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Sex, beauty and the orbitofrontal cortex

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Abstract

Face perception is mediated by a distributed neural system in the human brain. Attention, memory and emotion modulate the neural activation evoked by faces, however the effects of gender and sexual orientation are currently unknown. To test whether subjects would respond more to their sexually-preferred faces, we scanned 40 hetero- and homosexual men and women whilst they assessed facial attractiveness. Behaviorally, regardless of their gender and sexual orientation, all subjects similarly rated the attractiveness of both male and female faces. Consistent with our hypothesis, a three-way interaction between stimulus gender, beauty and the sexual preference of the subject was found in the medial orbitofrontal cortex (OFC). In heterosexual women and homosexual men, attractive male faces elicited stronger activation than attractive female faces, whereas in heterosexual men and homosexual women, attractive female faces evoked stronger activation than attractive male faces. These findings suggest that the OFC represents the value of salient sexually-relevant faces, irrespective of their reproductive fitness.

Keywords: Sexual preferences; Face perception; fMRI; Medial orbitofrontal cortex

1. Introduction

Face perception, a highly developed visual skill in humans, is mediated by activation in a distributed neural system that encompasses regions in the visual cortex, limbic system, and prefrontal cortex (Haxby et al., 2000; Ishai et al., 2005). The cortical network for face perception includes regions in extrastriate cortex that process the identification of individuals (Grill-Spector et al., 2004), the superior temporal sulcus, where gaze direction and speech-related movements are processed (Hoffman and Haxby, 2000), the amygdala and insula, where facial expressions are processed (Phillips et al., 1997; Ishai et al., 2004), regions in prefrontal cortex (Nakamura et al., 1998), and regions of the reward circuitry, including the nucleus accumbens and orbitofrontal cortex, where the assessment of facial beauty is processed (Aharon et al., 2001; Kampe et al., 2001; O'Doherty et al., 2003). Numerous studies have shown that neural activation in face-selective regions is modulated by cognitive factors such as expertise, attention, visual imagery, and emotion (Gauthier et al., 1999; Ishai et al., 2000, 2002; Vuilleumier et al., 2001). However, the effects of gender and sexual preference on face perception are currently unknown.

Social communication requires the accurate analysis of the intentions of other individuals. To this end, men and women should adopt strategies of "face reading" in order to successfully interact with potential sexual partners. Thus, given the benefits of facial beauty in mating (Perrett et al., 1998; Senior, 2003), it is reasonable to assume differential patterns of activation in the hetero- and homosexual brain in response to faces of the same- or opposite-sex. We therefore hypothesized that hetero- and homosexual subjects would respond more to their sexually preferred faces. Specifically, we predicted similar responses to male and female faces in the visual cortex, where facial identity is processed, but differential responses in the reward circuitry, where value is assigned to stimuli. To test this hypothesis, we have recently scanned 40 hetero- and homosexual men and women whilst they viewed faces or assessed facial attractiveness (Kranz and Ishai, 2006). In all subjects, male and female faces evoked similar neural responses within a distributed network of face-selective visual, limbic and prefrontal regions. An interaction between stimulus gender and the sexual preference of the subject was observed in the mediodorsal nucleus of the thalamus (mdT) and the OFC. In heterosexual

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women (HeW) and homosexual men (HoM) stronger activation was evoked by male than female faces, whereas in heterosexual men (HeM) and homosexual women (HoW) stronger activation was elicited by female than male faces, indicating that response to faces in the reward circuitry is modulated by sexual preference (Kranz and Ishai, 2006).

It has been recently shown that the OFC, a region involved in representing the reward value of various stimuli, responds more to beautiful faces, in particular to happy, attractive faces (O'Doherty et al., 2003). To test whether the OFC exhibits a three-way interaction between stimulus gender, beauty and the sexual preference of the observer, we compared responses evoked by Attractive, Neutral and Unattractive male and female faces in hetero- and homosexual men and women. We found that in HeW and HoM, Attractive Male faces evoked stronger activation than Attractive Female faces, whereas in HoW and HeM Attractive Female faces elicited stronger activation than Attractive Male faces, suggesting that the OFC represents the value of salient, sexually-relevant faces.

2. Experimental procedures

2.1. Subjects

Forty normal, right-handed subjects (10 heterosexual women, 10 heterosexual men, 10 homosexual women, 10 homosexual men, mean age and S.D. was 26±3 years) with normal vision participated in the study. All subjects gave informed written consent for the procedure in accordance with protocols approved by the University Hospital. Subjects were classified as hetero- or homosexuals based on their self-report in a modified version of the Sell questionnaire (Sell, 1996).

2.2. Stimuli and tasks

Stimuli were displayed using Presentation (www.neurobs.com, version 9.13) and were projected with a magnetically shielded LCD video projector onto a translucent screen placed at the feet of the subject. Subjects viewed gray scale photographs of 100 male and 100 female faces and pressed one of three buttons to indicate whether each face was Attractive, Neutral, or Unattractive. In each run, epochs of faces (30 s) were alternating with epochs of phase-scrambled faces (12 s). Each stimulus was presented for 3 s, with no blank periods between the stimuli. The order of runs was randomized across subjects.

2.3. Data acquisition

Data were collected using a 3T Phillips Intera whole body MR scanner (Philips Medical Systems, Best, The Netherlands). Changes in blood-oxygenation level-dependent MRI signal were measured by using sensitivity encoded gradient-echo echo planar sequence (Pruessmann et al., 1999), with 35 axial slices, TR = 3000 ms, TE = 35 ms, flip angle = 82°, field of view = 220 mm, acquisition matrix = 80 × 80, reconstructed voxel size = 1.72 × 1.72 × 4 mm, and SENSE acceleration factor R = 2. High-resolution spoiled gradient recalled echo structural images were collected in the same session for all the subjects (180 axial slices, TR = 20 ms, TE = 2.3 ms, field of view = 220 mm, acquisition matrix = 224 × 224, reconstructed voxel size = 0.9 × 0.9 × 0.75 mm). These high-resolution anatomical images provided detailed anatomical information for the region-of-interest (ROI) analysis and were used for 3D normalization to the brain atlas (Talairach and Tournoux, 1988).

2.4. Data analysis

Functional MRI data were analyzed in BrainVoyager QX Version 1.3 (Brain Innovation, Maastricht, The Netherlands). All volumes were realigned to the first volume, corrected for motion artefacts and spatially smoothed using a 5-mm FWHM Gaussian filter. The main effect of faces (activation evoked by faces vs. activation evoked by scrambled faces) was analyzed using multiple regression with box-car functions that were convolved with a canonical hemodynamic response function (Friston et al., 1995). A set of face-responsive ROIs was anatomically defined for each subject with clusters that showed a significant effect ($p<0.01$, uncorrected). These regions included the inferior occipital gyrus, lateral fusiform gyrus, amygdala, the mediodorsal nucleus of the thalamus, insula, inferior frontal gyrus, and the medial orbitofrontal cortex (see Kranz and Ishai, 2006). The contrast of faces vs. scrambled faces was orthogonal to the other contrasts and therefore the pre-selection of these regions did not bias inference about subsequent main effects and interactions. In each subject and each ROI, the face stimuli were sorted post-hoc, based on their attractiveness score, and mean parameter estimates were calculated for Attractive, Neutral, and Unattractive male and female faces. The parameter estimates were used for between-subjects random-effects analyses. For each group, separate repeated measures ANOVAs were used to examine the effect of stimulus gender (male or female) and assessment of attractiveness (Attractive, Neutral, or Unattractive). Finally, the three-way interaction between stimulus gender (male or female face), beauty (Attractive, Neutral, or Unattractive) and the sexual preference of the subject (hetero- or homosexual) was analyzed.

3. Results

The behavioral data collected while subjects assessed facial attractiveness are shown in Table 1. Regardless of their gender or sexual orientation, all subjects similarly rated both male and female faces, as reflected by the distribution of the attractiveness scores and by the response latencies. Longer reaction times were associated with Attractive rather than Unattractive faces ($p<0.0001$ for both male and female faces, in all groups of subjects). On average, all subjects rated 45% of the female faces as Neutral, 28% as Attractive and 27% as Unattractive. Similarly, all subjects rated 45% of the male faces as Neutral, 20% as Attractive and 35% as Unattractive. The interaction between the sexual preference of the subject and the attractiveness scores was not statistically significant ($F_{3,36}=0.308$, $p=0.82$).