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Report

Face Perception Is Modulated by Sexual Preference

Felicitas Kranz[1,2] and Alumit Ishai[1,2,*]
[1] Institute of Neuroradiology
University of Zurich
Zurich
Switzerland
[2] Institute for Biomedical Engineering
Swiss Federal Institute of Technology
Zurich
Switzerland

Summary

Face perception is mediated by a distributed neural system in the human brain [1, 2]. The response to faces is modulated by cognitive factors such as attention, visual imagery, and emotion [3–6]; however, the effects of gender and sexual orientation are currently unknown. We used fMRI to test whether subjects would respond more to their sexually preferred faces and predicted such modulation in the reward circuitry. Forty heterosexual and homosexual men and women viewed photographs of male and female faces and assessed facial attractiveness. Regardless of their gender and sexual orientation, all subjects similarly rated the attractiveness of both male and female faces. Within multiple, bilateral face-selective regions in the visual cortex, limbic system, and prefrontal cortex, similar patterns of activation were found in all subjects in response to both male and female faces. Consistent with our hypothesis, we found a significant interaction between stimulus gender and the sexual preference of the subject in the thalamus and medial orbitofrontal cortex, where heterosexual men and homosexual women responded more to female faces and heterosexual women and homosexual men responded more to male faces. Our findings suggest that sexual preference modulates face-evoked activation in the reward circuitry.

Results

Regardless of their gender or sexual orientation, all subjects assessed the attractiveness of both male and female faces in a similar way, as reflected by their response latencies (Figure 1). 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 (Table 1). The interaction between the sexual preference of the subject and the attractiveness rating was not statistically significant ($F_{3,36} = 0.308$, $p = 0.82$).

Face perception evoked activation in a distributed network that included regions in the visual cortex, limbic system, prefrontal cortex, and reward circuitry (Table 2). We found significant activation in multiple, bilateral face-responsive regions in all subjects and analyzed the effects of stimulus gender and attractiveness scores within these regions; Figure 2 shows the patterns of activation during the attractiveness rating in the lateral fusiform gyrus and the amygdala. In both regions, assessing the attractiveness of female and male faces evoked similar activation. Moreover, in both regions, attractive female faces evoked stronger activation than unattractive female faces ($p < 0.001$, in HeW [heterosexual women], HoW [homosexual women], and HeM [heterosexual men] groups). Similar findings were found in other face-selective regions (e.g., inferior occipital gyrus, superior temporal sulcus, insula, and inferior frontal gyrus), where the effects of stimulus gender (male or female face) and sexual preference (heterosexual or homosexual) were not statistically significant.

Consistent with our hypothesis, we found a significant interaction between stimulus gender and the sexual preference of the subject in two regions, namely the mediodorsal nucleus of the thalamus (mdT) and the medial orbitofrontal cortex (OFC). Within the OFC, attractive faces evoked significantly stronger activation (the mean response ± SEM, averaged across all subjects, was 0.97 ± 0.08) than neutral (0.84 ± 0.08, $p < 0.01$) and unattractive (0.86 ± 0.09, $p < 0.01$) faces. Because most faces presented during the attractiveness task were rated "neutral," our interaction analysis included the mean responses evoked by all male and all female faces. Figure 3 shows the patterns of activation in mdT (A) and the OFC (B). In both regions, although male faces evoked stronger responses than female faces in HeW and HoM, HoW and HeM responded more to female than to male faces. The mean amplitude of the fMRI signal in response to male and female faces, averaged across all subjects in a group whose members showed activation in each region, is shown in Figure 3C. In both regions, the difference between activation evoked by male faces and activation evoked by female faces was significant in HoW ($p < 0.04$), HeM ($p < 0.001$), and HoM ($p < 0.01$), but not in HeW. The interaction between stimulus gender (male or female face) and the sexual preference (hetero- or homosexual) of the subject was highly significant in mdT ($p < 0.01$) and in the OFC ($p < 0.001$). To illustrate the effects of sexual preference in each group, we subtracted the mean amplitude of the fMRI response evoked by male faces from the mean amplitude of the fMRI response evoked by female faces (Figure 3D).

Contrasting the response to male faces with the response to female faces did not reveal any significant cluster of activation in the brain, even when the threshold was lowered to $p < 0.05$ at both the subject and

*Correspondence: ishai@hifo.unizh.ch

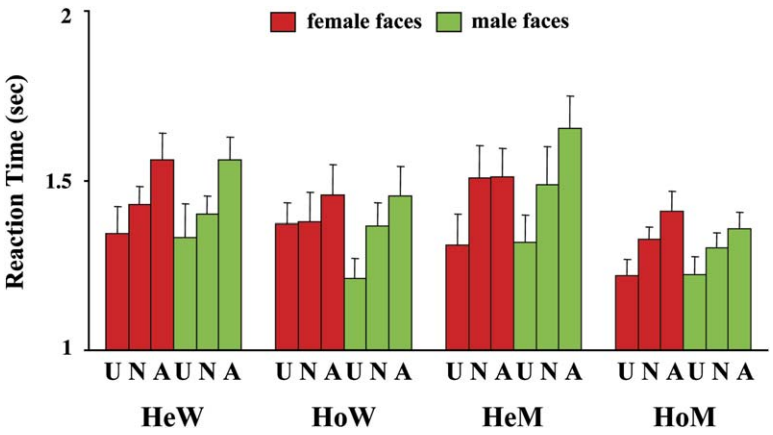

Figure 1. Behavioral Data

Mean reaction times averaged across ten subjects in each group (HeW = heterosexual women; HoW = homosexual women; HeM = heterosexual men; HoM = homosexual men). Subjects were presented with 100 male faces and 100 female faces and assessed their attractiveness by pressing one of three buttons to indicate whether each face was unattractive (U), neutral (N), or attractive (A). In this and subsequent figures, error bars indicate the standard error of the mean.

the group level. Furthermore, the interaction between the gender of the subject (male versus female), regardless of their sexual preference, and the gender of the stimulus (male vs. female faces) was not statistically significant. The patterns of activation in the mdT and the OFC therefore suggest that the response to faces within these regions was modulated by the sexual preference of the subject.

Discussion

Consistent with previous functional neuroimaging studies, our data indicate that face perception evokes activation in a distributed cortical network [1, 2] that includes regions in the visual cortex, limbic system, and prefrontal cortex, where invariant (facial identity) and variant (gaze direction and facial expression) features are processed [7–9], and regions in prefrontal cortex and the reward circuitry, where the assessment of facial beauty is processed [10–13]. Given the benefits of facial beauty in mating [14, 15], we postulated differential patterns of activation in the heterosexual and homosexual brain in response to faces of the same or opposite sex. Interestingly, all subjects, regardless of their gender or sexual preference, showed virtually identical patterns of neural activation within multiple, bilateral face-selective regions, where male and female faces elicited responses of similar magnitude. It therefore seems that the gender of face stimuli is processed similarly in the cortical network that mediates face perception.

Facial beauty is considered a marker for reproductive fitness [16]. Attributes such as symmetry [17] and sexually dimorphic features [14] contribute to the assessment of facial attractiveness. Not surprisingly, recent studies have reported that facial beauty evokes activation in the reward circuitry [11, 13]. It has been suggested 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 [15]. 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 the same and opposite sex. Similar behavioral findings were found in a group of heterosexual men [11] and a group of male and female subjects [13]. The virtually identical attractiveness rating of both male and female faces was reflected not only by the response latencies but, importantly, by the amplitude of the fMRI signal. Within a network of face-selective regions that included the lateral fusiform gyrus and the amygdala, unattractive, neutral, and attractive male and female faces elicited very similar activation.

In contrast with previous studies that assumed automatic processing of facial beauty and instructed subjects to judge the gender of face stimuli (e.g., [13]), we chose a different approach, namely explicit assessment of facial attractiveness, so that the gender of the face stimulus was irrelevant to the task. We postulated that if face processing is indeed modulated by the gender or sexual preference of the subject, an interaction with the gender of the stimulus would be observed in regions such as the amygdala and the OFC. To our surprise, we did not observe differences between the neural responses evoked by male faces and those evoked by female faces in the amygdala. We did, however, observe a significant interaction between stimulus gender and sexual preference in the mdT and in the OFC. The OFC receives projections from the mdT, with which it is reciprocally connected [18], and thus the similar patterns of activation observed in these regions can be explained in terms of their anatomical connections. The OFC is involved in representing the reward value of various sensory stimuli [19], including beautiful faces [13], and abstract positive and negative reinforcers [20]. A recent fMRI study has shown that passive viewing of various face stimuli is sufficient to evoke significant activation in the OFC [2]. The existence of face-selective neurons in the OFC [21] and the inability of patients with OFC lesions to identify

Table 1. Assessment of Facial Attractiveness

	Female Faces			Male Faces		
	U	N	A	U	N	A
HeW	25 (5)	47 (3)	28 (4)	34 (7)	45 (5)	21 (4)
HoW	18 (5)	47 (4)	35 (6)	42 (9)	43 (6)	15 (4)
HeM	30 (5)	42 (2)	28 (5)	33 (6)	50 (5)	17 (4)
HoM	36 (4)	45 (3)	19 (3)	33 (4)	42 (2)	25 (2)

Mean percentage of button presses, averaged across ten subjects in each group, is shown for unattractive (U), neutral (N) and attractive (A) faces. Standard deviations are indicated in parenthesis.

Table 2. A Network of Face-Responsive Regions

Region	N	Volume, cm^3 (Mean, SEM)	x (Mean, SEM)	y (Mean, SEM)	z (Mean, SEM)
L IOG	40	12.3 (0.3)	−36.0 (0.8)	−75.2 (1.0)	−12.9 (0.8)
R IOG	40	13.1 (0.1)	36.7 (0.8)	−74.7 (0.9)	−12.3 (0.7)
L FG	40	12.0 (0.3)	−36.8 (0.5)	−46.0 (0.7)	−18.5 (0.6)
R FG	40	12.9 (0.1)	37.3 (0.6)	−47.7 (0.9)	−17.9 (0.5)
L STS	24	4.7 (0.6)	−49.0 (0.9)	−44.9 (1.7)	7.6 (1.3)
R STS	36	5.4 (0.5)	46.2 (0.7)	−41.1 (1.4)	6.8 (0.9)
L AMG	38	9.2 (0.5)	−15.8 (0.4)	−7.8 (0.6)	−8.1 (0.7)
R AMG	39	9.6 (0.5)	16.6 (0.6)	−7.3 (0.4)	−9.1 (0.3)
L IPS	36	8.5 (0.7)	−31.4 (1.1)	−49.3 (1.5)	42.2 (0.9)
R IPS	36	8.7 (0.6)	31.3 (0.9)	−51.1 (1.5)	40.9 (0.9)
mdT	33	7.3 (0.7)	1.0 (0.2)	−11.5 (0.8)	12.8 (0.5)
L caudate	27	5.5 (0.6)	−11.9 (0.5)	−1.1 (1.0)	16.6 (0.8)
R caudate	32	4.8 (0.6)	12.7 (0.5)	−1.5 (1.0)	17.4 (0.7)
L IFG	40	7.9 (0.6)	−38.7 (0.7)	2.7 (1.2)	32.4 (0.9)
R IFG	39	10.6 (0.4)	40.5 (0.8)	1.4 (0.8)	32.0 (0.9)
L putamen	21	6.1 (0.7)	−20.4 (0.7)	4.8 (1.0)	3.3 (0.6)
R putamen	20	6.1 (0.8)	21.3 (0.7)	4.3 (0.8)	4.1 (0.9)
ACC	37	11.4 (0.3)	0.5 (0.4)	13.7 (1.2)	46.3 (1.0)
L insula	39	7.3 (0.5)	−33.2 (0.7)	19.1 (1.4)	6.7 (0.7)
R insula	40	8.9 (0.5)	35.3 (0.7)	17.9 (0.9)	7.0 (0.6)
OFC	35	8.9 (0.7)	1.1 (0.3)	58.5 (0.7)	1.2 (0.9)

Clusters were localized based on the main effect of faces ($p < 0.01$, uncorrected). N indicates the number of subjects who showed significant activation in each region. Volumes were calculated before spatial normalization. Coordinates are in the normalized space of the Talairach brain atlas [26]. The standard error of the mean is indicated in parentheses. L = left, R = right.

emotional facial expressions [22] 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.

It could be argued that the OFC is mediating the adaptive value of attractive, opposite-sex faces, and thus provides putative neural correlates for the assessment of potential mates for reproductive purposes. We, however, did not find neural evidence in support of such

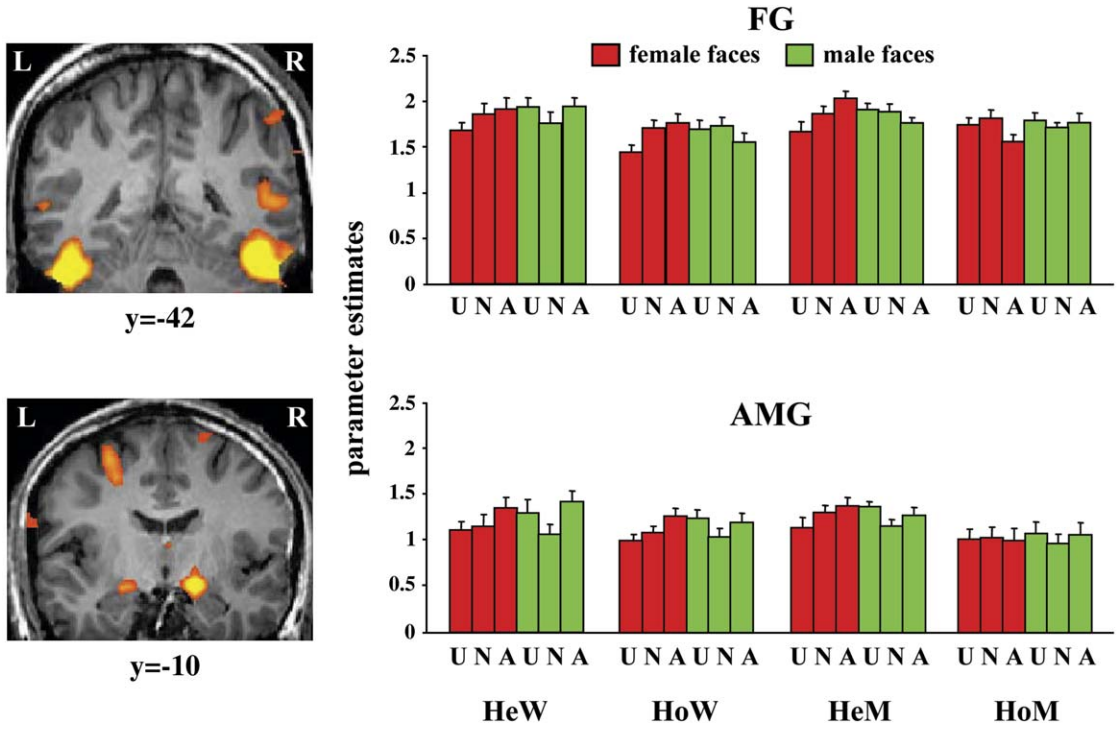

Figure 2. Activation Evoked by Faces in the Lateral Fusiform Gyrus and the Amygdala

Coronal sections, illustrating the main effect of faces ($p < 0.01$, uncorrected) in the fusiform (top) and the amygdala (bottom), were taken from two individuals. In each region, mean parameter estimates were averaged across all subjects who showed a significant response to faces. Male and female faces were sorted according to their rating as unattractive (U), neutral (N), or attractive (A). Data were averaged across the left and the right hemispheres.

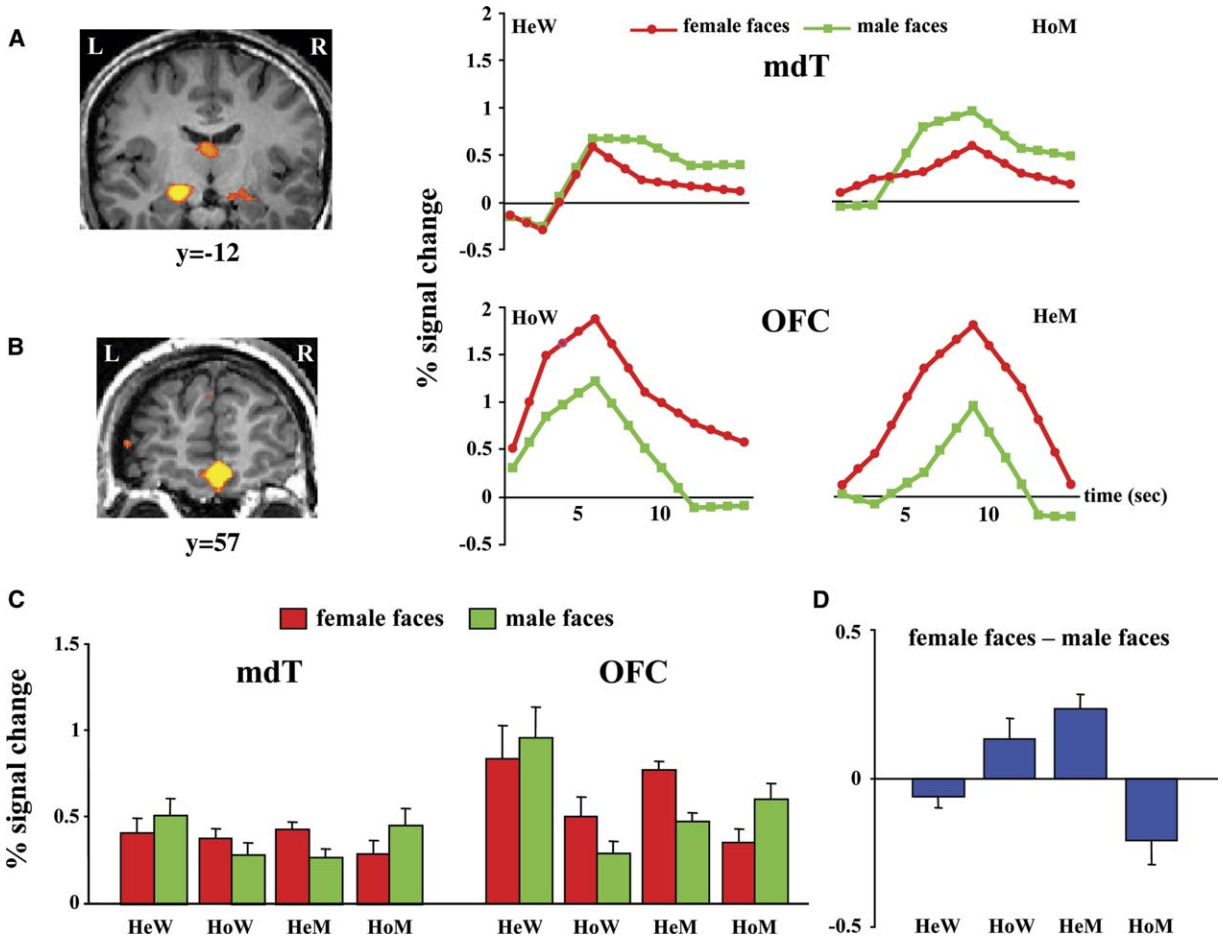

Figure 3. Response to Faces in the mdT and OFC

Coronal sections, illustrating the main effect of faces ($p < 0.01$, uncorrected) in the mdT (A) and OFC (B), were taken from two individuals. Time courses in the mdT and OFC are shown for one subject from each group for 15 s from stimulus onset. (C) Mean amplitude of the fMRI signal in the mdT and OFC. A significant response to faces was found in 9 HeW, 8 HoW, 8 HeM, and 8 HoM subjects in the mdT and in 8 HeW, 8 HoW, 10 HeM, and 9 HoM subjects in the OFC. (D) The difference between the amplitude of the fMRI response evoked by female faces and that evoked by male faces in the mdT and OFC. Negative values indicate stronger responses to male faces, whereas positive values indicate stronger responses to female faces.

dissociation between attractive opposite-sex faces that reflect evolutionary benefits and attractive same-sex faces that reflect aesthetic appraisal of beauty [15]. Rather, our findings demonstrate that the OFC has a more general role in representing the reward value of faces of potential sexual partners, including same-sex mates, irrespective of reproduction.

Our data indicate that although in heterosexual and homosexual men and women faces are similarly processed within a distributed cortical network, stronger activation in response to sexually preferred faces is found in the reward circuitry, where HeW and HoM respond more to male faces and HoW and HeM respond more to female faces. Although HeW exhibited the smallest difference between activation evoked by male faces and activation evoked by female faces, the differential neural responses in HeW were significantly different from the patterns of response in the HoW and were more similar to the activation patterns observed in HoM. Consistent with our findings, a recent study has shown that heterosexual women and homosexual men exhibited similar patterns of responses to putative pheromones [23]. Taken together, these results provide converging evidence that sexual preference, and not reproductive fitness, modulates neural responses to relevant stimuli in the adult human brain.

Conclusion

Male and female face stimuli evoke similar neural activation within a distributed cortical network that includes visual, limbic, and prefrontal regions. Sexually relevant faces elicit stronger neural responses in the reward circuitry, where the value of stimuli is represented.

Experimental Procedures

Subjects

Forty normal, right-handed subjects (ten heterosexual women, ten heterosexual men, ten homosexual women, and ten homosexual men; mean age and SD 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 heterosexuals or homosexuals based on their self report in a modified version of the Sell questionnaire [24].

Stimuli and Tasks

Stimuli were displayed with 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 grayscale photographs of faces (three runs) and assessed facial attractiveness (five runs). In each run, epochs of faces (30 s) were alternating with epochs of phase-scrambled faces (21 s in viewing, 12 s in attractiveness rating) and each stimulus was presented for 3 s, with no blank periods between the stimuli. During the viewing condition, 60 male and 60 female unfamiliar, famous, and emotional faces were presented. During the assessment of facial attractiveness, 100 male and 100 female faces were presented. Subjects pressed one of three buttons to indicate whether a face was attractive, neutral, or unattractive, and reaction times were recorded. The order of runs was randomized across subjects.

Data Acquisition

Data were collected with a 3T Philips Intera whole-body MR scanner (Philips Medical Systems, Best, The Netherlands). Changes in the blood-oxygenation-level-dependent MRI signal were measured with the sensitivity-encoded gradient-echo echoplanar sequence [25] (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, 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 [26].

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 artifacts, and spatially smoothed witha 5 mm FWHM Gaussian filter. The main effect of faces (activation evoked by faces compared to scrambled faces) was analyzed by multiple regression with box-car functions that were convolved with a canonical hemodynamic response function [27]. 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 (IOG), lateral fusiform gyrus (FG), superior temporal sulcus (STS), amygdala, intraparietal sulcus (IPS), caudate, putamen, the mediodorsal nucleus of the thalamus (mdT), anterior cingulate cortex (ACC), insula, inferior frontal gyrus (IFG), and medial orbitofrontal cortex (OFC). The contrast of faces versus 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 mean parameter estimates of face-selective responses were calculated separately for male and female faces. Additionally, for each subject, trials were sorted post-hoc according to their attractiveness score, and the mean of the parameter estimates was calculated for attractive, neutral, and unattractive male and female faces. The parameter estimates were used for between-subjects random-effects analyses. We also used separate repeated-measures ANOVAs to examine the effect of stimulus gender (male or female) and assessment of attractiveness (attractive, neutral, or unattractive) in each region and each hemisphere. Finally, the interaction between stimulus gender (male or female face) and the sexual preference of the subject (heterosexual or homosexual) was analyzed.

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