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Neural Responses to Sexual Stimuli in Heterosexual and Homosexual Men and Women: Men's Responses Are More Specific

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Abstract

Patterns of genital arousal in response to gendered sexual stimuli (i.e., sexual stimuli presenting members of only one sex at a time) are more predictive of men's than of women's sexual orientations. Additional lines of evidence may shed light on the nature of these differences. We measured neural activation in homosexual and heterosexual men and women using fMRI while they viewed three kinds of gendered sexual stimuli: pictures of nude individuals, pictures of same-sex couples interacting, and videos of individuals self-stimulating. The primary neural region of interest was the ventral striatum (VS), an area of central importance for reward processing. For all three kinds of stimuli and for both VS activation and self-report, men's responses were more closely related to their sexual orientations compared with women's. Furthermore, men showed a much greater tendency to respond more positively to stimuli featuring one sex than to stimuli featuring the other sex, leading to higher correlations among men's responses as well as higher correlations between men's responses and their sexual orientations. Whole-brain analyses identified several other regions showing a similar pattern to the VS, and none showed an opposite pattern. Because fMRI is measured identically in men and women, our results provide the most direct evidence to date that men's sexual arousal patterns are more gender specific than women's.

Keywords Sexual orientation · Sexual arousal · fMRI · Sex differences · Ventral striatum · Reward · Category specificity

Introduction

Female sexual orientation is more flexible than male sexual orientation. Women are more likely than men to report sexual attraction to people of their own sex (Bailey et al., 2016; Diamond, 2016). Women are more likely than men to report changes in their relative sexual attraction to men and women (Diamond, 2016). They are also more likely to show varying patterns across their self-reported sexual attractions, behaviors, and identities (Diamond, 2016). Men, on the other hand, are much more prone than women to exhibit highly directed and inflexible patterns of sexual attraction (e.g., paraphilias) over time (American Psychiatric Association, 2013).

Observations such as these have motivated at least two noteworthy theories. Diamond (2016) has focused on the dimension termed sexual fluidity or "a capacity for situation-dependent flexibility in sexual responsiveness, which allows individuals to experience changes in same-sex or other-sex desire across both short-term and long-term time periods." Sexual fluidity involves shifts in identity and attraction that can occur nonvoluntarily in response to changes in social environments, close relationships, or for other reasons. Women may be more likely than men to exhibit substantial degrees of sexual fluidity (Bailey et al., 2016). Baumeister (2000) has argued more generally that female sexuality—not just sexual orientation—is more socially influenced (and in that sense more flexible or "plastic") than male sexuality. Both lines of research have increased awareness of female sexual flexibility, especially with respect to partner sex. Neither line of research, however, has made great progress in elucidating the mechanisms behind this flexibility.

One candidate mechanism to explain women's sexual flexibility is their less specific pattern of sexual arousal (Bailey, 2009; Chivers, Rieger, Latty, & Bailey, 2004; Chivers, Seto, & Blanchard, 2007). In the initial research report on this phenomenon (Chivers et al., 2004), homosexual and heterosexual

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men and women were shown sexually explicit videos featuring actors of only one sex. Homosexual and heterosexual men generated opposite patterns of sexual arousal almost perfectly predictive of their self-reported sexual orientations. This was true whether sexual arousal was measured physiologically, (via genital measures) or subjectively (via self-report). In contrast, women's sexual arousal patterns were weakly correlated with their sexual orientations. Indeed, heterosexual women showed an indifferent pattern, with similar degrees of arousal to male and female stimuli. Homosexual women showed stronger subjective and genital arousal to female than to male stimuli, although their degree of bias was less than men's. These findings have been replicated in subsequent research (Chivers, 2017; Chivers et al., 2007; Rieger, Savin-Williams, Chivers, & Bailey, 2016; Rosenthal, Sylva, Safron, & Bailey, 2012; Suschinsky, Lalumière, & Chivers, 2009).

To the extent that relative sexual arousal to types of stimuli in the laboratory reflects sexual motivations in real-life situations, this research plausibly helps account for the greater sexual flexibility of women. However, an important limitation of the research concerned the comparability of measures in men and women. Genital arousal is objectively measured but must be assessed quite differently in men and women (Bailey, 2009). Although subjective sexual arousal is measured the same way in men and women, it must rely on self-report, and so comparability of scaling across the sexes cannot be assumed.

Although the comparability of genital arousal results for men and women may be limited, other studies have shown sex differences in sexual specificity using methods that are applied identically to men and women (Bailey et al., 2016; Chivers, 2017). Overall, objective measures of sexual interest administered identically in both sexes still show greater specificity in men, suggesting that the sex difference in concordance is not simply a reflection of different measurement methods. Measures which have found greater arousal specificity in men than in women have included time viewing female versus male images (Lykins, Meana, & Strauss, 2008; Rupp & Wallen, 2009), self-reported visual attention (Huberman, Maracle, & Chivers, 2014), and relative pupil dilation (Rieger & Savin-Williams, 2012).

The origins of the sex difference in specificity of genital response are not clear, although several hypotheses have been proposed (Chivers, 2017). These include the possibility that men's more specific and stronger arousal response serves a motivational function (i.e., to encourage mating with available partners as quickly as possible) that would be evolutionarily disadvantageous among women (Bailey, 2014). Other possible explanations include the greater erotic plasticity in women (Baumeister, 2000), that non-specific sexual responses in women represent a protective mechanism for vaginal penetration (Suschinsky & Lalumière, 2010), and that non-specific sexual responses reflect stronger identification with actors by women than men as a result of sex differences in theory of mind (Gallese, Keysers, & Rizzolatti, 2004).

fMRI of the Ventral Striatum: A Potential Window on Sexual Interest

fMRI is a particularly promising tool for trying to understand sex differences in sexual response. In addition to providing a converging line of evidence, fMRI also has particular methodological strengths, such as allowing the same measurement approach to be used in men and women, and allowing for the assessment of responses that are too brief (or too small in magnitude) to generate measurable physiological or subjective signals. Further, in contrast to other methods, fMRI provides multidimensional datasets capable of identifying which neural systems are involved in responding to particular experimental situations (e.g., when viewing a preferred or non-preferred sexual stimulus).

The ventral striatum (VS) is an especially promising brain region to consider in studying sex differences in sexual specificity, as this structure is strongly related to reward processing (Haber & Knutson, 2010). Previous studies attempting to differentiate general and sexual arousal have found that only the VS and hypothalamus are specifically associated with experiencing stimuli as erotic (Stark et al., 2005; Walter et al., 2008). Outside of the context of studies using sexual stimuli, these brain areas have been associated with motivation and appetitive states more generally (van der Laan, de Ridder, Viergever, & Smeets, 2011). While the VS is more narrowly associated with incentive motivation, the hypothalamus is best understood as a heterogeneous aggregation of organismic control nuclei, with some involved in sexual responses (LeVay, 1991; Roselli & Stormshak, 2010; Succu et al., 2007), but with other subsections—and sometimes populations of neurons within the same nucleus (Tye & Deisseroth, 2012)—involved in non-sexual processes such as aggression (Carmichael & Wainford, 2015; Ferris et al., 1997; Sewards & Sewards, 2003). However, it is difficult to differentiate among these heterogeneous processes within the hypothalamus with the limited spatial resolution of fMRI, and so inferences about sexual preferences would be tenuous. Although it is not specific to sexual responding, the VS is integral to action selection based on relative valuations as estimated from experience (Knutson, Wimmer, Kuhnen, & Winkielman, 2008; Mannella, Gurney, & Baldassarre, 2013).

The VS is consistently associated with motivational processes across many kinds of neuroimaging studies. VS activation is associated with craving food (Tang, Fellows, Small, & Dagher, 2012), craving drugs (Kühn & Gallinat, 2011), monetary reward (Spreckelmeyer et al., 2009), desiring to breathe in conditions of air deprivation (Evans et al., 2002), desiring to drink when thirsty (de Araujo, Kringelbach, Rolls, & McGlone, 2003), experiences of aesthetic attraction and appreciation (Kühn & Gallinat, 2012), compulsive videogame playing (Ko et al., 2009), and more. The factor underlying each of these conditions is reward, suggesting that the VS is a central contributor to a "common neural currency" of value (Diekhof, Kaps, Falkai, & Gruber, 2012; Haber & Knutson, 2010; Levy & Glimcher, 2012).

Although VS activity corresponds to a variety of motivating states, its activity can be reasonably concluded to correspond to sexual motivation while viewing sexual stimuli (Knutson et al., 2008; Lee, Jeong, Choi, & Kim, 2015; Oei, Both, van Heemst, & van der Grond, 2014). That is, greater VS activity toward either female or male erotic stimuli can be reasonably interpreted as suggesting relative gynephilic or androphilic preferences, respectively.

Support for the VS as a measure of sexual preferences is also evidenced by studies of heterosexual and homosexual men (Hu et al., 2008; Kagerer et al., 2011; Paul et al., 2008; Ponseti et al., 2006; Safron et al., 2007). In all of these studies, the VS showed greater activity in response to erotic stimuli featuring participants' preferred sex. Only one study of heterosexual and homosexual men failed to detect VS involvement in response to (non-erotic) pictures of attractive faces (Kranz & Ishai, 2006).

Fewer studies have investigated the specificity of women's brain activity (Ponseti et al., 2006; Safron et al., 2018), but the VS also consistently activates in women viewing sexual stimuli (Arnow et al., 2009; Hamann, Herman, Nolan, & Wallen, 2004; Karama et al., 2002). Research investigating women's VS responses also reflects patterns previously found in sexual psychophysiology research, including the relative specificity of gynephilic women's responses as compared to other women's responses (Safron et al., 2018).

The Present Study

We conducted a neuroimaging study with heterosexual and homosexual male and female participants in which we focused on the correspondence between VS activation to male versus female erotic stimuli and sexual orientation. We also examined subjective self-reports, to determine whether these yielded similar patterns to the neural measures. We included three types of gendered sexual stimuli in order to explore generality of effects. This also allowed us to examine patterns of covariation of both neural and subjective responses to the different kinds of stimuli.

Method

Participants

Participants included 26 heterosexual women, 25 homosexual women, 26 heterosexual men, and 25 homosexual men, recruited using internet advertisements. Participants were screened for inclusion using online questionnaires inquiring about sexual orientation, sexual interests, and personality and medical eligibility for fMRI research. No participants reported a transgender identity or medical history involving gender confirmation procedures. Participants were informed of the risks and nature of the study and agreed to participate in questionnaire, fMRI, and genital arousal portions of the research. Genital arousal and fMRI assessments were conducted separately from each other, on different days. All methods were approved by the Institutional Review Board of Northwestern University and carried out in accordance with its guidelines. Informed consent was obtained from each participant for every portion of the study in which they participated. Genital data for the male participants were reported in Rosenthal et al. (2012), fMRI data for the male participants were reported in Safron et al. (2017), and fMRI data for the female participants were reported in Safron et al. (2018). This is the first publication combining the male and female data used in these previous studies to explore sex differences in fMRI activation.

Participants' sexual orientation was assessed using a modified Kinsey score (Kinsey, Pomeroy, & Martin, 1948), which asked participants about their sexual fantasies throughout adulthood as well as in the past year (Chivers et al., 2004, 2007). The scale ranges from 0 to 6, with 0 corresponding to an exclusively heterosexual orientation and 6 corresponding to an exclusively homosexual orientation. Responses to the questions about adulthood and about the past year were averaged to create a Kinsey score for each participant. The average Kinsey score was .8 for heterosexual women (SD = .7, range = 0–2); 5.2 for homosexual women (SD = .68, range = 4–6); .4 for heterosexual men (*SD* = .46, range = 0–1.5); and 5.7 for homosexual men (SD = .45, range = 5–6). Self-reported sexual identities (i.e., "homosexual/gay/lesbian" and "heterosexual/straight") corresponded with the Kinsey score ranges for all participants.

Participants' ages ranged from 25 to 50 years old. Mean ages were 29.7 for heterosexual women (SD = 5.86, range = 25–46); 29.0 for homosexual women (SD = 3.12, range = 25–38); 32.3 for heterosexual men (SD = 6.75, range = 25–48); and 33.2 for homosexual men (SD = 6.4, range = 26–50). Among the participants, 66% identified as Caucasian, 14% as African American, 7% as Asian, 5% as Latino/a, and 8% identifying with another group or as multiracial. Ethnic identity did not differ significantly across combinations of sex and sexual orientation.

Our sample size was guided by two preliminary studies using fMRI to examine response to erotic stimuli (still images, combining both single nudes and sexually explicit couples): one of 24 men (12 heterosexual and 12 homosexual; Safron et al., 2007), and one of 22 women (11 heterosexual and 11 homosexual; Sylva et al., 2013). The latter article included analyses comparing participants in both studies and reported that for "a number of regions, the specificity of the response for men was reliably greater than for women." The present study's sample (51 men and 51 women) more than doubled the aggregate of the two preliminary studies.

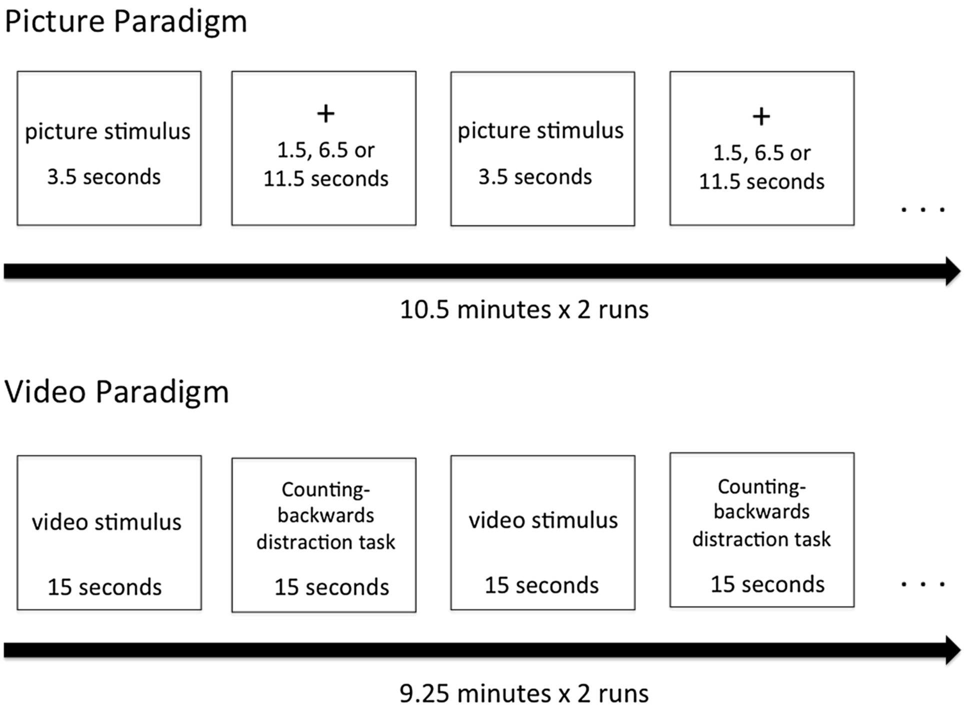

Fig. 1 Visual depiction of the scanner procedure used to present picture and video stimuli to the participants

Stimuli

We employed three different types of erotic stimuli: two consisting of pictures and one of videos.

Picture Stimuli

We employed a subset of the picture stimuli used in Safron et al. (2007). Eighty unique pictures depicted either single nude men, single nude women, or same-sex couples (i.e., either two men or two women) engaged in explicit sexual contact. Thus, each picture depicted persons of one sex only. In our previous research, we combined pictures of single individual men and male couples as "male erotic stimuli" and pictures of single individual women and female couples as "female erotic stimuli." In the current study, however, we have distinguished stimuli comprising pictures of single individuals from those of same-sex couples. This allowed us to examine whether patterns of activation vary across the two kinds of stimuli.

Video Stimuli

Video stimuli included 12 unique clips: six video clips depicting individual masturbating men and six video clips depicting individual masturbating women. Depicted individuals appeared sexually aroused but did not appear to reach orgasm. To estimate baseline responses, six natural landscape videos were shown.

Procedure

Viewing Erotic Pictures with fMRI Assessment

In each of two 10.5-min runs (ordering counterbalanced), participants viewed 40 erotic pictures featuring male actors and 40 erotic pictures featuring female actors. (Note that pictures of single individuals and of couples were interspersed during these runs. The aforementioned separation of pictures depicting individuals versus couples was done during data analysis.) Each picture was shown for 3.5 s, followed by a variable-duration fixation cross presented for either 1.5, 6.5, or 11.5 s. (For greater clarity, this scanner procedure is depicted in Fig. 1). During the presentation of each picture, participants used buttons held in their right hands to rate that image on a scale of −2 to +2 (respectively: "strongly disliked," "disliked," "liked," "strongly liked"), with no option of 0 for neutral ratings.

Viewing Erotic Videos with fMRI Assessment

In each of two 9.25-min runs (ordering counterbalanced), videos were presented for 15 s each, followed by a 15-s distraction task requiring participants to indicate via button-press when a number in a series decreased by an interval other than seven. This task was intended to facilitate a return to emotional and physiological baseline. (For greater clarity, this scanner procedure is depicted in Fig. 1).

After leaving the scanner, participants viewed the videos once more and provided ratings of each clip. Videos were rated using a 5-point scale for degree of sexual appeal, ranging from "not at all" (0) to "very much" (4), with a midpoint of "somewhat" (2). This rating scale differed from the picture stimuli rating scale. The picture rating scale was chosen to be consistent with previous investigations (Rosenthal et al., 2012). For the videos paradigm, we changed the word "liking" to "sexual appeal" in order to minimize ambiguity.

Data Analysis

fMRI Signal Extraction Methods

Image Acquisition A Siemens Trio 3T magnet and 12-channel RF head coil were used to collect T2*-weighted gradient-recalled EPI images from the whole brain (32 3-mm slices with a .99-mm interslice gap; TR = 2500 ms; TE = 20 ms; flip angle = 80°; FOV = 220 mm, 128 × 120 matrix). Slices were taken along the plane connecting the anterior and posterior commissures, with a 1.72 mm × 1.72 mm × 3.99 mm resolution, with more refined axial dimensions intended to produce less distortion and signal dropout in sub-cortical areas, although possibly at the expense of signal-to-noise ratio. During each picture run, 250 whole-brain volumes were collected, and during each video run, 220 whole-brain volumes were collected, with the first four volumes discarded to account for initial magnetization effects. For anatomical localization, a structural MRI scan consisting of T1-weighted images was conducted after the testing runs (160 1-mm axial slices; TR = 2.1 ms; TE = 4.38 ms; flip angle = 15°; FOV = 220 mm; 256 × 192 matrix).

Image preprocessing. Image preprocessing and analysis were performed using SPM 12b (Wellcome Trust Centre for Neuroimaging, London, UK) and implemented in MATLAB v 8.1.604 (The MathWorks Inc., MA, USA).

Functional (EPI) volumes were first corrected for slice timing. Each participant's volumes were then registered to the mean slice, after which the registered volumes were resliced, used to create a mean resliced image, and then co-registered to the mean structural (T1) image. All EPI images, including the mean resliced image, as well as the structural (T1) scans were then spatially normalized to Montreal Neurological Institute (MNI) space, and resampled to 3 × 3 × 3 mm (27 mm^3) resolution. Normalized functional images were then smoothed to an 8-mm full-width-at-half-maximum Gaussian kernel.

Data Exclusion and Loss

Signal-to-Noise Ratio and Head Coverage Exclusions To exclude participants with poor signal due to either head motion or scanner conditions, average signal-to-noise ratio (SNR) over time was calculated for each subject (after preprocessing, using a mask that included only voxels with appreciable EPI signal). The SNR ratio for each voxel (mean divided by SD) was averaged across all voxels in the brain (Parrish, Gitelman, LaBar, & Mesulam, 2000; Van Dijk, Sabuncu, & Buckner, 2012). Participants whose picture data SNR was more than one SD below the mean were excluded from picture analyses. Similarly, participants whose video data SNR was more than one SD below the mean were excluded from video analyses.

To check the validity of our SNR-exclusion criterion, head motion plots were visually inspected for all participants (Parrish et al., 2000). Excluded participants were confirmed to have highly variable head positions as compared to included participants. An additional validity check was performed using evoked responses to erotic pictures minus a fixation cross baseline. Excluded participants had substantially reduced activity in visual cortices as compared to included participants.

Based on these criteria, 13 participants (five heterosexual women, two heterosexual men, four homosexual women, and two homosexual men) were excluded from ROI-based fMRI picture analyses, and 15 participants (six heterosexual women, four heterosexual men, four homosexual women, and one homosexual man) were excluded from ROI-based fMRI video analyses.

For whole-brain analyses, mean functional scans were individually examined to identify participants with substantial cutoffs in head coverage. As a result, one homosexual male and one heterosexual female who had substantial frontal lobe cutoff were excluded from whole-brain analyses in addition to those participants excluded for SNR.

Thus, the total number of participants included in ROI-based fMRI picture analyses was 89, and the total number of participants included in ROI-based fMRI video analyses was 87. For whole-brain analyses, the total number of participants included was 87 for the picture paradigm and 85 for the video paradigm.

Subjective Data Loss One (heterosexual) male participant was excluded from subjective picture rating analyses due to insufficient subjective data resulting from a data recording error, and an additional (homosexual) male participant was excluded from subjective video rating analyses for the same reason. Unfortunately, substantial subjective data were lost for female participants due to a data recording error. Specifically, for a period during data collection participants' subjective responses were assessed but equipment failed to record them. For picture analyses, subjective data from 20 participants (12 heterosexual women and eight homosexual women) were lost. For video analyses, subjective data from two homosexual women were lost for the same reason. Thus, 81 participants were included in subjective picture analyses, and 99 participants were included in subjective video analyses. Although this degree of lost data for female participants in the picture paradigm was obviously unfortunate, this loss did not undermine our investigation or limit the conclusions

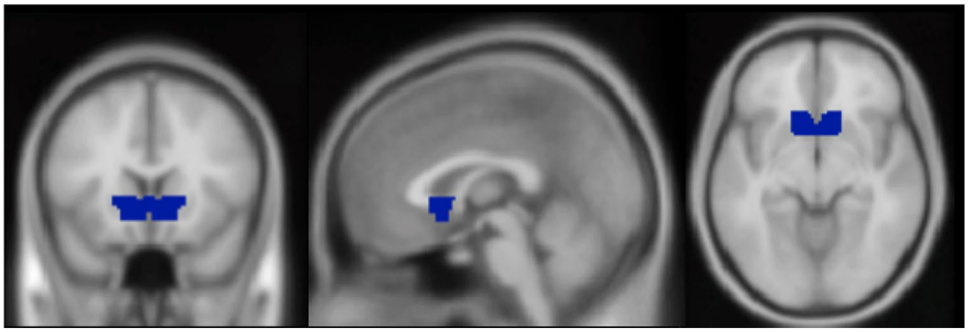

Fig. 2 Ventral striatum (VS) ROI mask drawn using an average brain in the WFU PickAtlas toolbox for SPM 8. MNI coordinates displayed: $x=0$, $y=17$, $z=-8$

we were able to draw. As we show in the Results, the general pattern of results was identical in the subjective and fMRI data and, if anything, the subjective results were more statistically robust despite the greater loss of data.

First-Level fMRI Analyses

For both the video and picture assessments, a standard general linear model (GLM) (Friston et al., 1994) was used to identify hemodynamic changes for each participant, and a high-pass filter (cutoff 128 s) was used to remove low-frequency temporal noise.

For the picture assessment, each participant's responses to each stimulus contrast of interest were concatenated within stimulus type, using data from both runs. Estimated average activity was calculated for each participant's separate responses to male pictures, female pictures, male videos, and female videos (contrasted with fixation cross for pictures and nature scenes for videos). These estimates were used for region of interest analyses.

Ventral Striatum (VS) Region of Interest Analyses

The VS ROI mask used in the present study was drawn on an MNI template brain using the WFU PickAtlas toolbox for SPM 8 (Maldjian, Laurienti, Kraft, & Burdette, 2003). It was anatomically defined as a dilated intersection of the ventral anterior caudate and putamen. This VS ROI is shown in Fig. 2.

Estimates of average VS activity for each participant were extracted using the MarsBar toolbox for SPM8 (Brett, Anton, Valabregue, & Poline, 2002). Extracted VS ROI data were analyzed using JMP Pro v11 (SAS Institute, Cary, NC).

Planned Contrasts

The primary question guiding this research was whether men's VS activation patterns are more strongly related to their sexual orientations than are women's. We conducted separate analyses for each of our six dependent variables.

Whole-Brain Analyses

We compared whole-brain activation patterns of women and men (combining data from homosexual and heterosexual orientation groups), contrasting differential activity to erotic stimuli depicting the preferred versus the non-preferred sex (averaging across erotic pictures and videos). We performed t-tests across all voxels in the brain, with family-wise error (FWE) corrections for multiple comparisons, using a significance threshold of $p < .05$ and a voxel extent threshold of $k = 5$. Peak activations and spatial extents of clusters were visually examined as overlays on slice and render maps. Neuroanatomical descriptions were determined based on agreement between two trained investigators, and checked against designations from the software and online atlases (Maldjian et al., 2003).

Results

We constructed dependent variables for each of the six combinations of stimuli (pictures of nude individuals; pictures of sexual interactions in same-sex couples; and videos of individuals masturbating) and type of measure (VS activation; self-rating of subjective feelings) by subtracting each participant's mean response to male stimuli minus the response to female stimuli. We refer to this variable throughout as the male–female contrast. Higher scores on this contrast represent more VS activation to male than to female stimuli (for the neural measures) and more positive feelings about the male than stimuli (for the self-report subjective ratings).

As a test of the sensitivity of our VS ROI for measuring reward-related activity, we compared it to an extrastriate occipitotemporal area, a commonly activated attention-modulated area in studies of sexual response (Georgiadis & Kringelbach, 2012; Georgiadis, Kringelbach, & Pfaus, 2012). While the extrastriate area showed differentiation between heterosexual and homosexual men toward erotic stimuli, our VS ROI showed differentiation between both heterosexual and homosexual men and heterosexual and heterosexual and homosexual women. However, the potential sensitivity of the VS as a measure of orientation is not the primary reason that motivated its selection

Table 1 Within-sex correlations among subjective and neural male–female contrasts, and between the contrasts and sexual orientation

	Subjective ratings			VS activation		
	Pictures of individuals[a]	Pictures of couples[a]	Videos	Pictures of individuals	Pictures of couples	Videos[b]
Subjective ratings						
Pictures of individuals		.56 (21)	.42 (20)	.31 (21)	.63 (21)	.06 (20)
Pictures of couples	**.97** (49)		.48 (20)	.26 (21)	.28 (21)	− ..28 (20)
Videos	**.96** (44)	**.98** (44)		.43 (39)	.15 (39)	.21 (38)
VS activation						
Pictures of individuals	.63 (45)	.63 (45)	.58 (44)		.24 (41)	.21 (38)
Pictures of couples	.68 (45)	.63 (45)	**.66** (44)	.50 (46)		.11 (38)
Videos	.49 (43)	**.48** (43)	.54 (44)	.49 (43)	.41 (43)	
Female sexual orientation[c]	.47 (21[a])	.23 (21[a])	.71 (41)	.37 (41)	.33 (41)	.23 (40)
Male sexual orientation[c]	**.96** (49)	**.96** (49)	**.96** (46)	**.68** (46)	**.72** (46)	.53 (45)

Correlations were computed with pairwise deletion, thus using all available cases. Bolded correlations indicate that the correlation for men was significantly higher than the respective correlation for women ($p < .05$, two-tailed). Results for males are below the diagonal. Results for females are above the diagonal. Sample sizes are below correlations in parentheses

[a] Data from 20 female subjects were either not collected, or were lost, due to mechanical error

[b] Results are presented with one outlier excluded (S126), a heterosexual man whose response on this variable was unusually high (in the predicted direction)

[c] Sexual orientation was dichotomous, with the higher number representing attraction to men

as a primary outcome measure. Rather, the most notable aspect of the VS is its specificity as a measure of valence (as opposed to salience, which could be either positively or negatively valenced), and the construct validity this provides for studies of sexual preferences.

Table 1 presents the correlations among male–female contrasts for both self-rated subjective responses and VS activation to our three categories of stimuli. In Table 1, results for women are above the diagonal, and those for men are below. For example, the first number on the first row, .56, represents the correlation among women of the difference of liking of male versus female pictures of individuals with the difference of liking of male versus female pictures of couples. The final number on that row, .06, represents the correlation among women of the difference of liking of male versus female pictures of individuals with the difference of VS activation to videos featuring males versus females. The final two rows of the table include the correlations between each male–female contrast and female and male sexual orientation (higher and lower row, respectively). For example, the first number in the final row, .96, is the correlation for men of the difference of liking of male versus female pictures of individuals with dichotomously-measured sexual orientation (with the positive value indicating that higher values of the contrast are associated with attraction to men).

The male correlations tended to be substantially higher, with 5 of the 15 respective correlations significantly so. The mean of the male correlations was .64, and the mean of the female correlation was .27. This difference was sustained for the three correlations involving only self-ratings ($M = .97$ vs. $M = .48$), the 9 correlations between self-ratings and neural activation scores ($M = .59$ vs. $M = .23$), and the 3 correlations among neural activation scores ($M = .47$ vs. $M = .19$). Thus, in general, the different measures cohered more for the male than for the female participants.

The magnitude of correlations tends to be larger in samples with greater true score variance. Thus, we examined whether the larger correlations in male participants reflected increased variability between homosexual and heterosexual men, relative to the variability between homosexual and heterosexual women. Specifically, we compared male and female variance for the key variables. For all six male–female contrasts, men were significantly and substantially more variable than women (Table 2), with the ratio of variances (male/female) ranging from 2.44 to 7.98.

We conducted the following analysis to test for a sex difference in response specificity: We regressed each male–female contrast on participant's sex (male/female), preference (male/female), and the interaction term. If men are more specific than women in their responses, then there should be larger differences between male- and female-preferring men than between male- and female-preferring women. This is tested via the interaction term. Table 3 and Fig. 3 present results of these analyses. All interaction terms were statistically significant, and in every case, the direction of effects was as predicted.

Table 3 also contains results of other potentially interesting, though statistically dependent, analyses. With one exception, heterosexual and homosexual participants of the same sex differed significantly in their male–female contrasts. The single

Table 2 Ratio of male-to-female variances in male–female contrasts

Variable	Ratio of variances (male/female)
Pictures of individuals (subjective ratings)	3.16
Pictures of couples (subjective ratings)	7.98
Videos (subjective ratings)	3.85
Pictures of individuals (VS activation)	2.44
Pictures of couples (VS activation)	2.87
Videos (VS activation)	2.68

All ratios were significantly greater than 1, $p < .01$

exception was women's VS activation to video stimuli. In general, VS activation to video stimuli appeared to discriminate relatively weakly. For example, this was the only stimulus/response variable for which homosexual females and heterosexual males had nonsignificant male–female contrasts.

Also, in Table 3, heterosexual women responded indifferently (i.e., their male–female contrasts did not differ significantly from zero), with one exception. Notably, in this exception (their self-reported subjective ratings of same-sex couples), they rated the female stimuli more positively.

Table 3 Summary of statistical results

	Subjective			Neural		
	Pictures of individuals	Pictures of couples	Videos	Pictures of individuals	Pictures of couples	Videos
Sex *x* preference interaction significant?	Yes	Yes	Yes	Yes	Yes	Yes
N_{Female}, N_{Male}	21[a], 49	21[a], 49	41, 46	41, 46	41, 46	40, 45[b]
F	50.30	113.59	76.98	8.93	14.42	5.46
p	$< .0001$	$< .0001$	$< .0001$	.004	.0003	.022
Male–female contrast significantly different between homosexual and heterosexual groups?						
Females	Yes	Yes	Yes	Yes	Yes	No
Males	Yes	Yes	Yes	Yes	Yes	Yes
Mean male–female contrast 95% CI						
Heterosexual females	−.57 −1.68 to .54	−.95 −1.80 to −.11	.28 −.19 to .76	.06 −.23 to .35	.02 −.19 to .23	.09 −.16 to .34
Homosexual females	−2.00 −2.83 to −1.16	−1.45 −2.15 to −.76	−1.89 −2.44 to −1.34	−.46 −.79 to −.13	−.36 −.65 to −.06	−.17 −.43 to .09
Heterosexual males	−2.79 −3.09 to −2.48	−2.73 −3.17 to −2.30	−2.85 −3.18 to −2.51	−.60 −.92 to −.28	−.54 −.81 to −.28	−.34 −.88 to .20
Homosexual males	2.34 1.99 to 2.70	3.16 2.86 to 3.46	2.95 2.59 to 3.31	.89 .49 to 1.29	.86 .53 to 1.19	.77 .53 to 1.00
Male–female contrast 95% CI includes 0?						
Heterosexual females	Yes	No[c]	Yes	Yes	Yes	Yes
Homosexual females	No	No	No	No	No	Yes
Heterosexual males	No	No	No	No	No	Yes
Homosexual males	No	No	No	No	No	No

[a] Data from 20 female subjects were either not collected, or were lost, due to mechanical error

[b] Results are presented with one outlier excluded (S126), a heterosexual man whose response on this variable was unusually high (in the predicted direction). With this outlier included, the analysis remained statistically significant in the predicted direction, $p = .013$

[c] Heterosexual women rated female couples more highly than they rated male couples

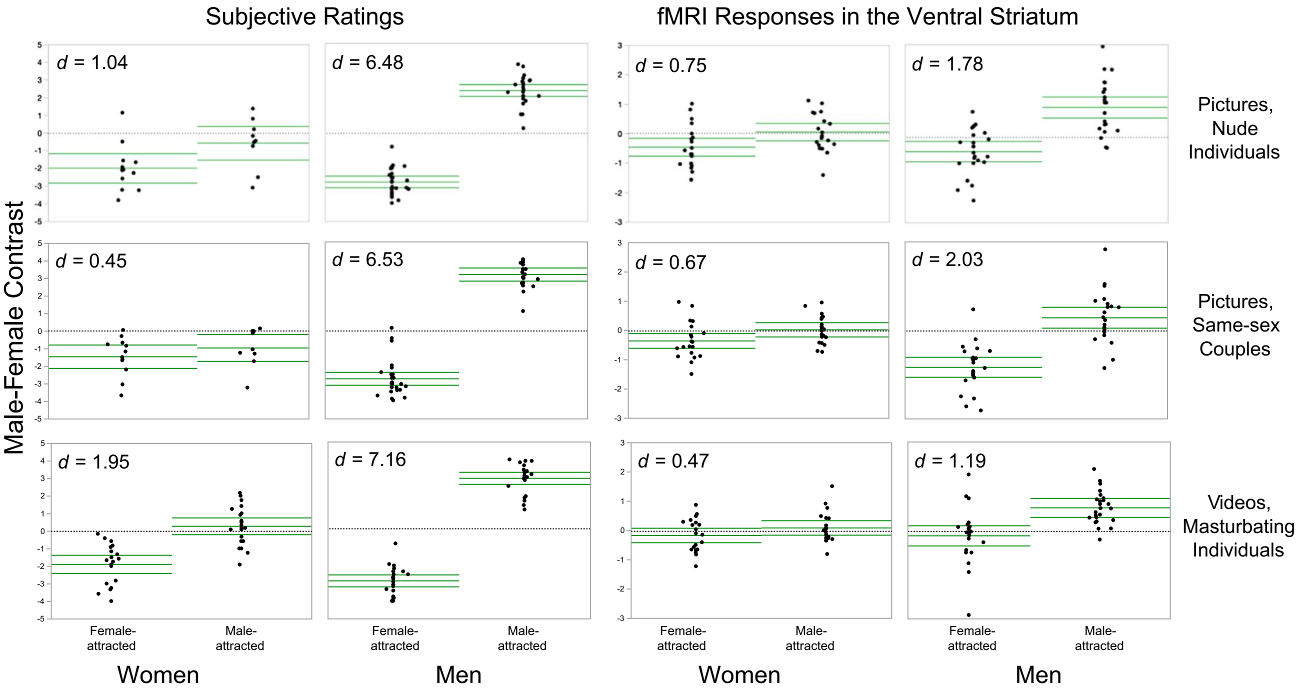

Fig. 3 Male–female contrasts for subjective ratings and VS activation to three categories of stimuli. Each point represents a participant's mean male–female contrast. For each group, the three lines represent the mean (middle line) and the 95% confidence interval. The line that extends across the female-attracted and male-attracted participants for each comparison represents a contrast value of zero

Whole-Brain Results

When responses were compared for contrasts between stimuli depicting the preferred versus the non-preferred sex, no areas showed significantly greater activity for women compared with men. Men, however, showed significantly greater differential activations for this subtraction in multiple brain areas (Table 4, Fig. 4). Occipital activations were likely indicative of visual attention (Sabatinelli, Flaisch, Bradley, Fitzsimmons, & Lang, 2004); hippocampus may have indicated either memory encoding or retrieval (Greene, Gross, Elsinger, & Rao, 2006); and caudate (including the ventral striatum) (Safron et al., 2017), thalamus (including the medial dorsal nucleus) (Metzger et al., 2010), subgenual anterior cingulate (Walter et al., 2008), and orbitofrontal (Kringelbach, 2005) activations likely indicated salience and reward processing.

Discussion

Results from both a priori region of interest ventral striatum (VS) and whole-brain analyses support and extend the view that men's responses to erotic stimuli are more specific than women's. That is, men's responses are more likely to correspond with their sexual orientations and identities. The current study focused on both self-rated subjective response and VS activation to gendered stimuli. Findings using the two measures converged on the same general conclusion: women were less disposed than men to find erotic stimuli of their preferred sex especially rewarding compared with their non-preferred sex.

Our results suggest that past studies demonstrating a sex difference in specificity of sexual arousal do not simply reflect female genital arousal measurement artifacts. That concern had stemmed, in part, from the much lower concordance of genital and subjective arousal in women than in men (Chivers, Seto, Lalumière, Laan, & Grimbos, 2010). Women can have relatively high genital arousal with low subjective arousal, and vice versa (Suschinsky & Lalumière, 2010). However, our results implicate the reward system as exhibiting similar patterns to those observed in the sexual psychophysiology literature.

Our findings clarify one likely reason why men's response patterns correlate more strongly, both among themselves and with sexual orientation: men's much greater variance in gender-biased response patterns. The median ratio of variances (male/female) of the various male–female contrasts in Table 2 is 3.02 (i.e., the average of 3.17 and 2.87). Because both the male and female samples comprise approximately half heterosexual and half homosexual participants, the smaller female variance indicates that women tend to generate responses to erotic stimuli that are much less gender-biased compared with men's responses. That is, a woman in our sample was less likely than a man to produce much stronger responses to one sex than to the

Table 4 Differential brain activations between male and female subjects toward erotic stimuli (preferred–non-preferred sex)

R/L	Region	BA	MNI	Voxels	Peak *T*
Women > men					
	No differential activations				
Men > women					
R	Middle occipital gyrus	BA 18	27 −94 2	377	7.09
R	Cuneus, middle occipital gyrus	BA 18, 17	18 −91 2		6.12
R	Middle occipital gyrus, inferior occipital gyrus, fusiform gyrus, lingual gyrus, declive	BA 19	27 −91 14		6.1
L	Caudate body		−21 −13 23	196	6.54
L	Caudate body		−24 −25 26		5.6
L	Thalamus (pulvinar, ventral lateral nucleus)		−21 −31 11		5.36
L	Middle occipital gyrus, cuneus	BA 18, 19, 17	−24 −94 11	276	6.31
L	Inferior occipital gyrus, middle occipital gyrus	BA 18	−33 −91 −7		5.74
L	Inferior occipital gyrus, fusiform gyrus, lingual gyrus, declive	BA 19	−33 −76 −7		5.34
R	Caudate body, thalamus (pulvinar, lateral posterior nucleus, ventral lateral nucleus)		21 −19 20	277	6.29
R	Caudate head, anterior cingulate	BA 25	15 29 −4		5.98
R	Caudate body		18 5 23		5.96
L	Ventral caudate head		−18 29 2	40	5.9
R	Hippocampus, caudate tail		33 −34 −1	25	5.73
L	Hippocampus, caudate tail		−30 −25 −7	15	5.58
R/L	Medial dorsal thalamic nucleus		0 −7 8	14	5.42
R	Ventral striatum, nucleus accumbens		9 8 −4	5	5.05
L	Subgenual cingulate, orbitofrontal cortex	BA 10	−12 41 −7	11	4.95
L	Posterior hippocampus		−36 −43 2	5	4.89

L left, *R* right, *BA* Brodmann area

Coordinates are in MNI space and designate points of peak activation. All clusters were significant with $p < .05$ FWE corrections

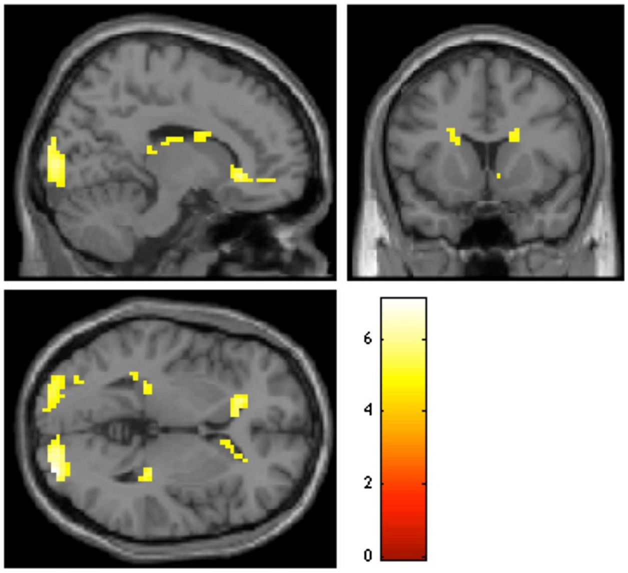

Fig. 4 Brain areas with greater gender-biased fMRI responses in men compared with women toward erotic stimuli (preferred sex > non-preferred sex). No brain areas showed greater gender-biased fMRI responses in women compared with men. Sagittal slice 52, coronal slice 39, and axial slice 37 are shown. Significance threshold: $p < .05$ FWE. Voxel threshold: $k = 5$

other. Psychometrically, increased variance in men's contrast scores likely reflected increased true score variance, relative to women's, as measures of sexual orientation. This suggests that women's brains and minds produce more varied (and potentially complexly determined) sources of measurable signal to gendered sexual stimuli than men's do. These differences may contribute to sex differences in the specificity of genital arousal.

Finally, the fact that our results for VS activation were quite similar to both results for subjective ratings of "liking" in the present study and to patterns of genital sexual arousal in past studies (e.g., Chivers et al., 2004) supports the construct validity of relative VS activation as an indicator of positive sexual incentive value. Furthermore, the consistency of our results for VS activation across the three kinds of stimuli suggests that the VS likely plays a role in the well-established, likely important, but so far poorly understood sex difference in the specificity of response to gendered sexual stimuli.

Limitations

The sample sizes in the present study, although substantially larger than those of prior fMRI studies of sexual orientation, were not large in an absolute sense. This was especially true with respect to subjective data, some of which were inadvertently lost. Nevertheless, effect sizes were consistently sufficiently large so that the primary effect of interest (the sex*preference interaction) was statistically significant in all six analyses. Furthermore, significance tests yielded smaller exact probabilities for the subjective data than for the neural data, even though the former sample sizes were smaller.

Our stimuli were all visual (although the video stimuli also had sound), and it is conceivable that our results are specific to this stimulus modality. That limitation applies to most of the relevant literature. It would be interesting to conduct similar research using different kinds of stimuli, such as text stories and audio stimuli.

One limitation concerning our subjective responses ratings for video stimuli was that ratings were collected outside the scanner. Thus, it is possible that discrepancies could exist between participants' reactions during the initial viewing and their ratings of the videos.

Conclusions

Bailey (2009) argued that men's sexual arousal patterns define their sexual orientations, proposing a thought experiment in which a man's well-measured genital arousal pattern clearly conflicted with his self-report and his behavioral choices. For example, a heterosexual-identified man whose genital arousal is consistently much stronger to male than to female stimuli would still in most cases be likely to have a homosexual orientation.[1] Furthermore, Bailey argued that men who must learn their sexual orientation identities (because they do not align with the heterosexuality that is expected for the majority) likely often do so via noticing their sexual arousal patterns. Although our study did not measure sexual arousal per se, its findings using the VS as an indicator of reward are quite similar to those of studies with genital arousal measures. For this reason, we henceforth refer to "sexual arousal/reward pattern," as either arousal or reward may guide men to similar conclusions about their sexual orientations.

Regardless of whether one accepts Bailey's argument about the central role of sexual arousal/reward patterns as the mechanism guiding male sexual orientation, the question remains what mechanisms guide female sexual orientation. Plausibly, a consistent pattern of sexual arousal/reward plays an important role among some homosexual women, who show some degree of response specificity, and who must (like homosexual men) discover the ways that they are different from the heterosexual majority; however, a driving role for arousal/reward patterns is less plausible for heterosexual women. Heterosexual women had a relatively indifferent response pattern, with no measured sexual or motivational response, whether subjective or neural, significantly favoring their preferred sex (men). Of course, our sample sizes of heterosexual women were small, ranging from 9 (for the subjective analyses with picture stimuli) to 22 (for the subjective analyses with video stimuli), thus precluding strong inference about failures to disprove null hypotheses. Still, our results support the view, consistently supported by past research, that heterosexual women's sexual orientation is weakly associated with their response to gendered sexual stimuli. Heterosexual women's behavioral choices are much more biased (toward men) than are their sexual arousal patterns and reward system responses to erotic stimuli. What mechanisms direct these choices? A growing, consistent body of research, including this study, suggests that the answers will not be found via research examining women's responses to the kinds of gendered sexual stimuli used so far.

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical Approval All procedures were performed in accordance with the ethical standards of Northwestern University and with the 1964 Helsinki declaration and its later amendments.

Informed Consent Informed consent was obtained from all individual participants included in the study.

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[1] It is important to stipulate that even the best objective measure of male sexual arousal, genital assessment, has measurement error (sometimes substantial error, especially when response is low). Thus, it is a man's score on the latent variable "sexual arousal pattern" and not that on any one assessment that defines his sexual orientation.

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