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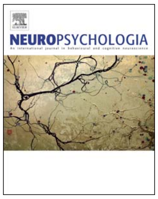

The non-linear development of the right hemispheric specialization for human face perception

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ABSTRACT

The developmental origins of human adults' right hemispheric specialization for face perception remain unclear. On the one hand, infant studies have shown a right hemispheric advantage for face perception. On the other hand, it has been proposed that the adult right hemispheric lateralization for face perception slowly emerges during childhood due to reading acquisition, which increases left lateralized posterior responses to competing written material (e.g., visual letters and words). Since methodological approaches used in infant and children typically differ when their face capabilities are explored, resolving this issue has been difficult. Here we tested 5-year-old preschoolers varying in their level of visual letter knowledge with the same fast periodic visual stimulation (FPVS) paradigm leading to strongly right lateralized electrophysiological occipito-temporal face-selective responses in 4- to 6-month-old infants (de Heering and Rossion, 2015). Children's face-selective response was quantitatively larger and differed in scalp topography from infants', but did not differ across hemispheres. There was a small positive correlation between preschoolers' letter knowledge and a non-normalized index of right hemispheric specialization for faces. These observations show that previous discrepant results in the literature reflect a genuine nonlinear development of the neural processes underlying face perception and are not merely due to methodological differences across age groups. We discuss several factors that could contribute to the adult right hemispheric lateralization for faces, such as myelination of the corpus callosum and reading acquisition. Our findings point to the value of FPVS coupled with electroencephalography to assess specialized face perception processes throughout development with the same methodology.

1. Introduction

Hemispheric lateralization of brain function is well established in humans as well as in other animal species. Yet the reasons for this lateralization are still largely unknown and debated (Corballis, 2009; Davidson and Hugdahl, 1995; Güntürkün et al., 2000). In humans, the right hemisphere (RH) is dominant in the perception of faces of conspecifics, a critical brain function for social interactions. This RH dominance for face perception has been initially supported by lesion studies, showing that a right ventral occipito-temporal lesion, typically associated with left upper visual field defects, is both necessary and sufficient to cause prosopagnosia, i.e., a severe and selective impairment at individual face recognition (Hecaen and Angelergues, 1962; Meadows, 1974; Sergent and Signoret, 1992; see Davies-Thompson et al., 2014; Rossion, 2014a for reviews). Divided visual field studies and chimeric face effects have also pointed to a right hemisphere advantage in face perception (Gilbert and Bakan, 1973; Hillger and Koenig, 1991; Kolb et al., 1983; Levy et al., 1972; Rizzolatti et al., 1971), a conclusion largely corroborated over the past two decades by numerous neuroimaging studies (Frässle et al., 2016; Kanwisher et al., 1997; Rossion et al., 2012a; Sergent et al., 1992) and high-density electroencephalographic (EEG) recordings on the human scalp (the right lateralized N170 potential evoked by faces; e.g., Bentin et al., 1996; Rossion and Jacques, 2011 for review). More recently, a strong right hemispheric dominance for face-selective responses in the human ventral occipito-temporal cortex (VOTC) has also been reported with intracerebral electrophysiological recordings (Jonas et al., 2016).

Since the critical brain regions involved in face perception are right lateralized in human adults, understanding *when* this right hemispheric lateralization emerges during human development and *which factors* drive this specialization is important to deepen our understanding of human face perception.

de Schonen and Mathivet (1989) initially proposed that the right hemispheric specialization for face perception emerges relatively *early*

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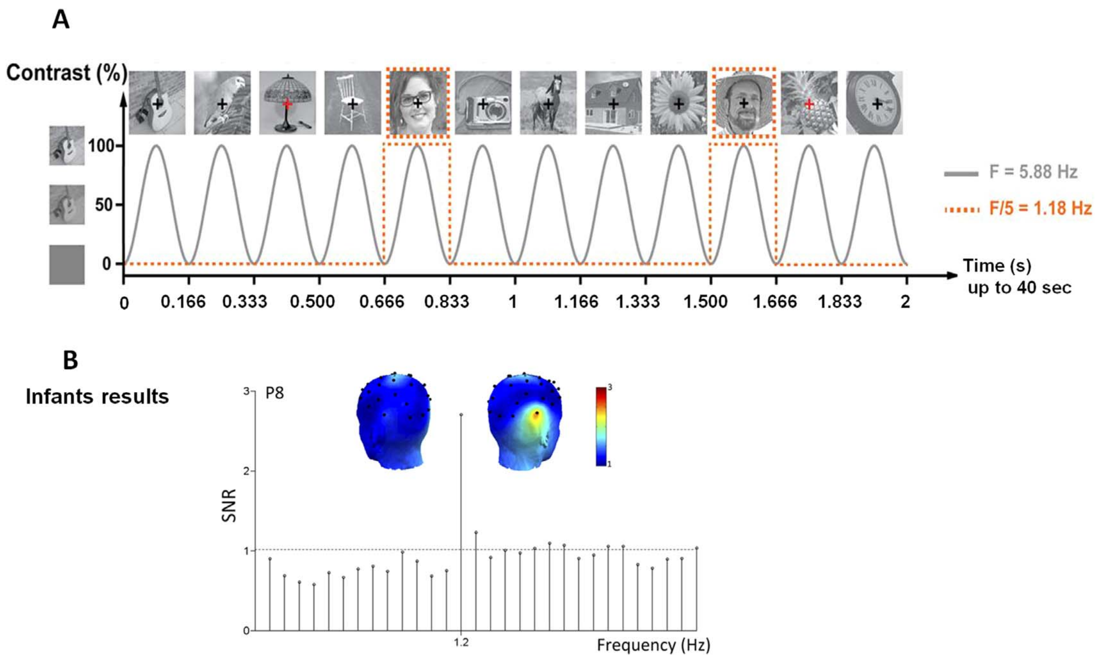

Fig. 1. Experimental Design. A. Example of a visual stimulation sequence where base stimuli are constituted of non-face objects, interspersed every 5 items with highly variable images of faces (various identities, viewpoints, …) (from de Heering and Rossion, 2015; Rossion et al., 2015). Stimuli are flickering on the screen at 6 Hz (6 stimuli per second) with a sinusoidal contrast modulation, with faces inserted every 5 stimuli (1.2 Hz). Each child viewed two 40-second stimulation sequences (i.e., 47 faces inserted in non-face objects). **B.** Results in 4- to 6-month-old infants (grand averaged frequency spectrum in signal-to-noise ratio (SNR) and topographies), with the same paradigm by de Heering and Rossion (2015), showing a clear peak of activation at 1.2 Hz located on the right occipito-temporal lobe, reflecting generic face categorization.

during development, i.e. being present already at a few months of age. Their proposal was based on the observation that 4- to 9-month-old infants saccade faster towards the picture of their mother's face than the matched picture of a stranger's face when these pictures are presented in the left visual field (LVF) but not in the right visual field (RVF; de Schonen and Mathivet, 1990; de Schonen et al., 1986). Along the same line, right hemisphere but not left hemisphere early deprivation of visual input for several months (between 6 weeks and 3 years) impairs the development of the adult expert (i.e., holistic/configural) face processing system (Le Grand et al., 2003). At the neural level, some studies using functional near-infrared spectroscopy (fNIRS) have also shown a significant RH advantage for faces over control visual stimuli in 5- to 8-month-old infants (e.g., Otsuka et al., 2007; see Otsuka, 2014 for a review). More recently, de Heering and Rossion (2015) exposed 4- to 6-month-old infants to numerous and highly variable natural images of faces inserted periodically (1 out of 5) in a fast (6 Hz) stream of non-face object images while recording their electroencephalogram (EEG) (Fig. 1A). Strikingly, infants' face-specific response to the frequency at which faces were presented in the sequence (1.2 Hz = 6 Hz/5) was the largest over their right occipito-temporal cortex (Fig. 1B). Importantly, this specific response to faces was not found for phase-scrambled images, ruling out potential low-level visual accounts of the effect (de Heering and Rossion, 2015).

Altogether, these observations support de Schonen and Mativet's hypothesis that the right hemisphere takes precedence over the left hemisphere at an early age, which might be the result of its faster maturation rate at a time at which the infants' visual system mainly extract low spatial frequencies, and therefore global information, from facial inputs (Sergent, 1982).

However, according to a recent hypothesis, the right hemispheric specialization for face perception would rather emerge relatively *late* during development, i.e. when children learn to read, and would gradually increase through adolescence (Behrmann and Plaut, 2015; Dundas et al., 2012; see also Dehaene et al., 2015). This hypothesis generally rests on the general view that right hemispheric specialization for faces – and of other functions such as spatial perception – follows the left lateralization for language functions (Corballis, 1991; Lhermitte et al., 1972). More specifically, it states that the right hemisphere becomes dominant for face perception due to the gradual specialization of the left VOTC after children's exposure to a written script during reading acquisition. This specialization would then compete with the representation of faces in the left hemisphere, resulting in face representations mainly located in the RH (Behrmann and Plaut, 2015). This view is supported by several findings. First, the behavioral left visual field advantage caused by the RH superiority for face processing correlates positively with reading competence in school children and young adolescent (Dundas et al., 2012). Second, children of 9–12 years of age show a positive correlation ($r^2 = 0.32$) between the amplitude of the left N170 for words and the right N170 for faces, although the N170 for faces is not significantly stronger in the right hemisphere (Dundas et al., 2014) Third, literacy changes the hemispheric balance of neural response to faces with a slight decrease of neural activity in the left fusiform gyrus and a clearer increase in the homologous area of the right fusiform gyrus (in adults: Dehaene et al., 2010; and 10-year-old children: Monzalvo, Fluss, Billard, Dehaene, and Dehaene-Lambertz, 2012; respectively). Finally, left-handed individuals, who as a group show greater variability with respect to hemispheric language dominance than right-handed individuals, also show greater variability in their degree of RH lateralization of faces as evidenced from both behavioral (Dundas et al., 2015) and neural measurements (fMRI: Bukowski et al., 2013; Frässle et al., 2016; EEG: Dundas et al., 2015).

In sum, there is a striking contrast between evidence collected in young infants, supporting the early emergence of a RH lateralization for face perception independent of reading acquisition, and evidence gathered from children, adolescents and adults, rather favoring a late and gradual RH lateralization of face perception emerging as a consequence of reading acquisition and reading skills.

So far, these views, based on different sets of evidence, have been difficult to reconcile. The major reason for this difficulty is that studies in infants and children have been conducted with different techniques and paradigms. For instance, while fNIRS, visual field dominance paradigms and visual preference/adaptation paradigms have been