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Pattern recognition reveals sex-dependent neural substrates of sexual perception

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Abstract

Sex differences in brain activity evoked by sexual stimuli remain elusive despite robust evidence for stronger enjoyment of and interest toward sexual stimuli in men than in women. To test whether visual sexual stimuli evoke different brain activity patterns in men and women, we measured hemodynamic brain activity induced by visual sexual stimuli in two experiments with 91 subjects (46 males). In one experiment, the subjects viewed sexual and nonsexual film clips, and dynamic annotations for nudity in the clips were used to predict hemodynamic activity. In the second experiment, the subjects viewed sexual and nonsexual pictures in an event-related design. Men showed stronger activation than women in the visual and prefrontal cortices and dorsal attention network in both experiments. Furthermore, using multivariate pattern classification we could accurately predict the sex of the subject on the basis of the brain activity elicited by the sexual stimuli. The classification generalized across the experiments indicating that the sex differences were task-independent. Eye tracking data obtained from an independent sample of subjects ($N = 110$) showed that men looked longer than women at the chest area of the nude female actors in the film clips. These results indicate that visual sexual stimuli evoke discernible brain activity patterns in men and women which may reflect stronger attentional engagement with sexual stimuli in men.

KEYWORDS

fMRI, MVPA, pattern-classification, sex differences, sexual arousal

1 | INTRODUCTION

Identification of potential mating partners is crucial for reproduction and species survival and relies strongly on visual cues in humans and other primates (Georgiadis & Kringelbach, 2012). Accordingly, visual sexual stimuli are rewarding and sexually arousing for humans (Wierzbica et al., 2015) and they trigger autonomic and genital

responses that prepare the body for sexual activity in both men and women (Chivers et al., 2010). Yet, human reproductive and sexual behavior is markedly dimorphic presumably because women carry significantly higher metabolic costs of reproduction while men have a higher capacity for conceiving offspring (Buss & Schmitt, 2019). Men have a stronger sexual motivation than women, as indicated by a higher desired frequency of sexual intercourse and a number of sexual

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partners, and more frequent masturbation and sexual fantasies (for a meta-analysis, see Baumeister et al., 2001). Accordingly, men experience stronger sexual arousal (Murnen & Stockton, 1997) and positive affect (Peterson & Janssen, 2007; Sarlo & Buodo, 2017) than women when viewing sexual stimuli depicting their preferred sex. Finally, men also consume erotica and pornography more than women (Rissel et al., 2017; Solano et al., 2020) and begin doing so at an earlier age (Hald, 2006). These sex differences in subjective experience and consummatory behavior suggest sexually dimorphic brain activity patterns to sexual signals. However, this issue remains hotly debated (Mitricheva et al., 2019; Poepl et al., 2020).

Meta-analyses of neuroimaging studies show that visual sexual versus neutral stimuli activate numerous cortical and subcortical regions spanning the emotion and reward circuits such as the brainstem, ventral striatum, amygdala, hypothalamus, thalamus, insula, cingulate, premotor cortex, and visual cortices (Mitricheva et al., 2019; Poepl et al., 2016). Most of these studies have been conducted on men, and the few studies comparing men and women have yielded mixed results. Early small-scale studies reported stronger activation in men compared with women in hypothalamus (Hamann et al., 2004; Karama et al., 2002), amygdala (Hamann et al., 2004), and extrastriate visual cortex (Sabatinelli et al., 2004) in response to erotic stimuli. More recent studies have found stronger activity in men in the thalamus, anterior and middle cingulate gyrus, and occipital and parietal cortices (Wehrum et al., 2013) as well as in nucleus accumbens (NAc) in response to erotic pictures (Wehrum-Osinsky et al., 2014). Other studies, however, have found no evidence for sex differences (Gillath & Canterberry, 2012; Stark et al., 2005). Meta-analyses have also yielded conflicting results regarding sex differences in the processing of visual sexual stimuli: Poepl et al. (2016) found stronger engagement of basal ganglia and hypothalamus in men whereas Mitricheva et al. (2019) found no evidence for sex differences. Thus, despite the marked sex differences in sexual behavior, the putative sex differences in the neural processing of visual sexual stimuli have remained elusive.

So far, all fMRI studies on sex differences in the processing of visual sexual stimuli have employed conventional mass-univariate general linear model (GLM) analysis. In contrast to the GLM approach, multivariate pattern analysis (MVPA) of fMRI data uses machine learning algorithms to capture activity patterns distributed across voxels that differentiate conditions or classes such as stimulus categories (Haxby et al., 2001), emotional and cognitive states (Putkinen et al., 2021; Saarimäki et al., 2015), and subject groups (Du et al., 2012; Shimizu et al., 2015). Since MVPA exploits information aggregated across voxels, this analysis approach is sensitive to spatially distributed group differences that are not detectable by conventional univariate analyses (Nummenmaa & Saarimäki, 2019). Accordingly, previous fMRI studies have successfully employed MVPA to reveal sex differences in resting state activity (Weis et al., 2020) as well as language-related tasks (Ahrens et al., 2014; Xu et al., 2020). Thus, even though univariate (voxel-wise) GLM analysis of brain responses to visual sexual stimuli may not reliably

differentiate men and women, multivariate brain activation patterns induced by such stimuli could be more sensitive to sex differences.

2 | THE CURRENT STUDY

Here we used multivariate pattern analysis in a large sample of subjects ($N = 91$, 46 men) to test whether men and women show different neural responses to sexual stimuli. In two experiments, subjects viewed sexual and nonsexual film clips and pictures while their haemodynamic brain activity was measured with fMRI. We found that men showed stronger activation than women particularly in the visual and prefrontal cortices in both experiments. Furthermore, using MVPA we could accurately predict the sex of the subject on the basis of the brain activity elicited by the sexual stimuli. The classification generalized across the experiments so that sex could be predicted when the classifier was trained on the data from one experiment and tested on the data from the other indicating that the sex differences were consistent across the experiments.

3 | METHODS

3.1 | Subjects

Altogether 91 volunteers participated in the study. Four additional participants were scanned but excluded because of neurological abnormalities revealed in their MRIs or unusable data due to a broken gradient coil. The final sample consisted of 46 men (mean age 31, range 20–57) and 45 women (mean age 32, range 20–56). All subjects reported either heterosexual ($N = 81$, 38 women) or bisexual ($N = 10$, 7 women) as their sexual orientation. The exclusion criteria included a history of neurological or psychiatric disorders, alcohol, and substance abuse, current use of medication affecting the central nervous system, and the standard MRI exclusion criteria. All subjects gave an informed, written consent and were compensated for their participation. The ethics board of the Hospital District of Southwest Finland had approved the protocol and the study was conducted in accordance with the Declaration of Helsinki.

3.2 | fMRI study design

To map the brain regions encoding sexual content in films, we used a paradigm (Karjalainen et al., 2017, 2019; Lahnakoski et al., 2012) in which the subjects were shown 96 movie clips with variable content (total duration 20 min). Nine movie clips (mean duration 11.9 s) were extracted from commercially available pornographic films and depicted female–male couples engaged in sexual intercourse. The other film clips (mean duration 17.8 s) were extracted from mainstream English language feature films and contained scenes with

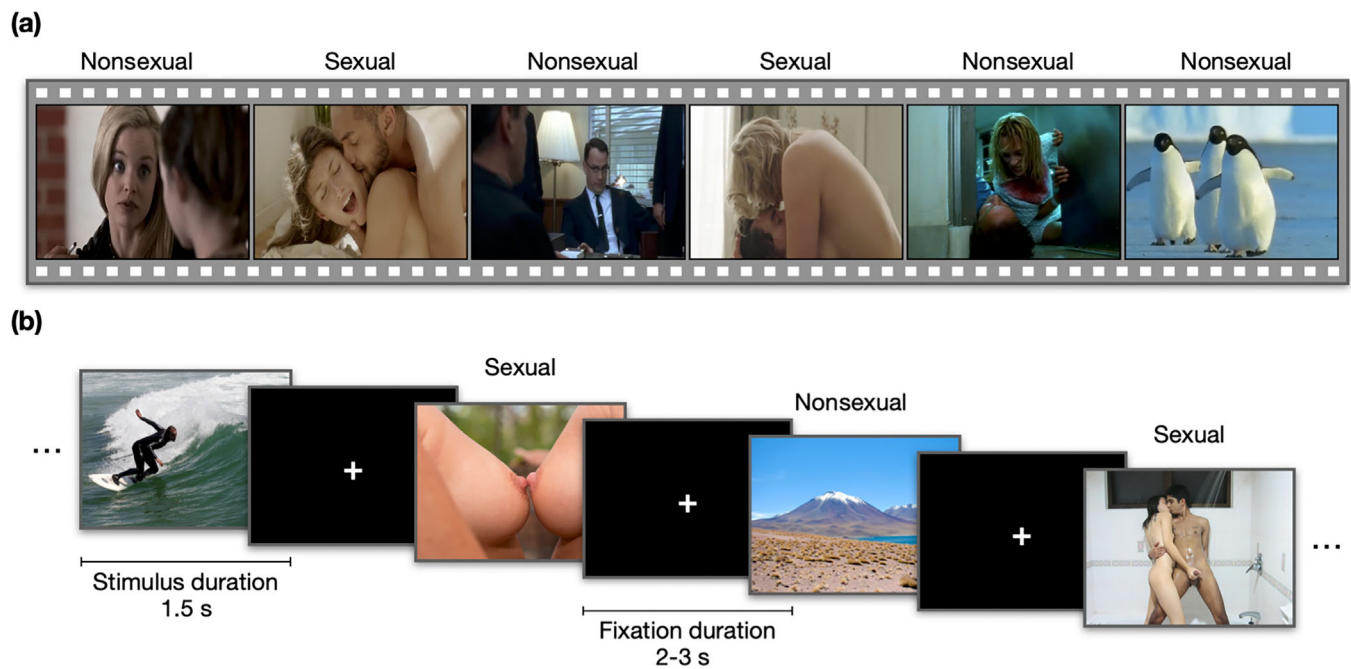


FIGURE 1 Experimental design and sample stimuli for the movie (a) and picture experiment (b). (a) Movie experiment: 96 erotic and nonerotic movie clips (task duration: 20 min). (b) Picture experiment: 324 erotic and nonerotic pictures (task duration: 22 min).

nonsexual human interaction (friendly discussion, arguing, violence), human actions not directly related to social interaction (e.g., eating, walking, driving), as well as scenes depicting nonhuman animals, landscapes and objects (Figure 1a).

The movie clips were presented in a fixed order without breaks. Dynamic ratings with a 4-s temporal resolution were obtained for the presence of sexual content (continuous scale from 0 to 100) in the film clips from a separate sample of subjects ($n = 6$) not participating in the fMRI study. The dynamics ratings for sexual content were averaged across subjects and then used as a regressor in the first-level GLM analysis (see below).

In the second fMRI experiment the subjects were shown 300 nonerotic images from Nencki Affective Picture System (NAPS) and 24 erotic images from Nencki Affective Picture System Erotic Subset (NAPS-ERO) data sets (Marchewka et al., 2014; Wierzbna et al., 2015) in a random order (total duration, 22 min) (Figure 1b). The erotic pictures depicted female–male, and female–female couples engaged in sexual intercourse or interaction. The nonerotic pictures depicted people engaged in nonsexual activities (e.g., sports) as well as animals, landscapes, and inanimate objects. Each picture was presented for 1.5 s followed by a fixation cross for 2–3 s. The data from this experiment were used to test the generalization of the multivariate pattern classification (see following text). All film clips and pictures were presented via NordicNeuroLab VisualSystem binocular display. For the film experiment, audio was presented binaurally via MRI-compatible headphones (Sensimetrics S14) at a comfortable level adjusted individually for each participant. The fMRI experiments were conducted during the same imaging session.

3.3 | MRI data acquisition

The MRI data were acquired using a Phillips Ingenuity TF PET/MR 3 T whole-body scanner. High-resolution (1 mm^3) structural images were obtained with a T1-weighted sequence (TR 9.8 ms, TE 4.6 ms, flip angle 7° , 250 mm FOV, 256×256 reconstruction matrix). 472 functional volumes were acquired with a T2*-weighted echo-planar imaging sequence (TR = 2600 ms, TE = 30 ms, 75° flip angle, 240 mm FOV, 80×80 reconstruction matrix, 62.5 kHz bandwidth, 3.0 mm slice thickness, 45 interleaved slices acquired in ascending order without gaps).

3.4 | Structural and functional MRI data preprocessing

MRI data were preprocessed using fMRIPrep 1.3.0.2 (Esteban, Markiewicz, et al. 2018). The following preprocessing was performed on the anatomical T1-weighted (T1w) reference image: correction for intensity non-uniformity, skull-stripping, brain surface reconstruction, spatial normalization to the ICBM 152 Nonlinear Asymmetrical template version 2009c (Fonov et al., 2009) using nonlinear registration with antsRegistration (ANTs 2.2.0) and brain tissue segmentation. The following preprocessing was performed on the functional data: coregistration to the T1w reference, slice-time correction, spatial smoothing with a 6 mm Gaussian kernel, automatic removal of motion artifacts using ICA-AROMA (nonaggressive) (Pruim et al., 2015), and resampling to the MNI152NL in 2009c Asym standard space.

3.5 | Full-volume GLM data analysis

The fMRI data were analyzed in SPM12 (Wellcome Trust Center for Imaging; <http://www.fil.ion.ucl.ac.uk/spm>). To reveal regions activated by sexual content in the films, a general linear model (GLM) was fit to the data where the mean sexual content ratings (resampled to one TR and convolved with the canonical HRF) were used as a regressor. For the picture experiment, the responses to the different picture categories (female–male couples, female–female couples, landscapes, non-sexual human activities, faces, and objects) were modeled separately with stick functions. For each subject, contrast images were generated for the main effect of sexual content in the films and for the sexual–minus–landscape contrast in the picture experiment and subjected to a second-level analysis where the contrast images were compared between men and women separately for the two experiments. Clusters surviving family-wise error (FWE) correction ($p < .05$) are reported. To control for putative sex differences in general social perception, we repeated the GLM analysis for the picture experiment using pictures of nonsexual human activities as the control stimulus. These analyses revealed essentially the same results as the main analysis with the sexual > landscape pictures contrast (see Data S1).

3.6 | Multivariate pattern classification analysis

For the main multivariate pattern analysis (MVPA), the subject-wise unthresholded beta maps obtained for the sexual stimuli in both experiments were used in classifying subjects' sex. Only gray matter voxels were included in the analysis. The gray matter mask was generated by segmenting the average normalized T1 image into gray and white matter and cerebrospinal fluid using SPM. The gray matter map was thresholded with an intensity threshold >0.25 and binarized to create a mask that included 189,114 voxels. The beta maps were normalized to have zero mean and unit variance before the application of MVPA. For all analyses except for the cross-classification between experiments (see below), a linear support vector machine (SVM) implemented in Python was used in the classification due to its ability to perform well in high-dimensional spaces. To test the performance of the classifier, leave-one-subject-out cross-validation was performed, where the classifier was trained on data from all except one subject and tested on the holdout subject data. Classification accuracy was defined as the proportion of correctly classified subjects. To determine whether the classification accuracy was above the theoretical 50% chance level, we generated a null distribution for the classification accuracy by repeating the analysis 1000 times while shuffling the category (male/female) labels (Pereira et al., 2009). Classification accuracy was determined significant if it was higher than 95% of the accuracies obtained with the randomly shuffled labels.

We also tested the generalizability of the sex classification by training the classifier on the film data and testing it with the data from the pictures experiment (contrast erotic pictures > landscapes) and

vice versa. This analysis was otherwise identical to the main MVPA described above, except that in the leave-one-subject-out cross-validation, the test data were taken from the pictures experiment if the classifier was trained on the film data, and from the film experiment if the classifier was trained on the pictures data. For the cross-classification between the film and picture experiment, a nonlinear kernel was employed as this produced higher classification accuracies than the linear kernel (with the linear kernel, the respective accuracies were 60% and 61% when the movie data was used for training and picture data for testing and vice versa).

Finally, we tested whether successful sex classification could be achieved also with nonsexual stimuli, and whether the sex-specific activation patterns would generalize across sexual and nonsexual stimuli. Specifically, the GLM analysis was performed with ratings for the presence of nonsexual human actions involving vocalizations (e.g., neutral discussion, laughter, arguing) as the regressor, and the subject-wise beta maps obtained for this control dimension were subjected to an identical MVPAs as those obtained for the sexual content in the film clips. Cross-classification was performed between the control dimension and responses to the sexual films and the sexual pictures. Successful cross-classification between the beta images for the sexual and nonsexual stimuli would require information about the subject sex that is shared across the two types of beta images. This would suggest that the successful classification with the beta images for sexual stimuli did not solely stem from the sexual content of stimuli but could reflect more general sex differences in visual or social perception.

3.7 | Eye tracking

To test for sex differences in attention allocation while viewing the sexual stimuli, we conducted an eye movement experiment. A total of 110 subjects (43 men, mean age 27 years) not participating in fMRI volunteered for the study. Subjects viewed a subset of the videos presented in the fMRI experiment (including all the erotic videos) while their eye movements were recorded using Eyelink 1000 eye-tracker (SR Research, Mississauga, Ontario, Canada; sampling rate 1000 Hz, spatial accuracy better than 0.5° , with a 0.01° resolution in the pupil-tracking mode). The total duration of the eye-tracking experiment was 15 min. A nine-point calibration and validation were completed at the beginning of the experiment and then after 1 of 3 and 2 of 3 of the experiment had elapsed. Saccade detection was performed using a velocity threshold of $30^\circ/s$ and an acceleration threshold of $4000^\circ/s^2$. Dynamic regions of interest (ROIs) were drawn frame-by-frame on the face, chest, genital, and buttocks areas of the male and female characters in the sexual scenes; the remaining clips were not analyzed in this study. We computed the clip-wise proportional dwell time (%) for each region of interest and analyzed the effects of ROI as well as actor and subject sex on the dwell times using linear mixed model (LMM).

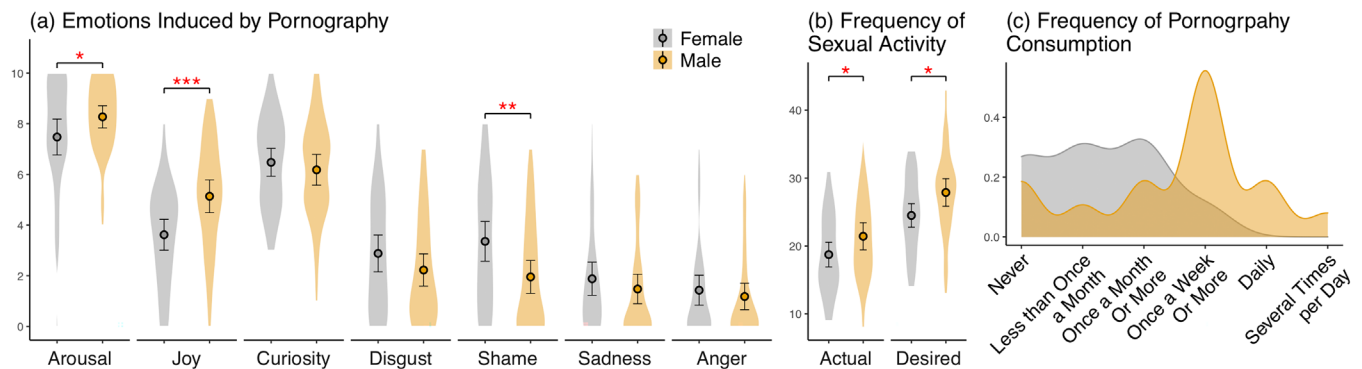


FIGURE 2 (a) Emotions induced by pornography in men and women participants. (b) The actual and desired frequency of various sexual activities. (c) Frequency of pornography consumption in men and women. * $p < .05$ ** $p < .01$, *** $p < .001$.

3.8 | Questionnaires

The fMRI study subjects filled out an online questionnaire about positive and negative emotions induced by pornography (full ratings were obtained from 86 participants, 44 men). Specifically, the subjects rated on a scale of 1–10 how strongly they felt sexual arousal, joy, curiosity, disgust, shame, sadness, and anger while viewing sexually explicit media. The subjects also reported how often they viewed pornography (never, less than once a month, less than once a week, once a week or more, daily, several times a day). Subjects also rated on how often they engaged or wanted to engage in kissing, masturbation, vaginal or anal intercourse, oral sex, and sexual fantasies on a scale ranging from never to several times a day (Derogatis & Melisaratos, 1979). Summary scores were computed for the actual and desired frequency of these sexual behaviors.

4 | RESULTS

4.1 | Emotions elicited by sexual stimuli in men and women

Both men and women reported high positive emotions and low negative emotions toward pornography and moderate-to-high levels of pornography consumption (Figure 2a). Men reported stronger sexual arousal ($t[85] = 2.01$, $p < .05$) and joy ($t[85] = 3.63$, $p < .001$) and less shame ($t[85] = 2.83$, $p < .01$) than women. Men also consumed pornography more frequently than women: the most typical answer for men was at least once a week while the most common answer for women was at least once a month ($\chi^2 [5, N = 86] = 25.5$, $p < .000$) (Figure 2c). The frequency of pornography consumption correlated positively with sexual arousal ($r = .44$) and joy ($r = .34$) and negatively with shame ($r = -0.24$) (Figure S5). Men also reported higher actual ($t[83.55] = 2.00$, $p < .05$) and desired ($t[83.55] = 2.53$, $p < .05$) frequency of sexual activities (Figure 2b).

4.2 | Brain responses to sexual stimuli in the whole sample

Modeling the BOLD data for the movie experiment with the sexual content regressor revealed activity in visual areas in the lateral occipital cortex extending to the inferior temporal and fusiform gyri. There was also extensive activation of regions associated with emotion and reward such as the amygdala, brainstem, thalamus, ventral striatum, insula, ACC, and OFC. Activation was also observed in sensorimotor regions in the precentral gyrus, SMA, and cerebellum (Figure 3a). Viewing erotic images in the picture experiment activated a largely overlapping network of cortical and subcortical regions (Figure 3b).

4.3 | Sex differences

In the film experiment, men showed stronger response to sexual content compared with women in the lateral occipital cortex, occipital pole, fusiform gyrus, frontal pole, middle frontal gyrus, intraparietal sulcus (IPS), and precentral gyrus/middle frontal gyrus including the putative location of the frontal eye field (FEF) (Figure 4a and Figure 5). In contrasts, women showed stronger activation than men in auditory cortical regions, parietal operculum and the right precentral gyrus (Figure 4a). In the picture experiment, men showed stronger response than women for the contrast erotic pictures > landscapes in largely the same areas which was activated more strongly in men in the movie condition (Figure 4b and Figure 5). These results were replicated with the erotic > nonerotic human pictures contrast (Figure S1). Unlike in the movie experiment, no region showed stronger activity in women than in men. The results of separate follow-up analyses for the female–male and female–female picture subcategories were concordant with the main analysis and are shown in Figure S2.

4.4 | Multivariate pattern classification

Men and women were classified above chance level based on their responses to both the erotic movie clips (mean accuracy = 76%)

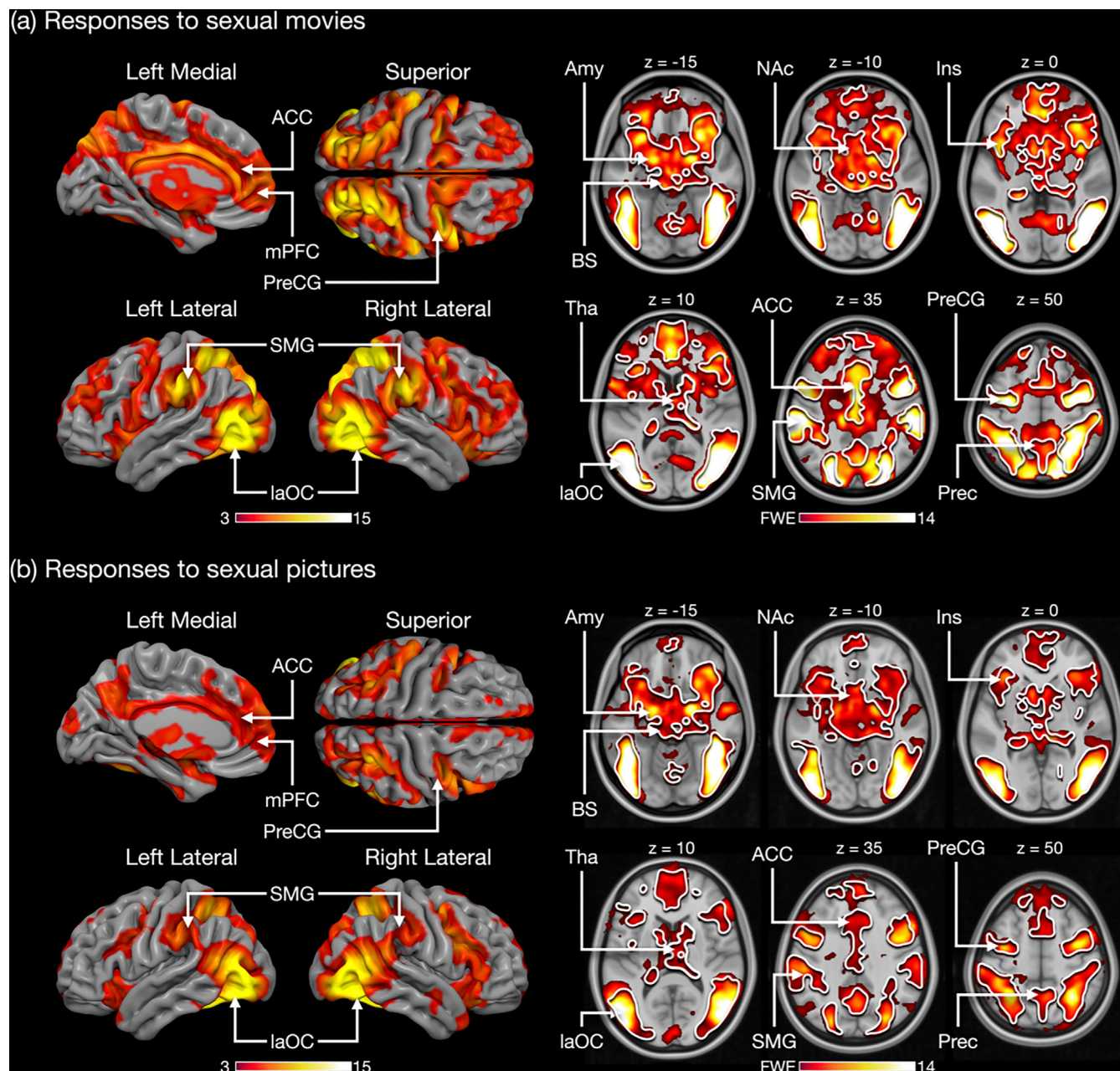


FIGURE 3 Brain regions responding to sexual content in the film clips (a) and pictures (b) in the whole sample (thresholded at $p < .05$, FWE corrected at cluster level). The white outline represents the overlap in activation across the movie and picture experiments. The colorbars represent the t -value. Amy, amygdala; ACC, anterior cingulate cortex; BS, brainstem; Ins, insula; laOC, lateral occipital cortex; mPFC, medial prefrontal cortex; NAc, nucleus accumbens; SMG, supramarginal gyrus; Tha, thalamus; Prec, precuneus; PreCG, precentral gyrus.

and pictures (mean accuracy = 64%; Figure 6). The classifier also generalized across the experiments: classification accuracy was above chance level even when the classifier was trained on the movie data and tested on the pictures data (mean accuracy 66%) and vice versa (mean accuracy 66%). We also tested whether misclassifications could be attributed to bisexual orientation but only one bisexual female participant was misclassified in the movie experiment. Similarly, self-reported emotions toward pornography or sexual drive were not associated with classification accuracy (see Data S1).

Classification was also accurate with the control dimension in the movie experiment (i.e., training and testing with the response to the control dimension, mean accuracy of 68%). However, the classification failed when the responses to the control dimension was used for training and the responses to erotic clips for testing and vice versa (mean accuracies 48% and 44%, respectively, see Figure S3) indicating that, in contrast to the cross-classification with erotic movies and pictures, the classification with the control dimension did not generalize to classification with responses to the sexual film clips. This indicates the successful sex classification with the sexual stimuli did not reflect

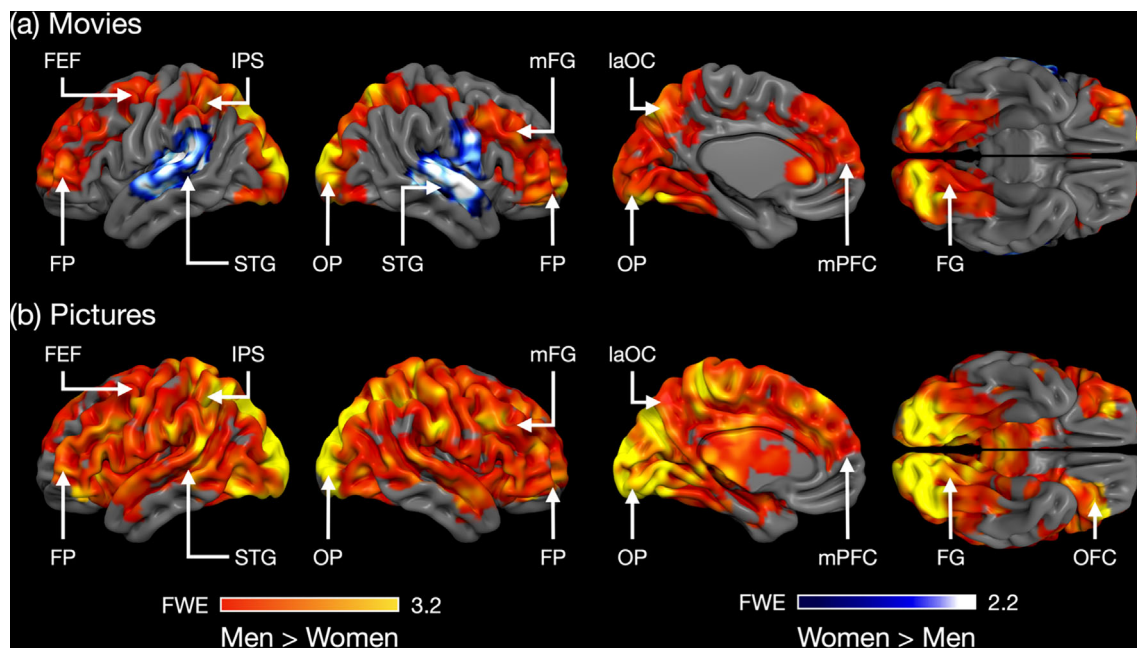


FIGURE 4 (a) Brain regions showing stronger responses to sexual content in men versus women (hot colours) and women versus men (cool colours) in the movie experiment. (b) Brain regions showing stronger responses in men than in women in response to the sexual pictures. The activation maps are thresholded at $p < .05$, FWE corrected at cluster level. The colorbars show the t -value. FEF, frontal eye field; FG, fusiform gyrus; FP, frontal pole; IPS, intraparietal sulcus; laOC, lateral occipital cortex; mFG, medial frontal gyrus; OFC, orbitofrontal cortex; OP, occipital pole; SMG, supramarginal gyrus; STG, superior temporal gyrus.

general sex differences in audiovisual processing but was based on the processing of the sexual content in the films and pictures.

4.5 | Eye tracking results

Compared with women, men looked longer at the female actors' chest region ($F[1107] = 11.089$, $p < .001$). Women looked longer at males actors' faces than men did ($F[1107] = 4.0619$, $p < .05$). No significant sex differences were found for the other areas of interest (Figure 7).

5 | DISCUSSION

Our main finding was that sexual stimuli elicit discernible patterns of brain activation in men and women. The GLM analysis revealed that sexual movie clips and pictures elicited widespread activation across the brain in both sexes: Activations were observed in regions associated with reward and emotion (e.g., brainstem, basal ganglia, thalamus, ACC, amygdala, and medial prefrontal cortex) and in somatosensory and motor cortices (pre- and postcentral gyrus, SMA) implicated in sexual arousal (Georgiadis & Kringelbach, 2012). Activations were also observed in visual regions in the occipital and inferior temporal cortices and in the dorsal attention network (frontal eye fields, FEF and intraparietal sulcus, IPS). Men showed stronger responses than women particularly in visual regions in the occipital cortex and fusiform gyri, in the dorsal attention network as well as in various

prefrontal regions. Notably, using multivariate pattern classification we were able to accurately predict the sex of the individual subjects. The classifier generalized across the movie and picture experiments, underlining the consistency of the sex-specific response patterns. These results indicate that, although visual sexual stimuli engage similar networks in men and women, brain activity patterns induced by such stimuli are different across sexes.

5.1 | Brain activity patterns induced by visual sexual stimuli predict individuals' sex

Using multivariate pattern classification of the brain responses to the sexual movies and pictures, we were able to accurately classify the subjects as men or women. This indicates that sex differences in the brain responses to sexual signals are robust enough to differentiate men and women at the individual subject level. To our knowledge, there are no previous studies employing sex classification with visual sexual stimuli, but the classification accuracies achieved in the current study are comparable with those obtained in sex classification with resting-state fMRI (Satterthwaite et al., 2015; Weis et al., 2020; Zhang et al., 2018; Zhang et al., 2020) and functional connectivity during a semantic decision task (Xu et al., 2020). The accuracy was better in the movie (76%) than in the picture experiment (66%). This likely reflects the fact that audiovisual movies are more representative of the natural sociosexual environment, and consequently activate the brain more strongly and consistently than still photos (Hasson

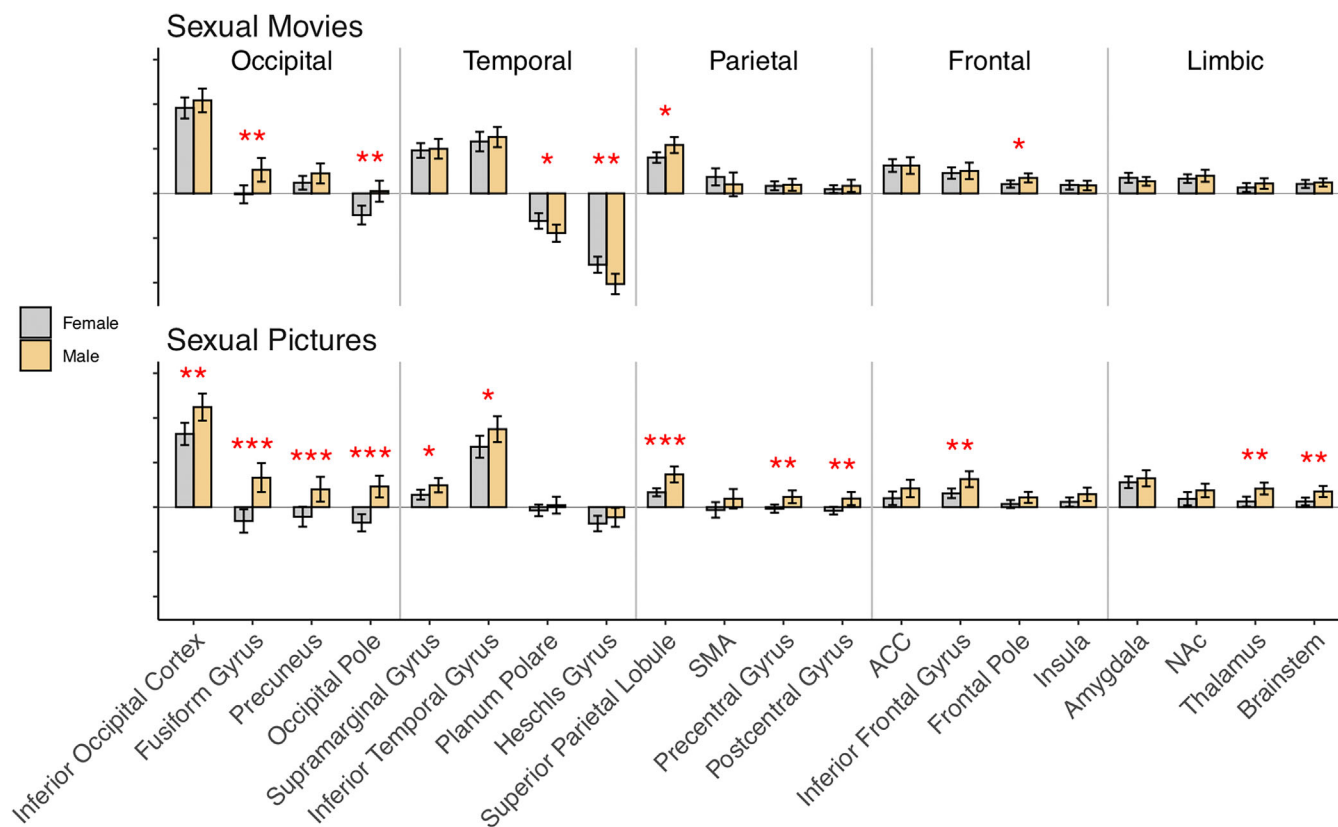


FIGURE 5 Mean beta weights (arbitrary scale) extracted from unthresholded first-level contrast images within anatomical ROIs derived from the Harvard-Oxford atlas. The error bars indicate 95% confidence intervals. Asterisks denote significant sex differences at the ROI level. The regional results are plotted only for visualization purposes to highlight sex differences obtained in the full-volume analysis. * $p < .05$, ** $p < .01$, *** $p < .001$.

et al., 2010). Importantly, above chance level classification was achieved even with cross-classification where the classifier was trained on the data from one experiment and tested on data from the other indicating that the male/female-typical brain activation patterns evoked by sexual signals were consistent across the experiments. This indicates that the sex-specific brain responses reflected the processing of the sexual content shared across the dynamic videos and still pictures.

Virtually the same regions showing sex differences in the GLM analysis (see below) also contributed the most to the classification with SVM in both experiments as indexed by the high correlation between the SVM weights and the beta values for the sex difference 2nd level contrasts ($r = .7$ for the movie experiment and $r = .6$ for picture experiment). Namely, occipital cortex and fusiform gyrus and frontal regions showed strong weights indicative of male category while temporal regions showed the strong voxel weights indicative of female category (see Figure S4). Interestingly, above chance level sex classification was obtained even with the responses to the control dimension. However, the cross-classification between the responses to the control dimension and the sexual stimuli was at chance level indicating that different activity patterns contributed to the sex classification for sexual versus nonsexual stimuli. In line with this, the spatial distribution of the SVM weight across the brain for the sexual

stimuli and the control dimension were dissimilar as illustrated by the low correlation between the voxel weight maps for the sexual stimuli and the control dimension ($r = -.17$ for the movie experiment and $r = .07$ for the pictures experiment).

Although the brain activity patterns evoked by visual sexual stimuli were predictive of subject sex, some subjects were misclassified demonstrating that these brain activity patterns were not fully sexually dimorphic (compare Joel & Fausto-Sterling, 2016). Classification accuracy is partly determined by methodological factors such as the training set sample size (Balki et al., 2019) but some previous studies suggest that sex misclassification may also reflect a characteristic cognitive or affective profile (Satterthwaite et al., 2015; Zhang et al., 2021). In the current study, the misclassified men reported lower negative emotions toward pornography than the correctly classified men, but no other differences were found between the correctly and incorrectly classified subjects (see Data S1). Interestingly, those subjects who identified themselves as bisexual were no more likely to be misclassified than those who identified themselves heterosexual suggesting that brain activity patterns evoked by sexual stimuli are not dependent on bisexual vs. heterosexual orientation. It is possible that factors such as sexual history or more nuanced sexual preferences may contribute to the misclassification.

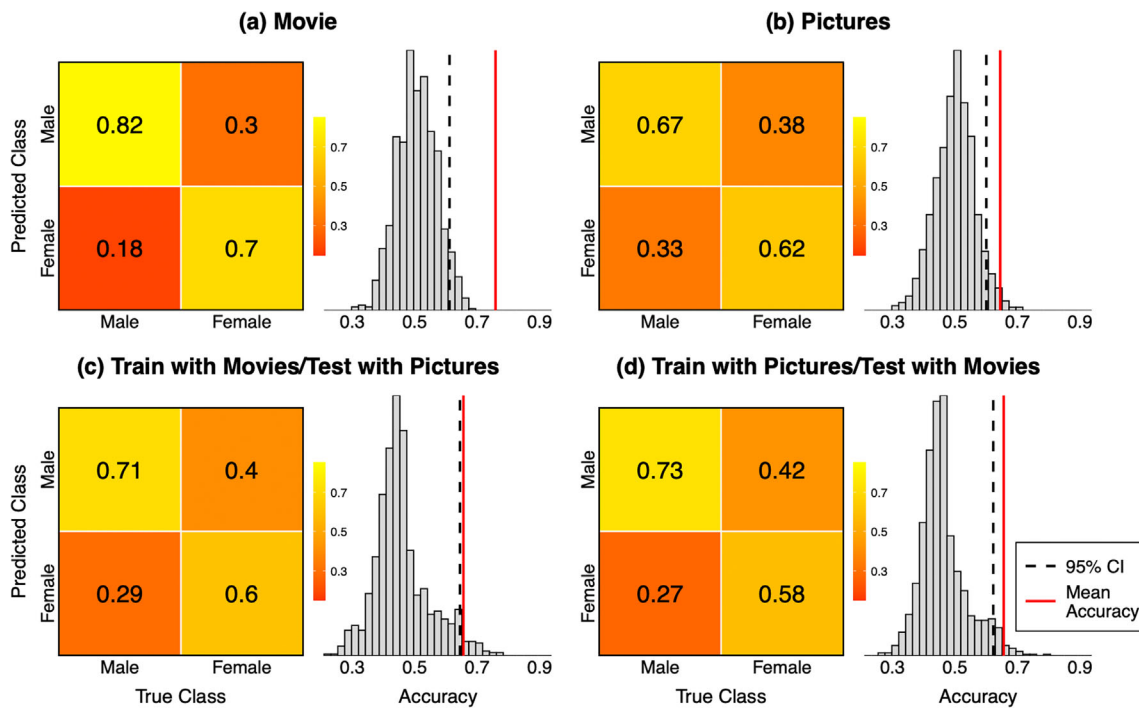


FIGURE 6 Confusion matrices and null distributions for the sex classification for the movie and pictures tasks and the cross-classification across these experiments. The numbers in the confusion matrices indicate the proportions of correct and false predictions for men and women. The histograms show the null distribution for the classification accuracy. The red vertical lines indicate the mean classification accuracy, and the dashed vertical line the upper confidence interval limit (95% quantile) of the null distribution.

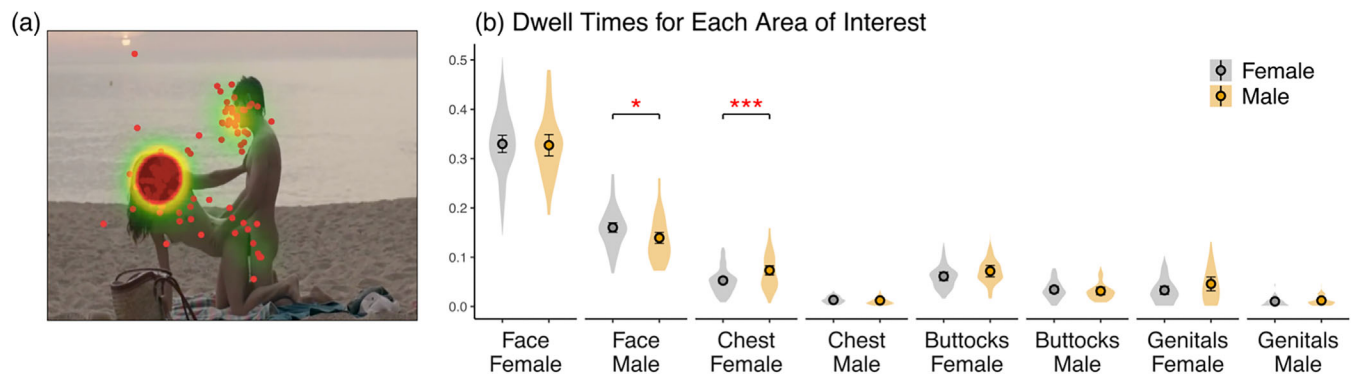


FIGURE 7 (a) Sample mean fixation distribution (heatmap) and individual fixations for the sexual movie clips. (b) Average dwell times for the different areas of interests for men and women.

5.2 | Sex-dependent activation of visual and attentional circuits

Sexual stimuli activated occipitotemporal visual regions consistently in both experiments, suggesting attentional modulation of visual cortical activity for sexually salient stimuli. Event-related potential studies indicate that human bodies with visible (vs. hidden) sexual signals induce amplified temporocortical responses already <200 ms from stimulus onset demonstrating facilitated processing of visual sexual cues early in visual processing stream (Alho et al., 2015; Hietanen et al., 2014; Hietanen & Nummenmaa, 2011). Occipital activity was

particularly strong in the putative body sensitive regions (the “extrastriate body area”) in the lateral occipital cortex (Downing et al., 2001) suggesting amplified processing of sexual information in the human body recognition systems (e.g., Ponseti et al., 2006). Men showed stronger activity than women in a cluster extended from V2 along the fusiform gyrus (compare Sabatinelli et al., 2004; Sylva et al., 2013; Wehrum et al., 2013) which suggests that sexual stimuli trigger stronger attentional amplification of visual cortical activity in men than in women. Heightened attention toward visual sexual cues facilitates sexual arousal (Dawson & Chivers, 2016) which may explain previous findings that the activation of occipitotemporal visual regions is

positively associated with measures of penile erection and subjective sexual arousal (Arnou et al., 2002; Moulrier et al., 2006).

Eye-tracking studies indicate that men show an attentional bias toward the explicitly sexual aspects of visual sexual stimuli (Nummenmaa et al., 2012; Rupp & Wallen, 2007). Our control experiment with eye tracking revealed that men looked longer at the chest area of the nude female actors in the movie clips than women did (approximately 7% vs. 5% of the video duration in men vs. women, respectively). Women, in turn, tended to look at the male actors faces slightly longer than men did. These subtle sex differences in the locus of attention may partly account for the sex differences in brain activation in the visual cortices (compare Dolcos et al., 2020; Ferri et al., 2013). Both the sexual videos and pictures activated intraparietal sulcus (IPS) and frontal eye fields (FEF) which are central nodes in the dorsal attention network supporting controlled, top-down attention (Corbetta & Shulman, 2002). In both experiments, men showed stronger activation in a parietal cluster that extended to the IPS as well as in middle frontal gyrus/precentral gyrus extending to the FEF suggesting that visual sexual stimuli engage dorsal attention network more strongly in men than in women. Interestingly, the eye tracking data also revealed that faces were the most attended regions in the sexual scenes. This accords with the well-known attentional bias towards faces and suggests that during sexual contact the partner's face conveys important information regarding enjoyment and sexual arousal thus warranting preferential attention over genitals and other erogenous zones.

Women showed stronger activation than men only in the movie experiment in auditory cortical regions. This result suggests that women responded more strongly to the audio track in the sexual video clips which consisted mostly of nonverbal female vocalizations communicating sexual pleasure. A number of studies have shown that affective vocalizations, including sexual ones (Fecteau et al., 2007), elicit stronger auditory cortical activity than neutral voices (Frühholz et al., 2016). Behavioral studies suggest a slight female advantage in emotion recognition from nonverbal emotional vocalizations (Thompson & Voyer, 2014) but sex differences in affective sound processing have not been studied extensively with neuroimaging (however, see Ethofer et al., 2007). Our results tentatively suggest that women respond stronger to nonverbal sexual vocalizations and thereby that the stronger male reactivity to sexual cues might be specific to visual domain. However, as attention toward visual stimuli attenuates auditory cortical activity (Johnson & Zatorre, 2006; Molloy et al., 2015), another explanation is that this group difference reflects stronger reduction in auditory cortical activity in men due to stronger attention toward the visual sexual cues in the videos in men compared to women. In line with this interpretation both men and women showed reduced auditory cortex activity for the sexual videos as indicated by the negative beta weights in auditory cortex (Figure 5).

Evolutionary accounts posit that men and women have evolved different mating strategies in domains where they have faced different adaptive challenges (Buss & Schmitt, 1993). Lower obligatory parental investment in men has presumably given rise to the stronger preference for short-term mating and sexual variation in men, as these

have increased the probability of genetic success more for men than for women. Men may also have evolved a preference for physical features associated with youth since such cues signal fertility and many years of potential future reproduction (Buss & Schmitt, 2019). The type of pornography consumed by men often simulates short-term sexual encounters with novel young women (Malamuth, 1996; Salmon & Diamond, 2012). Thus, men's higher attentional engagement with sexual stimuli might reflect evolved preferences for sexual variety and physical cues of reproductive potential. Such biological biases probably interact with cultural norms in shaping sex-typical preferences as evidenced by cross-cultural variation and changes across time in the magnitude of these sex differences (Buss & Schmitt, 2019; Petersen & Hyde, 2011).

5.3 | Emotion circuit activation in men and women

Both men and women experienced strong positive emotions and only weak negative emotions toward pornography although men reported slightly higher feelings of sexual arousal and joy and less shame than women. In accordance with the incentive value of sexual stimuli, both experiments activated limbic and mesolimbic regions associated with reward and emotion such as the ventral striatum and amygdala in both men and women. Unlike some previous studies, we did not observe sex differences in the activation of the amygdala (Hamann et al., 2004) or NAc (Wehrum-Osinsky et al., 2014) suggesting that activity evoked by visual sexual stimuli in these regions does not reliably differentiate men and women. The sexual stimuli also activated the primary and secondary somatosensory cortices and insula in both men and women in accordance with previous studies (Arnou et al., 2009; Ferretti et al., 2005). These regions contribute to emotion via the processing of bodily sensations and interoceptive feedback (Craig, 2002) and SII is more generally involved in the perception of touch (Keyser et al., 2010). We also observed activation in the ACC, which is a common finding in studies employing visual sexual stimuli (Stoléru et al., 2012) presumably because cingulate activity is coupled with autonomic arousal (Beissner et al., 2013). Overall, the sex differences observed in the GLM analysis were most consistent in cortical regions although activity in the brainstem and thalamus were also stronger in men than in women in the pictures experiment.

5.4 | Sex differences in neural substrates of sexual perception: State of the evidence

The recent meta-analysis of Mitricheva et al. (2019) found no evidence of sex differences in brain responses to visual sexual stimuli. However, Poepl et al. (2020) re-analyzed these data with a number of methodological improvements, such as the exclusion of ROI analyses, and found more consistent activation in ACC and hypothalamus in men and in lateral occipital cortex in women. We also found a sex difference in a frontal cluster partly overlapping with the ACC but did not replicate the hypothalamic and occipital effects.

One possible source of the discrepancies between our results and these meta-analyses is that the latter were not based on direct comparisons between sexes in the original studies. Instead, both meta-analyses compared separate Activation Likelihood Estimation (ALE) maps for men and women that were computed mostly from studies with only men or women as subjects. This approach can reveal sex differences in how consistently a given region is activated in different studies (i.e., sex difference in convergence), but cannot uncover the consistency of sex differences in brain activation across studies (i.e., convergence of sex differences) (Müller et al., 2018). Such meta-analyses may also be confounded by methodological differences between studies with only men or women as participants. A meta-analysis of direct comparisons between men and women is precluded by the scarcity of pertinent high-quality studies: Mitricheva et al included only 11 studies with both men and women, and most of these were underpowered for reliable group comparison (Hamann et al., 2004; Klucken et al., 2009) or did not perform a whole brain analysis of the sex differences (Strahler et al., 2018). Notably, the only study with a whole brain GLM analysis of sex differences and a sample size comparable to ours (Wehrum et al., 2013) revealed stronger responses to sexual pictures in men than women in the thalamus and occipital and parietal cortex in line with our results. Thus, we provide much-needed data on sex dependency of neural responses to sexual stimuli and pave way for robust meta-analyses of such sex differences.

5.5 | Limitations

Subject-specific emotion ratings and physiological arousal responses were not acquired from the participants in the fMRI experiment; thus we could not directly link the hemodynamic data with direct indices of sexual arousal. The current study specifically focused sex differences in brain responses to stimuli representative of “mainstream” pornography typically consumed more by men than women and we did not attempt to balance how sexually arousing or interesting the stimuli were for the male and female participants (cf. Janssen et al., 2003; Laan et al., 1994). The majority of our subjects identified as exclusively heterosexual and thereby we were unable to test the effects of sexual preference irrespective of gender and our results may not generalize to individuals with non-heterosexual preference.

6 | CONCLUSIONS

We conclude that sexual stimuli elicit discernible patterns of brain activation in men and women. Visual sexual stimuli engaged regions supporting reward, bodily sensations, attention, and visual processing irrespective of sex. However, sexual stimuli activated visual cortex and prefrontal regions more strongly in men than in women. Brain activity patterns induced by sexual movies and pictures contain information about the sex of the subject that allows accurate sex classification with multivariate pattern classification. Thus, despite substantial

overlap in regions activated by sexual stimuli in men and women, brain activity patterns associated with such stimuli differ between sexes.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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