Development of face recognition: Dynamic causal modelling of MEG data

Wei He\textsuperscript{a,b,⁎}, Blake W. Johnson\textsuperscript{a,b}

\textsuperscript{a} Department of Cognitive Science, Macquarie University, New South Wales 2109, Australia
\textsuperscript{b} Australian Research Council Centre of Excellence in Cognition and Its Disorders, Macquarie University, New South Wales 2109, Australia

1. Introduction

The human face conveys an extremely rich set of information concerning identity, gender, emotion, and other important social cues. Interpretation of this wealth of information is essential for social interactions and requires elaborative processes in multiple brain regions, with a bias toward right hemisphere structures (Haxby et al., 2000; Rossion, 2014). Functional magnetic resonance imaging (fMRI) studies in healthy adults show a stronger blood-oxygen-level dependent (BOLD) signal in the lateral inferior occipital gyrus (i.e., the occipital face area, OFA) and middle fusiform gyrus (i.e., fusiform face area, FFA; Kanwisher and Yovel, 2006) when processing faces or invariant facial aspects (e.g., eyes) compared to other object categories (e.g., cars). Moreover, evidence from fMRI-neural adaptation or repetition suppression studies demonstrates that BOLD activities in both the OFA and FFA are increased for a sequence of unique faces compared to repeated faces (Eger et al., 2004; Ewbank et al., 2012; Gauthier et al., 2000b; Schiltz and Rossion, 2006). Such “release from adaptation” suggests that similar populations of face-selective neurons may function in both categorizing (e.g., ‘it is a face, not a car’) and identifying faces (e.g., ‘it is face A, not face B’).

Electrophysiological recordings using magneto-/electro-encephalography (M/EEG) have provided information about the temporal sequencing of face-specific processing stages (Olivares et al., 2015; Rossion, 2014). Two important M/EEG components, the M/N170 and the M/N250, are believed to index structural (e.g., Bentin et al., 1996; Rossion and Jacques, 2008) and identity (e.g., Itier et al., 2006; Schweinberger et al., 2007, 2002; Walther et al., 2013) encoding stages of facial attributes. A recent MEG study in young adults reported that the right fusiform gyrus exhibits an early reduction in its activity at around 150 ms for category-level repetitions of face stimuli (e.g., face-to-different-face) and a late reduction between 200 and 300 ms for item-level repetitions (face-to-same-face) (Simpson et al., 2015). Taken together, the fMRI and MEG data suggest that a common population of neurons in the OFA and FFA carries out categorization and identification of faces in two sequential stages.

Given the social importance of face perception, one might assume the underlying brain regions should mature quite early. In fact, this issue is still strongly debated in the literature. Compelling support for early maturation has been reported by recent fMRI and M/EEG studies, showing that the activation and response patterns of the FFA (Cantlon et al., 2010; Haist et al., 2013) and the M/N170 (He et al., 2015; Kuefner et al., 2010) are stable from age 4–5 years (McKone et al., 2012). On the other hand, there is a wealth of fMRI data showing that the brain regions comprising the face network continue to mature to adolescence and beyond (Cohen Kadosh et al., 2013; Kadosh et al., 2013; McCandliss et al., 2003).

⁎ Corresponding author at: ARC Centre of Excellence in Cognition and its Disorders, Level 3, Australian Hearing Hub, 16 University Avenue, Macquarie University, NSW, 2109, Australia.
E-mail address: wei.he@mq.edu.au (W. He).

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Song et al., 2015). In adults, the repetition of unfamiliar faces is known to modulate the amplitude of M250, indicating the initial encoding of individual face exemplars (Schweinberger, 2011; Schweinberger et al., 2004, 2002; Walther et al., 2013). It remains unclear whether there is a comparable effect in children’s brain responses. One EEG study on 7-month-old infants reported a more negative N290 (a precursor of the adult N170) amplitude for novel female faces compared to 1-back repeated female faces (with one intervening different face) (Righi et al., 2014). However, a later infant EEG study using human faces, ape faces, and houses in an immediate repetition paradigm reported that, unlike the adult response, the N290 amplitude was modulated at the level of the basic categorization (human, ape, or house) but not the individual-level representation (Righi et al., 2014; Peykarjou et al., 2014). Another recent EEG study found no N290 amplitude effect, but did find a reduced N290 latency for repeated faces, which the authors interpreted to suggest faster processing of the repeated faces (Peykarjou et al., 2016).

In older children, two recent M/EEG studies using face repetition tasks have reported a frontal negative component between 250 and 600 ms in children as young as 8-years-old that is sensitive to face repetitions, with a larger amplitude for immediately repeated faces than novel/non-repeated faces (Itier and Taylor, 2004). Source reconstruction on a similar component in 6–7-year-olds showed enhanced activation in the right hippocampus to repeated (but unfamiliar) faces (Taylor et al., 2011b). It remains unclear how this frontally-distributed component may be related to the occipitotemporal M/N250 component reported in adults.

While there have been a few electrophysiological and neuroimaging studies of face repetition effects in infancy, and in school-aged children, there have been no studies of children of intermediate ages. There are two main reasons for the lack of neuroimaging studies on face recognition in early childhood. Firstly, preschool children have a limited capacity for the sustained attentive vigilance and behaviour control typically required in such experiments (Brown and Jernigan, 2012). Secondly, most neuroimaging systems with adult-sized head coils (fMRI) and helmet dewars (MEG) are poorly optimised for use with the smaller heads of children (Johnson et al., 2010). The advantage of using a custom-sized pediatric MEG system with pre-school aged children has been demonstrated in our previous work showing a robust face-sensitive M170 response in a group of 3- to 6-year-old children (He et al., 2014a,b; 2015); a response that has not been detected in previous studies using a conventional adult MEG system (Kylläinen et al., 2006; Taylor et al., 2010). Furthermore, using dynamic causal modelling (DCM), we were able to elucidate developmental changes in the connectivity of the core face network comprised of the OFA, FFA, and superior temporal sulcus (STS) (He et al., 2015).

In the present study, we aimed to extend our previous pediatric MEG work on the N170 to the subsequent M250 stage of face processing in healthy preschool aged children. To this end, we used a passive viewing repetition paradigm with an orthogonal visual detection task (Schweinberger et al., 2007). Repetitions were presented in a 0-lag and passive viewing design to minimise the cognitive and attentional demands on the children. We examined whether an M250 effect is detectable in children (using a pediatric MEG system); and compared the effective connectivity of the OFA and FFA underlying the neural responses obtained in both groups.

2. Material and methods

2.1. Participants

Data were collected from 10 typically-developing children (4 M, aged 5.3 ± 0.83 years, range 4–6 years) and 11 healthy adults (7 M, aged 24 ± 5.76 years, range 18–33 years). All participants were right-handed with normal or corrected to normal vision. Data from an additional 12 participants (10 children and 2 adults) were excluded due to non-compliance (6 children), excessive head movement (> 10 mm throughout the whole session causing loss of more than 40% of trials, 4 children), and technical problems during data acquisition (2 adults). The experimental procedures were approved by the Human Participants Ethics Committee at Macquarie University. Written informed consent was obtained from the adult participants and from the parents/guardians of the children prior to the experiment.

2.2. Experimental procedure

Upon arriving at the laboratory, participants were familiarized with the magnetically shielded room (MSR) where they were tested in a supine position with visual images projected onto a screen by video projectors situated outside the MSR room (child MEG projector: InFocus Model IN5108, Portland; Adult MEG projector: Sharp Notevision Model PG10S, Japan). Prior to MEG measurements, five head position indicators (HPI) were attached to a tightly fitting elastic cap. The 3D locations of the HPIs, fiducial landmarks and the shape of each participant’s head were measured with a pen digitizer (Polhemus Fastrack, Colchester, VT). Then, children were tested using the child custom-sized 64-channel whole-head axial gradiometer MEG system (Model PQ1064R-N2m, KIT, Kanazawa, Japan), and adults were tested using the 160-channel whole-head axial gradiometer MEG system (Model PQ1160RN2, KIT, Kanazawa, Japan). The gradiometers of both systems have a 50 mm baseline and a 15.5 mm diameter positioned in a glass fibre reinforced plastic cryostat for measurement of the normal component of the magnetic field from the human brain (Kado et al., 1999). In both systems, neighbouring channels are 38 mm apart, and 20 mm from the outer dural surface. The size of the dural helmet of the child system was 53.4 cm. This was designed to fit 90% of heads of 5-year olds (for more details please refer to Johnson et al., 2010).

Both systems were situated within the same MSR and therefore environmental noise was equivalent. Stimuli consisted of 84 colour pictures, including 43 unfamiliar faces (24 male) and 41 cartoon alien pictures. Faces were posed with neutral expression and without glasses, earrings, facial hair or make-up. All pictures were trimmed to remove any background, including clothing and hair. Four blocks of 63 pictures were presented with 86 trials of immediate repetitions (0-lag) and 86 trials of no repetitions. No individual face appeared more than 3 times within a block. To ensure that participants maintained vigilance, they were required to press a button for catch trials of cartoon aliens, randomly embedded into the image stream. Brain responses to the catch trials and to faces presented immediately before or after the catch trials were not analysed further. Repeated, non-repeated, and catch trials were presented in a pseudo-randomized order. Even though each face was repeated only once after a varying number of intervening stimuli, participants might develop expectations about the nature of the next stimulus. To examine this possibility, we compared responses for the first and last blocks of trials and found no significant differences (see section 1 in the Supplementary Materials).

The experiment was programmed using Experiment Builder software (SR Research Ltd., Mississauga, Ontario, Canada). All pictures were presented within a light grey frame fitted into a rectangular area that subtended a visual angle of 3.10° × 4.58° in the adult system and 2.64° × 3.90° in the child system. The monocular gaze of the participant’s right eye was monitored by an SR Research Eyelink 1000 eye-tracking system with a sampling rate of 1000 Hz (http://www.srresearch.com/EL_1000.html). Each trial began with a fixation point that appeared at the centre of the screen for 200 ms. Each stimulus was then presented for 1000 ms with the condition that eye fixations were maintained in the proximity of the fixation point. The mean inter-stimulus interval was 1000 ms (with a random jitter of 50 ms). Catch trials remained on the screen until a response was made or a maximum duration of 2000 ms occurred (Fig. 1). In both groups, participants responded to catch trials with accuracy greater than 98%.
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