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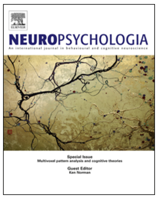

The functional architecture for face-processing expertise: FMRI evidence of the developmental trajectory of the core and the extended face systems

Frank Haist[a,b,*], Maha Adamo[b], Jarnet Han Wazny[b], Kang Lee[c], Joan Stiles[b,d]

[a] *Psychiatry Department, University of California, San Diego, 9500 Gilman Drive, La Jolla, CA 92093-0115, USA*
[b] *Center for Human Development, University of California, San Diego, 9500 Gilman Drive, La Jolla, CA 92093-0115, USA*
[c] *Dr. Eric Jackman Institute of Child Study, University of Toronto, 45 Walmer Road, Toronto, Ontario, Canada M5R 2X2*
[d] *Cognitive Science Department, University of California, San Diego, 9500 Gilman Drive, La Jolla, CA 92093-0115, USA*

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ABSTRACT

Expertise in processing faces is a cornerstone of human social interaction. However, the developmental course of many key brain regions supporting face preferential processing in the human brain remains undefined. Here, we present findings from an FMRI study using a simple viewing paradigm of faces and objects in a continuous age sample covering the age range from 6 years through adulthood. These findings are the first to use such a sample paired with whole-brain FMRI analyses to investigate development within the core and extended face networks across the developmental spectrum from middle childhood to adulthood. We found evidence, albeit modest, for a developmental trend in the volume of the right fusiform face area (rFFA) but no developmental change in the intensity of activation. From a spatial perspective, the middle portion of the right fusiform gyrus most commonly found in adult studies of face processing was increasingly likely to be included in the FFA as age increased to adulthood. Outside of the FFA, the most striking finding was that children hyperactivated nearly every aspect of the extended face system relative to adults, including the amygdala, anterior temporal pole, insula, inferior frontal gyrus, anterior cingulate gyrus, and parietal cortex. Overall, the findings suggest that development is best characterized by increasing modulation of face-sensitive regions throughout the brain to engage only those systems necessary for task requirements.

1. Introduction

Human beings are social animals by nature (Aristotle, 350 B.C. E.; Spinoza, 1677). That fact explains the increasing interest in the field of social neuroscience aimed at discovering the neural architecture supporting human social behavior. Faces are arguably the most important visual stimuli in our social environment. As the fulcrum of our social interaction with others, it is not surprising that adults are expert face processors. Adult expertise is characterized by the near universal ability to rapidly and accurately discriminate individuals from amongst thousands of highly similar faces encountered routinely and to extract extensive information about individuals from brief exposures to face stimuli.

Advances in functional neuroimaging are largely responsible for the significant increase in our understanding of the mature brain architecture for human face processing in typical and atypical populations (Avidan & Behrmann, 2009; Behrmann & Avidan, 2005; Haxby, Hoffman, & Gobbini, 2002; Kanwisher & Yovel, 2006; Tsao & Livingstone, 2008). Brain regions within the “core” face system process the invariant aspects of faces, such as facial features and identity (Haxby, Hoffman, & Gobbini, 2000). The core regions include the functionally defined fusiform face area (FFA) in the middle fusiform gyrus (see Kanwisher & Yovel, 2006), the occipital face area (OFA) in the lateral inferior occipital gyrus (see Gauthier et al., 2000; Rossion et al., 2003), and the posterior superior temporal sulcus (pSTS) (Haxby et al., 2000). Recent studies suggest that the fusiform gyrus may include multiple distinct face preferential processing regions occupying the posterior and anterior aspects of the middle fusiform gyrus (Pinsk et al., 2009; Weiner & Grill-Spector, 2012). We use the acronym FFA to infer all regions (i.e., voxels) within the fusiform gyrus that show a functionally defined preference to

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Abbreviations: FFA, fusiform face area(s); OFA, occipital face area; FG, fusiform gyrus; STS, superior temporal sulcus; VOT, ventral occipitotemporal cortex

[*] Corresponding author at: Psychiatry Department, University of California, San Diego, 9500 Gilman Drive, MC 0115, La Jolla, CA 92093-0115 USA.
Tel.: +1 858 822 5456; fax: +1 858 822 1602.
E-mail addresses: fhaist@ucsd.edu (F. Haist), madamo@ucsd.edu (M. Adamo), jarnet@ucsd.edu (J. Han Wazny), kang.lee@utoronto.ca (K. Lee), jstiles@ucsd.edu (J. Stiles).

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faces (e.g., face activity > activity to diverse objects). This approach closely aligns the present study with previous studies of development of the core face network regions. One important feature of the mature core system, particularly the FFA and OFA, is that these regions are activated when viewing faces largely regardless of specific task demands. That is, activation is observed whether the task requires active face processing, such as remembering or matching specific faces (Epstein, Higgins, Parker, Aguirre, & Cooperman, 2006; Gauthier, Curby, Skudlarski, & Epstein, 2005; Mazard, Schiltz, & Rossion, 2006; Xu, 2005; Yovel & Kanwisher, 2004, 2005), passive viewing (Grill-Spector, Knouf, & Kanwisher, 2004; Haist, Lee, & Stiles, 2010; Kanwisher, McDermott, & Chun, 1997; Kanwisher, Stanley, & Harris, 1999; Rhodes, Byatt, Michie, & Puce, 2004; Wojciulik, Kanwisher, & Driver, 1998), or implicit presentation (Cantlon, Pinel, Dehaene, & Pelphrey, 2011; Kouider, Eger, Dolan, & Henson, 2009; Morris, Pelphrey, & McCarthy, 2007). Activation of the pSTS is most closely associated with dynamic feature processing, such as monitoring eye gaze and mouth movements, and is thus observed in tasks in which these actions are factors (Ishai, Schmidt, & Boesiger, 2005; Rolls, 2007).

In contrast, the recruitment of brain areas within the mature “extended” face system tends to be task-specific (Fairhall & Ishai, 2007; Gobbini & Haxby, 2007; Haxby et al., 2000, 2001; Ishai et al., 2005). For example, activation of the amygdala, insula, and other limbic system areas occur when tasks require the analysis of the emotional content of faces (Bzdok et al., 2012; Gobbini & Haxby, 2007; Ishai, Pessoa, Bikle, & Ungerleider, 2004; Schulz et al., 2009). Recollection of semantic knowledge for faces may engage the inferior frontal gyrus, whereas episodic memory retrieval may recruit the precuneus, posterior cingulate cortex, and medial temporal lobe (Brambati, Benoit, Monetta, Belleville, & Joubert, 2010; Gobbini & Haxby, 2007; Leveroni et al., 2000). Analysis of intentions can activate the region of the temporal–parietal junction, whereas processing attitudes and mental states recruits the anterior cingulate cortex (Kaplan, Freedman, & Iacoboni, 2007; Redcay et al., 2010). Regions of the anterior temporal pole may be active in tasks requiring individuation of faces and biographical information retrieval (Gobbini & Haxby, 2007; Kriegeskorte, Formisano, Sorger, & Goebel, 2007; Nestor, Plaut, & Behrmann, 2011; Nestor, Vettel, & Tarr, 2008). In summary, recruitment of the regions included in the extended network presumably reflects the fact that many face tasks require processing of a wide array of information beyond the general appearance of the face.

In contrast to the adult literature, the body of evidence regarding the brain architecture of face processing in childhood is limited. Behavioral data show that the ability to process faces as distinctive visual stimuli begins in the first year of life. Newborns show a preference for and can discriminate faces from other classes of objects and abstract stimuli (Bushnell, Sai, & Mullin, 1989; Cassia, Turati, & Simion, 2004; Johnson & Morton, 1991; Turati, Simion, Milani, & Umiltà, 2002). By 3 months, infants can categorize faces by gender, race, and attractiveness (Kelly et al., 2005, 2007; Langlois, Ritter, Roggman, & Vaughn, 1991; Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002; Slater, Bremner et al., 2000; Slater, Quinn, Hayes, & Brown, 2000), and by 5 to 7 months they begin to rely on both featural and configural information for face identification (Cohen & Cashon, 2001). Despite these early abilities, the behavioral evidence is strong that expertise in face processing develops slowly and over many years (for review see Lee, Quinn, Pascalis, & Slater, 2013). For example, children have difficulty processing featural and configural information relevant to face identification through the school-age period (Mondloch, Le Grand, & Maurer, 2002). The pattern of children's featural processing reaches adult levels at about 10 to 11 years, before which they first rely on outer face features for face identification and then gradually shift to rely on inner face features (Want, Pascalis, Coleman, & Blades, 2003). Extraneous features such as clothing and hairstyle easily distract children under 10 to 11 years when identifying individual faces (Freire & Lee, 2001; Mondloch et al., 2002). In summary, the behavior literature suggests that face-processing expertise shows an extended developmental trajectory reaching into adolescence.

The emerging cognitive neuroscience literature is consistent with the behavioral evidence for the protracted development of face-processing expertise. Most of the neural imaging work using event-related potential (ERP) methodologies has revealed an early onset of neural markers specific for faces. For example, the N170, a negative deflection with peak latency of approximately 170 ms, is consistently observed in studies of face processing (for review see Lee et al. (2013)). However, despite their early onset, these markers undergo gradual development to reach the adult level only in adolescence (de Haan, Pascalis, & Johnson, 2002; Taylor, Batty, & Itier, 2004). In contrast to ERP methodologies that have exquisite temporal resolution but very poor spatial resolution, researchers have mainly relied on FMRI methodologies to study the cortical regions involved in the development of face processing expertise. Some FMRI studies have focused on development within the ventral posterior regions generally with findings showing a pattern of increasing specification in the location of face-selective regions (Aylward et al., 2005; Gathers, Bhatt, Corbly, Farley, & Joseph, 2004; Passarotti et al., 2003). One early study reported a shift from more diffuse to more focal activation within the ventral occipito-temporal cortex (VOT) (Passarotti et al., 2003). Subsequent studies suggest that the basic pattern of developmental change involves a shift in the locus of activation from divergent areas within the VOT to the fusiform gyrus (Aylward et al., 2005; Gathers et al., 2004; Golarai, Liberman, Yoon, & Grill-Spector, 2010; Scherf, Behrmann, Humphreys, & Luna, 2007). Many studies have focused on the FFA and OFA components of the core face network specifically; yet, there remains considerable controversy about the developmental trajectory of the FFA. Some studies of young school age children failed to find activation within the regions that are typically associated with the mature FFA, while others have reported adult-like FFA activation intensity in children. For example, two studies that included children as young as 4 years suggested the FFA reaches mature levels of activity and extent of fusiform gyrus (FG) activation by 7 years (Cantlon et al., 2011; Pelphrey, Lopez, & Morris, 2009). Nevertheless, the preponderance of evidence suggests significant developmental change within the FFA well beyond this time extending through mid to late adolescence. Gathers et al. (2004) reported that younger children (5–8 years) did not show reliably greater activation for faces relative to objects within the FFA, whereas older children (9–11 years) showed reliable face selectivity within the FFA. Similarly, Scherf et al. (2007) reported that children from 5 to 8 years do not activate the classic FFA, but instead tend to produce face-preferential activation in the posterior ventral processing system putatively involved in featural processing. Several groups have reported that development of face preferential activation in the fusiform gyrus is associated with systematic increases in the size (Brambati et al., 2010; Cohen Kadosh, Johnson, Dick, Cohen Kadosh, & Blakemore, 2013; Golarai et al., 2007; Peelen, Glaser, Vuilleumier, & Eliez, 2009; Scherf et al., 2007) and intensity of activation (Brambati et al., 2010; Cohen Kadosh, Cohen Kadosh, Dick, & Johnson, 2011; Golarai et al., 2007; Joseph, Gathers, & Bhatt, 2011). Developmental changes in face preferential activation in fusiform gyrus volume and intensity have also been found using FMRI adaptation paradigms (Cohen Kadosh, Henson, Cohen Kadosh, Johnson, & Dick, 2010; Scherf, Luna, Avidan, & Behrmann, 2011). Further, increases in FFA volume and activation intensity correlate with improvement in recognition memory for faces (Golarai et al., 2007, 2010). This underscores an issue that