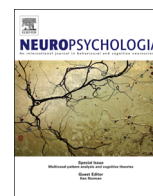




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Early visual deprivation from congenital cataracts disrupts activity and functional connectivity in the face network



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ABSTRACT

The development of the face-processing network has been examined with functional neuroimaging, but the effect of visual deprivation early in life on this network is not known. We examined this question in a group of young adults who had been born with dense, central cataracts in both eyes that blocked all visual input to the retina until the cataracts were removed during infancy. We used functional magnetic resonance imaging to examine regions in the “core” and “extended” face networks as participants viewed faces and other objects, and performed a face discrimination task. This task required matching faces on the basis of facial features or on the spacing between the facial features. The Cataract group (a) had reduced discrimination performance on the Spacing task relative to Controls; (b) used the same brain regions as Controls when passively viewing faces or making judgments about faces, but showed reduced activation during passive viewing of faces, especially in extended face-network regions; and (c) unlike Controls, showed activation in face-network regions for objects. In addition, the functional connections of the fusiform gyri with the rest of the face network were altered, and these brain changes were related to Cataract participants' performance on the face discrimination task. These results provide evidence that early visual input is necessary to set up or preserve activity and functional connectivity in the face-processing network that will later mediate expert face processing.

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1. Introduction

Adults are experts at recognizing the identity of faces despite changes in viewpoint, lighting, or facial expression, while at the same time being adept at detecting age, race, emotional expression and direction of gaze. This expertise appears to arise from processing faces, unlike objects, as holistic gestalts and from being exquisitely sensitive to the location of features within the face and to the shape of individual facial features (Maurer, Le Grand, & Mondloch, 2002). By adulthood, all these skills are better for upright than for inverted faces, a pattern suggesting that they are tuned by experience differentiating individuals in real world interactions (Hole, 1994; Mondloch, Le Grand, & Maurer, 2002, 2003b; Young, Hellawell, & Hay, 1987). Converging evidence for a role of experience comes from the findings that holistic processing is stronger for own-race and own-species faces than for the faces of other races or most other species (Michel, Rossion, Han, Chung,

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& Caldara, 2006; Tanaka, Kiefer, & Bukach, 2004; Taubert, 2009) and that sensitivity to feature spacing is better for human faces than for monkey faces, other-race faces and houses (Mondloch, Maurer, & Ahola, 2006; Mondloch et al., 2010a; Robbins, Shergill, Maurer, & Lewis, 2011).

At birth, infants' attention is drawn toward faces but that preference is mediated, at least in part, by general structural properties, such as top-heaviness and congruency, rather than an innate face module (Simion, Leo, Turati, Valenza, & Dalla Barba, 2007). Already at birth infants can discriminate two faces, likely making use of featural differences (Turati, Macchi Cassia, Simion, & Leo, 2006). During infancy, rudimentary versions of the skills underlying adult expertise emerge: holistic processing by 3 months of age (Turati, Valenza, Leo, & Simion, 2005) and sensitivity to large differences in feature spacing by 5 months of age (Bhatt, Bertin, Hayden, & Reed, 2005; Hayden, Bhatt, Reed, Corby, & Joseph, 2007), the emergence of which has already been shaped by experience because it is manifest for human and monkey upright faces but not inverted faces or houses (Zieber et al., 2013). However, recognition of facial identity continues to improve into adolescence, with improvements in recognition of a face in a novel point of view or lighting (de Heering, Rossion, & Maurer, 2012;

Mondloch, Geldart, Maurer, & Le Grand, 2003a), in sensitivity to differences in feature spacing (Mondloch et al., 2003a), and in the magnitude of differential sensitivity to upright versus inverted faces (de Heering et al., 2012; Robbins, Maurer, Hatry, Anzures, & Mondloch, 2012). The cause of the late changes may arise from additional experience individuating upright faces of one's own race or from more general improvements in attention and cognition that impact performance on the measurement tools (Crookes & McKone, 2009). The late maturation of the neural correlates of adults' expertise, e.g., the N170 in event-related potentials (Taylor, Batty, & Itier, 2004) and the face-specific activation in the fusiform gyrus in fMRI studies (see below) suggest that at least some of the behavioral changes during adolescence are face-specific.

When visual input is missing during infancy because of bilateral congenital cataracts, the adult pattern of expertise for face processing fails to emerge later in development. Such individuals are normal at detecting the structure of a face (Mondloch et al., 2003b, 2013) and discriminate with normal accuracy between faces differing in the shape of their features (de Heering & Maurer, 2014; Le Grand, Mondloch, Maurer, & Brent, 2001; Mondloch, Robbins, & Maurer, 2010b). However, they fail to show evidence of holistic processing during childhood (Le Grand, Mondloch, Maurer, & Brent, 2004), and even as adults have difficulty discriminating upright faces that differ only in feature spacing (de Heering & Maurer, 2014; Le Grand et al., 2001; Robbins, Nishimura, Mondloch, Lewis, & Maurer, 2010). In contrast, they are normal at discriminating feature spacing in inverted faces, monkey faces, and houses (de Heering & Maurer, 2014; Le Grand et al., 2001; Robbins et al., 2010). Perhaps as a result of these perceptual deficits, even as adults they have difficulty recognizing faces with an altered point of view (de Heering & Maurer, 2014; Geldart, Mondloch, Maurer, de Schonen, & Brent, 2002) and are poor at recognizing famous faces or faces recently learned in the lab (de Heering & Maurer, 2014). Additional evidence comes from the findings of less-than-normal shifts in perception in adaptation paradigms designed to test for norm-based coding (Nishimura, Maurer, Jeffery, & Rhodes, unpublished data) and for differential representation of upright and inverted faces (Robbins et al., 2012), and from evidence that normal face detection is accompanied by abnormally large P1 and N170 responses (Mondloch et al., 2013; but see Roder, Ley, Shenoy, Kekunnaya, & Bottari, 2013, for evidence of an absence of a face-specific N170 in a sample with much longer deprivation). This pattern of deficits suggests that early visual input may be necessary to set up the neural architecture underlying adults' face expertise. When that input is missing, people may have to rely on alternate pathways not as well suited to face expertise or on the normal, but damaged, pathways. The purpose of the current experiment was to use functional magnetic resonance imaging (fMRI) to assess those alternatives while adults with a history of early visual deprivation watched faces versus other categories and while they discriminated faces based on feature shape (a task on which they perform normally) or based on feature spacing (a task on which they have large deficits).

Previous fMRI studies of adults' ability to process faces indicate that this ability is mediated by activity in a variety of brain regions, particularly those in ventral occipito-temporal cortex. These studies have identified a region in the fusiform gyrus that responds more robustly to faces than to other types of visual stimuli (e.g., Downing, Chan, Peelen, Dodds, & Kanwisher, 2006; Grill-Spector, Knouf, & Kanwisher, 2004; Haxby et al., 1994; Kanwisher, McDermott, & Chun, 1997). This area has come to be known as the fusiform face area, or FFA. The magnitude of activity in FFA depends both on whether attention is directed to the faces (O'Craven, Downing, & Kanwisher, 1999; Wojciulik, Kanwisher, & Driver, 1998) and on the task demands involved in processing them (Druzgal & D'Esposito, 2003; Ishai & Yago, 2006; Lee, Anaki, Grady, & Moscovitch, 2012; Nestor, Vettel, & Tarr, 2008).

Despite agreement that the FFA is especially sensitive to faces, there has been considerable debate as to its precise role in face processing, including whether it is truly selective for faces, or rather mediates the differentiation of objects with which one has developed an expertise (Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Grill-Spector et al., 2004; Joseph & Gathers, 2002). There is evidence of FFA involvement in both holistic (Schiltz, Dricot, Goebel, & Rossion, 2010; Schiltz & Rossion, 2006) and part-based face processing (Yovel & Kanwisher, 2004). Although there is considerable evidence that the FFA is specialized for representing face identity (Grill-Spector et al., 2004; Mazard, Schiltz, & Rossion, 2006; Nestor, Plaut, & Behrmann, 2011; Nestor et al., 2008; Rhodes, Byatt, Michie, & Puce, 2004), some have argued that the FFA is involved in the individuation of non-face objects (Haist, Lee, & Stiles, 2010). There are also regions adjacent to FFA in the fusiform gyrus that appear to be involved in some aspects of face processing (Maurer et al., 2007b; Schiltz et al., 2010).

Despite the focus on the FFA, face processing in the brain goes quite a way beyond this one region. In addition to the FFA, visual representation of faces involves a region in posterior occipital cortex (the occipital face area, or OFA), thought to provide input to FFA (Nichols, Betts, & Wilson, 2010; Rossion et al. 2003), and the superior temporal sulcus (STS), which is involved in the processing of eye gaze (Hoffman & Haxby, 2000; Itier & Batty, 2009). Other regions that are thought to primarily represent non-face objects, such as the lateral occipital region (Grill-Spector, Kushnir, Edelman, Itzhak, & Malach, 1998; Malach et al. 1995), also show activity related to face processing (Axelrod & Yovel, 2012; Haxby et al., 2001; Natu, Raboy, & O'Toole, 2011). Indeed, there is evidence that distinct patterns of activity across the entire ventral occipito-temporal cortex can be used to predict when participants are viewing faces (Haxby et al., 2001). One recent model of face processing (Gobbini & Haxby, 2007) proposes that there is a "core" system concerned with the visual analysis of faces, and an "extended" system for extracting person knowledge and processing the emotional and reward aspects of faces. The core system includes the occipital and temporal areas that are sensitive to face stimuli (FFA, OFA, and STS), whereas the emotional part of the extended system includes the amygdala, insula, and striatum, all of which have been implicated in emotion or reward (e.g., Adolphs, Tranel, Damasio, & Damasio, 1994; Haber & Knutson, 2010; Lane, Reiman, Ahern, Schwartz, & Davidson, 1997; Phillips et al., 1997). The person-knowledge segment of the extended system consists of the anterior temporal cortex, medial prefrontal cortex, and medial parietal/posterior cingulate cortex (PCC), regions involved in personal semantics, self-reference and theory of mind (Graham, Lee, Brett, & Patterson, 2003; Grigg & Grady, 2010a; Northoff & Bermpohl, 2004; Spreng & Grady, 2010). In this model, the core system provides input to the two parts of the extended system, which in turn modulate the activation of the core system through feedback. Although this model does not include frontal regions, other work (Fairhall & Ishai, 2007; Ishai, Schmidt, & Boesiger, 2005) has suggested that the inferior frontal gyrus (IFG) and orbitofrontal cortex (OFC) should be considered as a part of the extended face network. The IFG may be involved in the semantic processing of faces (Ishai, Haxby, & Ungerleider, 2002; Leveroni et al., 2000) whereas the OFC is involved in reward, decision making and top down processing of faces (Fellows, 2007; Li et al., 2010; Rolls, 2000). Studies assessing functional connectivity of these regions, including the frontal areas, have provided further evidence for the idea that face processing is supported by an interacting network of regions (Fairhall & Ishai, 2007; Li et al., 2010; McIntosh et al., 1994).

Developmental neuroimaging studies have shown that the areas of ventral occipital cortex are responsive to faces even in

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