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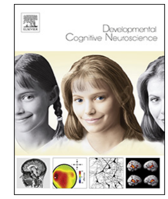

Age-related increase of image-invariance in the fusiform face area

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ABSTRACT

Face recognition undergoes prolonged development from childhood to adulthood, thereby raising the question which neural underpinnings are driving this development. Here, we address the development of the neural foundation of the ability to recognize a face across naturally varying images. Fourteen children (ages, 7–10) and 14 adults (ages, 20–23) watched images of either the same or different faces in a functional magnetic resonance imaging adaptation paradigm. The same face was either presented in exact image repetitions or in varying images. Additionally, a subset of participants completed a behavioral task, in which they decided if the face in consecutively presented images belonged to the same person. Results revealed age-related increases in neural sensitivity to face identity in the fusiform face area. Importantly, ventral temporal face-selective regions exhibited more image-invariance – as indicated by stronger adaptation for different images of the same person – in adults compared to children. Crucially, the amount of adaptation to face identity across varying images was correlated with the ability to recognize individual faces in different images. These results suggest that the increase of image-invariance in face-selective regions might be related to the development of face recognition skills.

1. Introduction

In our daily life we encounter and recognize a vast number of faces. In most cases, we manage to recognize faces with great ease – even across varying contexts including differences in facial expression, lighting or viewpoint. How does this astonishing ability develop and what are its neural underpinnings?

It has been shown that the ability to discriminate and recognize faces undergoes prolonged development from childhood to adulthood (Germine et al., 2011; Weigelt et al., 2014). Similarly, on a neural level, the regions belonging to the network that subserves face recognition undergo development from childhood to adulthood (Cohen Kadosh et al., 2013a, 2013b, Golarai et al., 2007, 2010, 2017; Scherf et al., 2007). As such, a core component of the face-selective network, the fusiform face area (FFA; Kanwisher et al., 1997) exhibits developmental changes from childhood to adulthood: the FFA increases in size (Golarai et al., 2007; Peelen et al., 2009; Scherf et al., 2007), develops a stronger category-selectivity (Golarai et al., 2010; Peelen et al., 2009) and becomes increasingly sensitive to face identity (Natu et al., 2016).

Recently, behavioral studies have indicated that the ability to recognize a face in varying images might follow a prolonged trajectory from childhood to adulthood (Laurence and Mondloch, 2016; Neil et al., 2016) thus suggesting that the development of this ability might be linked to the overall increase in face recognition skills. Behavioral studies on the development of face recognition across varying images employed versions of a paradigm previously developed by Jenkins et al. (2011), in which participants are asked to sort images of faces containing natural within-person variability into piles according to their perceived identities. Adults divided 40 images of two identities into more identities than actually present with 7.5 identities on average (Jenkins et al., 2011). Notably, six- to 14-year-old children divided the images into even more identities with 14.5 identities on average (Neil et al., 2016).

Which neural underpinnings might be driving these differences between children and adults in image-invariant face recognition? The face-selective functional region FFA has been shown to process invariant aspects of faces crucial for identity recognition (Haxby et al., 2000; Rotshtein et al., 2004). To investigate image-invariance in the FFA and other functional regions, researchers have used fMRI adaptation (Grill-Spector and Malach, 2001), which is based on the mechanism that a certain brain region will show an adapted response to a repeated presentation of a certain stimulus feature, if this brain region is involved in processing this particular stimulus feature. This approach has proven to be a useful tool for studying neurodevelopmental processes (e.g., Natu et al., 2016; for a review see Nordt et al., 2016) as it does not require collecting behavioral responses thus avoiding possible

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confounds due to performance differences across groups (Poldrack, 2000). In case of image-invariance in the FFA, this suggests that the signal in the FFA should adapt to repeated presentations of the same face even when presented in different images. Using this approach, studies in adults have found that the FFA exhibits image-invariance up to a certain degree (Davies-Thompson et al., 2013), thereby suggesting that the development of the ability to recognize the same face across different images (Laurence and Mondloch, 2016; Neil et al., 2016) might be related to an increase of image-invariance in the FFA.

To investigate differences in image-invariance in the FFA between children and adults, in the present study we addressed the neurodevelopmental foundation of the ability to recognize the same face identity across naturally varying images. To this end, seven- to 10-year-old children and adults watched series of faces in a blocked fMRI adaptation paradigm (Grill-Spector and Malach, 2001; Nordt et al., 2016), comprising (i) the repeated presentation of the same face shown in the exact same image, (ii) the repeated presentation of the same face but in different images, and (iii) images of different faces. To obtain two independent measures of the development of invariance in face-selective regions, we employed both functional and structural approaches of defining face-selective regions in ventral temporal cortex (Weiner et al., 2014). Based on behavioral evidence (Laurence and Mondloch, 2016; Neil et al., 2016), we expected to find less adaptation for faces presented in varying images in children's face-selective regions compared to adults. Thus, we hypothesized, that from childhood to adulthood face-selective regions exhibit greater invariance to image variability, that is to say, they become more proficient in recognizing the same face across varying images. Furthermore, we test if the amount of adaptation to the same face identity across different images is related to the behavioral ability of recognizing individual faces in different images.

2. Materials and methods

2.1. Participants

Child participants were recruited via newspaper articles and via a participant pool of families, who had already participated in other studies of the lab. Adult participants were recruited via announcements at the university. Data of 14 children (aged seven to 10 years, mean age = 8.36, *SD* = 0.81) and 14 adults (aged 20–23 years, mean age = 21.21, *SD* = 0.94) were included in the analyses. Three additional children were scanned but had to be excluded: Two datasets were excluded due to high head motion (motion > 3 mm) in the functional runs and one dataset had to be excluded due to technical error during data acquisition. Data of six adults were excluded due to the following reasons: one of them reported a psychiatric disorder (after being scanned) and data of five adults were discarded because their score on the Cambridge Face Memory Test was more than two standard deviations below the mean, thereby hinting at abnormal face processing (cutoff for prosopagnosia: 42.1 points or 58.47%, see Bowles et al., 2009).

As child participants are more difficult to recruit than adult participants, we included both right and left handed children and consecutively matched the adult sample to the child sample based on the parameters of handedness (Willems et al., 2010), gender and age range. Furthermore, we aimed at including similar amounts of data from children and adults to make sure that differences across groups are not due to differences in statistical power. After obtaining 14 data sets with high quality (indicated by low motion) in children, we matched the data of adult participants to that of children with regard to the factors handedness, gender, age range (four years in each age group) and number of participants across the age groups. By excluding additional five adult participants we achieved matching of groups for handedness (five left-handed participants in each age group), gender (4 female participants in each group) and age range (four years in each group). These datasets were excluded prior to any analyses (after checking for head motion values).

The remaining participants had normal or corrected vision and were free of neurological or psychiatric disorders. In each of the age groups four participants were left-handed (as indicated by self or – in case of child participants – parent report) and four participants were female. Adults' performance on the Cambridge Face Memory Test (Duchaine and Nakayama, 2006) was on average 79.07% (*SD* = 8.87%, range: 62.5–94.44%) and children's performance on the Cambridge Face Memory Test for Children (Croydon et al., 2014) was on average 81.68% (*SD* = 8.16%, range: 70.83–95.83%), demonstrating normal face recognition abilities in both groups.

Child participants were rewarded with a small present and a gift card and adult participants received course credit or monetary compensation for their participation. All participants or – in case of child participants – one of their caregivers gave informed written consent to participate in the study. Ethical approval was obtained from the local institutional review board.

2.2. Stimuli

2.2.1. Adaptation paradigm

Stimuli used in the adaptation paradigm consisted of 208 color images of the faces of 128 different individuals. Of those 128 individuals 112 were shown in only one image, while the remaining 16 individuals were depicted in six different images each. Half of the stimuli were taken from the internet and half of the stimuli were taken from two face databases including the PUT Face database (Kasiński et al., 2008) and the database "A lifespan database of adult facial stimuli" (Minear and Park, 2004). Faces taken from the internet were of sport team members of teams largely unknown in Germany (for examples of stimuli from the databases and from the Internet, see Supplementary material 1). All stimuli depicted faces of Caucasian adults. Both half of the stimuli from the internet and half of the stimuli from the database depicted male faces, while the other half depicted female faces. In all stimuli the face was seen in front view, with frontal gaze and with a neutral or friendly expression. Multiple images of the same individual differed only slightly from each other with small rotations of the head (approximately less than 5° from the front view). Furthermore, there were small changes of haircut, age and emotional expression across the six different images of the same individual. Images stemming from the internet contained a higher degree of variability compared to the images taken from the databases (for analyses of the effects of image variability see supplementary material 2). This was confirmed by the results of a simple rating task. In this task 12 adult participants, who did not take part in the fMRI adaptation paradigm, were given 16 small pieces of paper. On each piece six varying images of one face identity were printed in a row. Participants were asked to sort the pieces of paper (responding to the 16 identities) with regard to the variability of the six images of each face identity, from top indicating a high degree of variability to bottom indicating a low degree of variability. Results showed that images of faces from the internet were ranked as more variable compared to the images taken from the databases: 10 out of 12 participants sorted all 8 rows of images from the internet on the top 8 ranks, and the remaining 2 participants sorted 7 out of 8 image rows from the internet on the top eight ranks.

Image processing was done in Adobe Photoshop CS5 Extended. In a first step, the face (including the hair) was cropped. Subsequently, those images were scaled to a maximum image height of 207 pixels. The cropped face was then centered in a 250 × 250 pixels-sized square on a grey background. As the participants task was to press a button for blue-washed images, which occurred at a random time point within the block (see, Section 2.4.2 Task), we created "blue-washed" versions of all stimuli for the task using Photoshop. While these blue versions had the same grey background as the regular stimuli, the part of the image depicting the face had a slight transparent blue overlay. For examples of the stimuli, see Fig. 1. Scrambled versions of all images were made. The scrambled versions of blue-washed images were further edited with an