UD, UK, ³Centre for Brain and Cognitive Development, Department of Psychological Science, Birkbeck, University of London, Henry Wellcome Building, Malet Street, London WC1E 7HX, UK

Address correspondence to Kathrin Cohen Kadosh, Department of Experimental Psychology, University of Oxford, Oxford, UK.
Email: kathrin.cohenkadosh@psy.ox.ac.uk

In this combined structural and functional MRI developmental study, we tested 48 participants aged 7–37 years on 3 simple face-processing tasks (identity, expression, and gaze task), which were designed to yield very similar performance levels across the entire age range. The same participants then carried out 3 more difficult out-of-scanner tasks, which provided in-depth measures of changes in performance. For our analysis we adopted a novel, systematic approach that allowed us to differentiate age- from performance-related changes in the BOLD response in the 3 tasks, and compared these effects to concomitant changes in brain structure. The processing of all face aspects activated the core face-network across the age range, as well as additional and partially separable regions. Small task-specific activations in posterior regions were found to increase with age and were distinct from more widespread activations that varied as a function of individual task performance (but not of age). Our results demonstrate that activity during face-processing changes with age, and these effects are still observed when controlling for changes associated with differences in task performance. Moreover, we found that changes in white and gray matter volume were associated with changes in activation with age and performance in the out-of-scanner tasks.

Keywords: Brain development, Cortical specialization, Developmental neuroimaging, Face processing

Introduction

Human faces potentially provide a plethora of social information, including identity, emotional expression and direction of eye gaze. Studies have shown that the ability to extract basic face information develops gradually (Mondloch et al. 2006) and is mirrored at the neural level by slowly emerging cortical networks (Scherf et al. 2007; Cohen Kadosh et al. 2011). In recent years, much research has focused on the behavioral and neural basis of face-processing in infants and young children (Cohen Kadosh and Johnson 2007; Pelphrey et al. 2009; Cantlon et al. 2011). A smaller number of studies have suggested that face-processing abilities continue to improve during adolescence (Monk et al. 2003; Yurgelun-Todd and Killgore 2006; Pfeifer et al. 2011), with some studies observing a dip in face-processing proficiency in early adolescence (Carey et al. 1980; Thomas et al. 2007). Among the developmental milestones associated with adolescence are changes in social information processing, when new aspects of face processing such as judgements of attractiveness, or social status, become increasingly important. It has been suggested that a better understanding of the developmental changes in face processing during adolescence could provide

a good model for understanding the transition of social information processing from childhood through adulthood (Scherf et al. 2012). The aim of the current study was to investigate the development of the neural circuitry associated with face processing across a wide age range from childhood to adulthood, and to attempt to disentangle age-related changes from those associated with improvements in task performance.

There is evidence that the prolonged trajectory of becoming proficient at processing faces is mirrored at the neural level by slowly emerging cortical face networks (Cohen Kadosh and Johnson 2007). In 1 study, children, adolescents, and adults passively viewed photographic images of faces versus objects, places or abstract patterns (Golarai et al. 2007). The results showed an age-related increase in the activation within right fusiform cortex [fusiform face area (FFA)], with adults showing more activation than child groups and the adolescent group exhibiting an intermediate pattern. In addition, an expansion of FFA volume was correlated with a behavioral improvement in recognition memory for facial identity. In a different study, Scherf et al. (2007) showed children, adolescents, and adults short movie clips of faces, places, and objects, and observed an age-related increase in face-selective FFA activation between childhood and adolescence, as well as an increase in face-selective activation in the superior temporal sulcus (STS). Somewhat in contrast, Cantlon et al. observed a robust FFA response in 4-year-old children for faces in comparison to other categories, such as shoes, letters, numbers, or scrambled images (Cantlon et al. 2011).

Patterns of effective connectivity within the core face-network regions also change over development (Cohen Kadosh et al. 2011). While the basic configuration of the core face-network is present from 7 years, between ages 7 and 11 there is an increase in the degree to which functional network connections are modulated by current task demands. More specifically, it was found that different task demands [e.g. focus on extracting a facial identity selectively strengthened the network path that connected the inferior occipital gyrus (IOG) to the fusiform gyrus (FG), whereas extracting an emotional expression modulated path strength from the IOG to the STS].

In the current study, we analyzed data from 48 children, adolescents, and young adults who were instructed to selectively process facial identity, expression, or gaze in 3 different face-processing tasks. Our first aim was to pinpoint the developmental trajectories from mid-childhood to adulthood for the processing of each face aspect. We assumed that during development 2 types of change can occur: changes due to practice or experience and changes due to the chronological age of participants. First, task performance may improve due

to practice, and this “training effect” might be associated with changes in underlying neural circuitry. This kind of training effect could be independent of age and thus be seen with performance changes at any age. While this may be difficult to assess in practice, because adults tend to show near ceiling performance on most face-processing tasks, we would expect to see performance-related changes in more challenging face-processing tasks in which individual differences become clearer. This kind of principle has already been shown in individuals with developmental prosopagnosia, who never develop typical adult-level face-processing abilities in the absence of any obvious sensory or intellectual deficit or brain injury (Avidan et al. 2005; Behrmann and Avidan 2005). Participants with developmental prosopagnosics reliably activate face-specific regions in the cortex while also recruiting additional brain areas [e.g. the inferior frontal gyrus (IFG); Avidan et al. 2005] and it is interesting to note that IFG activation is routinely observed in studies testing children (Passarotti et al. 2003; Gathers et al. 2004; Passarotti et al. 2007). This suggests that in a participant group with adult-like levels of functional and structural brain maturation, there are persistent differences in brain responses that could be attributed to the use of alternative processing strategies.

A second type of change that could occur is chronological age-related changes in the neuronal circuitry that are independent from experience (sometimes termed “maturation”). These age-dependent plasticity effects most likely reflect changes in gray matter, such as axon sprouting, or synaptic pruning and synaptogenesis, while white matter (WM) changes may be due to changes in myelination, fiber organization (Giedd et al. 1999; Harris et al. 2011; Lebel and Beaulieu 2011; Petanjek et al. 2011). It is important to attempt to differentiate performance and age-related changes when investigating development in the neural circuitry on any task in order to obtain a clear picture of which changes are experience dependent and which are simply due to ongoing brain maturation during the first 3 decades of life (Schlaggar et al. 2002; Brown et al. 2005; Church et al. 2010; Cohen Kadosh 2011).

Thus, our second aim was to separate out age from task performance effects by including 2 specific covariates in our design that represented the level of task performance for the 3 face aspects in the functional magnetic resonance imaging (fMRI) in-scanner tasks and 3 additional out-of-scanner face tasks. The in-scanner tasks were designed to be simple in order to allow all participants to perform at similar proficiency levels while using task-specific cognitive strategies. In contrast, the 3 out-of-scanner tasks were more challenging, eliciting greater variation in performance and were used to assess more detailed changes in task performance at different ages. This approach allowed us to assess changes in brain activation as a function of task performance separately from general age effects. We note that the results in the current study pertain only to changes that are associated either with task performance (independent of age) or with age (independent of task performance). Our analysis approach was not designed to reveal changes associated with *both* performance and age. While this approach may lead us to miss regions involved in the interaction between these factors, it nevertheless represents an important step towards differentiating the factors that contribute to the emerging network for face processing.

Our third aim was to assess how functional changes with age and task performance are related to changes in underlying gray and WM. While it has often been suggested that developmental changes in brain function may reflect—and contribute to—changes in brain structure (Cohen Kadosh 2011; Crone and Ridderinkhof 2011; Scherf et al. 2012), no studies have directly investigated this with regard to face-processing abilities.

Our research approach to investigating these aims was based on recent paradigm shifts, which have prompted research to focus less on comparing developmental changes in specific brain regions, but rather to look at development from a more general perspective, such as comparing connectivity patterns in large brain networks. This shift has been motivated by several factors, including: First, new theoretical frameworks, such as the neural re-use theory (Anderson 2007a, 2007b, 2010) and more established theories such as the interactive specialization approach (Johnson 2001, 2011), have suggested that postnatal functional brain development relies not only on the slow maturation of particular core areas, but also on a process of specialization and fine-tuning of a network of cortical areas. It has been suggested that this specialization process reflects a continuous reorganization process during which systematic connections between cortical areas are strengthened and core areas become increasingly specialized (Cohen Kadosh 2011). A too narrow focus on specific brain regions that are commonly found in the mature brain might lead to missing important developmental effects, such as age or performance effects, as the research findings for the IFG reviewed above have impressively demonstrated. There is already some empirical support for these new theoretical approaches in the face literature [see the DCM face-processing study reviewed above (Cohen Kadosh et al. 2011)], and this network approach to brain organization has also been investigated for other cognitive domains, such as resting state and cognitive control (Fair et al. 2007, 2008). Second, in addition to assessing developmental changes from a network perspective, research has begun to delineate different factors that affect network formation, such as structural and functional brain development, age, puberty onset, performance differences, individual differences, genes, etc. While this work had begun for other domains of cognition, such as word generation or intelligence (Brown et al. 2005; Shaw et al., 2008), there is still a need to highlight the importance of using such a systematic approach in developmental neuroimaging studies in order to allow for comparability across studies and to minimize confounds. The current study is one of the first studies to address these issues for face-processing research. In turn, this approach may also allow us to reconcile apparently contradictory findings, such as the ones reported above.

Materials and Methods

Participants

A total of 48 participants aged 7–37 years (mean age 16.1, SD = 7.7; 26 females; 2 left-handed) took part in this fMRI study. An additional 11 children were tested in the age range of 7–11 years, but excluded from further analysis due to early termination of the scanning session (5 participants) or excessive motion during the scans. Note that none of the adults or children included in this data set exhibited >3-mm deviation in the centre of mass in any direction.

We also conducted an additional, age group-specific analysis of the behavioral results (for both the in- and out-of-scanner tasks), in which the sample was divided into 3 age groups: 20 children, 7–11 year olds (mean age = 9.9 years, SD = 1.3 years; 10 females), 14 adolescents, 12–17 year olds (mean age = 14.0 years, SD = 1.7 years, 8 females) and 14 adults (mean age = 27.0 years, SD = 4.2 years, 8 females). All participants had normal or corrected to normal vision. The study was approved by the local ethics committee and informed consent was obtained from all participants (or the primary caregiver in the case of minors) prior to testing. We note that part of the functional activation data from the child and adult age groups has previously been published (Cohen Kadosh et al. 2011). However, the structural data and the analyses in the current paper are novel.

Stimuli

fMRI Tasks

A stimulus set was created from 27 color photographs taken under standard lighting conditions (3 women × 3 emotional expressions (happy, angry, neutral) × 3 directions of eye-gaze (right, left, direct)). All pictures were cropped to show the face in frontal view and to exclude the neck and haircut of the person; any differences in the face stimuli were adjusted by comparing the means and standard deviations in the histograms for each RGB value using Adobe Photoshop 7 (mean/SD: R = 52.2/3.3; G = 36.2/1.6; B = 24.4/1.7) (see Cohen Kadosh et al. 2010, for the same procedure). The stimulus size of 6.3 × 7 cm corresponded to a visual angle of 9.5° × 11° when presented to the participants in the scanner. The stimuli were presented on a dark gray background of a computer screen. Experimental procedure and stimulus presentation were controlled using Matlab (Mathworks, MA).

Participants were required to detect a specified target in a stream of consecutively presented standard stimuli: in the Identity task, participants had to detect a specific identity; in the Expression task, a happy face; in the Gaze task, a face with direct gaze (Fig. 1). Each task was presented in a separate block. The experiment therefore consisted of 3 consecutive blocks, and block order was counterbalanced across participants. At the beginning of each task, a 10 s instruction cue informed participants of the relevant dimension to attend to (“Identity task,” “Expression task,” or “Gaze task”). Each stimulus was presented for 500 ms, with an inter-stimulus interval of 1 s. The standard stimuli were arranged in mini-blocks of approximately 15 s, containing on average 9 standard stimuli (SD ± 2 standard stimuli) and 1 target stimulus. Target stimuli occurred in a pseudo-randomized order in the mini-blocks, but targets never appeared before the presentation of at least 5 standard stimuli. Each block consisted of 30 mini-blocks. Finally, 6 periods of 10 s of a blank screen baseline condition were inserted into each block, at randomly selected breaks between mini-blocks. The same images were used for all 3 tasks. Since stimuli were presented in mini-blocks the 2 other,

task-irrelevant dimensions for each task were varied systematically and presented for an equal amount of times to ensure that the repetitions in task-irrelevant face aspects would be identical across the 3 tasks.

Out-of-Scanner Tasks

As our in-scanner tasks were designed so that the performance across the entire age range would be matched, we also conducted 3 more demanding out-of-scanner tasks [the Benton Facial Recognition test, an Expression categorization task and a Gaze direction detection task (Cohen Kadosh et al. 2011)] to assess developmental differences in processing task performance for each face aspect.

Benton Facial Recognition Test

The Benton facial recognition test is widely used in clinical and research settings to diagnose face recognition abilities in adults following brain injury. The paper and pencil test consisted of a cardboard book with 27 pages and a scoring sheet. On each page of the test book, 6 black and white photographs were shown of either male or female faces. Participants were required to recognize a specific target face, which was shown amongst 5 distracter stimuli on the opposite page. As the test progresses, it became increasingly difficult to recognize the target face amongst the distracter stimuli, as the heads are rotated and photographic light effects cast shadows. The test was self-paced and participants were encouraged to turn over the pages after settling on a particular standard stimulus. The short version of the test took no more than 5 min to administer for all age groups.

The Expression Categorization Task

The Expression categorization task was created to assess age-dependent differences in the categorization of emotional expressions. Twenty color photographs of female and male students were chosen from the Battery of Japanese and Caucasian Facial Expressions of Emotion (JACFEE) and Neutral Faces (JACNeuF) by Matsumoto and Ekman (1988), which is an updated version of the widely used Ekman faces (Ekman and Friesen 1976) and has been cross-culturally validated. Note that only Caucasian faces were used for the present study. The photographs were presented in a random order, depicting 4 happy, angry, sad, fearful, and neutral faces. The task was self-paced and the photographs were presented individually on a computer screen against a black background for an unlimited amount of time. Participants had to categorize each photograph and testing time did not exceed 5 min for all age groups.

Gaze Direction Detection Task

The Gaze direction detection task was constructed to assess developmental differences in gaze direction detection that vary as a function of head orientation. The task was based on a version of the Pegs task (Leekam et al. 1997) but was modified as outlined: A stimulus set was

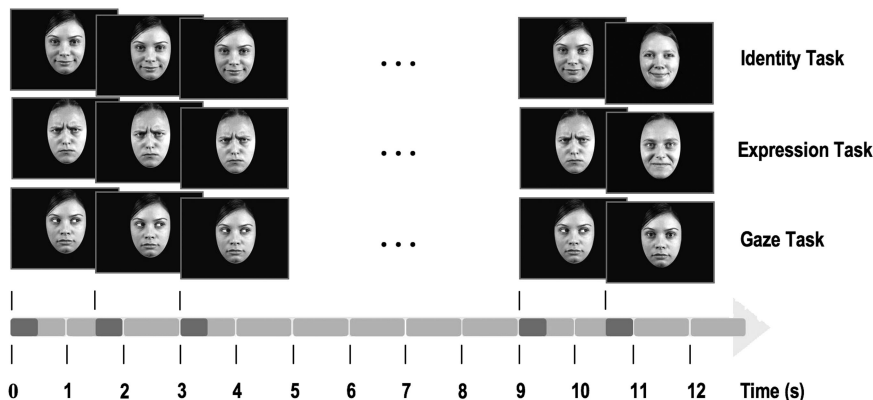


Figure 1. Example trials from the 3 fMRI target detection tasks (Identity task, Expression task, and Gaze task). The target stimulus is presented on the right for illustrative purposes only, as it could occur at any time point within the presentation block.

created of 18 color photographs, which depicted a female model facing 3 different rods. The different color rods (red, blue, and yellow) were spaced either 20° or 10° apart and the model's eyes were directed to 1 of the rods. In addition, in half of the pictures the model's head was rotated by either 10° or 20° from the centre. Each test item was shown against a dark background on a computer screen and participants had to name the color of the rod that the model was looking at. The test was self-paced and the experimenter noted the responses on a separate response sheet. For both child and adult participants, testing times did not exceed 3 min.

fMRI Data Acquisition and Data Analysis

A Siemens 1.5T Avanto MRI scanner (Siemens, Erlangen, Germany) was used to acquire gradient echo-planar images (29 oblique slices covering the occipital, temporal, and most of the parietal lobes; TR = 2500 ms; TE = 50 ms; flip angle = 90°; field-of-view = 192 × 192 mm; voxel size: 3.0 × 3.0 × 4.5 mm). Following the functional scans, a T₁-weighted structural image (1 mm³ resolution) was acquired for coregistration and display of the functional data and for the voxel-based morphometry (VBM) analysis.

Our fMRI analysis assessed overall task differences [3 regressors for the 3 tasks, as well as the relationship between the covariates for age and accuracy rates (both fMRI tasks and out-of-scanner tasks)] and these tasks. In a first step we therefore contrasted overall task activation for each task and then conducted separate analyses, which independently assessed age and performance effects that are specific for each of the 3 tasks. Last, we related specific age or proficiency effects to structural effects using VBM analysis.

Data were analyzed using SPM8 (Wellcome Department of Imaging Neuroscience, London; <http://www.fil.ion.ucl.ac.uk/spm>). The analysis followed the same steps as in a previous work that employed the same paradigm with adult participants (Cohen Kadosh et al. 2010). The 3 in-scanner tasks were run in a randomized order in 3 consecutive blocks during the same scanning session. For each block, we used an auto-align procedure to keep slice positioning consistent for all blocks. For the data preprocessing, the EPI volumes were spatially realigned to an early image within each block using a least-square approach and the 6 rigid body parameter to correct for movement artefacts. The EPI volumes were then normalized to the Montreal Neurological Institute (MNI) standard space (Ashburner and Friston 2003a, 2003b) and smoothed using an 8-mm full-width, half-maximum Gaussian kernel.

At the first (single-subject) level, a general linear model (GLM) was computed for each participant, with 6 regressors total. These modeled each task (identity, expression, gaze) as well as the presence of a particular target (happy face in the emotion task, a particular person in the identity task, and a direct gaze in the gaze task). For the present study, we report only results for the standard rather than the target trials, as the response to the target trials involves confounding attentional and motor-related effects. Each mini-block was modeled as an epoch of 12 s and convolved with a canonical hemodynamic response function. To account for residual movement artifacts, the model also included 6 further regressors representing the rigid-body parameters estimated during realignment. Voxel-wise parameter estimates for these regressors were obtained by restricted maximum-likelihood estimation, using a temporal high-pass filter (cut-off 128 s) to remove low-frequency drifts, and modeling temporal autocorrelation across scans with an AR(1) process.

The images from the individual analysis were then input into a group GLM with 3 regressors for the 3 tasks (i.e. β_1 *(Identity task); β_2 *(Expression task); β_3 *(Gaze task)), plus 3 covariate vectors for: (i) age in months; (ii) mean accuracy rates for the 3 fMRI tasks and (iii) the mean accuracy for the out-of-scanner tasks. Note that the 3 out-of-scanner tasks were combined into 1 covariate where the Benton test accuracy rates was covaried with the activation in the Identity task [β_{10} *(Identity task × Out-of-scanner Benton task)], the Expression categorization task accuracies was covaried with the activation in the Expression task [β_{11} *(Expression task × Out-of-scanner Expression categorization task)] and the Gaze direction detection task accuracies was covaried with the activation in the Gaze task [β_{12} *(Gaze task ×

Out-of-scanner Gaze direction detection task)]. The inclusion of these 3 covariate vectors allowed us to assess age effects in the 3 tasks while simultaneously controlling for task performance effects, and vice versa (see Table 1 for all regressors and contrasts). Note that despite that fact that there were no overall behavioral difference in the in-scanner tasks (as intended), we nevertheless chose to include them in the analysis of the age effects in order to control for differences in cognitive strategy at different age points.

VBM Analysis

A VBM analysis (Ashburner and Friston 2000) was conducted to investigate developmental changes in gray and WM tissue volumes in specific regions-of-interest (ROIs) in all participants using the SPM8 VBM8 toolbox (<http://dbm.neuro.uni-jena.de/vbm/>). First, each participant's structural T₁ image was normalized to the standard T₁ MNI template. Then segmentation was performed using prior tissue probability maps and all scans were segmented into cerebro-spinal fluid and gray and WM, using Jacobian determinants for the nonlinear warping modulation. All images were smoothed with an 8 mm full-width, half-maximum Gaussian kernel. We extracted the mean gray and WM adjusted volumes in 6 mm radius ROIs for the brain regions showing significant task differences in the assessment of the task × covariate interactions (Table 3). Using MarsBaR toolbox (<http://marsbar.sourceforge.net/>), each ROI was centered on the peak voxel of an orthogonal contrast (all conditions against baseline) in order to avoid any dependency in our statistical analysis. The gray and WM-adjusted volumes were then included in a multiple regression analysis whether differences in underlying brain structure would predict linear or nonlinear changes in brain activation as a function of age or task performance on the tasks. Note that we excluded outliers (± 2 standard deviations) in our ROI analysis.

Results

Behavioral Data

fMRI Tasks

For the analysis of the behavioral results, we compared accuracy and reaction times (RT) across the entire age range in the 3 tasks. Across all ages, RT differed between the 3 tasks [main effect of task: $F(2, 94) = 5.35, P = 0.006$]; the main effect of task was due to longer RTs in the Expression task in comparison to the identity task [$t(47) = 3.28, P = 0.002$]. A similar trend was seen in the Expression task in comparison to the Gaze task [$t(47) = 1.94, p = 0.058$]. Accuracy did not differ between the 3 tasks [main effect of task: $F(2, 94) = 0.60, P = 0.52$; see also Table 2 for all behavioral results). Across all participants, RTs and accuracy rates were not correlated, thus excluding the possibility of a speed-accuracy trade-off [Spearman's $\rho(48) = -0.05, P = 0.70$].

We also conducted an analysis of the behavioral results with the entire sample divided into 3 age groups (see Methods). A mixed model repeated-measures ANOVA was conducted for RT with within-subject factor task (3 levels: identity, expression, and gaze) and between-subject factor age group (3 levels: 7–11 years, 12–17 years, and adults). Only the main effect of task was significant [$F(2,90) = 4.35, P = 0.016$], while neither the main effect of age group nor the interaction between task and age group was significant [all $F < 1.0$, all $P > 0.4$]. Accuracy was analyzed in the same way, and none of the main effects or the interaction was significant [all $F < 2.5$, all $P > 0.08$] (see Table 2 for all effects). This finding was further supported by an analysis which looked at the behavioral results separately for each task which further established that there were no significant main effects of age

Table 1
fMRI design regressors and contrasts

Δ % BOLD=	$\beta 1^*$ (ID task)	$\beta 2^*$ (E \times P task)	$\beta 3^*$ (GA task)	$\beta 4^*$ (Age \times ID task)	$\beta 5^*$ (Age \times EXP task)	$\beta 6^*$ (Age \times GA task)	$\beta 7^*$ (Acc IN-scanner \times ID task)	$\beta 8^*$ (Acc IN-scanner \times EXP task)	$\beta 9^*$ (Acc IN-scanner \times GA task)	$\beta 10^*$ (Acc OUT-scanner \times ID task)	$\beta 11^*$ (Acc OUT-scanner \times EXP task)	$\beta 12^*$ (Acc OUT-scanner \times GA task)
Main effect ID task	+	-	-									
Main effect EXP task	-	+	-									
Main effect GA task	-	-	+									
ID task: Age effects				+	-	-						
EXP task: Age effects				-	+	-						
GA task: Age effects				-	-	+						
ID task: Acc effects							+	-	-			
EXP task: Acc effects							-	+	-			
GA task: Acc effects							-	-	+			
ID task: Acc effects										+	-	-
EXP task: Acc effects										-	+	-
GA task: Acc effects										-	-	+

Acc, accuracy; EXP, expression; GA, gaze; ID, identity; IN, in-scanner tasks; OUT, out-of-scanner tasks.

for either task [all $F < 2.85$, all $P > 0.07$]. In addition, we found no evidence of a speed-accuracy trade-off when analyzing the behavioral results for each age group in each task [all $rho < 0.38$, all $p > 0.18$] (see Supplementary Table S2 for all additional analyses).

Out-of-Scanner Tasks

For the analysis of the Benton test, the mean scores for each participant were entered into an ANOVA with between-subject factor age group (7–11 years, 12–17 years, adults). The main effect of age was significant [$F(2,43) = 10.08$, $P < 0.001$]. Simple effects tests showed that this was due to significantly higher accuracy for the adult participants in comparison to the children and adolescents [children: 22.2% errors; adolescents: 18.4% errors; adults: 6.7% errors; adults vs. children: $t(32) = 4.67$, $P < 0.001$; adults vs. adolescents: ($t(24) = 3.16$, $P = 0.004$)]. The children and adolescents did not differ in their accuracy ($t(30) = 0.89$, $P = 0.376$).

For the Expression categorization test, the correct categorizations were calculated for each participant and were entered into an ANOVA with between-subject factor age (children, adolescents, and adults). The main effect of age approached significance [$F(2,43) = 3.08$, $P = 0.056$]. Planned comparisons revealed that the children made significantly more mistakes

than the adolescents (children: 9.8% errors; adolescents: 2.9% errors; $t(30) = 2.32$, $P = 0.027$), but not the adults (children: 9.8% errors; adults: 5.7% errors; $t(32) = 1.35$, $P = 0.188$). The adolescents did not differ significantly from the adult group ($t(24) = 1.18$, $P = 0.248$).

For the Gaze detection task, the mean accuracy scores were analyzed using an ANOVA with between-subject factor age group (children, adolescents, and adults). The main effect of age was significant [$F(2,43) = 3.59$, $P = 0.036$]; this was due to significantly lower accuracy in children compared with adults (children: 12.8% errors; adults: 5.2% errors; $t(32) = 2.50$, $P = 0.018$), but not between the children and adolescents (children: 12.8% errors; adolescents: 7.9% errors; $t(30) = 1.42$, $P = 0.166$) or the adolescents and adults ($t(24) = 1.11$, $P = 0.277$).

Neuroimaging Data

In a first step, we contrasted the 3 face tasks with each other (e.g. Identity task minus Expression task and Gaze task) across the entire group, to assess task-specific activation at the whole-brain level. This analysis step enabled us to look at differential brain activation that was significantly stronger in 1 task in comparison to the 2 other tasks. We note that this differential activation is in addition to the commonly reported

Table 2

Behavioral results for the fMRI tasks and the out-of-scanner tasks. Bold font indicates significant effects

fMRI tasks	Identity task	Expression task	Gaze task	Effect
	Accuracy rates percentage and standard deviation for children/teens/adults			Main effect of task [$F(2,88) = 2.57, P = 0.082$] Main effect of age group [$F(2,44) = 1.28, P = 0.288$]
	87.5/82.3/89.3 23.0/28.4/15.5	79.0/75.9/91.1 12.9/28.2/9.0	85.3/88.2/92.3 12.7/25.9/12.7	
	RTs (average and standard deviation for children/teens/adults)			Interaction task \times age group [$F(4,88) = 0.931, P = 0.441$]
	811/796/929 310/95/195	928/838/979 267/84/189	869/822/939 261/123/165	Main effect of task [$F(2,90) = 4.35, P = 0.016$]
				Main effect of age group [$F(2,45) = 0.616', P = 0.652$] Interaction task \times age group [$F(4,90) = 0.931, P = 0.441$]
Out-of-scanner tasks	Benton test 77.8/81.6/91.3 4.7/5.0/3.3	Expression test	Gaze test	Main effect of age group [$F(2,43) = 10.08, P < 0.001$]
		90.2/97.1/94.3 9.5/4.5/7.0		Main effect of age group [$F(2,43) = 3.083, P = 0.056$]
			87.2/92.1/94.8 10.5/7.3/5.0	Main effect of age group [$F(2,43) = 3.594, P = 0.036$]

activation of face regions in the occipital-temporal face network (Ishai 2008; Cohen Kadosh et al. 2011) that was found when each task was contrasted against a baseline condition (see Fig. 2). We used these particular contrasts [for the Identity task for example, the beta weights were [Identity task 2 – (Expression task 1 + Gaze task 1)]] to differentiate the 3 tasks from each other. This approach was chosen, as we were particularly interested in singling out those brain regions that are special for each task (i.e. not shared between tasks), and then to systematically assess what drives the change in BOLD signal in these brain regions. This represents the opposite approach to the analysis depicted in Figure 2, which shows the *overlap* in activation for the 3 tasks.

We found that both the Identity and the Expression tasks yielded areas of specific greater activation when each was compared with the other 2 tasks (Table 3). There was more activation during the Identity task than in expression or gaze over a widespread set of regions over the occipital, temporal, and frontal lobes, as well as in the cerebellum. The Expression task-specific activation was restricted to portions of the frontal lobe and the caudate nucleus (see Table 3).

Separating Age Effects From Task Performance Effects

In a second step, we then assessed to what extent the observed differences in task-specific activation found in the previous step could be further differentiated into: (a) *age-dependent differences in task activation*, that is, brain regions in which activation in the 3 tasks varies with age (while controlling for task performance); and (b) *performance-dependent differences in task activation* (based on the accuracy rates) for the 3 fMRI tasks and the 3 out-of-scanner tasks (while controlling for age effects).

Age-Dependent Task Differences (Controlling for Task Performance Differences)

In this analysis, we looked at age effects that were specific to each fMRI task. By systematically contrasting the 3 tasks with each other (see also Table 1 for an overview of all contrasts), we found task-specific age differences for the Expression task in the left FG and the right inferior temporal gyrus (ITG), as well as the cerebellum (see Fig. 3, Tables 4 and 5). We then

used linear and nonlinear multiple regression analyses and found that the observed age effects on fMRI activation in the FG and the ITG were associated with an age-related increase in WM volume, as well as changes in gray matter (GM) volume in the FG (FG: [$R^2 = 0.50$; GM: $t(44) = -0.21, P = 0.042$; WM: $t(44) = 6.01, P < 0.001$]; ITG: [$R^2 = 0.20$; GM: $t(44) = -0.022, P = 0.982$; WM: $t(44) = 2.82, P = 0.007$], regression coefficients indicate BOLD and GM/WM relationships, for curve fitting results see Tables 4 and 5). In both FG and ITG, WM volume increased linearly with increased functional responses with greater age, whereas gray matter followed a quadratic trajectory in the FG.

For the Gaze task, we found a significant age effect (i.e. increase with age) in the left supramarginal gyrus, which was not related to changes in brain morphology [$R^2 = 0.01$; GM: $t(44) = -0.32, P = 0.75$; WM: $t(44) = 0.79, P = 0.43$].

The Identity task did not yield significant age effects.

Task Performance-Dependent Task Differences (Controlling for Age Differences)

Changes in brain activation as a function of processing task performance for the 3 face aspects were analyzed separately for the accuracy rates in the in-scanner and out-of-scanner tasks [e.g. $\beta 7^*(\text{Identity task} \times \text{in-scanner Identity task accuracy})$, see Table 2 for all regressors and contrasts]. The different performance effects for each task are listed in Table 3. See also Figure 4 for an illustration of activation as a function of performance in the Identity task. We found performance differences for all 3 face aspects, as described below.

The Identity task \times in-scanner performance effect showed effects on activation in the right IOG, the left medial occipital gyrus and the bilateral ITG. Task performance effects in the Identity task \times out-of-scanner Benton task were widespread, modulating activation in regions in the face network and beyond (Table 3).

The Expression task \times in-scanner performance effects on activation were found in the cerebellum. Last, only the bilateral insula and the rolandic operculum exhibited differential activation related to the Gaze task \times out-of-scanner Gaze detection task interaction.

Multiple regression analysis for those ROIs that fell within the core and extended face network (Haxby et al. 2000;

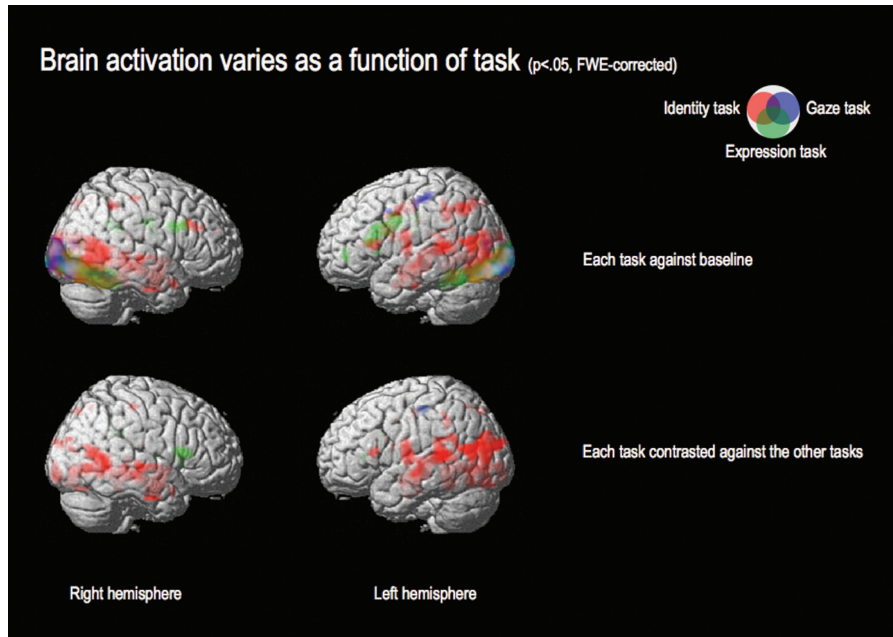


Figure 2. Brain networks exhibiting activation for the 3 fMRI tasks. Upper row: activation for each task against baseline. Lower row: activation for each task minus the combined activation for the other 2 tasks [e.g. identity task minus (expression plus gaze task)]. All maps are $P < 0.05$ Family-Wise-Error (FWE) corrected for peak height.

Fairhall and Ishai 2007; Ishai 2008; Tables 4 and 5) showed that the IFG activation in the out-of-scanner Benton task was associated with WM changes that followed an inverse trajectory [$R^2 = 0.22$; GM: $t(37) = -1.50$, $P = 0.143$; WM: $t(37) = 2.19$, $P = 0.035$], whereas activation changes in the insula in the out-of-scanner Gaze detection task was related to linear age-related increase in GM [$R^2 = 0.17$; GM: $t(43) = 2.88$, $P = 0.006$; WM: $t(43) = 0.254$, $P = 0.801$] (Table 5).

Discussion

This study assessed the developmental trajectory of the neural processing of 3 aspects of face processing from childhood through adulthood, and investigated whether these developmental effects in face-processing-related brain activity were associated with changes in task performance, chronological age, or brain structure. While age-dependent changes in activation were primarily observed in occipito-temporo-parietal regions, changes in activation related to task performance were widespread across occipital and temporal cortex and the limbic system, with additional frontal loci for the Identity task. Finally, both age and performance effects in the out-of-scanner tasks were associated with changes in underlying gray and WM volume.

While the in-scanner tasks were designed with the aim that participants would use task-specific cognitive strategies for each face aspect, they were also kept deliberately simple to yield similar performance levels between the 3 age groups. However, our more challenging out-of-scanner face-processing tasks showed clear developmental differences. Children performed less accurately at processing all 3 face aspects and adolescents showed lower task performance for recognizing faces than did adults.

Our fMRI results show that all 3 in-scanner tasks reliably activated the established core face-network regions (Fig. 2)

(Haxby et al. 2000; Fairhall and Ishai 2007; Cohen Kadosh et al. 2010, 2011). Further, our analysis also revealed differential patterns of behavior and neural activation for all these tasks beyond mid-childhood which we will discuss in detail below.

Expression and Gaze Processing Show Specific Age Effects

The age-dependent effects in the Expression task were concentrated in brain regions that support face emotion processing in the mature brain, including the FG and the adjacent ITG (Haxby et al. 2000; Cohen Kadosh et al. 2010). Activation in both the FG and the ITG in the Expression task was best fitted with a logarithmic developmental trajectory (Fig. 3). Specifically, an initially increasing response to facial expression was followed by a plateau. This suggests that this response pattern becomes increasingly specialized with age, that is, selectively activated in a particular task context only (Johnson et al. 2009; Cantlon et al. 2011). For the Gaze task, age effects were also found in the left supramarginal gyrus, a region that has been shown in recent modeling studies to be part of an extended cortical eye gaze network (Nummenmaa et al. 2010). The findings of developmental changes in neural responses in the core face-network regions are also in line with the predictions made by theoretical frameworks for human functional brain development, such as neural re-use or Interactive Specialization models (Johnson 2001, 2011; Anderson 2007a, 2007b).

For the Expression task, age-dependent activation in FG and ITG brain regions was accompanied by structural brain changes, in particular an increase in WM (Fig. 3). This finding runs in line with longitudinal MRI studies that found gray and WM changes in the occipital and temporal lobe beyond the second decade of life (Giedd et al. 1999; Sowell et al. 2004; Raznahan et al. 2011; Hedman et al. 2011). The observed

Table 3Main effects for task, and effects for age and proficiency covariates in each task (FWE, $P < 0.05$, >5 contiguous voxels)

Effect	Brain regions (L/R)	MNI (x, y, z)	Approx. Brodman area	Cluster size	t	
<i>Identity task (Expression and Gaze task)</i>						
	L superior temporal gyrus	-66, -42, 12	22	8853	9.45	
	R lingual gyrus	15, -96, -9	19		7.73	
	Cerebellum	-6, -81, -15	-		7.97	
	R lingual gyrus	18, -81, -6	19		7.25	
	L medial occipital gyrus	-45, -81, 6	18		6.91	
	R middle temporal gyrus	-51, -69, 15	21		7.49	
	L FG	-24, -69, -12	20		6.05	
	R medial occipital gyrus	57, -66, 12	18		6.66	
	R V1	30, -60, 0	17		7.16	
	L middle temporal gyrus	-60, -60, 13	21		5.97	
	R middle temporal gyrus	60, -51, 0	21		6.08	
	L lingual gyrus	-24, -48, -3	19		7.08	
	L FG	-18, -42, -12	20		7.22	
	L superior temporal gyrus	-51, -42, 12	22		7.04	
	R superior temporal gyrus	60, -21, 0	22		7.18	
	R hippocampus	39, -21, -9	28		7.11	
	L middle temporal gyrus	-48, -21, -6	21		6.03	
	R ITG	51, -12, -30	20		6.57	
	L Heschls gyrus	-60, -9, 9	41		6.65	
	R superior temporal gyrus	54, -9, 0	22		6.2	
	R parahippocampal gyrus	33, -6, -30	20		8.71	
	R hippocampus	21, -6, -13	28		7.2	
	R pallidum	21, -3, -3	-		7.43	
	R precuneus	3, -78, 51	7		234	5.45
	R middle cingulate cortex	0, -39, 45	-		4.61	
	R precentral gyrus	21, -27, 57	4		85	5.11
	R precentral gyrus	33, -27, 54	4		4.96	
	L middle frontal gyrus	-24, -9, 49	9/10		85	5.08
	L IFG	-39, 9, 24	47		4.72	
Identity task: Age effects						
No significant activation clusters						
Identity task: In-scanner task proficiency effects						
	R IOG	51, -75, -3	19	234	6.13	
	R ITG	60, -60, -6	20		5.66	
	R ITG	44, -44, -12	20		5.01	
	L medial occipital gyrus	-21, -99, 3	18	181	5.55	
Identity task: Out-of-scanner Benton test proficiency effects						
	R parahippocampal gyrus	33, -6, -30	20	8643	9.23	
	R lingual gyrus	15, -96, -9	19		8.57	
	Cerebellum	-6, -81, -15	-		7.25	
	L medial occipital gyrus	-45, -81, 6	18		6.24	
	L IOG	-42, -81, -9	19		5.93	
	L middle temporal gyrus	-54, -72, 9	21		7.58	
	L FG	-39, -72, -17	20		6.13	
	R middle temporal gyrus	63, -54, 6	21		6.13	
	L FG	-30, -51, -18	20		6.23	
	Cerebellum	-18, -48, -18	-		6.05	
	Cerebellum	3, -45, -15	-		6.28	
	L inferior parietal lobe	-42, -45, 39	40		6.22	
	R inferior parietal lobe	48, -45, 48	19		6.02	
	L middle temporal gyrus	-66, -42, 9	21		8.34	
	R supramarginal gyrus	51, -42, 45	40		6.15	
	R hippocampus	36, -21, -9	28		6.03	
	R hippocampus	21, -6, -15	28		6.68	
	L IFG	-39, 9, 24	47		6.85	
	R medial temporal pole	51, 9, 24	38		6.05	
	IFG	51, 24, 30	47		111	5.31
Expression task (Identity and Gaze task)						
	R IFG	45, 18, 12	47		458	6.45
	R caudate nucleus	18, 18, 3	-			5.36
	L IFG	-33, 30, 9	47	199		4.94
Expression task: Age effects						
	L FG	-30, -33, -24	20	59	5.2	
	Cerebellum	33, -51, -24	-	68	4.63	
	R ITG	48, -57, -12	20	78	4.28	
Expression task: In-scanner task proficiency effects						
	Cerebellum	3, -42, -15	-	60	5.08	
	Cerebellum	12, -39, -18	-		4.61	
Expression task: Out-of-scanner proficiency effects expression categorization task						
No significant activation clusters						
Gaze task (Identity and Expression task)						
No significant activation clusters						
Gaze task: Age effects						
	Supramarginal gyrus	-42, -33, 24	40	64	4.6	
Gaze task: In-scanner task proficiency effects						
No significant activation clusters						
Gaze task: Out-of-scanner proficiency effects gaze direction task						
	L insula	-27, 30, 9	13	104	4.98	
	R insula	27, 33, 12	13	68	4.80	
	R rolandic operculum	51, 3, 9	43	65	4.08	

L/R, Left or right hemisphere; MNI, Montreal Neurological Institute.

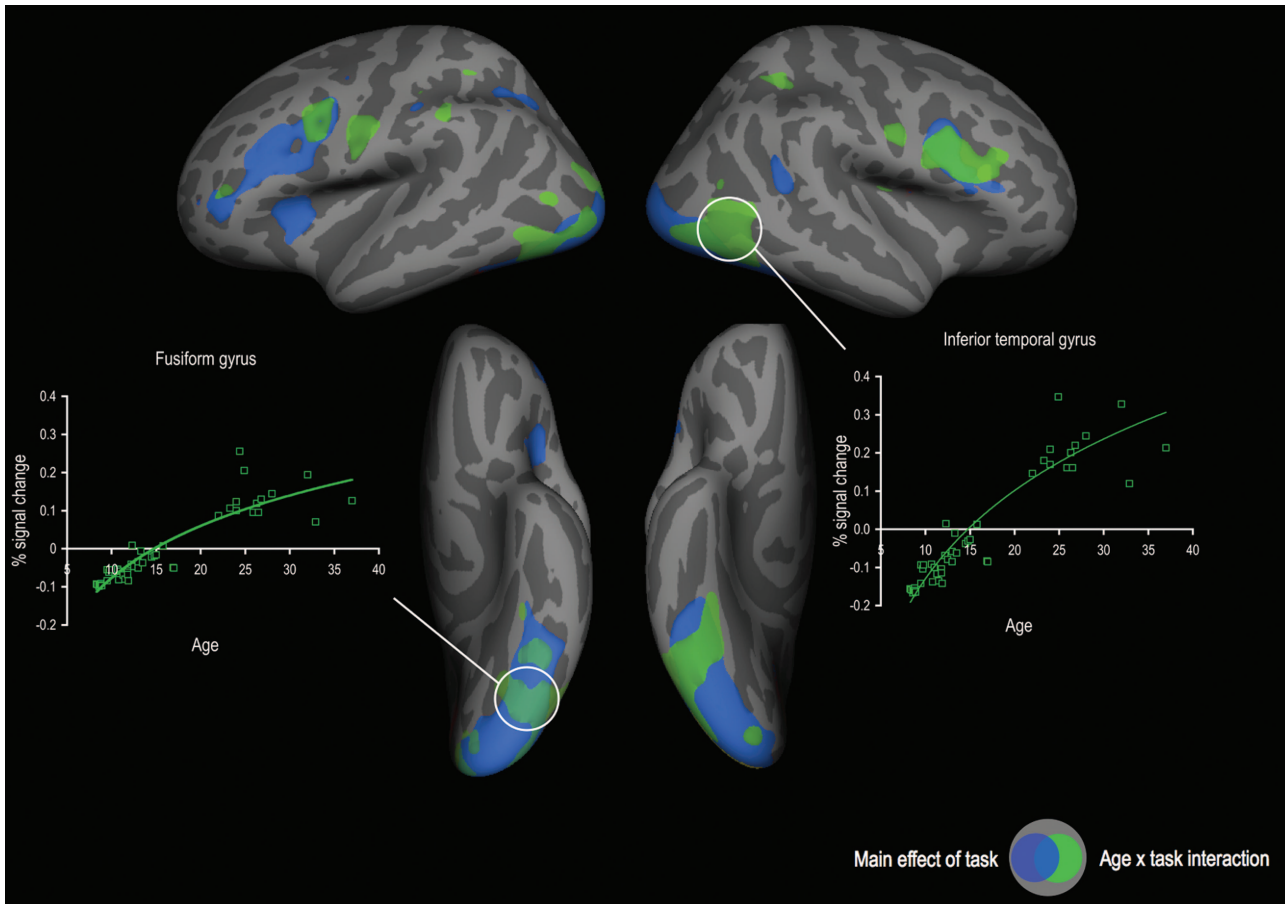


Figure 3. Brain activation as a function of task and age in the Expression task. Activation for the main effect of task [β_2^* (Expression task) – (β_1^* (Identity task) + β_3^* (Gaze task))] is shown in blue, and activation in brain regions that can be explained by the concurrent interaction between task \times age [β_5^* (Expression task \times Age)] is shown in green. For 2 selected brain regions, changes in activation are shown as a function of age. Note that we controlled for outliers (± 2 standard deviations) in this analysis. Map threshold is $P < 0.001$ uncorrected for peak height, extent threshold $P < 0.05$, corrected. Both hemispheres are shown in a lateral (top) and inferior (bottom) view. The right hemisphere is depicted on the right.

Effect	Brain regions	MNI (x, y, z)	Cluster size	T	VBM analysis, beta values for grey matter (GM), WM
Table 4 Voxel-based morphometry (VBM) analysis for specific brain regions within the core and extended face network. (FWE, $P < 0.05$, >5 contiguous voxels)					
<i>Proficiency effects in the In-scanner Identity task</i>					
	IOG	51, -75, -3	234	6.13	$R^2 = 0.02$; GM: $t(41) = -0.802, P = 0.427$; WM: $t(41) = -0.107, P = 0.915$
	ITG	60, -60, -6		5.66	$R^2 = 0.06$; GM: $t(41) = 1.33, P = 0.190$; WM: $t(41) = -1.06, P = 0.295$
<i>Proficiency effects in Out-of-scanner Benton test</i>					
	FG	-30, -51, -18		6.23	$R^2 = 0.04$; GM: $t(37) = -0.991, P = 0.329$; WM: $t(37) = 1.01, P = 0.321$
	IOG	-42, -81, -9		5.93	$R^2 = 0.01$; GM: $t(38) = -0.694, P = 0.492$; WM: $t(38) = 0.362, P = 0.720$
	IFG	51, 24, 30	111	5.31	$R^2 = 0.22$; GM: $t(37) = -1.50, P = 0.143$; WM: $t(37) = 2.19, P = 0.035$
<i>Age effects in the In-scanner Expression task</i>					
	FG	-30, -33, -24	59	5.2	$R^2 = 0.50$; GM: $t(44) = -0.21, P = 0.042$; WM: $t(44) = 6.01, P < 0.001$
	ITG	48, -57, -12	78	4.28	$R^2 = 0.20$; GM: $t(44) = -0.022, P = 0.982$; WM: $t(44) = 2.82, P = 0.007$
<i>Age effects in the In-scanner Gaze task</i>					
	Supramarginal gyrus	-42, -33, 24	64	4.6	$R^2 = 0.01$; GM: $t(44) = -0.320, P = 0.751$; WM: $t(44) = 0.794, P = 0.432$
<i>Proficiency effects in Out-of-scanner Gaze direction task</i>					
	Insula	-27, 30, 9	104	4.98	$R^2 = 0.17$; GM: $t(43) = 2.88, P = 0.006$; WM: $t(43) = 0.254, P = 0.801$

Bold font indicates significant effects.
MNI, Montreal Neurological Institute.

dynamic relationship (an initial increase, followed by a subsequent plateau) between developmental BOLD change in FG and ITG along with changes in both gray and WM might speculatively be the result of the concurrent increase in myelination and synaptic pruning in these brain regions (Huttenlocher 1984; Bourgeois and Rakic 1993; Schmithorst and Yuan 2010; Petanjek et al. 2011).

Changes in Neural Activity Associated with Task Performance

In contrast to the age effects discussed above, all 3 tasks showed patterns of brain activity that were linked to task performance, and particularly for identity processing in both the in-scanner and out-of-scanner tasks. These performance effects were associated with widespread activation patterns,

Table 5

Trend analysis for functional responses in specific brain regions within the core and extended face network

Brain regions	MNI	BOLD vs. GM	BOLD vs. WM	BOLD vs. Age	BOLD vs. Performance
<i>Proficiency effects in the In-scanner Identity task</i>					
IOG	51, -75, -3	No relationship	No relationship	Not tested	Linear: [$R^2 = 0.072$; $F(1,40) = 3.12, P = 0.085$]
ITG	60, -60, -6	No relationship	No relationship	Not tested	Linear: [$R^2 = 0.072$; $F(1,40) = 3.12, P = 0.085$]
<i>Proficiency effects in Out-of-scanner Benton test</i>					
FG	-30, -51, -18	No relationship	No relationship	Not tested	Quadratic: [$R^2 = 0.043$; $F(2,38) = 0.847, P = 0.437$]
IOG	-42, -81, -9	No relationship	No relationship	Not tested	Cubic: [$R^2 = 0.083$; $F(3,36) = 1.09, P = 0.366$]
IFG	51, 24, 30	No relationship	Inverse: [$R^2 = 0.20$; $F(1,37) = 9.24, P = 0.004$]	Not tested	Cubic: [$R^2 = 0.083$; $F(3,36) = 1.09, P = 0.366$]
<i>Age effects in the Expression task</i>					
FG	-30, -33, -24	Quadratic: [$R^2 = 0.18$; $F(2,42) = 4.50, P = 0.017$]	Linear: [$R^2 = 0.45$; $F(1,44) = 36.5, P < 0.001$]	Logarithmic: [$R^2 = 0.83$; $F(1,46) = 218, P < 0.001$]	Not tested
ITG	48, -57, -12	No relationship	Linear: [$R^2 = 0.121$; $F(1,44) = 6.067, P = 0.018$]	Logarithmic: [$R^2 = 0.83$; $F(1,46) = 218, P < 0.001$]	Not tested
<i>Age effects in the In-scanner Gaze task</i>					
Supramarginal gyrus	-42, -33, 24	No relationship	No relationship	Inverse: [$R^2 = 0.13$; $F(1,43) = 6.44, P = 0.015$]	Not tested
<i>Proficiency effects in Out-of-scanner Gaze direction task</i>					
Insula	-27, 30, 9	Linear [$R^2 = 0.17$; $F(1,41) = 8.45, P = 0.006$]	No relationship	Not tested	Quadratic: [$R^2 = 0.09$; $F(2,41) = 2.03, P = 0.145$]

Bold font indicates significant effects.

GM, grey matter; WM, white matter.

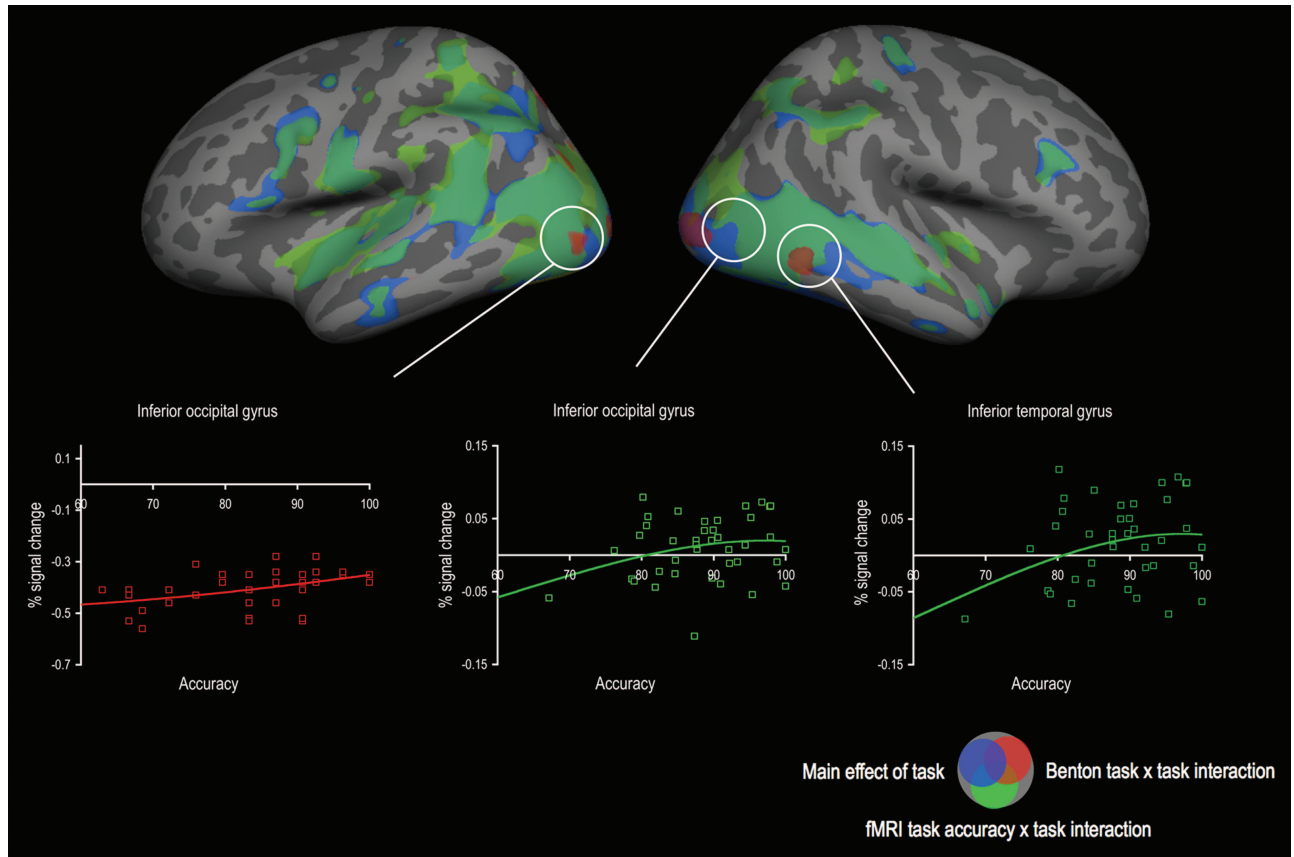


Figure 4. Brain activation as a function of task and task performance in the Identity task. Activation for the main effect of task [$\beta_1^*(\text{Identity task}) - \beta_2^*(\text{Expression task}) + \beta_2^*(\text{Gaze task})$] is shown in blue, while activation in brain regions that can be explained by the concurrent interaction of task with task performance is rendered in green [$\beta_7^*(\text{Identity task} \times \text{In-scanner task accuracy})$] and in red [$\beta_{10}^*(\text{Identity task} \times \text{Out-of-scanner Benton test})$]. For 3 selected brain regions, changes in activation are shown as a function of task performance. Note that we controlled for outliers (± 2 SDs) in this analysis. Map threshold is $P < 0.001$ uncorrected for peak height, extent threshold $P < 0.05$, corrected. Both hemispheres are shown in the lateral view. Note that the right hemisphere is depicted on the right side.

which included several regions outside the commonly reported core face-network in the mature brain (Fig. 4) (Fairhall and Ishai 2007). One possible explanation is that activation in these brain regions reflects the use of heterogeneous cognitive strategies for processing the 3 face properties (Cohen Kadosh et al. 2010). While the present study did not find overt behavioral differences in processing different face properties in the 3 in-scanner tasks for the different age groups (i. e. no significant a task \times age interaction), it may be that the observed differential task performance effects in the BOLD response were driven by the use of additional or alternative face-processing strategies and possibly different strategies at different ages (Mondloch et al. 2002; Monk et al. 2003). This is based on the assumption that changes associated with performance should be seen at any age. The notion of performance differences reflecting the use of heterogeneous strategies is also in line with previous studies that reported prolonged trajectories in face-processing behavior during childhood through adulthood, including an adolescent dip in face-recognition abilities (Carey et al. 1980). Note that the use of heterogeneous strategies would not necessarily result in observable differences in accuracy, given that the 3 In-scanner tasks were deliberately constructed to yield equal performance across the age range. Rather, these may reflect changes in social information processing at different developmental stages, such as what information is extracted from a face. In the current study, the bilateral insular cortex was one of the few regions that exhibited changes in activation as a function of task performance level in the Gaze task. The anterior insula has been shown to be part of a cortical network supporting eye gaze perception (Pitskel et al. 2011) and one possible interpretation of this finding is that the achievement of high-performance levels in the processing of eye gaze are related to greater engagement of these brain regions. Alternatively, the observed change in BOLD response may also partially explained by underlying gray matter development, which showed a linear increase in this brain region.

It has been shown in recent studies that effective cortical networks are continuously strengthened and reorganized throughout development (Fair et al. 2007; Cohen Kadosh et al. 2011) and it may be that the widespread activation patterns in the Identity task reflect this reorganization process throughout the developmental trajectory (Cohen Kadosh 2011). This interpretation is supported by the behavioral literature, which shows that recognizing faces relies on specific cognitive processing strategies whose acquisition requires extensive training and exposure (Maurer et al. 2002; Mondloch et al. 2003). Last, prolonged development for facial recognition abilities can also be seen as an adaptive strategy, as it can accommodate the changing criteria for facial recognition throughout development. For example, facial identity may be processed differently during adolescence when aspects such as attractiveness or trustworthiness become more important (Scherf et al. 2012). The results from our analysis approach, which allowed us to isolate effects of age and performance separately, support this interpretation: we found widespread activation differences related to performance level in the Identity task.

Conclusions

In summary, the results from our study indicate that the developmental trajectories for extracting social information from

faces extend well into adolescence and possibly beyond. By testing a large sample of participants from 7 through to 37 years, we showed that the behavioral and neural basis for 3 basic aspects of face perception follows differential developmental trajectories, and that these can be partially attributed to underlying structural brain development that extends well into the third decade of life. Further studies are needed to pinpoint the continuous trajectories for face-processing abilities during and beyond early adulthood. We were also able to identify the developmental changes in functional brain activation that were distinct from changes in task performance. Our results supported the notion of a continuous development in core and extended cortical networks supporting basic face-processing abilities throughout the first 3 decades of life. More specifically, we were able to demonstrate that neural activity during face-processing tasks changes with age, and these developmental changes were different from changes associated with improved task performance. Finally, the fact that we found significant changes associated with either age or task performance in our study validates our approach, and suggests that separating these influences on development can further elucidate the emergence of face networks.

Supplementary Material

Supplementary material can be found at: <http://www.cercor.oxfordjournals.org/>.

Acknowledgements

The authors acknowledge funding from the Birkbeck-UCL Centre for NeuroImaging; the Economic and Social Research Council (PTA-026-27-2329) and the European Union (MEST-CT-2005-020725) to K.C.K.; from the Medical Research Council to M.H.J. (G0701484) and F.D. (G0400341); R.C.K. is a Wellcome Trust Career Development Fellow (0883781); and S.-J.B. is a Royal Society University Research Fellow.

Funding

Funding to pay the Open Access publication charges for this article was provided by a Wellcome Trust Career Development Fellowship to R.C.K.

Notes

Conflict of Interest: None declared.

References

- Anderson ML. 2007a. Evolution of cognitive function via redeployment of brain areas. *Neuroscientist*. 13:13–21.
- Anderson ML. 2007b. The massive redeployment hypothesis and the functional topography of the brain. *Philos Psychol*. 21:143–174.
- Anderson ML. 2010. Neural reuse: A fundamental organization principle of the brain. *Behav Brain Sci*. 33:245–266.
- Ashburner J, Friston KJ. 2000. Voxel-based morphometry—the methods. *NeuroImage*. 11:805–821.
- Ashburner J, Friston KJ. 2003a. Rigid body transformation. In: Frakoviak RS, Friston KJ, Frith C, Dolan RJ, Price C, Zeki S, Ashburner J, Penny W, eds. *Human brain function*. 2nd ed. Oxford: Academic Press. p. 635–654.
- Ashburner J, Friston KJ. 2003b. Spatial normalization using basis functions. In: Frakoviak RS, Friston KJ, Frith C, Dolan RJ, Price C,

- Zeki S, Ashburner J, Penny W, editors. Human brain function. 2nd ed. Oxford: Academic Press. p. 655–672.
- Avidan G, Hasson U, Malach R, Behrmann M. 2005. Detailed exploration of face-related processing in congenital prosopagnosia: 2. functional neuroimaging findings. *J Cogn Neurosci*. 17:1150–1167.
- Behrmann M, Avidan G. 2005. Congenital prosopagnosia: face-blind from birth. *Trends Cogn Sci*. 9:180–187.
- Bourgeois JP, Rakic P. 1993. Changes in synaptic density in the primary visual cortex of the macaque monkey from fetal to adult stage. *J Neurosci*. 13:2801–2820.
- Brown TT, Lugar HM, Coalson RS, Miezin FM, Petersen SE, Schlaggar BL. 2005. Developmental changes in human cerebral functional organization for word generation. *Cereb Cortex*. 15:275–290.
- Cantlon JF, Pineda P, Dehaene S, Pelphrey KA. 2011. Cortical representations of symbols, objects, and faces are pruned back during early childhood. *Cereb Cortex*. 21:191–199.
- Carey S, Diamond R, Wood B. 1980. Development of face recognition—a maturational component. *Dev Psychol*. 16:257–269.
- Church JA, Petersen SE, Schlaggar BL. 2010. The “Task B Problem” and other considerations in developmental functional neuroimaging. *Hum Brain Mapp*. 31:852–862.
- Cohen Kadosh K. 2011. What can emerging cortical face networks tell us about mature brain organisation? *Dev Cogn Neurosci*. 1:246–255.
- Cohen Kadosh K, Cohen Kadosh R, Dick F, Johnson MH. 2011. Developmental changes in effective connectivity in the emerging core face network. *Cereb Cortex*. 21:1389–1394.
- Cohen Kadosh K, Henson RNA, Cohen Kadosh R, Johnson MH, Dick F. 2010. Task-dependent activation of face-sensitive cortex: an fMRI adaptation study. *J Cogn Neurosci*. 22:903–917.
- Cohen Kadosh K, Johnson MH. 2007. Developing a cortex specialized for face perception. *Trends Cogn Sci*. 11:267–269.
- Crone EA, Ridderinkhof KR. 2011. The developing brain: from theory to neuroimaging and back. *Dev Cogn Neurosci* 1:101–109.
- Ekman P, Friesen W. 1976. Pictures of facial affect. Palo Alto, CA: Consulting Psychologists Press.
- Fair DA, Cohen AL, Dosenbach NUF, Church JA, Miezin FM, Barch DM, Raichle ME, Petersen SE, Schlaggar BL. 2008. The maturing architecture of the brain’s default network. *Proc Natl Acad Sci USA*. 105:4028–4032.
- Fair DA, Dosenbach NUF, Church JA, Cohen AL, Brahmbhatt S, Miezin FM, Barch DM, Raichle ME, Petersen SE, Schlaggar BL. 2007. Development of distinct control networks through segregation and integration. *Proc Natl Acad Sci USA*. 104:13507–13512.
- Fairhall SL, Ishai A. 2007. Effective connectivity within the distributed cortical network for face perception. *Cereb Cortex*. 17:2400–2406.
- Gathers AD, Bhatt R, Corbly CR, Farley AB, Joseph JE. 2004. Developmental shifts in cortical loci for face and object recognition. *NeuroReport*. 15:1549–1553.
- Giedd JN, Blumenthal J, Jeffries NO, Castellanos FX, Liu H, Zijdenbos A, Paus T, Evans AC, Rapoport JL. 1999. Brain development during childhood and adolescence: a longitudinal MRI study. *Nat Neurosci*. 2:861–863.
- Golarai G, Gharemani DG, Whitfield-Gabrieli S, Reiss A, Eberhardt JL, Gabrieli JDE, Grill-Spector K. 2007. Differential development of high-level visual cortex correlates with category-specific recognition memory. *Nat Neurosci*. 10:512–522.
- Harris JJ, Reynell C, Attwell D. 2011. The physiology of developmental changes in BOLD functional imaging signals. *Dev Cogn Neurosci*. 1:199–216.
- Haxby JV, Hoffman EA, Gobbini MI. 2000. The distributed human neural system for face perception. *Trends Cogn Sci*. 4:223–233.
- Hedman AM, van Haren NEM, Schnack HG, Kahn RS, Hulshoff Pol HE. 2011. Human brain changes across the life span: a review of 56 longitudinal magnetic resonance imaging studies. *Hum Brain Mapp*.
- Huttenlocher PR. 1984. Morphometric study of human cerebral cortex development. *Neuropsychologia*. 28:517–527.
- Ishai A. 2008. Let’s face it: It’s a cortical network. *NeuroImage*. 40:415–419.
- Johnson MH. 2001. Functional brain development in humans. *Nat Rev Neurosci*. 2:475–483.
- Johnson MH. 2011. Interactive specialization: A domain-general framework for human functional brain development? *Dev Cogn Neurosci*. 1:7–21.
- Johnson MH, Grossmann T, Cohen Kadosh K. 2009. Mapping functional brain development: Building a social brain through Interactive Specialization. *Dev Psychol*. 45:151–159.
- Lebel C, Beaulieu C. 2011. Longitudinal development of human brain wiring continues from childhood to adulthood. *J Neurosci*. 31:10937–10947.
- Leekam S, Baron-Cohen S, Perrett D, Milders M, Brown S. 1997. Eye-direction detection: A dissociation between geometric and joint attention skills in autism. *Br J Dev Psychol*. 15:77–95.
- Matsumoto D, Ekman P. 1988. Japanese and Caucasian Facial Expressions of Emotion (JACFEE) and Neutral Faces (JACNEUF). Oakland, CA. CD-rom.
- Maurer D, Le Grand R, Mondloch CJ. 2002. The many faces of configural processing. *Trends Cogn Sci*. 6:255–260.
- Mondloch CJ, Geldart S, Maurer D, Le Grand R. 2003. Developmental changes in face processing skills. *J Exp Child Psychol*. 86:67–84.
- Mondloch CJ, Le Grand R, Maurer D. 2002. Configural face processing develops more slowly than featural face processing. *Perception*. 31:553–566.
- Mondloch CJ, Maurer D, Ahola S. 2006. Becoming a face expert. *Psychol Sci*. 17:930–934.
- Monk CS, McClure EB, Nelson EE, Zarahn E, Bilder RM, Leibenluft E, Charney DS, Ernst M, Pine DS. 2003. Adolescent immaturity in attention-related brain engagement to emotional facial expressions. *NeuroImage*. 20:420–428.
- Nummenmaa L, Passamonti L, Rowe J, Engell AD, Calder AJ. 2010. Connectivity analysis reveals a cortical network for eye gaze perception. *Cereb Cortex*. 20:1780–1787.
- Passarotti AM, Paul BM, Bussiere JR, Buxton RB, Wong EC, Stiles J. 2003. The development of face and location processing: an fMRI study. *Dev Sci*. 6:100–117.
- Passarotti AM, Smith J, DeLano M, Huang J. 2007. Developmental differences in the neural bases of the face inversion effect show progressive tuning of face-selective regions in the upright orientation. *NeuroImage*. 15:1708–1722.
- Pelphrey KA, Lopez J, Morris JP. 2009. Developmental continuity and change in responses to social and nonsocial categories in human extrastriate visual cortex. *Front Hum Neurosci*. 3:1–9.
- Petanjek Z, Judas M, Simic G, Rasin MR, Uylings HBM, Rakic P. 2011. Extraordinary neoteny of synaptic spines in the human prefrontal cortex. *Proc Natl Acad Sci USA*. 108:13281–13286.
- Pfeifer JH, Masten CL, Moore WE, Oswald TM, Mazziotta JC, Iacobini M, Dapretto M. 2011. Entering adolescence resistance to peer influence, risky behavior, and neural changes in emotion reactivity. *Neuron*. 69:1029–1036.
- Pitskel NB, Bolling DZ, Hudac CM, Lantz SD, Minschew NJ, Vander Wyk BC, Pelphrey KA. 2011. Brain mechanisms for processing direct and averted gaze in individuals with autism. *J Autism Dev Disord*. 41:1686–1693.
- Raznahan A, Lerch JP, Lee N, Greenstein D, Wallace GL, Stockman M, Clasen L, Shaw PW, Giedd JN. 2011. Patterns of Coordinated Anatomical Change in Human Cortical Development: A Longitudinal Neuroimaging Study of Maturational Coupling. *Neuron*. 72:873–884.
- Scherf SK, Behrmann M, Dahl R. 2012. Facing changes & changing faces in adolescence: investigating the neural basis of key developmental shifts in social-information processing. *Dev Cogn Neurosci* 2:199–219.
- Scherf KS, Behrmann M, Humphreys K, Luna B. 2007. Visual category-selectivity for faces, places and objects emerges along different developmental trajectories. *Dev Sci*. 10:F15–F31.
- Schlaggar BL, Brown TT, Lugar HM, Visscher KM, Miezin FM, Petersen SE. 2002. Functional neuroanatomical differences between

- adults and school-age children in the processing of single words. *Science*. 296:1476–1479.
- Schmithorst VK, Yuan W. 2010. White matter development during adolescence as shown by diffusion MRI. *Brain Cogn*. 72: 16–25.
- Shaw P, Kabani NJ, Lerch JP, Eckstrand K, Lenroot R, Gogtay N, Greenstein D, Clasen L, Evans A, Rapoport J *et al*. 2008. Neurodevelopmental trajectories of the human cerebral cortex. *J Neurosci*. 28:3586–3594.
- Sowell ER, Thompson PM, Leonard CM, Welcome SE, Kan E, Toga AW. 2004. Longitudinal mapping of cortical thickness and brain growth in normal children. *J Neurosci*. 24:8223–8231.
- Thomas LA, De Bellis MD, Graham R, LaBar KS. 2007. Development of emotional facial recognition in late childhood and adolescence. *Dev Sci*. 10:547–558.
- Yurgelun-Todd DA, Killgore WDS. 2006. Fear-related activity in the prefrontal cortex increases with age during adolescence: a preliminary fMRI study. *Neurosci Lett*. 406:194–199.