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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 ($F_{3,36}=0.308$, $p=0.82$).

Table 1
Assessment of facial attractiveness

	Button presses (%)						Reaction time (s)					
	AF	NF	UF	AM	NM	UM	AF	NF	UF	AM	NM	UM
HeW	28 (4)	47 (3)	25 (5)	21 (4)	45 (5)	34 (7)	1.56 (0.08)	1.43 (0.05)	1.34 (0.08)	1.56 (0.07)	1.39 (0.05)	1.33 (0.09)
HoW	35 (6)	47 (4)	18 (5)	15 (4)	43 (6)	42 (9)	1.45 (0.09)	1.38 (0.08)	1.37 (0.06)	1.45 (0.09)	1.37 (0.07)	1.21 (0.06)
HeM	28 (5)	42 (2)	30 (5)	17 (4)	50 (5)	33 (6)	1.51 (0.08)	1.50 (0.09)	1.31 (0.09)	1.65 (0.09)	1.49 (0.11)	1.32 (0.08)
HoM	19 (3)	45 (3)	36 (4)	25 (2)	42 (2)	33 (4)	1.41 (0.06)	1.32 (0.04)	1.22 (0.05)	1.36 (0.05)	1.30 (0.04)	1.22 (0.05)

Mean percentage of button presses and reaction times, averaged across 10 subjects in each group, are shown for Unattractive (U), Neutral (N) and Attractive (A) female (F) and male (M) faces. Standard errors of the mean are indicated in parentheses.

Face perception evoked activation in a distributed cortical network that includes visual, limbic and prefrontal regions (Fig. 1A). As we have recently shown, although assessing the attractiveness of female faces evoked similar activation to assessing the attractiveness of male faces in all face-responsive regions, a significant interaction between stimulus gender and the sexual preference of the subject was found in two regions, namely the mdT and the OFC (Kranz and Ishai, 2006).

To test whether the OFC exhibits a three-way interaction between stimulus gender, beauty and sexual preference, the mean activation evoked by Attractive, Neutral and Unattractive male and female faces was compared. Although most subjects showed activation in the OFC (Table 2), as only 28% of the female faces and 20% of the male faces presented in the experiment were rated "Attractive", the activation was averaged across all subjects and both face genders (Fig. 1B). Attractive male and female faces elicited stronger activation than Neutral and Unattractive male and female faces ($p<0.01$). Next, the mean response evoked by Attractive Female faces was compared with the mean response elicited by Attractive Male faces (Fig. 1C). Although in each group a the trend of higher

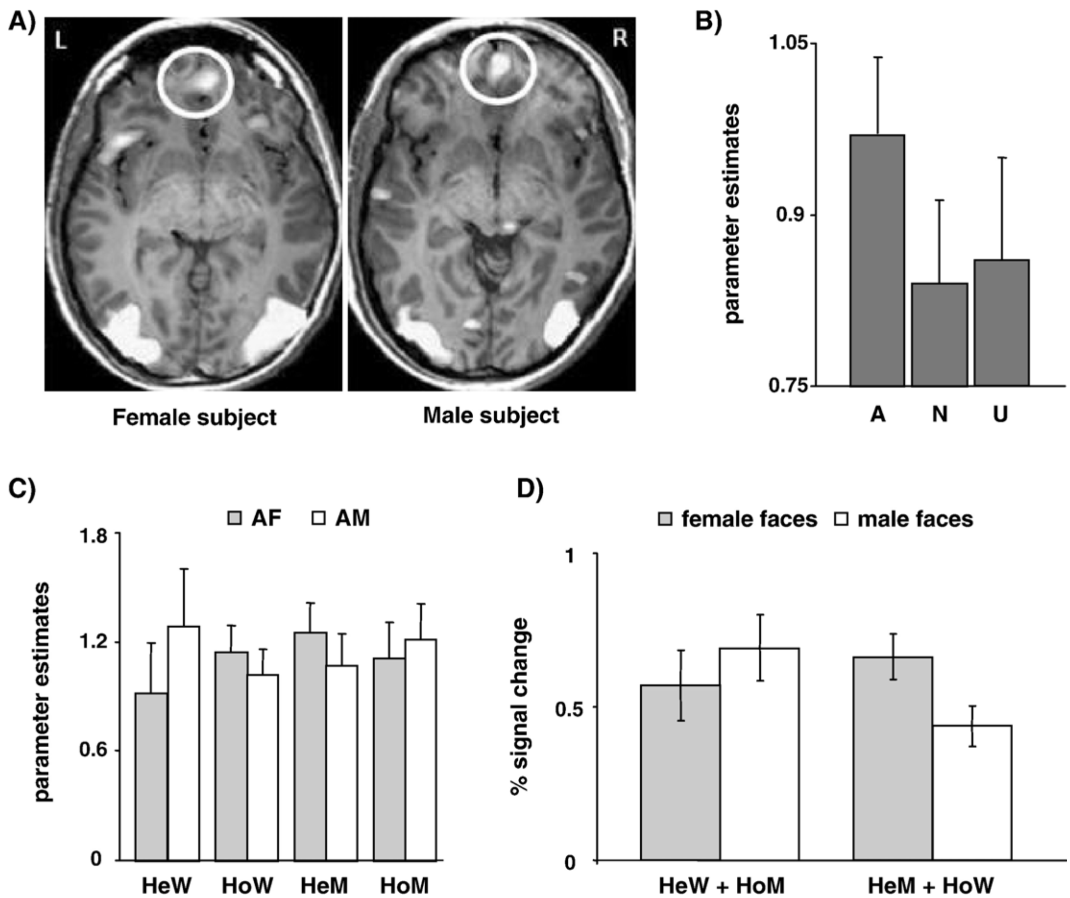

Fig. 1. Response to faces in the OFC. A) Axial sections, illustrating the main effect of faces ($p<0.01$, uncorrected) were taken from two individuals. The OFC is indicated by the white circle. B) Mean response to Attractive (A) Neutral (N) and Unattractive (U) faces. Data were averaged across both face genders and across all subjects. C) Mean response to attractive female (AF) and attractive male (AM) faces in each group of subjects. HeW = heterosexual women; HoW = homosexual women; HeM = heterosexual men; HoM = homosexual men. D) Differential responses to male and female faces. The mean amplitudes of the fMRI response evoked by male and female faces were averaged across groups with similar preference: HeW and HoM showed stronger response to male than to female faces, whereas HeM and HoW responded significantly more to female than male faces. Error bars indicate standard errors of the mean.

Table 2
Activation elicited by faces in the OFC

	N	Volume (cm^3)	x	y	z
HeW	8	8.4 (1.2)	1.5 (0.9)	58.6 (1.7)	1.4 (1.2)
HoW	8	7.5 (1.9)	−0.1 (0.8)	57.9 (0.8)	−0.9 (1.9)
HeM	10	9.7 (1.3)	1.4 (0.4)	58.1 (1.4)	0 (1.8)
HoM	9	9.6 (1.1)	1.7 (0.5)	59.2 (1.1)	4.2 (2.0)

Clusters were localized based on the main effect of faces ($p<0.01$, uncorrected). *N* indicates the number of subjects in each group who showed significant activation in the OFC. Volumes were calculated before spatial normalization. Coordinates are in the normalized space of the Talairach and Tournoux (1988) brain atlas. Standard errors of the mean are indicated in parentheses.

response to the sexually-preferred Attractive faces was observed, the difference between activation evoked by Attractive Female faces and activation evoked by Attractive Male faces did not reach statistical significance, probably due to the small group size. Nevertheless, when the groups with similar sexual preference were combined, this difference was statistically significant. Thus, in HeW and HoM the response to Attractive Male faces was stronger than the response to Attractive Female faces ($p<0.04$). Similarly, in HoW and HeM, the response to Attractive Female faces was stronger than the response to Attractive Male faces ($p<0.01$).

As most faces shown in the experiment were rated by all subjects "Neutral", the mean amplitudes of the fMRI signal, evoked by *all* male and female faces, were compared (Fig. 1D). Hew and HoM responded significantly more to male than to female faces, whereas HoW and HeM responded significantly more to female than to male faces. This interaction between stimulus gender (male or female face) and the sexual preference of the subject (hetero- or homosexual) was highly significant ($p<0.001$).

Taken together, the patterns of activation observed in the OFC suggest that all subjects responded more to their sexually preferred faces, particularly to those they found attractive.

4. Discussion

Face perception evokes activation in a distributed cortical network (Haxby et al., 2000; Ishai et al., 2005) that includes visual, limbic and prefrontal regions, where facial identity, gaze direction and facial expression are processed (e.g., Grill-Spector et al., 2004; Hoffman and Haxby, 2000; Phillips et al., 1997; Ishai et al., 2004) and regions in prefrontal cortex and the reward circuitry, where the assessment of facial beauty is processed (Nakamura et al., 1998; Aharon et al., 2001; Kampe et al., 2001; O'Doherty et al., 2003). Interestingly, we have recently found virtually identical patterns of neural activation within multiple, bilateral face-selective regions, where male and female faces elicit similar responses in all subjects, regardless of their gender or sexual preference. Furthermore, an interaction between stimulus gender and sexual preference was observed in the mdT and the OFC (Kranz and Ishai, 2006).

The OFC is involved in representing the reward value of various sensory stimuli (Rolls, 2004), including abstract positive and negative reinforcers (O'Doherty et al., 2001) and beautiful faces (O'Doherty et al., 2003). The existence of face-selective neurons in the OFC (Thorpe et al., 1983) and the inability of patients with OFC lesions to identify emotional facial expressions (Hornak et al., 1996) further suggest that this region has an important role in the processing of facial cues required for social communication. Modulation by sexual preference of the response to faces within the OFC extends its role in social behavior.

Facial beauty is considered a marker for reproductive fitness (Thornhill and Gangestad, 1999). Attributes such as symmetry (Langlois and Roggman, 1990) and sexually dimorphic features (Perrett et al., 1998) contribute to the assessment of facial attractiveness. Recent functional brain imaging studies have reported that facial beauty evokes activation in the reward circuitry (Aharon et al., 2001; O'Doherty et al., 2003), where direct eye gaze (Kampe et al., 2001) and happy expressions (O'Doherty et al., 2003) increase the appeal of attractive faces. In contrast with a recent study in which the attractiveness of face stimuli was rated post-scanning (O'Doherty et al., 2003), our subjects explicitly judged the attractiveness while in the MR scanner. We observed in all subjects enhanced responses to attractive rather than neutral or unattractive faces of both genders, a finding that can be explained in terms of their pleasing and rewarding value. Furthermore, all subjects responded more to their sexually preferred faces, in particular to those they found attractive, suggesting that the OFC represent relevant, salient stimuli, in order to guide or motivate social behavior.

It has been proposed that the rewarding, adaptive value of an attractive face can be dissociated from its aesthetic value. An attractive opposite-sex face may signal that a potential sexual partner has a healthy genotype, whereas an attractive, same-sex face cannot have such reproductive benefits (Senior, 2003). Our subjects, regardless of their gender or sexual orientation, similarly assessed the attractiveness of both male and female faces, suggesting that men and women equally notice and respond to beauty of same- and opposite-sex. Similar behavioral findings were found in a group of heterosexual men (Aharon et al., 2001) and a group of male and female subjects (O'Doherty et al., 2003). The OFC may represent the adaptive value of attractive, opposite-sex faces, thus providing putative neural correlates for the assessment of potential mates for reproductive purposes. Our data, however, do not support such neural dissociation between attractive faces of the opposite-sex that reflect evolutionary benefits and attractive faces of the same-sex that reflect aesthetic appraisal of beauty (Senior, 2003). Rather, our findings demonstrate that the OFC represents the reward value of faces of potential sexual partners, including same-sex mates, irrespective of reproduction. Consistently, a recent study has shown that heterosexual women and homosexual men show similar patterns of responses to putative pheromones (Savic et al., 2005). Taken together, these novel findings provide converging evidence that sexual preference, and not reproductive fitness, modulates neural responses to relevant stimuli in the adult human brain.

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