

Developmental Changes in Effective Connectivity in the Emerging Core Face Network

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Little is currently known about the postnatal emergence of functional cortical networks supporting complex perceptual and cognitive skills, such as face processing. The present study examined the emergence of the core cortical network underlying face processing in younger and older school-age children as well as young adults. Participants performed 3 functional magnetic resonance imaging target detection tasks where they either had to detect a specific facial identity, expression, or direction of eye gaze in a stream of consecutively presented faces. We compared the connectivity of the face network using dynamic causal modelling and observed that it emerges gradually during childhood. Further, we found that while the relative strength of functional network connections were differentially modulated by task demands in adults, there was no such modulation of this network in either older or younger children. These results were independent of the behavioral performance in the 3 age groups. We suggest that the emergence of the face network is due to continuous specialization and fine-tuning within the regions of this network. The current results have important implications for future studies investigating trajectories of brain development and cortical specialization both in typically and atypically developing populations.

Introduction

The comparatively prolonged sequence of postnatal structural brain development in humans has also been revealed in developmental changes in cortical activation patterns for several domains of perception and cognition (Schlaggar and McCandliss 2007). However, despite such examples of emerging specialization within individual cortical regions during development, it remains unclear how these regions become recruited into specialized cortical networks. For example recent studies have shown developmental increases in functional intrahemispheric connectivity and long-range connections with a concurrent decrease in short-range connections in “default” intrinsic brain networks (Fair et al. 2008; Superkar et al. 2009) and the control network (Fair et al. 2007), which were attributed to changes in myelination (Giedd et al. 1999) and synaptic pruning (Huttenlocher et al. 1982; Chugani et al. 1987). In contrast, not much is known yet about the emerging trajectories of coordinated activity in functional networks that “actively” support specific perceptual and cognitive functions (Superkar et al. 2009).

Currently, one of the best-studied examples of emerging cortical specialization is face processing in the fusiform face area (Golarai et al. 2007; Scherf et al. 2007). Faces represent an ideal case study to study more fundamental patterns of cortical specialization as they are of high social relevance, rely on specific cognitive processing strategies, and are processed

within a well-described core network in the adult brain (e.g., Haxby et al. 2000). Recently, several studies have shown that while face-dependent activation within the core face network is observed from at least mid-childhood (Cohen Kadosh and Johnson 2007), face-specific response patterns continue to undergo a prolonged process of fine-tuning and they vary as a function of age and processing proficiency levels (Golarai et al. 2007). For example, behavioral face processing abilities in 10-year-old children still differ from adults (Mondloch et al. 2002, 2003, 2006) but see McKone et al. (2009). Moreover, some studies have even reported a dip in behavioral performance at puberty, with adolescents performing worse than younger children (Carey et al. 1980; McGivern et al. 2002).

Several studies have found that face-specific responses in the cortex change significantly throughout childhood and early adolescence, in comparison to other stimulus categories such as human bodies, objects, or landscapes that recruit similar (fusiform body area for human bodies) or adjacent areas (parahippocampal place area for landscapes or the lateral occipital cortex for objects) (Golarai et al. 2007; Scherf et al. 2007; Pelphrey et al. 2009; Peelen et al. 2009). A recent study, however, found evidence for adult-like face responses (in comparison to shoes, letters, or numbers) in children as young as 4 years of age (Cantlon et al. 2010), suggesting that the developmental trajectory is less straightforward than previously thought. Therefore, it remains an open question how the changing patterns of activation come to approximate the mature adult network and to what extent this pattern depends on proficiency and age and on the specific face properties processed. While the effective connectivity of the core face network has been studied in adults (Fairhall and Ishai 2007; Rotshtein et al. 2007), its development is unknown and has not yet been described. Moreover, the investigation of changing patterns of effective connectivity with age can inform a recent trend in the adult neuroimaging literature, which has moved toward interpreting neural response properties with regard to a given region’s pattern of interconnectivity with others (Johnson et al. 2009).

The present study used three functional magnetic resonance imaging (fMRI) target detection tasks (Cohen Kadosh et al. 2010) to assess face-property-specific neural processing within the core face-processing network in children aged 7–8, 10–11 years, and in adults. Participants had to detect a specific identity, emotional expression, or direction of eye gaze in a stream of consecutively presented faces. This allowed us also, for the first time in children, to characterize the processing of different face properties in the same individual simultaneously. As the 3 target detection tasks were designed to tap into face-property-specific processing strategies while minimizing age-dependent proficiency differences and thus maximizing comparability across age groups, 3 additional out-of-scanner

behavioral tasks were conducted to independently assess face-property-specific proficiency (see Supplementary Material for a description).

In a first step, we conducted a region of interest (ROI) analysis to probe face-property-dependent fMRI activation within the regions of the core network, both as a function of age and face property (via a regression analysis with behavioral tasks). Then, dynamic causal modeling (DCM) analysis was used to probe the patterns of effective connectivity in the core face network in children and adults. DCM analysis represents a novel approach to interpret functional neuroimaging data that can be used to assess the effective connectivity patterns between different brain regions. For example, it allows one to determine how task demands (e.g., the instruction to process the identity and not the emotional expression of a face) modulate the connectivity between these regions (Friston et al. 2003).

Materials and Methods

Participants

Twenty-two children (ten 7- to 8-year olds, average age = 8.5 years, standard deviation [SD] = 0.3 years; twelve 10- to 11-year olds, average age = 10.8 years, SD = 0.9 years) and 14 adults (average age = 25.5 years, SD = 4.3 years) participated in the fMRI tasks. All participants had normal or corrected to normal vision. The study was approved by the UCL Ethics Committee, and informed consent was obtained from all participants (or the primary caregiver in the case of minors) prior to testing.

Experimental Procedure

In the target detection task, 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). Each task was a separate session, the experiment therefore consisted of 3 sessions, which took all place on the same day. 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"). Each stimulus was presented for 500 ms, with an interstimulus interval of 1 s. The standard stimuli were arranged in miniblocks of about 15 s, containing on average 9 standard stimuli (SD \pm 2 standard stimuli) and 1 target stimulus. Target stimuli occurred in a pseudorandomized frequency in the miniblocks, but targets never appeared before the presentation of at least 5 standard stimuli. Each session consisted of about 30 miniblocks. Finally, 6 periods of 10 s of blank screen "baseline condition" were inserted into each session, at randomly selected breaks between miniblocks.

fMRI Data Acquisition

A Siemens 1.5T Avanto MRI scanner (Siemens) was used to acquire gradient echo-planar images (EPIs) (29 oblique slices covering the occipital, temporal, and most of the parietal lobes; time repetition [TR] = 2500 ms; time echo [TE] = 50 ms; flip angle = 90°; field of view = 192 \times 192 mm; voxel size: 3.0 \times 3.0 \times 4.5 mm). Following the functional scans, a T_1 -weighted structural image (1 mm³ resolution) was acquired for coregistration and display of the functional data.

Data Analysis

Data were analyzed using SPM5 (Wellcome Department of Imaging Neuroscience; <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). EPI volumes were spatially realigned to correct for movement artifacts, normalized to the Montreal Neurological Institute (MNI) standard space (Ashburner and Friston 2003a; Ashburner and Friston 2003b) and

smoothed using an 8-mm Gaussian kernel. A general linear model was computed with 6 regressors, one for each condition in the design (3 tasks) plus one for targets trials for each of the 3 tasks. In addition, a covariate was included with the mean accuracy rates for each participant (collapsed across task, as the main effect of task or the interaction between task \times age group was not significant) to prevent the possibility of age-dependent proficiency differences affecting the fMRI results.

Each miniblock was modeled as an epoch of 12 s and convolved with a canonical hemodynamic response function. Because of the short SOA, this means that the regressors for the conditions of interest effectively model the mean response during a miniblock (with the exception of target trials). To account for (linear) residual movement artifacts, the model also included 6 further regressors representing the rigid-body parameters estimated during realignment (note that none of the adults or children included in this data set exhibited greater than 3-mm deviation in the centre of mass in any direction). Voxel-wise parameter estimates for these regressors were obtained by restricted maximum-likelihood estimation (ReML), using a temporal high-pass filter (cut-off 128 secs) to remove low-frequency drifts, and modelling temporal autocorrelation across scans with an Auto-regression (1) process. Finally, to obtain the areas for the connectivity analyses, three 6-mm VOIs were localized in each participant individually and closest to the group local maxima within the core face network in the right hemisphere (coordinates are for x , y , and z , in MNI space): fusiform gyrus (FG): 39, -50, -20; inferior occipital gyrus (IOG): 42, -78, -9; superior temporal sulcus (STS): 48, -42, 12 (see Supplementary Table S5).

DCM Model Construction and Assessment

Three models were constructed based on the core model structure proposed by Fairhall and Ishai (2007), which differed with regard to the modulatory influence of each face-processing task on the different brain regions. The specific task influences were modeled based on the results of a previous fMRI adaptation study (Cohen Kadosh et al. 2010) that used the same experimental design and stimuli and on the literature (Bruce and Young 1986; Haxby et al. 2000; Allison et al. 1994).

DCM Model Selection

For the current analysis, a Bayesian model selection procedure was adopted to choose the model that represented the best balance between data fit and model complexity (but see Ramsey et al. 2010). This procedure quantifies the relative goodness of 2 competing models, model 1 and model 2, by computing the Bayes factor (BF), which is the ratio between the evidence-favoring model 1 and the evidence-favoring model 2. Comparing model 1 to model 2, if $BF > 1$ the data favors model 1 over model 2, and when $BF < 1$, the data favors model 2 over model 1. Thus, BF is a summary of the evidence provided by the data in favor of one prediction, represented by a statistical model, as opposed to another.

Just as a culture has developed around the use of P values in classical statistics, so one has developed around the use of BF; $1 < BF < 3$ is considered as a weak evidence for one model over another, $3 \leq BF < 20$ as a positive evidence, $20 \leq BF < 150$ as strong evidence, and $BF > 150$ is considered as very strong evidence (Penny et al. 2004). For each participant, the best model represents an optimal balance between accuracy (i.e., fit) and complexity (i.e., parsimony). Two indexes can be used to compare the models across participants: 1) group Bayes factor (GBF)—the arithmetic mean of the BF and 2) positive evidence ratio—the number of participants who showed (at least) positive evidence ($BF \geq 3$) for one model divided by the number of participants who showed positive evidence for model 2.

The selected model parameters were assessed for intersubject consistency using the GBF values (Supplementary Table S6). In a second step, t -tests were conducted to establish whether all model parameters were significantly different from zero. Then specific age differences were assessed by comparing model parameters across groups using t -tests (Supplementary Table S7). Note that all t -tests were 2 tailed and Bonferroni corrected for multiple comparisons.

Results

A Huynh-Feldt-corrected, repeated-measures ANOVA with the between-subject factor “age” (3 levels) and the within-subject factor “task” (3 levels) established that the reaction times did not differ between 3 age groups: none of the main effects were significant, and there was no interaction between the factors age and task. For the accuracy rates, we only found a significant main effect of age ($F_{2,26} = 8.17, P = 0.002$). Planned comparisons revealed that the main effect of age was due to significant accuracy increases between the 7- to 8 and the 10- to 11-year groups ($t(14) = 2.21, P = 0.044$), between the 7- to 8-years group and the adults ($t(19) = 2.91, P = 0.009$) but not between the 10- to 11-year olds and the adults ($t(19) = 0.520, P = 0.609$). This suggests that while all 3 age groups detected the task-relevant face property at comparable speeds, proficiencies continue to improve until at least mid-childhood (Supplementary Table S1). As no main effect of task was found, the behavioral results for all 3 target detection tasks were collapsed for the correlation analyses. Moreover, in order to remove any differences due to overall lower accuracies, the mean accuracies collapsed across all 3 fMRI target detection tasks were included as a covariate in the fMRI ROI analysis.

ROI Analysis

In line with previous studies, which have commonly reported a right-hemisphere bias for face-related activation (Allison et al. 1994; Haxby et al. 2000), the ROI analysis focused on brain regions in the right hemisphere. Specifically, we examined age- and task-related differences in the core face-processing areas, a network based in the right hemisphere comprising the FG, the IOG, and the right STS. While none of the task \times age interactions reached significance within the specific ROIs, a significant main effect of age was found in the IOG ($F_{2,33} = 12.56, P = 0.001$). A trend toward a main effect of age was also observed in the FG ($F_{2,33} = 3.00, P = 0.064$). The STS showed a significant main effect of task ($F_{2,66} = 3.23, P = 0.046$) (Figure 1, Supplementary Tables S2 and S3). Planned comparison for these areas (Supplementary Table S3) showed that the source of the main effect for age in the IOG and FG was a significant lower activation for both the children groups in

comparison to the adult group (all $P < 0.05$). Finally, between-task comparisons in the right STS showed that main effect for task was due to increased activation for the expression task in comparison to the other tasks (Table 1).

A regression analysis using the accuracy rates for the out-of-scanner tasks assessed the differential influence of age or processing proficiency on activation within ROIs. Nonparametric stepwise regressions were conducted. All 3 brain regions correlated significantly with each other (all Spearman's $r_s > 0.50$, all $P < 0.001$), a finding that further supports the network character of this activation (Supplementary Table S4). Using a stepwise model, we found that the age group explained a significant amount of the activation differences in all 3 brain regions (FG: $r(36) = 0.352, P = 0.035$; IOG: $r(36) = 0.578, P < 0.001$). That is, neural activation increased significantly with age. The inclusion of additional variables, such as task accuracy in any of the tasks, correlated positively with neural activation but did not increase the explained variance significantly. This suggests that while high processing proficiency might result in stronger neural responses, age was the main predictor of activation within the regions of the face network.

Dynamic Causal Modeling

In the next step, we used DCM to pinpoint the developmental changes in effective connectivity patterns within the network and to assess how differing task demands modulated this effective connectivity. The model selection procedure confirmed the same basic model for all age groups. That is, the IOG

Table 1

Correlations between neural activation \times accuracy in the core face network

	R IOG MNI (42, -78, -9)	R FG MNI (39, -50, -20)
Age	$r(36) = 0.578, P < 0.001$	$r(36) = 0.352, P = 0.035$
ACC fMRI tasks	$r(36) = 0.312, P = 0.064$	$r(36) = 0.039, P = 0.821$
ACC Benton test	$r(36) = 0.408, P = 0.013$	$r(36) = 0.246, P = 0.148$
ACC expression task	$r(36) = 0.256, P = 0.132$	$r(36) = 0.212, P = 0.215$
ACC gaze task	$r(36) = 0.229, P = 0.0178$	$r(36) = -0.020, P = 0.908$

Note: ACC, accuracy; L, left; R, right.

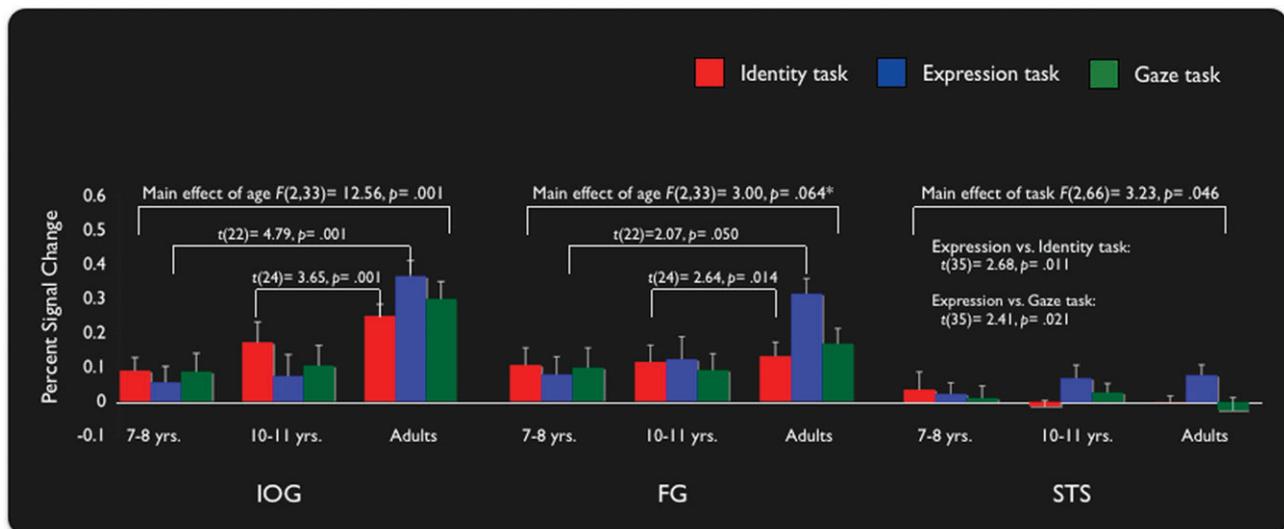


Figure 1. Changes in activation as a function of age group \times task in the 3 core regions of the brain network.

exerted an intrinsic influence (i.e., independent of the specific cognitive top-down influence) on activation in the FG and STS along 2 separate pathways (Fig. 2*a,b*). This shows that overall patterns of dynamic connectivity are similar to adults already at the age of 7–8 years. However, both groups of children showed substantially weaker connectivity between the IOG and FG and had no significant effective connectivity between the IOG and the STS. More notably, with regard to the developmental trajectories, no evidence was found for the influence of task demands on the effective connectivity within the network in the 2 child groups (Fig. 2*a*). That is, whereas in the adults the identity task selectively increased the influence of the IOG on the FG, while the expression task changed the influence of the IOG along the other path (via the STS), no such effect was observed for the child groups in any of the tasks (Fig. 2). Therefore, while both child groups exhibited similar network structures, no evidence was found for top-down task influences.

Finally, we conducted 3 additional analyses to rule out that the developmental effects were due to 1) a smaller sample size in the case of the 2 child groups, 2) a lower number of activated voxels in the VOIs in the case of the children, or 3) greater variation in the activation within the VOIs in the children. A power analysis was conducted to assess whether the developmental effects were due to a lack of statistical power as a consequence of the slightly smaller size of the child groups. The comparison of Cohen's *d*'s for each network path indicated that this was not the case (7- to 8-year olds: IOG–FG = 2.91; IOG–STS = 0.95; 10- to 11-year olds: IOG–FG = 1.87; IOG–STS = 0.23; adults: IOG–FG = 7.33; IOG–STS = 1.62) (Fig. 2*c*). Namely, the observed differences are not driven by a lack of statistical power due to smaller sizes. We note that while both

child groups showed reduced connection strength compared with the adults in the 2 network paths, the 10- to 11-year olds exhibited even weaker connection strengths than the younger children, a finding which might be due to the previously reported performance dip in face-processing skills in early adolescence (Carey et al. 1980; McGivern et al. 2002).

We then assessed whether the child groups showed less face-sensitive activation by calculating the number of face-responsive voxels in each volume of interest (VOI). Our analysis showed that the 3 age groups did not differ in the number of face-responsive voxels per VOI in the FG and the STS but that the 10- to 11-year-old children showed significantly less activation in the IOG in comparison to the other 2 groups. (FG: $F_{2,29} = 1.08$, $P = 0.355$ [mean/SD of activated voxels: 7–8 years = 16/8; 10–11 years = 14/7; adults = 19/9]; STS: $F_{2,29} = 0.655$, $P = 0.528$ [7–8 years = 8/6; 10–11 years = 12/7; adults = 11/8]; IOG: $F_{2,29} = 6.95$, $P = 0.04$ [7–8 years = 19/6; 10–11 years = 11/4; adults = 24/10]). The effect for the IOG was due to significant differences between the 7- to 8-year olds and the 10- to 11-year olds ($t(14) = 2.62$, $P = 0.02$) and the 10- to 11-year group and the adults ($t(19) = 3.46$, $P = 0.003$) but not between the 7- to 8-year olds and the adults ($t(19) = 1.56$, $P = 0.136$).

Finally, to assess the degree of variation across age, we compared the data time series (via the SDs for the 3 age groups) in the VOIs and found no significant difference for the IOG: $F_{2,31} = 2.326$, $P = 0.114$ (7- to 8-year olds: 0.147; 10- to 11-year olds: 0.208; adults: 0.162), the FG: $F_{2,31} = 0.50$, $P = 0.612$ (7- to 8-year olds: 0.167; 10- to 11-year olds: 0.183; adults: 0.158), or the STS: $F_{2,31} = 1.538$, $P = 0.231$ (7- to 8-year olds: 0.124; 10- to 11-year olds: 0.091; adults: 0.103). This suggests that the observed developmental changes are not due to greater

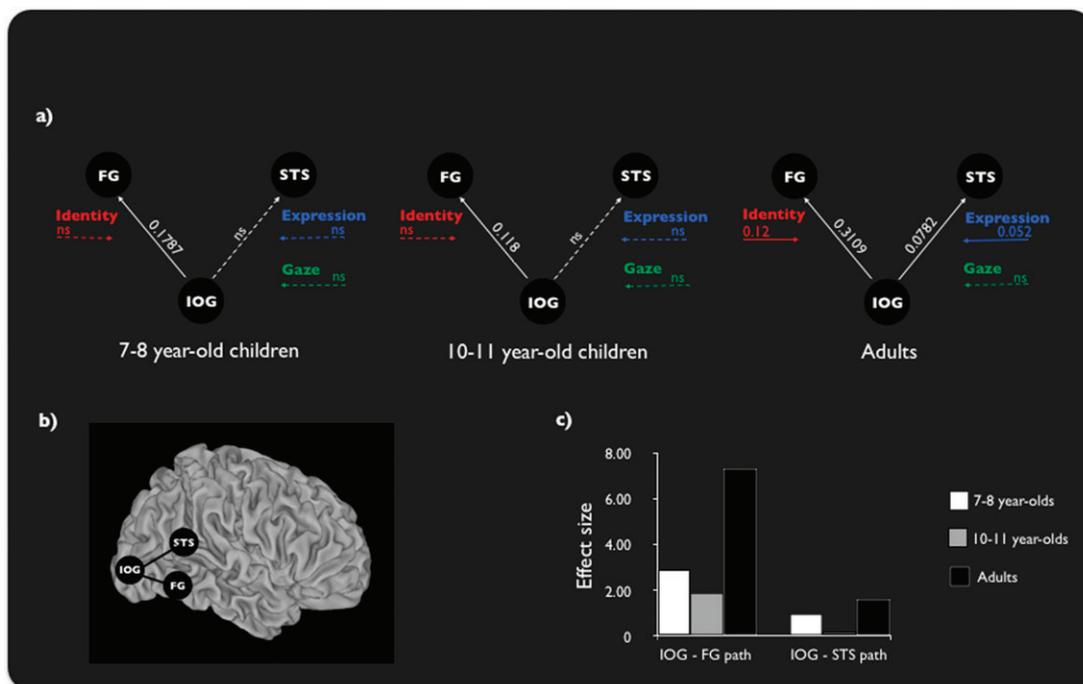


Figure 2. *a*) Color-coded task effects for each age group in the DCM model (Identity task = red; Expression task = blue, Gaze task = green). Solid arrows indicate significant effects and dotted arrows indicate nonsignificant effects. Black arrows indicate the intrinsic connection between the areas of interest. Colored arrows indicate modulatory effects of each task on the connection between the areas. *b*) Lateral schematic view of the face network in the brain. *c*) Effective connectivity strength for both network paths as a function of effect size. Color coding: white = 7- to 8-year-olds; gray = 10- to 11-year olds; black = adults.

variability in the younger participant (note that even descriptively in all the cases the adults group did not yield the smallest SD).

Summary and Discussion

In the current study, we investigated the changes in neural response patterns for different face properties and tasks in the core face network in children and adults and supplemented it with an examination of the developmental changes of the effective connectivity in a stimulus-specific related perceptual network. Our ROI analysis established that activity within the network increases with age and independently of the specific face property that is processed. The DCM analysis then confirmed that while the overall structure of the final mature network is already present in mid-childhood (i.e., the same basic network structure was found for all 3 groups), specific patterns of interregional connectivities are not established until at least 11 years of age. We then examined the modulation of the network resulting from different task demands and observed that detecting changes in identity and expression, but not gaze direction, significantly influenced the effective connectivity of the network in the adult participants, confirming previous analysis of the adult participants that face-sensitive cortical activation varies according to specific task demands (Cohen Kadosh et al. 2010).

The current results also revealed that neither child group showed the task-dependent modulation of effective connectivity seen in adults, indicating that activation of the emerging core network is less selectively tuned to task demands in children. This lack of modulation may contribute to, or reflect, the lower face-processing proficiency levels at this age (Fig. 2*a*, and as shown in the out-of-scanner tasks). Similarly, it might be that in children, compensatory connections exist outside the core network for processing the specific face properties (Gathers et al. 2004; Johnson et al. 2009). The age-dependent increase in activation that was observed in the ROI analysis appeared to be mainly driven by an increase for the expression task condition, possibly reflecting stronger connectivity between the FG and the amygdala in the adults.

While the current study offered an initial survey of task-dependent changes in network modulation of the face-processing regions, future studies should focus on possible age-dependent variations and/or extensions of these networks as face processing in the brain becomes increasingly structured and proficient. We note that the lack of task influence in the children cannot be explained by overall differences in accuracy as these were removed by including a covariate in the fMRI model. This conclusion is further supported by the finding that the 3 cognitive tasks differentially influenced the different network paths in the adult participants.

While we know that resting state networks expand and refine with postnatal development (Fair et al. 2008), the current findings extend these results to coordinated networks supporting active perception and cognition. As these functional networks strengthen, they may also incorporate new regions that are frequently coactive or lose nodes that become decorrelated with the rest of the network (Johnson 2001). Similarly, the lower number of specialized voxels may reflect a higher number of diffuse connections with other regions, which will need to be “pruned” for maximum efficiency. This interpretation has received some support from recent studies

(Simmons et al. 2007; Cantlon et al. 2010), and they speak to the predictions made by the interactive specialization (IS) framework (e.g., Johnson 2001). The IS view of human functional brain development (Johnson 2001) suggests that the activation of networks of regions may become increasingly selective or tuned to particular task demands or contexts during childhood.

Our results also provide some important insights in the neural response characteristics of the mature face-processing network. Namely, rather than supporting the notion of a network with segregated functional regions for different face stimulus properties (e.g., Haxby et al. 2000), they suggest that face-property-specific processing in the adult brain is modulated by task and dependent on a network of highly integrated regions. This interpretation is supported by a recent fMRI adaptation study (Cohen Kadosh et al. 2010) that found flexible task-dependent adaptation patterns for the IOG, FG, and STS using the same experimental design as the current study. Another study used transcranial magnetic stimulation to investigate the functional role of the IOG in the processing of the identity, expression, and gaze in the IOG at different time points (Cohen Kadosh et al. 2010). It was found that IOG integrates information across different face properties and that TMS affected the integrative processing of facial identity and expression at a mid-latency processing stage, suggesting that it relies both on feedforward and reentrant feedback processing. These findings again support the integrative network character of face processing in the brain and emphasize the importance of future work on not only the spatial but also the temporal, characteristics of neural face processing both in the mature and the developing brain.

Supplementary Material

Supplementary materials and Tables S1-S7 can be found at: <http://www.cercor.oxfordjournals.org/>.

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Notes

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