

Sex differences in the neural correlates of child facial resemblance: an event-related fMRI study

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Received 6 September 2004; revised 1 December 2004; accepted 7 December 2004

Available online 25 February 2005

Detection of genetic relatedness (i.e. kinship) impacts the social, parental, and sexual behavior of many species. In humans, self-referent phenotype matching based on facial resemblance may indicate kinship. For example, faces that resemble ours are perceived as more trustworthy and attractive. Sex differences in behavioral reactions to facial resemblance among children have also been demonstrated and are consistent with evolutionary theory suggesting that resemblance might serve as a paternity cue. Using event-related fMRI, we show that specific regions of the brain are implicated in processing facial resemblance and a sex difference in cortical response to facial resemblance expressed in children. We found a consistent activation in the fusiform gyrus across all face conditions, which is consistent with previous research on face processing. There were no sex differences in overall response to faces in the fusiform gyrus, and also to faces that did not resemble subjects. When resemblance was not modeled, females showed greater activation to child faces than males. Consistent with parental investment theory and theories of sexual selection, males showed greater cortical activity than females in response to children's faces that resembled them. These data suggest natural selection may have crafted a sexually differentiated neuro-sensory module implicated in detection of facial resemblance that may serve as a kin detection and paternity cue. This process may capitalize on neural substrates involved in self-referent processing and familiarity detection.

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Keywords: Facial resemblance; Kin detection; Paternity cue

Introduction

Kin discrimination mechanisms allow individuals to modify their behavior with respect to genetic relatedness (Lehman and Perrin, 2002) and have been shown to impact social (DeBruine, 2002, 2003, 2004; Hauber and Sherman, 2001), sexual (Lacy and

Sherman, 1983; Neff and Sherman, 2002), and parental behavior (Platek et al., 2002, 2003, 2004b; Daly and Wilson, 1982, 1998; Regalski and Gaulin, 1993; Volk and Quinsey, 2002; but see DeBruine, 2004). In humans, facial resemblance may serve as a kin identifier and has been shown to increase ratings of trustworthiness (DeBruine, 2002) and attractiveness (DeBruine, 2003). Further, sex differences in reactions to facial resemblance in children have also been documented (Platek et al., 2002, 2003, 2004a,b).

Parental investment theory (Trivers, 1972) suggests that sex differences in parental investment exist because of evolved mechanisms that involve parental certainty. Because of concealed ovulation, internal fertilization, and female infidelity among humans, parental certainty is asymmetrical: unlike females who can always be certain of maternity, males can never be certain of paternity. Current estimates of extra-pair paternity in humans are between 1 and 20%, with most estimates at about 10% (Baker and Bellis, 1995; Cerda-Flores et al., 1999; Neale et al., 2002; Sasse et al., 1994; Sykes and Irven, 2000); that is, approximately 1 in 10 children are the product of female infidelity (Platek and Shackelford, under contract; Shackelford et al., 2002 for review). A survey conducted in 1999 by the American Association of Blood Banks reported that as many as 30% of children are fathered by extra pair copulation (1999 Annual Report Summary, <http://www.aabb.org>). As a result of paternal uncertainty, males of many species, including humans, have evolved paternal assurance strategies to limit, control, prevent, and correct the incidence of female infidelity (Gallup et al., 2003; Goetz et al., in press; Platek and Shackelford, under contract), thereby increasing the likelihood that they only provision children that they have sired (Buchanan et al., 2003).

Platek et al. (2002, 2003) demonstrated that males utilize facial resemblance as a self-referent phenotype when asked to make hypothetical parental investment decisions. Additionally, Platek et al. (2004a,b) demonstrated, using a block design, a sex difference in BOLD response to self-resemblance among children's faces. This study revealed that child self-facial resemblance induced greater left anterior frontal activation in males when compared to females. Females showed significantly less activation over the whole brain.

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Available online on ScienceDirect (www.sciencedirect.com).

It has been reported (DeBruine, 2002, 2003; Platek et al., 2002, 2003, 2004a,b) that responses to facial resemblance occur at levels below conscious awareness and the cognitive processes involved in detection of facial resemblance are still unclear (see also Keenan et al., 2003). However, detection of self-resemblance may involve an integrated process that taps neural substrates involved in both self-face recognition and detection of facial familiarity. Sugiura et al. (2000) investigated passive and active recognition of one's own face in nine subjects using H₂O-15 PET. When comparing active and passive viewing of self-face to an unknown face, activation in left fusiform gyrus, right supramarginal gyrus, left putamen, and right hippocampus was reported. Direct contrast of active discrimination vs. passive viewing of self-face showed activation in right inferior and medial frontal gyri, and right anterior cingulate. More recently, Platek et al. (2004a,b) contrasted fMRI response to self-face and famous faces and found activation in right superior frontal gyrus. In the most extensive investigation of the neural substrates involved in self-face to date, Kircher et al. (2001) investigated activation to self-face when contrasted with activation to familiar (romantic partner) faces and found greater bilateral activation including the left inferior frontal gyrus, middle temporal gyrus, supramarginal and inferior parietal lobe and right insula and hippocampus (see also Kircher et al., 2000). Platek et al. (under review) recently improved upon existing studies of self-face recognition by controlling for familiarity as well as employing a fast event-related design. In this study, the direct contrast of self-face with a personally familiar sex-matched face (participant's fraternity brother) revealed activation in the right superior frontal gyrus, inferior parietal and medial frontal lobe, and left anterior middle temporal gyrus. These studies suggest that regions in the right frontal and parietal lobes are implicated in processing self-face. Furthermore, several studies have also implicated medial cortical structures in self-processing (e.g., Gusnard et al., 2001; Lou et al., 2004; Northoff and Bermpohl, 2004; Seger et al., 2004; Vogeley et al., 2000). For example, Vogeley et al. (2000) demonstrated that medial prefrontal regions are associated with taking one's own (first person) perspective and another person's (third person) perspective when solving an avatar task. Gusnard et al. (2001) demonstrated that activation in medial prefrontal and anterior cingulate regions vasculate depending upon attentional demands to self-referent or externally cued conditions.

Facial resemblance may also tap processing involved in detection of facial familiarity. Existing data suggest that detection of facial familiarity differs from detection of general face processing in two ways. First, the degree of activation in regions of the so-called face centers (FFA, fusiform face area/fusiform gyrus and inferior occipital gyrus) has been shown to be reduced when viewing familiar faces (Gobbini et al., 2004; Rossion et al., 2003); second, amygdala activation is associated more often with novel face detection than familiar face detection; that is, amygdala activation is attenuated when viewing familiar faces (Schwarz et al., 2003). It has also been suggested that neural responses to personally familiar faces activate a system involved in theory of mind and social cognition (Gobbini et al., 2004) when contrasted with famous familiar faces. Unfortunately, all of the studies that employed personally familiar faces as experimental stimuli used faces of family and friends, so we have no way of knowing what the unique neural contribution to familial faces is. This would be particularly important in light of our hypothesis that detection of familial relationships (i.e., kin recognition) through facial resemblance may serve as a means with which to detect kin that activates

specific neural substrates and behavioral response patterns. That being said, Gobbini et al. (2004) studied activation to faces of family members and friends and showed significant activation in anterior paracingulate gyrus, middle frontal gyrus, and fusiform gyrus, which have been associated with activation to self-referential stimuli (e.g., Kircher et al., 2001; Platek et al., under review).

Here, we used fMRI to investigate whether there were sex differences in the neural correlates of responding to facial resemblance. We hypothesized that: (1) contrasting faces, collapsing across conditions, with our baseline scrambled face condition would activate the fusiform face area (e.g., fusiform gyrus and inferior occipital gyrus), (2) collapsing across gender, there would be no sex difference when responding to faces as a function of age (main effect for child vs. adult), (3) collapsing across facial resemblance would activate regions implicated in self- and familiar face processing, and (4) self-resemblance in children would activate more cortical substrates in males when contrasted with females. Specifically, based on our previous study (Platek et al., 2004a,b), we predicted that males would show greater left frontal activation to self-resembling child faces than females, which may be interpreted as being associated with approach-type behavioral response patterns (Davidson, 1997).

Methods

Subjects

Fourteen (7 male, 7 female; Mean age: 24.79; Age range 21–33) healthy (screened for drug use, neurological and neuropsychiatric illness, and contraindications with MRI) right-handed students volunteered to participate in this study. All subjects gave written informed consent and the study was approved by the local Institutional Review Board. No subjects had children at the time of the study.

Pictures and morphing

All subjects consented to have their picture taken as part of the study. High-resolution pictures of subjects were taken using a Hewlett Packard (Model 315) 2.1 megapixel digital camera under uniform lighting conditions. Subjects were asked not to smile or frown, and to try to maintain a neutral unexpressive face; if a subject blinked or made a facial expression (e.g., smiled) the photo was re-taken. Images were processed using a 1.9-GHz laptop computer (Dell), Adobe Photoshop Elements (Version 2.0), and Ulead MorphEditor (Version 1.0) software, and were presented in color and matched for luminance. Images were cropped (using the magnetic lasso tool in Photoshop) just under the chin, from ear to ear, and just below the hairline so that only the face was cropped. Images were then feathered (10 pt) onto a black background and mounted on a canvas of consistent size; image aspect ratio was maintained to eliminate distortion via forced warping to a standardized "face space."

Each subject's picture was morphed (Ulead Morph Editor, version 1.0) with 1 child's face (1.75 years of age) and 1 adult face (25 years of age), so that each stimulus image combined 50% of the subject's face and 50% of the child/adult's face (see Fig. 1; see also Platek et al., 2002). A null/baseline condition consisted of a luminance matched scrambled face. Images were presented using

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