



Differential face-network adaptation in children, adolescents and adults

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ABSTRACT

Faces are complex social stimuli, which can be processed both at the categorical and the individual level. Behavioral studies have shown that children take more than a decade of exposure and training to become proficient at processing faces at the individual level. The neurodevelopmental trajectories for different aspects of face-processing are still poorly understood. In this study, we used an fMR-adaptation design to investigate differential processing of three face aspects (identity, expression and gaze) in children, adolescents and adults. We found that, while all three tasks showed some overlap in activation patterns, there was a significant age effect in the occipital and temporal lobes and the inferior frontal gyrus. More importantly, the degree of adaptation differed across the three age groups in the inferior occipital gyrus, a core face processing area that has been shown in previous studies to be both integral and necessary for individual-level face processing. In the younger children, adaptation in this region seemed to suggest the use of a predominantly featural processing strategy, whereas adaptation effects in the adults exhibited a more strategic pattern that depended on the task. Interestingly, our sample of adolescents did not exhibit any differential adaptation effects; possibly reflecting increased heterogeneity in processing strategies in this age group. Our results support the notion that, in line with improving behavioral face-processing abilities, core face-responsive regions develop throughout the first two decades of life.

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Introduction

Faces convey much information to the viewer, such as identity, emotional state and direction of attention via eye gaze. Faces are also a unique stimulus type in that they are consistently processed both at the categorical and the individual level. For a categorical assessment, holistic processing strategies that detect the basic face layout (e.g. two eyes above a nose, above a mouth) help rapidly to differentiate a face from a house. An individual assessment allows one to identify a specific individual or emotional expression, and depends on configural processing strategies that operate on distances between specific facial features (Calder and Young, 2005; Calder et al., 2000; Maurer et al., 2002). Lastly, eye gaze can be processed by focusing on the eye region using a simple featural strategy (Cohen Kadosh et al., 2010; Mondloch et al., 2003). We note that while the terms featural and configural are often found in the face processing literature, they may only represent descriptive approximations of the actual underlying cognitive processing styles.

The developmental trajectories of these face-processing abilities extend well into late childhood and adolescence, and some research has suggested that children experience difficulty in extracting configural face information until the age of 10 (Durand et al., 2007; Karayanidis et al., 2009; Mondloch et al., 2002, 2003; Thomas et al., 2007). In one study, 6-, 8- and 10-year-old children and adults were asked to compare a limited set of female faces when stimuli differed either in terms of the spacing between the face properties (configural set) or with regards to specific features (featural set) (Mondloch et al., 2002). While all child groups exhibited greater difficulties than adults with the configural set, the 6- and 8-year-olds also showed lower accuracies in the featural set. These age differences persisted when controlling for factors such as poor encoding efficiency, limited memory span and low saliency in the stimulus changes (Mondloch et al., 2004). In a different study of 139 5–15 year-old children and adults, different stimulus samples were designed for the different age groups (to accommodate possible age-dependent difference in memory and executive function) in a facial identity and expression matching task (Karayanidis et al., 2009). There was a significant increase in accuracy with age, with children aged 12 years or younger being worse at matching facial identities than older children or adults. These results suggest that the observed developmental differences can be attributed to differences in face-specific processing

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strategies, and not simply to improvements in general cognitive abilities.

Face networks in the brain

Face processing relies on a core network of brain regions, including the inferior occipital gyrus (IOG), the fusiform gyrus (FG) and the superior temporal sulcus (STS) (Cohen Kadosh et al., 2011a; Haxby et al., 2000; Ishai, 2008). A recent fMR-adaptation study from our group showed that the processing of different face aspects overlaps within this network (Cohen Kadosh et al., 2010). fMR-adaptation designs are based on the finding that repeated presentation of a stimulus, or of certain stimulus characteristics, leads to a reduced BOLD signal (signal decrease), and the assumption that this BOLD reduction reflects reduced activity in neurons that represent that specific stimulus or stimulus characteristic. In other words, fMR adaptation effects tend to be specific to certain characteristics of the stimulus, such that the BOLD signal recovers to normal levels as soon as these characteristics change (Sawamura et al., 2006). Hence, it has been proposed that fMR-adaptation paradigms can be used to test preferential tuning characteristics within a particular brain region (i.e., a decrease in neural response during repeated presentation of a specific stimulus characteristic, which is reversed and followed by an increase and recovery in signal when the specific stimulus characteristic is varied again), thereby improving the spatial resolution of fMRI (Naccache and Dehaene, 2001). Note that adaptation effects can refer to both, a decrease or increase in neural response in a specific brain region. In the present study however, we will focus on adaptation effects due to an increase in signal response as a function of stimulus characteristic variation.

Most importantly for present purposes, fMR-adaptation designs can also help differentiate changes in bottom-up, purely-stimulus driven responses from changes in top-down, cognitive processing strategies. For example, if stimulus presentation is kept constant while task instructions are varied, then the observed recovery from adaptation can be attributed to a change in the cognitive demands brought about by the task instruction (Grill-Spector et al., 1999, 2006). Ganel et al. (2005) found that the FG exhibited recovery from adaptation for task-irrelevant changes in emotional expression during an identity-processing task (for which participants are believed to rely on configural processing, which should also lead to processing of facial expression). Cohen Kadosh et al. (2010) subsequently replicated this effect of lower adaptation in the FG (and IOG) to task-irrelevant but strategically-relevant expression changes during an identity-processing task, but furthermore showed recovery from adaptation in IOG and FG for both identity changes and gaze changes during an expression-processing task (for which participants are believed to rely on both configural and featural processing). These differential adaptation effects that varied as a function of task (e.g., whether a specific task encouraged the use of a configural or featural processing strategy) suggest that the core face network does not process different face aspects in segregated brain regions, but rather that different brain regions are recruited flexibly, depending on specific task requirements.

The protracted acquisition of face processing abilities observed in children and adolescents at the behavioral level has been proposed to be mirrored at the neural level by prolonged cortical specialization within the regions of the face network (see Cohen Kadosh and Johnson, 2007; Kanwisher, 2010 for a review). In one fMRI study, children, adolescents and adults passively viewed photographic images of faces, objects, places or abstract patterns (Golarai et al., 2007). Age affected the spatial extent of BOLD activation within right FG, with adults showing more extensive activation than child groups, and the adolescent group exhibiting an intermediate pattern. In addition, the expansion of the fusiform face area (FFA) into surrounding cortex with age was correlated with behavioral improvement in recognition memory for facial identity. An fMR-adaptation study (Scherf et al., 2011) found evidence for categorical and individual-level adaptation

for faces in the bilateral FFA in adults, while adolescents (11–14 years) showed categorical adaptation bilaterally and individual-level adaptation only in the left FFA. Last, a group of children (6–10 years) exhibited neither categorical nor individual-level adaptation in either left or right FFA. These findings suggest a shift from categorical to individual level face processing, as well as a shift from a bilateral to a more specialized right-lateral processing with development.

The current study

The current study assessed developmental changes in neural face processing in a group of children, adolescents and adults in three face processing tasks (identity task, expression task and gaze task). Based on the behavioral literature which shows that children will rely mostly on featural processing strategies for processing faces up until mid-childhood (Cohen Kadosh, in press; Mondloch et al., 2002), we designed each task to encourage either configural or featural face processing strategies. Specifically, we expected adults to use configural face information in the identity task, featural information in the gaze task and both types of information in the expression task, as changing expression affect both, the overall facial configuration, but also single facial features, such as the mouth in a happy face. For the two younger groups, we expected to observe age-specific differential response patterns, which would reflect the slow acquisition of face processing abilities and, in turn, the age-group's preferential use of specific face processing strategies (e.g., predominantly featural processing in the younger children). As noted above, we are aware that the terms featural and configural processing are merely critical for testing the preferential extraction of different face information. The current study cannot provide direct evidence that these are indeed the only cognitive strategies used and we only use these terms to describe the preferential processing styles that we infer may be used by the participants. We used the increased spatial resolution offered by fMR-adaptation (Grill-Spector and Malach, 2001) to look at changes in the core face regions as a function of age and cognitive strategy. Our design had sequences of faces within which a given face aspect (identity, expression or gaze) was either repeated or changed across trials, and compared mean BOLD signal for these different types of blocks across each of the three tasks, in which target stimuli were defined according to one of these three face aspects. A significant adaptation effect is taken to mean that changing a particular face aspect during a mini-block leads a recovery from adaptation, and hence an increase in BOLD signal. For our three age groups, we predicted that: 1) adaptation would reflect the age-specific processing ability. In particular, we expected that in the younger age groups there would be less adaptation to changes in face aspects that rely on featural processing strategies, such as gaze changes, whereas the adults would show less adaptation to changes in face aspects that rely on featural as well as configural processing. 2) Similarly, we expected that with improving performance, we would also observe less adaptation to changes in strategy-relevant, but task-irrelevant face aspects, such as identity changes in the expression task, or expression changes in the gaze task. The current study therefore used adaptation techniques in two ways: first, we varied a face aspect directly, e.g. by changing an emotional expression from happy to angry, to elicit an increase in brain response in the brain region(s) sensitive to the relevant emotional information, and second, we varied our tasks to encourage the use of the top-down cognitive strategy that was used for extracting facial information. The latter approach was used to reveal adaptation effects in the brain region(s) that supports a specific processing strategy (e.g. a more configural strategy in the identity task), rather than the processing of a specific face aspect per se. In addition, the second approach allowed us to look not only at differential adaptation patterns in the core face network, but also to look at whether age-dependent differences in using cognitive strategies affect neural responses.

Methods

Participants

Fourteen adults (average age: 27 years, $SD = 4.21$ years; 9 females; 1 left-handed), 12 adolescents (average age: 14 years, $SD = 1.65$ years; 5 females) and 16 children (average age: 10 years; $SD = 1.4$ years, 6 females) participated in the study. Participants were recruited from an academic environment and from the greater London area via newspaper advertisements. All participants had normal or corrected to normal vision and reported no history of neurological illness. They received monetary compensation (£10 per hour) for participating in the experiment. The study was approved by the local ethics committee (Department of Psychology, Birkbeck College and University College London) and each participant gave informed consent before participating in the study. We note that, while the adaptation effects for the adult group have been published previously (Cohen Kadosh et al., 2010), the data from the two younger groups and, most importantly, the analyses across the three age groups, are novel.

Stimuli

A stimulus set was created from 27 color photographs taken under standard lighting conditions (3 women \times 3 emotional expressions (happy, angry, neutral) \times 3 directions of eye-gaze (right, left, direct); see Fig. S1 for all conditions). We chose to use only female faces in order to keep any task-irrelevant variation to a minimum, as it has been shown that changes in gender influence identity processing (Ganel and Goshen-Gottstein, 2002).¹ 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 : $R = 52.2/3.3$; $G = 36.2/1.6$; $B = 24.4/1.7$). The stimulus size of 6.3×7 cm corresponded to a visual angle of $9.5^\circ \times 11^\circ$ 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, Massachusetts, USA).

Experimental procedure

The 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 they had to detect a happy face, in the gaze task they had to detect a face with direct gaze). Each task was run as a separate session (run) within the same visit. The order of the tasks was counterbalanced across participants. At the beginning of each task, a short message (10 s) informed the participants of the relevant dimension to attend to (e.g., ‘Identity task’, ‘Expression task’, ‘Gaze task’). The same set of stimuli was used for all three tasks, but the stimulus presentation order varied, as the choice of target depended on the particular task. That is, one of the three different identities served as the target stimuli in the identity task, while the two remaining stimuli served as standard stimuli. The same was true for the two other tasks. In order to achieve maximum experimental control, the same target stimuli were used for each participant. We chose the target identity at random as we did not have any a priori expectations regarding their differentiability.

¹ We note that, in order to avoid confounding memory demands in the identity task, we only introduced three different facial identities and participants had sufficient time to familiarize themselves with the identities, as well as the expressions and gazes. It is important to point out that we found no significant performance differences between the tasks in either reaction time or accuracy across the three age groups, which suggests that we succeeded in creating three tasks of that were sufficiently easy for all groups to perform.

Each stimulus was presented for 500 ms, with an inter-stimulus interval (ISI) of 1 s. The standard (non-target) stimuli were arranged in mini-blocks of about 15 s (Wenger et al., 2004), containing on average 9 standard stimuli ($SD \pm 2$ standard stimuli) and 1 target stimulus (note that each session contained a small number of mini-blocks with zero or two targets). The number of standard and target stimuli in the mini-blocks was varied to disguise the different adaptation conditions and to minimize explicit strategies. In addition, the mini-blocks were presented successively without temporal gaps to give the impression of a constant flow of stimuli; this further disguised the mini-block structure. Target stimuli occurred in a pseudo-randomized frequency in the mini-blocks, but targets never appeared before the presentation of at least 5 standard stimuli, thus ensuring sufficient time for adaptation to occur (note that the number and position of the targets was balanced over all conditions). Another reason for keeping the targets apart was that we tried to include as many adaptation periods as possible, thus ensuring maximum design efficiency. Each session consisted of about 30 mini-blocks. Finally, 6 periods of 10s of blank screen were inserted into each session, at randomly selected breaks between mini-blocks during which participants were instructed to fixate on the fixation cross.

In order to make use of the fMRI adaptation technique (Grill-Spector and Malach, 2001), different aspects of the standard stimuli either varied or were kept constant within a mini-block, to create 12 conditions in total (Fig. S1). For example, in the identity task, identity remained constant over trials within each mini-block, but emotional expression, eye-gaze, both, or neither varied with each trial. For each task, we had therefore one baseline condition (no change in task-irrelevant face aspects) and 3 differential change conditions (with either one or two face aspects changing). This resulted in a 3 (experimental tasks) \times 4 (adaptation conditions) quasi-factorial design, with the following adaptation conditions:

- Identity task: baseline (no change) (–), Expression change (E), Gaze change (G), Expression/Gaze change (E/G);
- Expression task: baseline (no change) (–), Identity change (I), Gaze change (G), Identity/Gaze change (I/G);
- Gaze task: baseline (no change) (–), Identity change (I), Expression change (E), Expression/Identity change (E/I).

We note that the adaptation conditions for each task differed in one respect only: the task-relevant face property was not varied throughout a mini-block but was held constant. Task-relevant changes were not included because they would have triggered a disproportionately large recovery from adaptation due to attentional differences (Henson et al., 2002). Instead, only the task-irrelevant face aspects, such as emotional expression and/or eye-gaze in the identity task, varied throughout a mini-block. This approach allowed us to compare how different cognitive processing strategies influence the processing of different face aspects across the developmental trajectory, while avoiding attentional confounds. Nevertheless, it is important to note that we included an identical baseline condition in all three tasks (no change [–]) for comparison between adaptation conditions.

fMRI experiment

We used a Siemens 1.5 T Avanto MRI scanner with 12-channel head coil (Siemens, Erlangen, Germany) to acquire gradient echo-planar images (EPIs) (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 = $192 \text{ mm} \times 192 \text{ mm}$; voxel size: $3 \times 3 \times 4.5$ mm). Following the functional scans, a T1-weighted structural image (1 mm^3 isotropic resolution) was acquired for coregistration and display of the functional data.

Data analysis

Data were analyzed using SPM8 (Wellcome Department of Imaging Neuroscience, London; <http://www.fil.ion.ucl.ac.uk/spm8>). EPI volumes

were spatially realigned to correct for movement artifacts, normalized to the Montreal Neurological Institute (MNI) standard space (Ashburner and Friston, 2003a,b), and smoothed using an 8-mm Gaussian kernel. Statistical analysis was performed in two stages. In the first stage, we computed a General Linear Model (GLM) with 15 regressors, one for each condition in the semi-factorial design (3 tasks \times 4 adaptation conditions) plus one for target trials for each of the three tasks. Note that in the current study, we were interested in the activation to the standard trials and we did not analyze the target trials further, because the response to these targets 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. Because of the short SOA, the regressors for the conditions of interest effectively model the mean response during a mini-block (bar target trials). This is likely to be a sufficient measure of any fMRI adaptation that occurred during mini-blocks, because the inclusion of additional regressors to capture linear or quadratic changes across trials within each mini-block did not add significant findings. In other words, adaptation appeared to saturate quickly, most likely within the first few trials. To account for (linear) residual movement artifacts, the model also included six further regressors representing the rigid-body parameters estimated during realignment. Voxel-wise parameter estimates for these regressors were obtained by restricted maximum-likelihood estimation (ReML), 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 (see also Cohen Kadosh et al., 2010 for a similar procedure).

Images of these parameter estimates comprised the data for a second level GLM that treated participants as the only random effect. This GLM included only the 12 conditions of interest, using a single pooled error estimate, whose nonsphericity was estimated using ReML as described in Friston et al. (2002).

ROI analysis

The ROI analysis was performed using MarsBaR (<http://marsbar.sourceforge.net/>). First, we used the statistical parametric map (SPM) for the average response to 12 adaptation conditions (with the implicit blank screen periods serving as baseline), $p < .05$ Family-Wise-Error (FWE) corrected for peak height, to localize the functional ROIs (clusters) in each participant individually. Note that, because of the balanced

design and modeling of correlations (nonsphericity) in the error term, the contrast of all conditions against baseline that was used to identify ROIs is orthogonal to subsequent contrasts between conditions and therefore avoids the problem of double dipping (Kriegeskorte et al., 2009). We chose to embed the localizer contrast within the main experiment in order to control for effects of time, task, fatigue and practice, while maximizing statistical efficiency. By embedding our localizer contrast in the design, we could focus our analysis on brain regions that are involved in the within-category processing of faces, as opposed to brain regions that show a selectively stronger between-category response, such as faces vs. houses (Friston et al., 2006). In addition, we confirmed that our ROIs were close to the coordinate ranges for core face network regions in previous studies (for all ROI coordinates see Table 4 and below). We then selected three clusters from the overall activation map that corresponded to anatomical regions of theoretical interest in the right and left hemisphere (Haxby et al., 2000): the anterior fusiform gyrus (FG) (centroid MNI coordinates: $-39, -51, -18$; and $+39, -51, -18$), the inferior occipital gyrus (IOG) ($-36, -87, -12$; and $+42, -81, -9$) and the superior temporal sulcus (STS) ($+60, -27, +15$). The parameter estimates were averaged across voxels within a 6-mm spherical volume centered on these maxima, and entered into a 3-way mixed-effects, Huynh-Feldt-corrected Analysis of Variance (ANOVA), with factors “task” (3 levels), “adaptation condition” (4 levels) and “age group” (3 levels). In case of a significant interaction, we conducted simple effects analyses (Keppel, 1991), which, where appropriate (e.g., simple main effect), were followed by two-tailed t-tests in order to understand the source of the interaction. Note that 3 children and 2 adolescents were excluded from the ROI analysis for some tasks, leaving a final sample of 14 adults (all three tasks), 13 children (Identity task $n = 11$; expression and gaze task $n = 13$) and 10 adolescents (identity task $n = 9$; expression and gaze task $n = 11$) for the ROI analysis.

Results

Behavioral results

Mean reaction times (RTs) were calculated for correct trials only. These were subjected to a 2-way ANOVA with the factors “task” (3 levels), and “age group” (3 levels). Only the main effect of task was significant

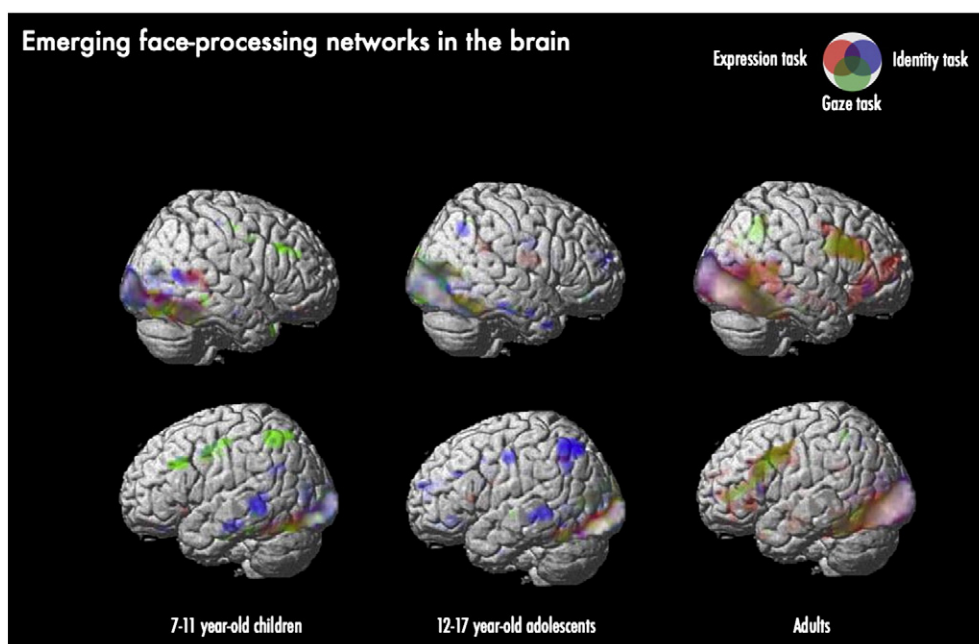


Fig. 1. Brain activation for the three fMRI face-aspect tasks against baseline in each age group. All maps are $p < .05$ Family-Wise-Error (FWE) corrected for peak height.

[$F(2,88) = 4.37$, $p = .016$], but not the main effect of age [$F(2,43) = 1.60$, $p = .213$], nor the interaction of task \times age [$F(4,88) = .662$, $p = .620$], (see also Table 1). Further analysis of the main effect of task revealed that RTs were faster for the identity task in comparison to the expression task [$t(46) = 3.21$, $p = .002$] but not in the gaze task [$t(46) = 1.54$, $p = .131$], and they did not differ between the gaze task and the expression task [$t(46) = 1.74$, $p = .089$]. None of the main effects (main effect of task: [$F(2,86) = 2.93$, $p = .066$]; main effect of age: [$F(2,43) = 1.27$, $p = .290$]) nor the interaction was significant for accuracy [$F(4,86) = 1.10$, $p = .359$]. These results suggest that all three tasks involved comparable levels of difficulty across age groups.

fMRI results

Our fMRI analysis consisted of two steps, a whole-brain analysis that looked for overall task-related differences in the three age groups and a functionally-defined ROI analysis that looked for adaptation effects in selected regions in the core face network. These adaptation effects were investigated to assess differences in adaptation conditions across tasks (task-dependent changes) and within tasks (stimulus-dependent changes, i.e. adaptation effects), as well as across age groups (age-dependent changes).

Whole-brain analysis

The whole-brain analysis yielded widespread activation for the main effect of age in both occipital lobes and the ventral-temporal stream, as well the right precuneus and the right inferior frontal gyrus (Table 2). However, no significant clusters were found for the main effect of task, nor the interaction between task \times age group, thus confirming the results from an earlier study which showed a consistent overlap between the three tasks (see also Fig. 1).

ROI analysis

Figs. 2–5 show the mean response for each task and age group in the core face-network regions. As can be seen in these figures, while overall signal responses are comparable across the different age groups, there were differential effects of recovery from adaptation for each task. Here, a significant effect is taken to mean that changing a particular face aspect during a mini-block leads a recovery from adaptation, and hence an increase in BOLD signal. Of the five functionally defined ROIs, all showed a main effect of task; in addition, left and right IOG and right STS showed a significant interaction between task \times adaptation condition \times age group (see Tables 3, 4 and 5 for all effects). The right IOG also showed a main effect of age group. Further analyses focused on these three ROIs. Below, we consider each ROI in turn.

Left IOG

The left IOG (Fig. 2) showed a trend towards an interaction between task, adaptation condition and age group [$F(12,186) = 1.86$;

Table 1
Behavioral results fMRI tasks.

	Group	Accuracy rates		Reaction times	
		Mean	SD	Mean	SD
Identity task	Children	88.1	23.5	805.6	317.7
	Adolescents	82.3	28.4	795.9	95.1
	Adults	89.3	15.5	929.5	195.0
Expression task	Children	77.0	12.0	924.7	273.5
	Adolescents	76.0	28.3	838.0	84.1
	Adults	91.1	9.0	978.9	189.0
Gaze task	Children	85.3	13.4	876.0	266.5
	Adolescents	88.2	25.9	821.9	123.1
	Adults	92.3	12.7	938.9	165.1

Table 2

Main effects for age, task, and interaction between age \times task ($p < .05$ Family-Wise-Error (FWE) corrected for peak height). MNI: Montreal Neurological Institute.

Effect	Brain regions	MNI (x, y, z)	Cluster size	Z
Main effect of age	Inferior occipital gyrus	42 – 81 – 9	2172	Inf
	Middle occipital gyrus	30 – 93 18		Inf
	Lingual gyrus	18 – 81 – 6		7.82
	Lingual gyrus	21 – 75 – 3		7.48
	Middle occipital gyrus	33 – 84 6		7.47
	Fusiform gyrus	30 – 54 – 18		7.31
	Cerebellum	33 – 36 – 27		6.74
	Middle occipital gyrus	27 – 99 6		6.63
	Calcarine gyrus	21 – 96 3		6.4
	Superior occipital gyrus	27 – 75 30		5.83
	Middle occipital gyrus	30 – 69 33		5.74
	Lingual gyrus	18 – 60 – 6		5.57
	Middle occipital gyrus	30 – 72 21		5.55
	Middle occipital gyrus	33 – 66 34		4.8
	Precuneus	15 – 48 6		4.74
	Middle occipital gyrus	– 36 – 87 0	1305	Inf
	Middle occipital gyrus	– 27 – 96 15		Inf
	Lingual gyrus	– 21 – 81 – 15		7.1
	Fusiform gyrus	– 36 – 72 – 15		6.2
	Calcarine gyrus	– 12 – 93 – 6		6.4
	Middle occipital gyrus	– 30 – 75 30		4.6
	Fusiform gyrus	42 – 48 – 18	44	6.44
	Inferior frontal gyrus	39 3 27	149	5.74
	Calcarine gyrus	– 12 – 57 9	138	4.92
	Inferior occipital gyrus	42 – 81 – 9	2172	Inf
	Middle occipital gyrus	30 – 93 18		Inf
	Lingual gyrus	18 – 81 – 6		7.82
	Lingual gyrus	21 – 75 – 3		7.48
Main effect of task	No significant activation clusters			
Interaction age \times task	No significant activation clusters			

$p = .054$] (see Table 5 for all other effects and Supplementary Tables 3 and 4 for all simple main effects between adaptation conditions). Further analyses were conducted based on a priori hypotheses regarding age differences in adaptation patterns to probe each age group separately.

Children. For the child participants, the main effect of task and the main effect of adaptation condition were significant (main effect of task: [$F(2,20) = 4$; $p = .034$]; main effect of adaptation condition: [$F(3,30) = 4.98$; $p = .006$]). The interaction between task \times adaptation condition was also significant [$F(6,60) = 3.25$; $p = .015$].

Children – Identity task. The simple main effect of adaptation condition was significant [$F(3,30) = 5.31$; $p = .007$]. Planned comparisons showed that the left IOG exhibited a significant release from adaptation when gaze changed [$t(10) = 3.53$, $p = .005$] and when gaze changed together with expression [$t(10) = 4.33$, $p = .001$]. No significant release from adaptation was observed when only expression changed [$t(10) = -1.64$, $p = .132$].

Children – Expression task. The simple main effect of adaptation condition was not significant [$F(3,36) = .903$; $p = .447$].

Children – Gaze task. The simple main effect of adaptation condition was significant [$F(3,36) = 4.08$; $p = .014$], and further comparisons revealed that this effect was due to a release from adaptation when identity and expression changed simultaneously, as opposed to a change in identity or expression only [identity and expression change vs. identity change $t(12) = 2.92$, $p = .013$; identity and expression change vs. expression change $t(12) = 3.02$, $p = .011$].

Adolescents. For the adolescent group, none of the main effects nor the interaction between task \times adaptation condition was significant [all $F_s < 2.52$, all $p_s > .112$].

Adults. Planned comparisons found a significant main effect of task [$F(2,26) = 8.95$; $p = .002$], but the main effect of adaptation condition

Adaptation effects in the left inferior occipital gyrus

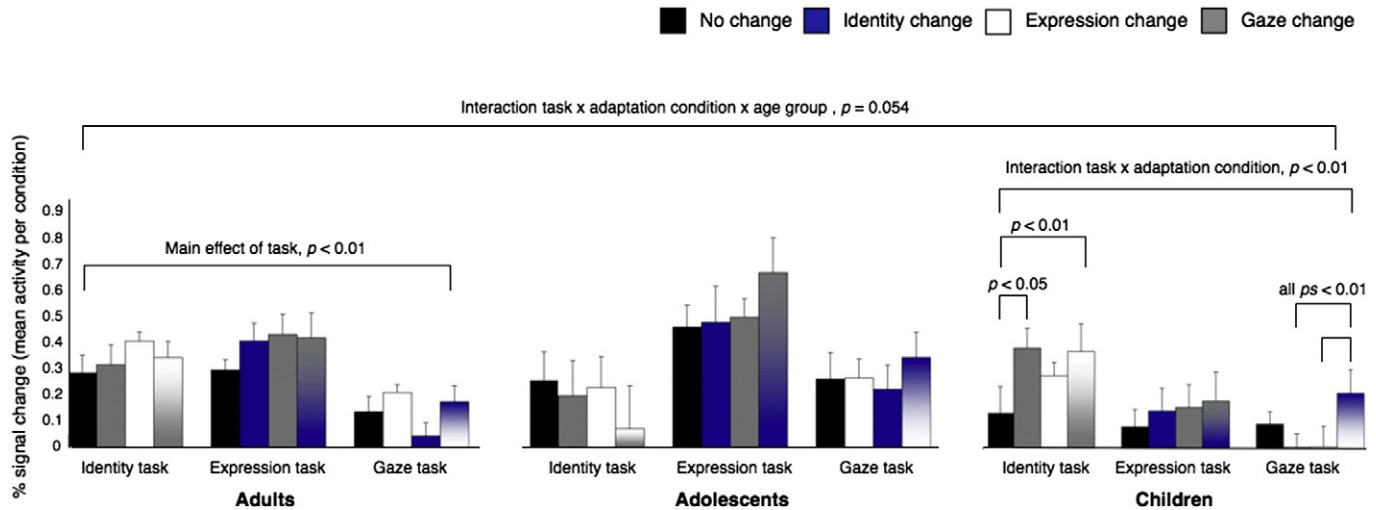


Fig. 2. Adaptation effects in the left inferior occipital gyrus for the three face-aspect tasks in each age group. Shown are percent signal changes (i.e., mean activity for each adaptation condition), where a value higher than no change suggests release from adaptation). Mean activity is shown for each face aspect that was varied in a particular task (for example, expression changes in the identity task; see legend for color coding for the different adaptation conditions). Significant differences in adaptation conditions are highlighted. See also Table 5 for all effects.

and the interaction between the two was not significant [all $F_s < 1.82$, all $p_s > .121$].

Right IOG

The right IOG (Fig. 3) showed an interaction between task, adaptation condition and age group [$F(12,186) = 1.87$; $p = .042$] (see Table 5 for all other effects and Supplementary Tables 3 and 4 for all simple main effects between adaptation conditions). Further analyses were conducted to probe the underlying source of this interaction in each age group separately.

Children. For the child participants, the main effect of task but not the main effect of adaptation condition was significant (main effect of

task: [$F(2,20) = 3.63$; $p = .045$]; main effect of adaptation condition: [$F(3,30) = .801$; $p = .443$]). The interaction between task \times adaptation condition was also significant [$F(6,60) = 3.24$; $p = .008$].

Children – Identity task. The simple main effect of task was not significant [$F(3,30) = 1.923$; $p = .147$].

Children – Expression task. The simple main effect of task was not significant [$F(3,36) = 1.126$; $p = .351$].

Children – Gaze task. For the gaze task, the simple main effect of task was significant [$F(3,36) = 3.25$; $p = .033$]. Moreover, we observed a significant release from adaptation when identity and expression changed simultaneously, but not separately (Identity and expression change vs. identity change [$t(12) = 2.40$, $p = .033$]; identity and expression change vs. expression change [$t(12) = 2.33$, $p = .038$]).

Adaptation effects in the right inferior occipital gyrus

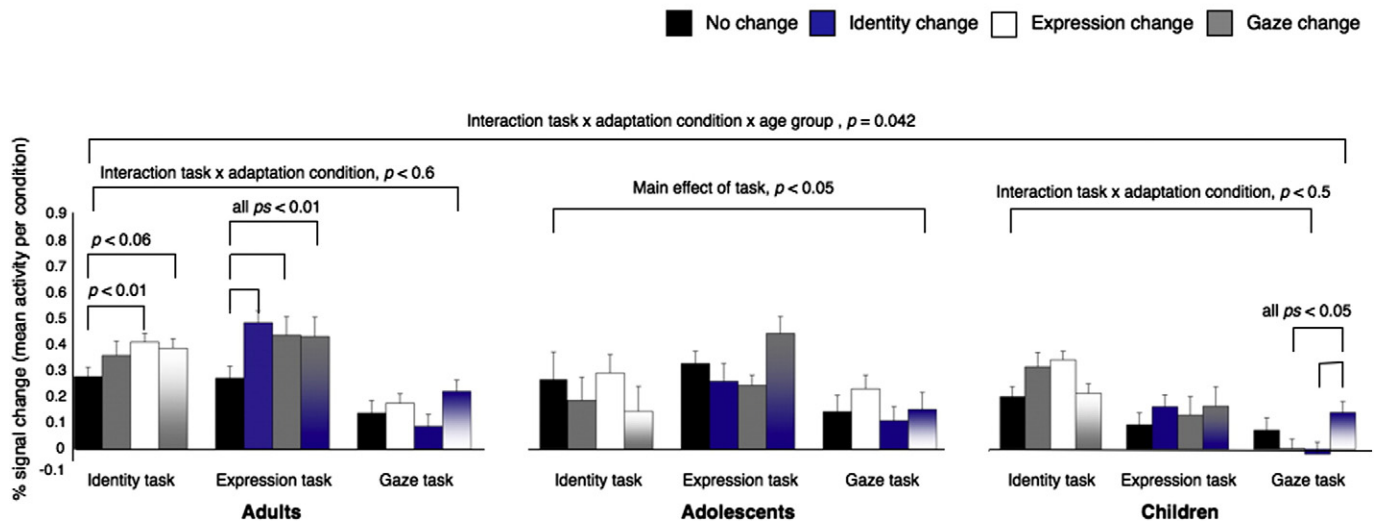


Fig. 3. Adaptation effects in the right inferior occipital gyrus for the three tasks in each age group. Shown are percent signal changes (i.e., mean activity for each adaptation condition), where a value higher than no change suggests release from adaptation). Mean activity is shown for each face aspect that was varied in a particular task (for example, expression changes in the identity task; see legend for color coding for the different adaptation conditions). Significant differences in adaptation conditions are highlighted. See also Table 5 for all effects.

Adaptation effects in the right fusiform gyrus

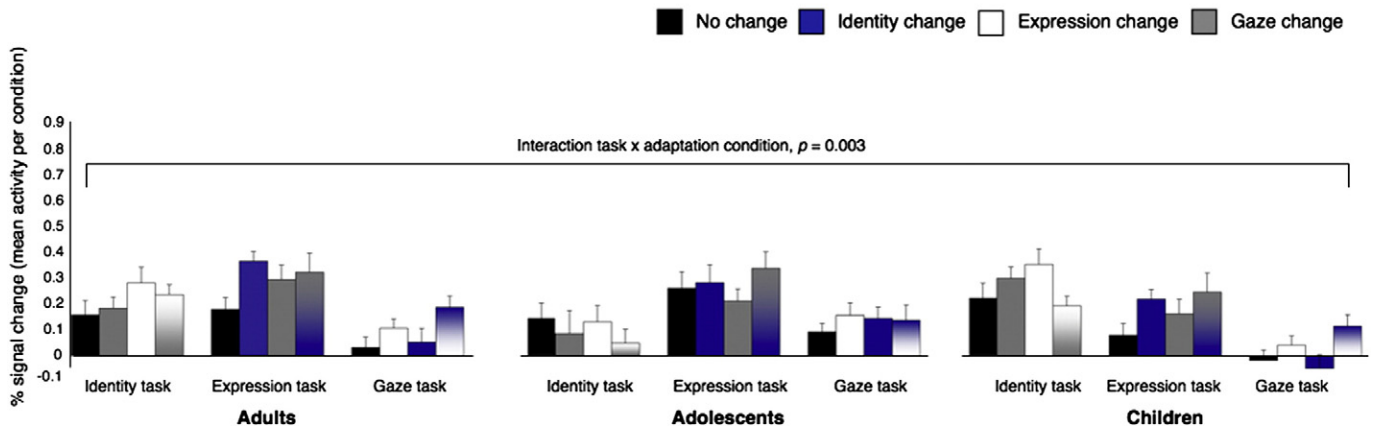


Fig. 4. Adaptation effects in the right fusiform gyrus for the three tasks in each age group. Shown are percent signal changes (i.e., mean activity for each adaptation condition), where a value higher than no change suggests release from adaptation). Mean activity is shown for each face aspect that was varied in a particular task (for example, expression changes in the identity task; see legend for color coding for the different adaptation conditions). Significant differences in adaptation conditions are highlighted. See also Table 5 for all effects.

Adolescents. For the adolescent group, only the main effect of task was significant [$F(2,16) = 6.19$; $p = .019$].

Adults. The main effect of task and the main effect of adaptation condition were significant [main effect of task: $F(2,26) = 16.9$; $p < .001$; main effect of adaptation condition: $F(3,39) = 6.42$; $p = .002$]. The interaction between task \times adaptation condition showed a trend towards significance [$F(6,78) = 2.36$; $p = .065$].

Adults – Identity task. The simple main effect of task was significant [$F(3,39) = 2.84$; $p = .050$]. Further decompositions showed that the right IOG exhibited release from adaptation when expression changed either separately [$t(13) = 3.20$, $p = .007$], or together with gaze [$t(13) = 2.04$, $p = 0.062$] in comparison to baseline. No release from adaptation was found for a simple change in gaze [$t(13) = -1.39$, $p = .188$].

Adults – Expression task. The simple main effect of task was significant [$F(3,39) = 7.65$; $p < .001$]. Additional comparisons revealed a significant release from adaptation when any face aspect changed in this

task in comparison to baseline (Identity change $t(13) = 5.04$, $p < .001$; gaze change: $t(13) = 3.38$, $p = .005$; combined identity and gaze change: $t(13) = 3.97$, $p = .002$).

Adults – Gaze task. For the gaze task, the simple main effect of task was not significant [$F(3,39) = 1.81$; $p = .167$].

Right STS

The right STS (Fig. 5) showed a significant interaction between task, adaptation condition and age group [$F(12,186) = 2.08$; $p = .020$] (see Table 5 for all other effects and Supplementary Tables 3 and 4 for all simple main effects between adaptation conditions).

Children. For the child participants, none of the main effects nor the interaction between task \times adaptation condition was significant [all $F_s < .685$; all $p_s > .568$].

Adolescents. For the adolescent group, none of the main effects was significant [all $F_s < 1.75$, all $p_s > .209$], but the interaction between

Adaptation effects in the right superior temporal sulcus

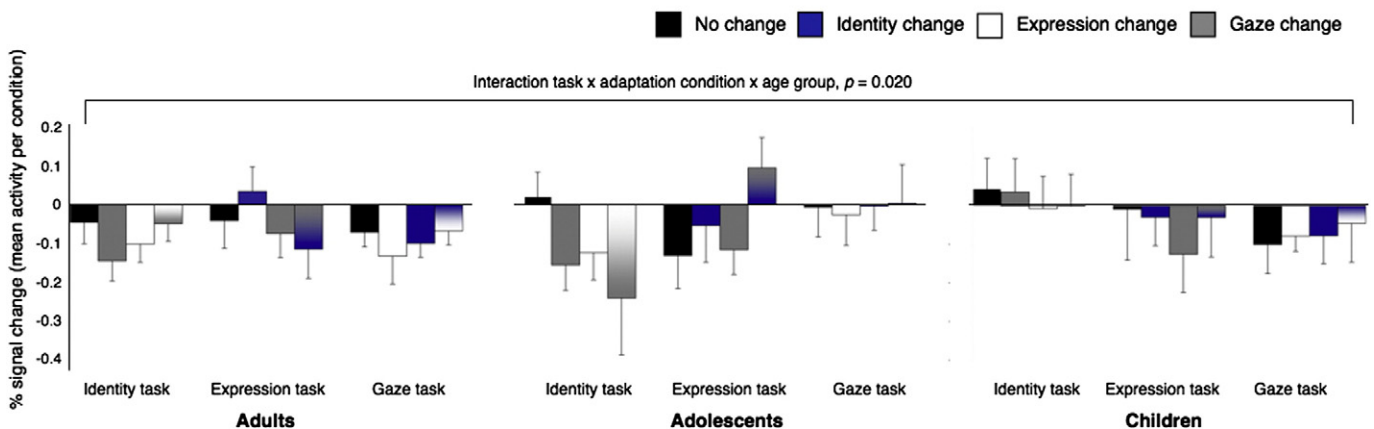


Fig. 5. Adaptation effects in the right superior temporal gyrus for the three tasks in each age group. Shown are percent signal changes (i.e., mean activity for each adaptation condition), where a value higher than no change suggests release from adaptation). Mean activity is shown for each face aspect that was varied in a particular task (for example, expression changes in the identity task; see legend for color coding for the different adaptation conditions). Significant differences in adaptation conditions are highlighted. See also Table 4 for all effects.

Table 3

Region-of-interest analysis for the regions of the core face-network. Bold font indicates a significant effect.

Effect	
Main effect of brain region	F(4,124) = 48.44; p < .001
Main effect of age group	F(2,31) = 2.29; p = .118
Interaction brain region × age group	F(8,124) = 2.53; p = .030
Main effect of task	F(2,62) = 11.1; p < .001
Interaction task × age group	F(4,62) = 4.43; p = .004
Main effect adaptation condition	F(3,93) = 4.06; p = .010
Interaction adaptation condition × age group	F(6,93) = .677; p = .666
Interaction brain regions × task	F(8,248) = 4.96; p < .001
Interaction brain regions × task × age group	F(16,248) = 1.22; p = .269
Interaction brain regions × adaptation condition	F(12,372) = 2.60; p = .006
Interaction brain regions × adaptation conditions × age group	F(24,372) = .879; p = .609
Interaction task × adaptation condition	F(6,186) = 3.204; p = .008
Interaction task × adaptation condition × age group	F(12,186) = 1.75; p = .073
Interaction brain regions × task × adaptation condition	F(24,744) = 1.70; p = .040
Interaction brain regions × task × adaptation condition × age group	F(48,744) = 1.38; p = .079

task × adaptation condition was significant [$F(6,48) = 2.62$; $p = .046$]. However, further decomposition for each task separately showed that none of the simple main effects was significant (Identity task: $F(3,24) = 2.60$; $p = .109$; Expression task: $F(3,27) = 2.33$; $p = .097$; Gaze task: $F(3,29) = .029$; $p = .990$).

Adults. None of the main effects of task or adaptation condition was significant [all $F_s < .558$, all $p_s > .594$]. The interaction between task × adaptation condition showed a trend towards significance [$F(6,78) = 2.02$; $p = .073$].

Discussion

The current study investigated developmental changes in adaptation patterns for different face aspects (identity, expression and gaze). As previous studies have shown that these face aspects rely to a varying extent of configural or featural face information, we predicted that adaptation patterns would reflect the improving processing proficiencies for face-specific configural processing. Moreover, along with the improving processing abilities with age, we predicted that adaptation patterns would increasingly reflect changes in strategy-relevant (but task-irrelevant) face aspects across the different tasks.

At the behavioral level, we found no significant accuracy or reaction time differences in the processing of the three face aspects for the three age groups, suggesting that our three tasks presented comparable difficulty levels to all participants. These comparable performance levels in the three age groups allow us to interpret more clearly the effects of age that we found in the fMRI data (Brown et al., 2005; Church et al., 2010).

Table 4

Region-of-interest analysis for the regions of the core face-network. Montreal Neurological Institute coordinates in parentheses. Abbreviations: FG = Fusiform gyrus; IOG = inferior occipital gyrus; STS = superior temporal sulcus. Bold font indicates a significant effect.

Effect	Left FG (−39, −51, −18)	Left IOG (−36, −87, −12)	Right FG (39, −51, −18)	Right IOG (42, −81, −9)	Right STS (60, −27, 15)
Main effect of task	F(2,62) = 4.98; p = .012	F(2,62) = 11.3; p < .001	F(2,62) = 9.75; p = .001	F(2,62) = 10.84; p < .001	F(2,62) = .172; p = .012
Main effect of age	F(2,31) = 1.29; p = .289	F(2,31) = 3.04; p = .062	F(2,31) = .408; p = .668	F(2,31) = 8.46; p < .001	F(2,31) = .390; p = .681
Interaction task × age group	F(4,62) = 4.26; p = .006	F(4,62) = 4.08; p = .005	F(4,62) = 2.38; p = .073	F(4,62) = 2.52; p = .050	F(4,62) = 1.22; p = .311
Main effect adaptation condition	F(3,93) = 4.12; p = .009	F(3,93) = 4.65; p = .005	F(3,93) = 4.45; p = .006	F(3,93) = 2.36; p = .077	F(3,93) = 1.44; p = .237
Interaction adaptation condition × age group	F(6,93) = .728; p = .627	F(6,93) = .850; p = .531	F(6,93) = .969; p = .451	F(6,93) = 1.35; p = .242	F(6,93) = .111; p = .995
Interaction task × adaptation condition	F(6,186) = 1.57; p = .166	F(6,186) = 2.69; p = .023	F(6,186) = 3.64; p = .003	F(6,186) = 3.34; p = .004	F(6,186) = 1.49; p = .182
Interaction task × adaptation condition × age group	F(12,186) = .738; p = .701	F(12,186) = 1.86; p = .054	F(12,186) = 1.09; p = .368	F(12,186) = 1.87; p = .042	F(12,186) = 2.08; p = .020

The whole-brain analysis showed that all three tasks were associated with overlapping BOLD activations (in that there was no significant main effect of task), but there were significant differences associated with age. We interpret this pattern as suggesting that the three tasks activated the same core face network regions, but that participants recruit additional brain regions at different ages. In a previous study (Cohen Kadosh et al., in press), we were able to show that neural activity during face processing tasks changes with age, and that these age effects could be differentiated from changes in improving task performance, which can be observed at all ages. These developmental age effects have been suggested to reflect chronological age-related changes in the neuronal circuitry (sometimes termed “maturation”) (Cohen Kadosh et al., 2011a; Giedd et al., 1999; Harris et al., 2011; Petanjek et al., 2011).

Differential adaptation in the core face network in children

In line with previous studies, most regions of the core face-network showed differential adaptation effects for the different stimulus conditions (a main effect of adaptation), or different adaptation effects for the three tasks (an interaction between task and adaptation) (see also Table 3) (Cohen Kadosh et al., 2010; Ganel et al., 2005; Rotshtein et al., 2005; Winston et al., 2004). However, only the bilateral IOG showed a clear pattern of age effects in adaptation across the three tasks, with the three age groups exhibiting differential processing of face aspects in each task (the right STS also showed an omnibus interaction, but no significant simple effects, so is not discussed further). The IOG is an integral and necessary part of the face network, and it has been suggested that it receives feed-forward and re-entrant feedback from face sensitive areas, including the FFA (Cohen Kadosh et al., 2010; Rossion et al., 2003; Rotshtein et al., 2007; Schiltz and Rossion, 2006). Previous work has shown that this region may be involved not only in the initial detection and categorization, but also in the integrative analysis of face stimuli and in particular facial identity and emotional expressions (Cohen Kadosh et al., 2011b). Interestingly, in our study, the FG did not show age-dependent adaptation effects. This finding runs in line with the results from the developmental fMRI-adaptation study by Scherf et al. (2011), where only adults exhibited clear individual level adaptation effects in the bilateral FG.

The adaptation results confirmed our first hypothesis of varying adaptation effects with age. We found clear adaptation effects in the bilateral IOG of both adults and children at the level of individual face aspects (i.e. identity, expression or gaze, rather than just at the level of face vs. house categories). While differential adaptation effects for identity, expression and gaze were previously shown for the IOG in adults (Cohen Kadosh et al., 2010), the current study is the first to show face-aspect-specific adaptation patterns in children aged 7–10 years that differ significantly from those observed in adults. This means that not only do children process different face aspects in the core regions from the age of 7, but also that these regions process faces differently from adolescents or adults, possibly reflecting the use of different

Table 5

Region-of-interest analysis for the regions of the core face-network. Abbreviations: IOG = inferior occipital gyrus; STS = superior temporal sulcus. Bold font indicates a significant effect.

Age group	Effect	Left IOG (−36, −87, −12)	Right IOG (42, −81, −9)	Right STS (60, −27, 15)
Children	Main effect of task	$F(2,20) = 4.00$; $p = .034$	$F(2,20) = 3.63$; $p = .045$	$F(2,20) = .456$; $p = .636$
	Main effect of adaptation condition	$F(3,30) = 4.98$; $p = .006$	$F(3,30) = .801$; $p = .443$	$F(3,30) = .685$; $p = .568$
	Interaction task × adaptation condition	$F(6,60) = 3.25$; $p = .015$	$F(6,60) = 3.24$; $p = .008$	$F(6,60) = .377$; $p = .891$
Adolescents	Main effect of task	$F(2,16) = 2.52$; $p = .112$	$F(2,16) = 6.19$; $p = .019$	$F(2,16) = 1.75$; $p = .209$
	Main effect of adaptation condition	$F(3,24) = .234$; $p = .872$	$F(3,24) = .403$; $p = .680$	$F(3,24) = .318$; $p = .786$
	Interaction task × adaptation condition	$F(6,48) = 1.65$; $p = .160$	$F(6,48) = 1.55$; $p = .197$	$F(6,48) = 2.62$; $p = .046$
Adults	Main effect of task	$F(2,26) = 8.95$; $p = .002$	$F(2,26) = 16.9$; $p < .001$	$F(2,26) = .532$; $p = .594$
	Main effect of adaptation condition	$F(3,39) = 1.62$; $p = .212$	$F(3,39) = 6.42$; $p = .002$	$F(3,39) = .558$; $p = .618$
	Interaction task × adaptation condition	$F(6,78) = 1.86$; $p = .121$	$F(6,78) = 2.36$; $p = .065$	$F(6,78) = 2.02$; $p = .073$

processing strategies in this age group. Specifically, in the children, the left IOG showed increased processing for featural gaze changes in the identity task. This means that the IOG did not only process the task-relevant identity information in a specific face, but also task-irrelevant gaze information. Similarly, we found bilateral IOG adaptation effects in the gaze task for identity and expression change. The fact that we found adaptation effects related to task-irrelevant gaze changes could speculatively be taken to suggest that children in our study adopted a predominantly featural processing strategy to process different face aspects. This interpretation is supported by the behavioral literature, which shows that children will rely mostly on featural processing strategies for processing faces up until mid-childhood (Cohen Kadosh, *in press*; Mondloch et al., 2002).

We were also able to confirm our second hypothesis for the adults: we found right-lateralized adaptation effects in the identity and expression tasks in the adults. In the identity task, these adaptation effects reflected task-irrelevant, but strategy-relevant expression changes, whereas in the expression task, both task-irrelevant changes in identity and gaze prevented adaptation. These findings run in line with previous findings that showed that the IOG processes different face aspects, depending on the cognitive task strategy (Cohen Kadosh et al., 2010). This was not the case for the child and adolescent groups in the current study, a result that we interpret to reflect the lower processing proficiency especially for extracting configural face information in this age range (Mondloch et al., 2002, 2003) and possibly the higher heterogeneity in processing strategies used (Maurer et al., 2002). We note that no adaptation effects were observed in our group of adolescents. Whether this is a result of increased variability in processing strategies in this age range, and/or due to the previously found changes in performance (Carey et al., 1980; Thomas et al., 2007), which have been suggested to reflect a shift in cognitive strategy (Scherf et al., 2012), remains to be determined. We note that, because we only examined significant interactions in a multi-factorial analysis, differences in the number of participants within each group cannot explain the differences found between groups. Nonetheless, additional analyses with matched group sizes yielded similar effect patterns, thereby confirming our differential adaptation effects across the three age groups (see Supplementary Tables 1 and 2).

Differences in hemispherical specialization in children

In the current study, children exhibited lower levels of hemispherical lateralization for processing different face aspects in comparison to the other age groups (Meng et al., 2012), for example, the left IOG exhibited differential adaptation patterns in the child group, whereas this was not found for the other two age groups.² This

suggests that children still use the bilateral IOG for an in-depth face analysis, whereas adolescents and adults do not. This finding runs in line with other studies that found stronger bilateral activation in children vs. adults and a shift from bilateral to more specialized right lateral face processing with age (Passarotti et al., 2003; Scherf et al., 2011).

Conclusions

The current study used an fMR-adaptation design to investigate differential processing patterns for three face aspects in children, adolescents and adults. We found that adaptation patterns did differ for the three age groups in the bilateral IOG, a core face processing area, which has been shown in previous studies to be both integral and necessary for in-depth face processing. In the younger children, adaptation effects in this region seemed to suggest the use of a predominantly featural processing strategy, whereas adults exhibited a more general pattern of strategy-relevant adaptation in core face processing regions. Taken together, our results support the notion that, in line with improving processing abilities, core face regions develop continuously during the first two decades of life.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2012.11.060>.

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References

- Ashburner, J., Friston, K.J., 2003a. Rigid body transformation. In: Frakoviak, R.S., Friston, K.J., Frith, C., Dolan, R.J., Price, C., Zeki, S., Ashburner, J., Penny, W. (Eds.), *Human Brain Function*, 2nd ed. Academic Press, Oxford, pp. 635–654.
- Ashburner, J., Friston, K.J., 2003b. Spatial normalization using basis functions. In: Frakoviak, R.S., Friston, K.J., Frith, C., Dolan, R.J., Price, C., Zeki, S., Ashburner, J., Penny, W. (Eds.), *Human Brain Function*, 2nd ed. Academic Press, Oxford, pp. 655–672.
- Brown, T.T., Lugar, H.M., Coalson, R.S., Miezin, F.M., Petersen, S.E., Schlaggar, B.L., 2005. Developmental changes in human cerebral functional organization for word generation. *Cereb. Cortex* 15, 275–290.
- Calder, A.J., Young, A.W., 2005. Understanding the recognition of facial identity and facial expression. *Nat. Rev. Neurosci.* 6, 641–651.
- Calder, A.J., Young, A.W., Keane, J., Dean, M., 2000. Configural information in facial expression perception. *J. Exp. Psychol. Hum. Percept. Perform.* 26 (2), 527–551.
- Carey, S., Diamond, R., Wood, B., 1980. Development of face recognition — a maturational component. *Dev. Psychol.* 16 (4), 257–269.
- Church, J.A., Petersen, S.E., Schlaggar, B.L., 2010. The “Task B Problem” and other considerations in developmental functional neuroimaging. *Hum. Brain Mapp.* 31, 852–862.

² Differences in hemispheric specialization were also supported by an additional ANOVA, which showed a significant interaction for brain region × task × adaptation condition × age group [$F(12,186) = 1.86$, $p = .047$], and specifically a trend towards an interaction for hemispheric × task × adaptation condition × age group [$F(12,186) = 1.72$, $p = .066$] in the bilateral IOG.

- Cohen Kadosh, K., 2012. Differing processing abilities for specific face properties in mid-childhood and adulthood. *Front. Psychol.* 2, 400. <http://dx.doi.org/10.3389/fpsyg.2011.00400>.
- Cohen Kadosh, K., Johnson, M.H., 2007. Developing a cortex specialized for face perception. *Trends Cogn. Sci.* 11 (9), 267–269.
- Cohen Kadosh, K., Henson, R.N.A., Cohen Kadosh, R., Johnson, M.H., Dick, F., 2010. Task-dependent activation of face-sensitive cortex: an fMRI adaptation study. *J. Cogn. Neurosci.* 22 (5), 903–917.
- Cohen Kadosh, K., Cohen Kadosh, R., Dick, F., Johnson, M.H., 2011a. Developmental changes in effective connectivity in the emerging core face network. *Cereb. Cortex* 21, 1389–1394.
- Cohen Kadosh, K., Walsh, V., Cohen Kadosh, R., 2011b. Investigating face-property specific processing in the right OFA. *Soc. Cogn. Affect. Neurosci.* 6 (1), 58–65.
- Cohen Kadosh, K., Johnson, M. H., Dick, F., Cohen Kadosh, R., Blakemore, S.-J., in press. Effects of age, task performance and structural brain development on face processing. *Cereb. Cortex*.
- Durand, K., Gallay, M., Seigneure, A., Robichon, F., Baudouin, J.-Y., 2007. The development of facial emotion recognition: the role of configural information. *J. Exp. Child Psychol.* 97, 14–27.
- Friston, K.J., Rotshtein, P., Geng, J.J., Sterzer, P., Henson, R.N.A., 2006. A critique of functional localizers. *Neuroimage* 30, 1077–1087.
- Friston, K.J., Penny, W., Phillips, C., Kiebel, S., Hinton, G., Ashburner, J., 2002. Classical and Bayesian inference in neuroimaging: theory. *NeuroImage* 16 (2), 465–483.
- Ganel, T., Goshen-Gottstein, Y., 2002. Perceptual integrality of sex and identity of faces: further evidence for the single route hypothesis. *J. Exp. Psychol. Hum. Percept. Perform.* 28, 854–867.
- Ganel, T., Valyear, K.F., Goshen-Gottstein, Y., Goodale, M.A., 2005. The involvement of the “fusiform face area” in processing facial expression. *Neuropsychologia* 43, 1645–1654.
- Giedd, J.N., Blumenthal, J., Jeffries, N.O., Castellanos, F.X., Liu, H., Zijdenbos, A., Rapoport, J.L., 1999. Brain development during childhood and adolescence: a longitudinal MRI study. *Nat. Neurosci.* 2 (10), 861–863.
- Golarai, G., Gharemani, D.G., Whitfield-Gabrieli, S., Reiss, A., Eberhardt, J.L., Gabrieli, J.D.E., Grill-Spector, K., 2007. Differential development of high-level visual cortex correlates with category-specific recognition memory. *Nat. Neurosci.* 10 (4), 512–522.
- Grill-Spector, K., Malach, R., 2001. fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychol.* 107, 293–321.
- Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzhak, Y., Malach, R., 1999. Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron* 24, 187–203.
- Grill-Spector, K., Henson, R., Martin, A., 2006. Repetition and the brain: neural models of stimulus-specific effects. *Trends Cogn. Sci.* 10 (1), 14–23.
- Harris, J.J., Reynell, C., Attwell, D., 2011. The physiology of developmental changes in BOLD functional imaging signals. *Dev. Cogn. Neurosci.* 1 (3), 199–216.
- Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. The distributed human neural system for face perception. *Trends Cogn. Sci.* 4 (6), 223–233.
- Henson, R.N.A., Shallice, T., Gorno-Tempini, M.L., Dolan, R.J., 2002. Face repetition effects in implicit and explicit memory tests as measured by fMRI. *Cereb. Cortex* 12, 178–186.
- Ishai, A., 2008. Let's face it: it's a cortical network. *Neuroimage* 40, 415–419.
- Kanwisher, N., 2010. Functional specificity in the human brain: a window into the functional architecture of the mind. *Proc. Natl. Acad. Sci.* 107 (25), 11163–11170.
- Karayanidis, F., Kelly, M., Chapman, P., Mayes, A., Johnston, P., 2009. Facial identity and facial expression matching in 5–12-year-old children and adults. *Infant Child Dev.* 18, 404–421.
- Keppel, G., 1991. Design and Analysis: A Researchers Handbook, 3rd ed. Prentice Hall, Upper Saddle River.
- Kriegeskorte, N., Simmons, W.K., Bellgowan, P.S., Baker, C.I., 2009. Circular analysis in systems neuroscience: the dangers of double dipping. *Nat. Neurosci.* 12 (5), 535–540.
- Maurer, D., Le Grand, R., Mondloch, C.J., 2002. The many faces of configural processing. *Trends Cogn. Sci.* 6 (6), 255–260.
- Meng, M., Cherian, T., Singal, G., Sinha, P., 2012. Lateralization of face processing in the human brain. *Proc. R. Soc. B.* <http://dx.doi.org/10.1098/rspb.2011.1784>.
- Mondloch, C.J., Le Grand, R., Maurer, D., 2002. Configural face processing develops more slowly than featural face processing. *Perception* 31, 553–566.
- Mondloch, C.J., Geldart, S., Maurer, D., Le Grand, R., 2003. Developmental changes in face processing skills. *J. Exp. Child Psychol.* 86, 67–84.
- Mondloch, C.J., Dobson, K.S., Parsons, J., Maurer, D., 2004. Why 8-year-olds cannot tell the difference between Steve Martin and Paul Newman: factors contributing to the slow development of sensitivity to the spacing of facial features. *J. Exp. Child Psychol.* 89, 159–181.
- Naccache, L., Dehaene, S., 2001. The priming method: imaging unconscious repetition priming reveals an abstract representation of number in the parietal lobes. *Cereb. Cortex* 11 (10), 966–974.
- Passarotti, A.M., Paul, B.M., Bussiere, J.R., Buxton, R.B., Wong, E.C., Stiles, J., 2003. The development of face and location processing: an fMRI study. *Dev. Sci.* 6 (1), 100–117.
- Petanjek, Z., Judas, M., Simic, G., Rasin, M.R., Uyilings, H.B.M., Rakic, P., 2011. Extraordinary neoteny of synaptic spines in the human prefrontal cortex. *Proc. Natl. Acad. Sci.* 108 (32), 13281–13286.
- Rossion, B., Caldara, R., Seghier, M., Schuller, A.-M., Lazeyras, F., Mayer, E., 2003. A network of occipito-temporal face sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. *Brain* 126, 1–15.
- Rotshtein, P., Henson, R.N.A., Treves, A., Driver, J., Dolan, R.J., 2005. Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. *Nat. Neurosci.* 8 (1), 107–113.
- Rotshtein, P., Vuilleumier, P., Winston, J., Driver, J., Dolan, R., 2007. Distinct and convergent visual processing of high and low spatial frequency information in faces. *Cereb. Cortex* 17, 2713–2724.
- Sawamura, H., Orban, G.A., Vogels, R., 2006. Selectivity of neuronal adaptation does not match response selectivity: a single-cell study of the fMRI adaptation paradigm. *Neuron* 49, 307–318.
- Scherf, S.K., Luna, B., Avidan, G., Behrmann, M., 2011. “What” precedes “which”: developmental neural tuning in face- and place-related cortex. *Cereb. Cortex* 21 (9), 1963–1980.
- Scherf, S.K., 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 (2), 199–219.
- Schiltz, C., Rossion, B., 2006. Faces are represented holistically in the human occipito-temporal cortex. *Neuroimage* 32, 1385–1394.
- Thomas, L.A., De Bellis, M.D., Graham, R., LaBar, K.S., 2007. Development of emotional facial recognition in late childhood and adolescence. *Dev. Sci.* 10 (5), 547–558.
- Wenger, K.K., Visscher, K.M., Miezin, F.M., Petersen, S.E., Schlaggar, B.L., 2004. Comparison of sustained and transient activity in children and adults using a mixed blocked/event-related fMRI design. *Neuroimage* 22, 975–985.
- Winston, J.S., Henson, R.N.A., Fine-Goulden, M.R., Dolan, R.J., 2004. fMRI-adaptation reveals dissociable neural representations of identity and expression in face perception. *J. Neurophysiol.* 92, 1830–1839.