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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.

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.