Behavioral Neuroscience
2007, Vol. 121, No. 2, 237–248

0735-7044/07/$12.00 DOI: 10.1037/0735-7044.121.2.237

Neural Correlates of Sexual Arousal in Homosexual and Heterosexual Men

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Men exhibit much higher levels of genital and subjective arousal to sexual stimuli containing their preferred sex than they do to stimuli containing only the nonpreferred sex. This study used event-related functional magnetic resonance imaging to investigate how this category-specific pattern would be reflected in the brains of homosexual ($n = 11$) and heterosexual ($n = 11$) men. Comparisons of activation to preferred sexual stimuli, nonpreferred sexual stimuli, and sports stimuli revealed large networks correlated with sexual arousal, spanning multiple cortical and subcortical areas. Both homosexual and heterosexual men exhibited category-specific arousal in brain activity. Within the amygdala, greater preference-related activity was observed in homosexual men, but it is unclear whether this is a cause or a consequence of their sexuality. In a subsequent analysis of regions hypothesized to support arousal, both participant groups demonstrated widespread increases in evoked activity for preferred stimuli. Aggregate data from these regions produced significant differences between stimulus types in 16 out of 22 participants. Significant activational differences matched reported sexual orientation in 15 of these 16 participants, representing an advance in psychophysiological measures of arousal.

Keywords: fMRI, event-related, sexual arousal, category specificity, sexual orientation

Sexual arousal is a highly coordinated set of reactions that prepare an organism for reproductive behavior. It is a dynamic process characterized by widespread changes in an organism's neurophysiological state such that adaptive responses are achieved. Attentive, affective, and motivational systems are optimized for the successful selection and engagement of sexual stimuli.

Men show category-specific genital and self-reported subjective sexual arousal in response to visual sexual stimuli, and their greatest sexual arousal is to the categories of people with whom they prefer to have sex (Chivers, Rieger, Latty, & Bailey, 2004; Freund, 1963). Heterosexual men experience higher genital and subjective arousal to women than to men (thus, they prefer female sexual stimuli), but homosexual men show the opposite pattern (and thus prefer male sexual stimuli). The most influential biological theory of sexual orientation is that hormones influence (largely prenatally) the development of neural structures that regulate sexual behavior (Ellis & Ames, 1987; LeVay, 1997). By this model, certain aspects of neurohormonal development proceed in a sex-atypical manner in homosexual individuals, resulting in psychological differences such as atypical triggers for sexual arousal.

Although homosexual and heterosexual men become aroused to different sexual stimuli, there are also substantial similarities in their sexual psychology and behavior. In studies of evolutionarily relevant mating psychology, men of both orientations reported similar interests in uncommitted sex and visual sexual stimuli, and they valued physical attractiveness to similar degrees (Bailey, Gaulin, Agyei, & Gladue, 1994). Furthermore, as noted above, men of both orientations exhibit category-specific sexual arousal to visual sexual stimuli. These data suggest that the factors leading to differences in sexual orientation may not produce differences in other aspects of sexual behavior. The current study explored the neural mechanisms of sexual arousal in homosexual and heterosexual men. We examined both similarities and differences in their patterns of neural activation to preferred versus nonpreferred visual sexual stimuli.

Previous Neuroimaging Studies

Several imaging studies have identified neural correlates of sexual arousal (Arnow et al., 2002; Beauregard, Levesque, & Bourgouin, 2001; Ferretti et al., 2005; Gizewski et al., 2006; Hagemann et al., 2003; Hamann, Herman, Nolan, & Wallen, 2004; Holstege et al., 2003; Karama et al., 2002; Park et al., 2001; Ponseti et al., 2006; Redoute et al., 2000, 2005; Sabatinelli, Flaisch, Bradley, Fitzsimmons, & Lang, 2004). These studies depict sexual arousal as a composite psychophysiological state correlated with functional changes in several brain regions (Redoute et al., 2000).

Fewer studies have compared sexual arousal in heterosexual men and women. When participants viewed erotic film excerpts, Karama et al. (2002) found activation in the thalamus and hypothalamus in men but not in women. Men, however, reported higher perceived sexual arousal compared with women, thus making interpretations of gender differences problematic. A magnetoencephalographic (MEG) study by Costa, Braun, and Birbaumer (2003) found that the magnitudes of contingent negative variation and visual-evoked magnetic fields were higher for preferred than for nonpreferred sexual stimuli in men and women. Differences in

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We thank Joan Linsenmeier for her comments on an earlier draft of this article.

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magnitudes were greater in men than women for the first component of the visual-evoked magnetic fields at 126 ms. More recently, Hamann et al. (2004) found amygdala differences between men and women in response to visual sexual stimuli. Although they attempted to control for differential arousal through the selection of stimuli with similar subjective ratings, weak correlations between subjective and genital arousal in women make this approach uncertain (Chivers et al., 2004). Gizewski et al. (2006) found greater visual sexual stimuli induced activations in men than women in the thalamus, amygdala, anterior cingulate, orbitofrontal cortex, parahippocampal, and insular cortices. Interpretations of group differences remain challenging because it is unclear whether observed differences represent different levels of arousal or different processing during similar levels of arousal.

Three neuroimaging studies have explored sexual arousal in homosexual men. Savic, Berglund, and Lindstrom (2005) found that homosexual men and heterosexual women displayed activation of sexually dimorphic hypothalamic nuclei in response to a testosterone derivative found in male sweat, whereas heterosexual men did not. Kranz and Ishai (2006) found that heterosexual men and homosexual women responded more to female faces and homosexual men and heterosexual women responded more to male faces in the medial dorsal nucleus of the thalamus and medial orbitofrontal cortex. Most recently, Ponseti et al. (2006) studied arousal in homosexual and heterosexual women and men using an event-related design with images of naked male or female trunks displaying signs of genital arousal. Across groups, the ventral striatum, centromedian thalamus, and ventral premotor cortex showed stronger neuronal responses to preferred relative to nonpreferred stimuli. Together, these studies provide strong evidence that category-specific arousal patterns are reflected in brain activity.

An event-related design was used to study sexual arousal in homosexual and heterosexual men. Most previous studies used blocks over 20 s in length for eliciting mental states. Although longer periods of stimulation may allow for deeper states of arousal, they are prone to expectancy biases, habituation effects, and distracting thought processes. Through the use of shorter stimulus presentations (3,500 ms), the current investigation is designed to examine earlier stages of the arousal process and avoid confounds associated with longer blocks. Our stimulus presentation time was chosen to maximize arousal while still providing the advantages of event-related design.

Regions of Interest (ROIs)

In our investigation, brain regions implicated in previous studies were organized a priori into a hypothesized network supporting sexual arousal and sexually dimorphic behavior (see Table 1). Regions targeted for examination included the basolateral–medial amygdala, sublenticular extended amygdala, midbrain, hippocampal complex, medial orbitofrontal cortex, nucleus accumbens–subcallosal cortex, rostral anterior cingulate, medial dorsal thalamic nucleus, hypothalamus, and visual cortex (Brodmann areas [BAs] 17 and 18). It is possible that other locations may also exhibit increased activity in response to visual sexual stimuli when measured with functional magnetic resonance imaging (fMRI); however, we focused on the aforementioned areas in order to conduct a priori statistical tests of whether these brain areas reflect category-specific sexual arousal and whether their activation patterns differ between homosexual and heterosexual participants. Regions that figure robustly in prior imaging studies of arousal–affect–reward were ideal to test whether activation is increased (or decreased) to preferred or nonpreferred sexual stimuli. Regions with differing morphologies or functionalities between men and women were of particular interest because the neurohormonal hypothesis of sexual orientation suggests that these areas may differ between homosexual and heterosexual men.

Method

Participants

Twenty-four right-handed, male volunteers (12 heterosexual, 12 homosexual) between the ages of 20 and 26 (heterosexual $M = 21$, homosexual $M = 21$) were recruited from the Northwestern University community and screened for compatibility with MRI. All participants were screened to ensure experience (and presumably comfort) with sexual images. Participants provided written informed consent for participation in the research study, following the procedures of the Northwestern University Institutional Review Board. Sexual orientation was assessed using Kinsey scale reports of sexual activity and feelings (Kinsey, Pomeroy, & Martin, 1948/2003). All participants indicated exclusive or nearly exclusive sexual activity and feelings for either women (heterosexual) or men (homosexual) during adulthood. Each participant was in good health and free from neurological and psychiatric problems. All data from 2 participants (1 heterosexual, 1 homosexual), and runs from 5 participants (3 heterosexual, 2 homosexual) were not used because of poor signal-to-noise ratio (SNR) during fMRI data acquisition (see below).

Stimuli

Visual stimuli were collected from a variety of Web sites on the World Wide Web. Sexual stimuli consisted of photographs depicting male and female nudity and sexual activity. To ensure that arousal was associated with only one sex at a time, only male–male or female–female sexual interactions were used. This method has been validated in phallometric studies of male sexual arousal (e.g., Chivers et al., 2004). Sexual stimuli were prescreened to maximize appetitive and minimize aversive responses. Nonsexual stimuli consisted of photographs of male and female sports activity. As with the sexual stimuli, males and females were never depicted together within a single image. All images had identical dimensions.

To examine where and to what extent the brain shows category-specific activation, we displayed sexual stimuli of the participants' preferred and nonpreferred sexes. (The preferred sexual stimuli depicted males for homosexual men and females for heterosexual men; the nonpreferred sexual stimuli depicted females for homosexual men and male stimuli for heterosexual men.) To further characterize the networks underlying sexual arousal, we used neutral sports images as a baseline condition to control for possible aversive reactions to the nonpreferred stimuli.

Procedure

Stimuli were presented in an event-related design consisting of four runs containing 100 stimuli each. Each stimulus was pre-

Table 1
Hypothesized Arousal Network Based on a Review of the Previous Literature

Region, Talairach coordinates, radius	Functional significance/background	Arousal/reward literature
AC (BA 24); (0, 36, 3); 9 mm	Extensive connections with the amygdala and projects to autonomic brainstem nuclei and forebrain regions controlling autonomic functions (Devinsky, Morrell, & Vogt, 1995).	Sexual arousal (Arnow et al., 2002; Ferretti et al., 2005; Karama et al., 2002; Ponseti et al., 2006; Redoute et al., 2000). Cocaine craving (Risinger et al., 2005).
Amy; (±23, −5, −15); 9 mm	Receives sensory information from the thalamus, hippocampus, and cortex and then activates or modulates synaptic transmission in target areas appropriate for the reinforcement signal with which the sensory information has been associated (Davis & Whalen, 2001). Medial nuclei are particularly sensitive to gonadal steroid hormones and are a likely site for regulation of sexually dimorphic social behavior (Cooke & Woolley, 2005). Lesion leads to abnormal sexual behavior in primates (Kluver & Bucy, 1939/1997).	Sexual arousal (Beauregard et al., 2001; Ferretti et al., 2005). Cocaine craving (Bonson et al., 2002). *More strongly activated in men than in women when viewing sexual stimuli (Hamann et al., 2004). Sex-related hemispheric lateralization for emotionally influenced memory and differing functional activity during rest (Cahill et al., 2004; Kilpatrick et al., 2006).*
Hip; (±30, −24, −9); 10 mm	Memory formation; encoding can be modulated by amygdalar activity (McIntyre, Marriott, & Gold, 2003). Shows activity for retrieval of autobiographical memories (Addis, Moscovitch, Crawley, & McAndrews, 2004).	Increased activity for sexually arousing stimuli (Hamann, Ely, Grafton, & Kilts, 1999).
Hyp; (0, 2, −7); 6 mm	A diverse set of nuclei regulating emotional, autonomic, and endocrine functioning with morphology that varies as a function of sex and orientation (Byne et al., 2001; LeVay, 1991). Responsive to olfactory signals of a sexual nature (Ferris et al., 2001).	Sexual arousal (Arnow et al., 2002; Beauregard et al., 2001; Ferretti et al., 2005; Karama et al., 2002; Redoute et al., 2000). Expectancy and experience of monetary gains (Breiter et al., 2001). *More strongly activated in men than in women when viewing sexual stimuli (Karama et al., 2002).*
MDTN; (±9, −16, 8); 7 mm	Connects limbic structures with cingulate and prefrontal cortices (Berridge, 2003). In hamsters, lesions result in inappropriate and inefficient sexual behavior (Sewards & Sewards, 2003).	*More strongly activated in men than in women (trend) when viewing sexual stimuli (Karama et al., 2002).* Category-specific activation for viewing of faces in homosexual and heterosexual women and men (Kranz et al., 2005). Sexual arousal (Ponseti et al., 2006).
Midbrain; (0, −16, −10); 9 mm	Contains diffuse neuromodulatory systems capable of releasing dopaminergic reward signals throughout the mesolimbic reinforcement system (Morgane, Galler, & Mokler, 2005), lowering thresholds in sensory systems through acetylcholine, and increasing vigilance with norepinephrine (Davis & Whalen, 2001). Necessary for sexual desire in the rat (Sewards & Sewards, 2003).	Self-stimulation site necessary for positive affect and liking (Berridge, 2003). Eating chocolate (Small et al., 2001). Expectancy and experience of monetary gains (Breiter et al., 2001).
mOFC; (±9, 36, −12); 9 mm	In nonhuman primates, this region has extensive connections with the hypothalamus, which allows for top-down regulation of limbic activity (O'Doherty et al., 2003).	Cocaine craving (Bonson et al., 2002; Risinger et al., 2005). Expectancy and experience of monetary gains (Breiter et al., 2001). Sexual arousal (Karama et al., 2002; Ponseti et al., 2006; Redoute et al., 2000). Attractive faces (O'Doherty et al., 2003).
NAc; (±9, 8, −8); 6 mm	Involved in processing reward value for multiple types of stimuli; associated dopaminergic activity in a variety of addictive-compulsive behaviors (Salamone, Correa, Mingote, & Weber, 2003).	Passive viewing of beautiful faces (Aharon et al., 2001). Expectancy and experience of monetary gains (Breiter et al., 2001). Cocaine craving (Breiter et al., 1997; Risinger et al., 2005).
SLEA; (±14, 4, −8); 6 mm	An extensive forebrain continuum establishing specific neuronal circuits with the medial prefrontal-orbitofrontal cortex and medial temporal lobe, characterized by a system of intrinsic association fibers, and a variety of downstream projections to the hypothalamus and brainstem; ideally structured to generate endocrine, autonomic, and somatomotor aspects of emotional and motivational states (Heimer, 2003; Heimer, Harlan, Alheid, Garcia, & de Olmos, 1997).	Expectancy and experience of monetary gains (Breiter et al., 2001). Positive and negative emotionally salient stimuli (Liberzon, Phan, Decker, & Taylor, 2003; Phan et al., 2003).
Visual (±13, −85, 4); 10 mm	Diffuse neuromodulatory systems may lower neuronal thresholds to increase visual information processing (Davis & Whalen, 2001).	Sexual arousal (Ferris et al., 2001; Karama et al., 2002; Mouras et al., 2003; Sabatinelli et al., 2004). Activated in motivated attention (Bradley et al., 2003).

Note. Regions were chosen based on having functional significance that would be relevant to the arousal process, or based on showing sexually dimorphic activation between men and women (*italics*). AC = rostral anterior cingulate; BA = Brodmann area; Amy = basolateral/medial amygdala; Hip = hippocampal complex; Hyp = hypothalamus; MDTN = medial dorsal thalamic nucleus; mOFC = medial orbitofrontal cortex; NAc = nucleus accumbens/subcallosal cortex; SLEA = sublenticular extended amygdala.

sented for 3,500 ms with a 1,500-ms intertrial interval. In addition, 50 fixation periods of 5,000 ms each were pseudorandomly interspersed among the stimuli to facilitate the deconvolution of evoked responses to each trial type. On each trial, participants indicated a preference rating by pressing one of four buttons (left hand, middle finger = strongly dislike; left hand, index finger = dislike; right hand, index finger = like; right hand, middle finger = strongly like). Practice trials familiarized participants with the rating procedure and minimized any initial startle effects from stimuli.

Imaging

Stimuli were projected onto a rear-projection screen and viewed through a mirror. A Siemens Trio 3T magnet and radio-frequency head coil were used to collect T2*-weighted gradient-recalled echoplanar images (EPI) from the whole brain (44 3-mm slices; return time = 2,500 ms, echo time = 20 ms, flip angle = 90°, field of view = 22 cm). Slices were oriented along the plane connecting the anterior and posterior commissures (slightly oblique from transverse) with a resolution of 3.44 mm × 3.44 mm × 3.00 mm. In each run, 310 whole-brain volumes were collected (four initial volumes to allow for signal saturation, and six additional volumes to observe the final hemodynamic responses). For anatomical localization, T1-weighted images (160 1-mm axial slices; return time = 2.1 ms, echo time = 4.38 ms, flip angle = 15°, field of view = 220 mm; 256 × 192 matrix) were acquired after the testing runs.

Whole Brain Analysis

Whole-brain SNR values were calculated for all runs and all participants. Any run with an SNR value lower than the midpoint between the highest and lowest observed SNRs of all runs was removed from the analysis. Five individual runs, each from different participants, were eliminated because of low brainwide SNR for that specific run. In addition, 2 participants were removed entirely because the average of their four runs was less than the cutoff value.

Images were coregistered through time using a three-dimensional registration algorithm (Cox, 1996). Functional volumes were spatially smoothed with a 6.88-mm (two voxels) full-width half-maximum Gaussian kernel to improve the SNR and accommodate residual anatomical differences across participants. Within each run, voxels were eliminated if the SNR was less than 20 across the scan (i.e., the mean EPI signal was not at least 20× greater than the variance). Each of the remaining runs was transformed (Collins, Neelin, Peters, & Evans, 1994) to conform approximately to the atlas of Talairach and Tournoux (1988; using the MNI-305 reference model) with a final resolution of 2.5 mm^3. All available runs of functional data (usually four) were concatenated into a single time series for each participant. The average response to each trial type was estimated using a general linear model analysis (Ward, 2006) that included the onset of each trial type and several control variables; the mean and linear drift in the EPI signal were estimated in each voxel for each of the four runs, and estimates of corrected motion for each time point were used to remove signal changes correlated with head–brain motion. Differences between trial types were estimated by contrasting the average peak response within the window of 5,000–10,000 ms after stimulus onset (to account for hemodynamic delay). Differences between trial types were estimated for each participant individually and then combined in a second-pass random-effects analysis that identified differences in evoked responses that were consistent across participants. The reliability threshold for the whole-brain analysis was set by identifying the false positive rate in Monte Carlo analysis of matched noise data (i.e., simulated datasets composed of random numbers matched to the observed data in mean and variance on a voxel by voxel basis). That analysis found a whole-brain false positive rate of less than .05 for clusters in which each voxel exhibited reliable activity at $t > 4.25$ ($p < .001$, uncorrected) in a cluster of at least 340 mm^3 in volume. These values were used as the cutoff criteria for all contrasts.

ROI Analysis

To compare activity in the hypothesized arousal network for heterosexual and homosexual men, we identified 10 ROIs anatomically. For each ROI, a sphere was centered on the loci with a radius chosen appropriate to the anatomical region. Spheres were drawn on the averaged brain that were slightly larger than the size of the region to encompass all of the relevant neural tissue and make up for variations in alignment of regions during normalization. The ROIs selected for analysis and rationale for their use are described in Table 1.

The SNR in each ROI for each participant was assessed to ensure that adequate signal was observed to support the preference analysis. Although the ROIs did vary from each other (e.g., the medial orbitofrontal cortex had lower average SNR than the anterior cingulate cortex or visual cortex ROIs), there was no systematic variation between groups.

To test the discriminative validity of the cognitive model, we combined the activation from all regions and determined the average evoked responses to different trial types. Peak hemodynamic response from 5,000–10,000 ms from sexual female trial types was subtracted from corresponding response to sexual male trial types. Negative scores indicated greater responses to female sexual stimuli and were considered to reflect a heterosexual pattern of brain activity, and positive scores indicated greater responses to male sexual stimuli and were considered to reflect a homosexual pattern. Predicted orientation was then compared with self-report to determine the sensitivity and specificity of the network.

Additional individual tests were performed to determine whether the network would vary on the basis of subjective report. A subset of trials was chosen contingent on the condition of preferred stimuli being strongly liked (SL preferred) and nonpreferred stimuli being strongly disliked (SD nonpreferred). Considering that ROIs were chosen on the basis of attentional, affective, and motivational significance, the use of extreme ratings on the liking scale should help control for variations in liking across participants and may enhance differential processing in those areas.

We averaged the data obtained within the ROI into a single time course and estimated the peak response to each stimulus type to determine responsiveness to different trial types. We then analyzed these estimates with 2 ×2 analyses of variance (ANOVAs) using stimulus sex (preferred, nonpreferred) and orientation (heterosexual, homosexual) as factors. To test whether the inclusion of subjective data would yield different neural responses, we per-

formed additional ANOVAs for SL preferred and SD nonpreferred stimuli.

Results

Subjective Responses

Figure 1 depicts the results of the subjective measures of liking. Participants reported liking their preferred stimulus types more than their nonpreferred stimulus types, $F(1, 20) = 405$, $p < .001$. This pattern was found in all participants. The magnitude of the differences between preferred and nonpreferred stimulus types did not differ significantly between homosexual and heterosexual men, $F(1, 20) = 1.59$, $p = .222$. When absolute ratings of nonpreferred stimuli were compared, however, heterosexual participants gave lower ratings to male stimuli than homosexual participants did to female stimuli, $F(1, 20) = 4.90$, $p < .05$. No difference was found for ratings of preferred stimuli, $F(1, 20) = .006$, $p = .949$.

Although heterosexual participants gave approximately equal ratings to male and female sports stimuli, $F(1, 20) < .001$, $p = .990$, homosexual participants gave more positive ratings to male than female sports stimuli, $F(1, 20) = 7.19$, $p < .05$. Because of this difference in reported valance, subsequent analyses used only female sports stimuli as comparisons for the heterosexual participants and male sports stimuli as comparisons for the homosexual participants. Ratings of male sports stimuli by homosexual participants and ratings of female sports stimuli by heterosexual participants were similar, $F(1, 20) = 1.60$, $p = .220$.

When the responses given to different stimulus types were examined in individual participants, Participant 16 showed unusually positive evaluations for nonpreferred stimuli. This participant, a self-reported heterosexual, had 10 instances in which he gave positive evaluations to nonpreferred stimuli, whereas other heterosexual men averaged 0.6 positive evaluations. He also tended to give less negative evaluations for nonpreferred stimuli compared with other heterosexual men (the percentages rated "strongly dislike" were 48% and 66%, respectively). Furthermore, he rated preferred stimuli less positively compared with other heterosexual men (the percentages rated "strongly like" were 46% and 82%, respectively).

Whole Brain Analysis

The preferred versus nonpreferred comparison ($N = 22$) identified greater activity for preferred stimuli in a large number of brain regions (see Figure 2 and Table 2), including widespread visual regions (BA 17, BA 18, BA 19), posterior cingulate, precuneus, left superior parietal lobule, left globus pallidus, thalamus, left putamen, left insula, bilateral caudate (head and body), left claustrum, left dorsal amygdala/sublenticular extended amygdala, anterior cingulate, hypothalamus, nucleus accumbens/subcallosal cortex, left superior frontal gyrus, and left cerebellum.

The only areas with greater activity to nonpreferred stimuli likely reflected the use of the left hand to press the "dislike" and "strongly dislike" buttons (sensory–motor areas of right pre-/postcentral gyri). Corresponding greater activation for preferred stimuli was seen in the matching ipsilateral regions.

For the preferred versus sports comparison (see Figure 2b and Table 3), preferred stimuli elicited greater activation than sports stimuli in a widespread parieto–occpito–temporal network: BA 17, BA 18, BA 19, left sensory–motor cortex, bilateral anterior cingulate, bilateral caudate/putamen/thalamus, left insula, left posterior cingulate, and right inferior parietal cortex. As in the previous comparison, the only area with greater activation for sports stimuli was the right sensory–motor cortex, reflecting the greater tendency to use the left hand to respond to those stimuli.

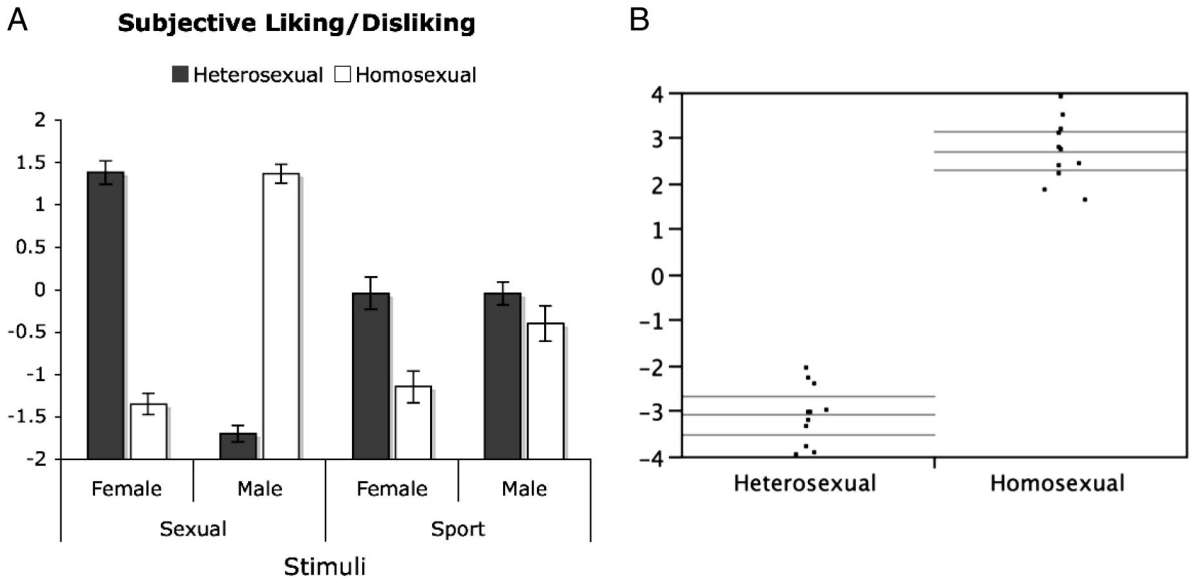

Figure 1. A: Average preference ratings (± *SE*) of homosexual and heterosexual participants to the preferred and nonpreferred sexual stimuli; −2 corresponds to strongly disliking a stimulus and +2 corresponds to strongly liking a stimulus. B: Individual participants' average differences in ratings of preferred and nonpreferred stimuli. For each group, the middle line represents the mean, and the outer lines mark the 95% confidence intervals.

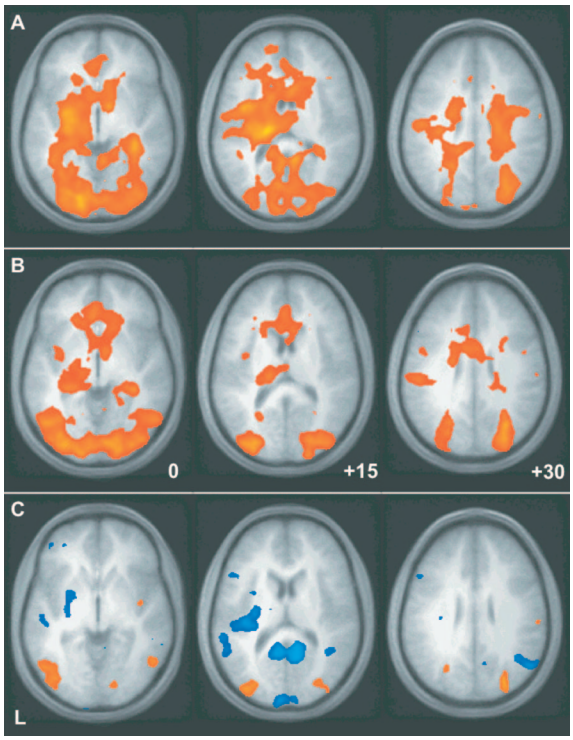

Figure 2. Areas of differential activity to preferred versus nonpreferred stimuli (A; increased activity to preferred stimuli shown in red), preferred versus sports stimuli (B; increased activity to preferred stimuli shown in red), and nonpreferred versus sports stimuli (C; increased activity to sports stimuli shown in blue). Sports images contained actors of the participants' preferred sex. Axial slices are at $z = 0$, $+15$, and $+30$.

For the nonpreferred versus sports comparison (see Figure 2 and Table 4), greater activity for sports stimuli was observed in the posterior cingulate bilaterally, left sensory–motor cortex, left insula, right inferior parietal lobule, left middle and superior temporal gyrus, left parahippocampal gyrus, left middle frontal gyrus, left middle occipital gyrus, left precuneus, cerebellum, and right middle temporal gyrus. Greater activity was observed for nonpreferred stimuli in the left inferotemporal cortex, right precuneus, and right sensory–motor cortex. Differential activity in pre-/postcentral gyri likely reflects motor activity (as above).

In the whole-brain analysis, the pattern of greater evoked activity for preferred stimuli did not differ reliably across the participant groups (i.e., the comparison of activity to female and male stimuli for heterosexual participants was similar to the comparison of activity to male and female stimuli for homosexual participants). No significant clusters were found at the whole brain level for the preferred–nonpreferred, preferred–sports, and nonpreferred–sports, homosexual–heterosexual double subtractions.

ROI Analysis

Differences between the participant groups were assessed with greater sensitivity in the network of areas hypothesized to be involved in arousal using an ROI analysis. When category-specific activity was assessed over the entire network (see Figure 3 and Table 5), 16 out of 22 participants exhibited significant differential activation between stimulus types; of those 16 participants, 15 showed greater activation for stimuli featuring their preferred sex. The one individual whose predicted brain activity did not correspond with reported sexual orientation was Participant 16.

When differential activation was assessed for SL preferred and SD nonpreferred stimuli (see Table 5), participants tended to show larger magnitudes of activation than when subjective preference was not used to select trials, $F(1, 21) = 3.77$, $p = .067$. Eight participants, however, did not show reliable differences between SL preferred and SD nonpreferred stimuli. The larger magnitude contrasts and fewer significant results may be explained by the smaller number of trials that went into these analyses.

Table 6 depicts the results of the ROI analysis. All regions in the hypothesized arousal network exhibited greater activity for preferred stimuli than for nonpreferred stimuli. Group differences were found in the amygdala for the preferred–nonpreferred comparison with homosexual men showing category-specific activation to male sexual stimuli and heterosexual men showing tonic activation across stimulus conditions (see Figure 4). When subjective data were used to select SL preferred and SD nonpreferred stimuli, the interaction between stimulus type and sexual orientation fell below significance and became a trend, $F(1, 20) = 3.18$, $p = .091$. An additional test was performed without Participant 16 to ensure that an anomalous data point was not skewing the results. These results were still significant for the preferred–nonpreferred comparisons including all trials, but not the subjectively filtered preferred–nonpreferred contrasts, $F(1, 20) = 4.41$, $p < .05$, and, $F(1, 20) = 3.53$, $p = .077$, respectively.

Discussion

Homosexual and heterosexual men exhibited category-specific networks of activity when viewing male and female sexual stimuli. The finding of large networks of activity spanning multiple anatomical domains suggests that the neurophysiological state of sexual arousal involves coordination of cognitive/affective/sensory–motor systems such that increased vigilance, positive affect, and motivational responses are triggered by salient stimuli. When sexual stimuli matched the participant's stated preference, dramatically increased activity was observed across multiple cortical and subcortical regions.

Most previous studies mapped arousal by comparing sexual stimuli with neutral stimuli. This study, however, used three conditions (preferred, nonpreferred, and neutral sports) and three comparisons to examine the neural correlates of sexual arousal. The preferred–nonpreferred subtraction yielded the most widespread network of activity, with greater activation to preferred stimuli. Although men sometimes report aversion to nonpreferred sexual stimuli (Freund, Langevin, Cibiri, & Zajac, 1973; Freund, Langevin, & Zajac, 1974), no regions of consistently greater activity to the nonpreferred stimuli were identified (outside of motor areas, because of the method of reporting arousal level). Brain regions regulating aversion may have been insufficiently activated in the context of this study. Another possibility is that aversion activates some of the same regions as the appetitive response, but to a smaller degree.

When nonpreferred sexual stimuli were compared with sports stimuli, however, greater activity to the nonpreferred stimuli was

Table 2
Areas Exhibiting Differential Activity to Preferred and Nonpreferred Stimuli

Region	BA	*X*	*Y*	*Z*	Size (mm^3)
Preferred > Nonpreferred					
Very large cluster including:					239,203
L middle occipital gyrus	18/19	−28	−85	−5	
		−32	−84	14	
R middle occipital gyrus	18/19	34	−82	−4	
L primary visual cortex	17	−18	−89	1	
R primary visual cortex	17	−21	−89	4	
R superior occipital gyrus/precuneus	19	29	−85	24	
L precuneus	19	−22	−83	35	
L posterior cingulate		−12	−53	22	
R posterior cingulate		12	−56	22	
L precuneus/inferior parietal cortex	7	−9	−61	64	
R hippocampus		31	−41	−2	
L basal gangalia/thalamus		−27	−24	−1	
		−19	−15	−1	
L thalamus		−19	−23	7	
L claustrum/pulvinar/insula		−24	−25	17	
L caudate head		−14	7	14	
L caudate body		−19	−18	27	
R caudate head		9	9	16	
R caudate body		18	−17	27	
L insula	13	−33	2	18	
		−29	27	17	
L anterior cingulate	24/32	−1	26	21	
R anterior cingulate	24/32	10	20	21	
L sensory–motor cortex		−36	−32	52	
	4	−38	−17	58	
		−39	−43	65	
		−16	−36	66	
		−27	−38	65	
R cerebellum		26	−40	−34	
		26	−53	−24	
L superior frontal gyrus	8	−19	19	48	3,625
R cingulate	24/32	17	1	36	672
R superior frontal gyrus	8	16	23	45	672
R middle frontal gyrus	46	45	21	26	562
Nonpreferred > Preferred					
R sensory–motor cortex	4	34	−30	63	8,266

Note. L = left; R = right; BA = Brodmann area.

observed in areas associated with visual processing and attention, including the inferotemporal cortex and precuneus. Greater activity in the inferotemporal cortex for nonpreferred stimuli compared with sports stimuli may reflect responses to faces and bodies in the sexual images (Downing, Jiang, Shuman, & Kanwisher, 2001). Greater activity in the cerebellum and basal ganglia during the viewing of sports stimuli might reflect a tendency for participants to engage in mental rehearsal of motor routines relating to the particular sport (Decety et al., 1994).

Our results suggest that the neural processes underlying arousal quickly, specifically, and robustly activate in response to sexual stimuli of a preferred nature. Beauregard et al. (2001) found that the superior frontal cortex and the anterior cingulate were involved in the conscious self-regulation of sexual arousal. In the current study, those areas did not show elevated activation to nonpreferred stimuli compared with preferred or sports stimuli. Thus, we think it is unlikely that conscious regulation of sexual arousal accounts for the category-specific pattern we obtained. Furthermore, the short stimulus presentation times (3,500 ms) and rapid succession of images (5,000 ms between onsets) should ensure that we are studying the initial stages of arousal, which seems especially likely to reflect automatic processes. Finally, Ponseti et al. (2006) generated category-specific arousal using an even shorter image presentation with a 300-ms trial onset and 2,700-ms intertrial interval. Because MEG studies have shown category-specific neuronal activity to visual sexual stimuli at as early as 126 ms (Costa et al., 2003), it seems likely that category-specific arousal does not rely on conscious control for its expression.

Examination of previous reports on arousal-related neural activity suggested a network of specific regions participating in the arousal response (see Table 1). Each of these regions exhibited category-specific activity that was higher for the preferred stimuli than for the nonpreferred stimuli (see Table 6). Group differences were found in the amygdala, a region that has shown differential activation between men and women in previous neuroimaging studies (Cahill, Uncapher, Kilpatrick, Alkire, & Turner, 2004; Hamann et al., 2004; Kilpatrick, Zald, Pardo, & Cahill, 2006). If neural structures are organized differently in homosexual and heterosexual men in accordance with the neurohormonal hypothesis of sexual orientation, then it is possible that these variations

Table 3
Areas Exhibiting Differential Activity to Preferred and Sports Stimuli

Region	BA	*X*	*Y*	*Z*	Size (mm^3)
Preferred > Sports					
Large cluster including:					67,797
L early visual cortex	17	−4	−90	−3	
R early visual cortex	17	11	−90	−3	
L middle occipital gyrus	18	−31	−88	−4	
L middle occipital gyrus	18/19	−34	−88	9	
R middle occipital gyrus	19	27	−90	4	
R cuneus/middle occipital gyrus	17/18/19	22	−89	9	
R precuneus/inferior parietal cortex	7/19	27	−84	24	
L sensory/motor cortex		−38	−39	56	27,453
Bilateral anterior cingulate/caudate		−1	21	15	18,281
L basal ganglia/thalamus		−22	−26	5	6,781
L basal ganglia		−14	0	−6	1,062
L insula	13	−37	−3	4	969
L posterior cingulate		−20	−62	7	625
R caudate tail		16	−34	28	484
R inferior parietal cortex	40	56	−26	38	359
Sports > Preferred					
R sensory–motor cortex		29	−29	64	1,359

Note. L = left; R = right; BA = Brodmann area.

could manifest as differential activation in sexually dimorphic regions. Although the amygdala differences we found are consistent with the hypothesis that homosexual men's brains show atypical patterns of activation in sexually dimorphic regions, these results do not paint a simple picture of homosexual men having "female brains."

Interpretation of group differences remains challenging because such variations may represent either dissimilar levels of arousal or dissimilar processing during similar levels of arousal. A social alternative to the sexual dimorphism explanation is suggested by the finding that heterosexual men rated the nonpreferred stimuli lower than did homosexual men. Group differences in amygdala functioning may be due to negative attitudes toward homosexuality on the part of heterosexuals. However, a significant trend persisted when we restricted the analysis to those trials on which heterosexual and homosexual men gave similar ratings. Our finding of a group difference in the amygdala needs to be replicated before much energy is exerted to explain it. Assuming the difference is replicable, evidence from functional imaging is unable to resolve whether the difference is due to innate or social factors or to both.

Table 4
Areas Exhibiting Differential Activity to Sports and Nonpreferred Stimuli

Region	BA	*X*	*Y*	*Z*	Size (mm^3)
Sports > Nonpreferred					
R cerebellum		20	−47	−30	6,391
Bilateral posterior cingulate	30	9	−52	11	4,375
L sensory–motor cortex		−31	−32	65	4,031
L insula	13	−40	−30	20	2,125
R inferior parietal lobule	7/39	40	−68	41	1,344
L middle temporal gyrus	22/38	−54	−2	−16	1,156
L postcentral gyrus		−51	−21	45	875
L superior temporal gyrus	22	−55	−47	11	875
L parahippocampal gyrus	36	−24	−34	−14	812
L middle frontal gyrus	6	−12	−17	74	656
L middle occipital gyrus	18	−10	−102	11	578
L cerebellum		−41	−59	−40	484
L precuneus		−1	−69	39	469
L middle frontal gyrus	9	−52	17	32	422
R middle temporal gyrus	22	58	−43	0	406
L middle frontal gyrus	10/46	−38	48	11	391
Nonpreferred > Sports					
R sensory–motor cortex		43	−32	54	3,859
L inferior occipital/temporal cortex	37	−46	−70	−5	2,359
R cuneus/precuneus	19	26	−85	26	766

Note. L = left; R = right; BA = Brodmann area.

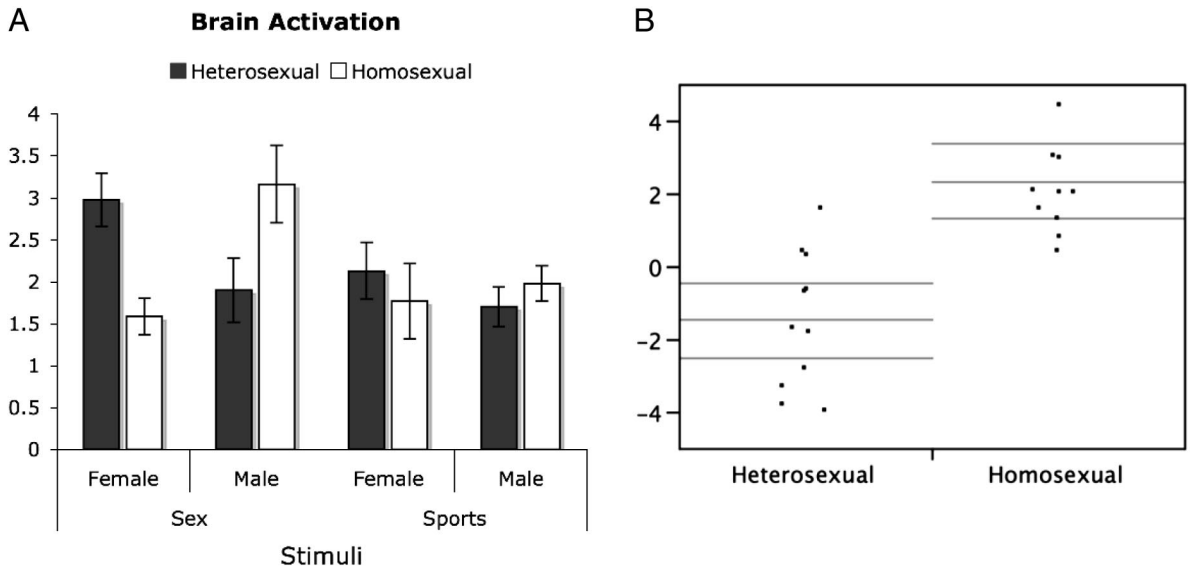

Figure 3. Differential activity averaged across all regions of interest. A: Average raw activity (± *SE*) for each stimulus type for homosexual and heterosexual participants. B: Differences in activation to the male sexual stimuli minus activation to the female sexual stimuli for individual participants. For each group, the middle line represents the mean, and the outer lines mark the 95% confidence intervals.

Activity assessed across these ROIs was a reliable predictor of self-reported sexual orientation, with greater responses to female stimuli for heterosexual men and greater responses to male stimuli for homosexual men in 15 out of 16 participants in this study (with 6 additional participants failing to exhibit significant differences between conditions). Although patterns of stated liking seemed to perfectly track self-reported sexual orientation, this association may be inflated by factors unrelated to arousal that influence both

Table 5
Discriminative Validity Test for Different Regions Hypothesized to be Involved in the Arousal Response

#	Orientation	Sexual female rating	Sexual male rating	Sexual male − Sexual female		Strongly liked preferred − Strongly disliked non-preferred	
				LC[0]	*F*(1, 1,152)	LC[0]	*F*(1, 1,152)
2	Hetero	1.98	−1.99	−1.770	5.47*	1.790	2.33*
3	Hetero	0.65	−1.39	−3.290	13.40***	6.220	10.30***
4	Hetero	1.14	−1.83	−0.615	0.52	3.530	3.18***
5	Hetero	1.98	−1.92	0.332	0.51	−0.310	0.43
7	Hetero	1.32	−2.00	−1.670	10.20**	2.560	16.10***
8	Hetero	1.18	−2.00	−3.750	26.60***	4.130	21.50***
9	Hetero	1.68	−1.33	−0.655	0.15	1.050	1.76
11	Hetero	1.84	−1.93	−2.790	28.80***	3.270	33.90***
14	Hetero	1.35	−1.70	−3.930	8.54**	1.350	0.62
16	Hetero	1.26	−1.14	1.610	4.09*	0.080	0.01
20	Hetero	0.77	−1.48	0.435	0.65	0.620	0.44
10	Homo	−1.93	1.57	1.320	5.80*	1.430	5.14*
12	Homo	−0.88	1.53	3.070	24.10***	0.760	0.41
13	Homo	−1.53	1.60	2.060	4.72*	2.870	6.04*
15	Homo	−1.56	1.66	1.620	7.65**	2.720	14.40***
17	Homo	−1.40	1.06	0.820	2.38	1.490	3.45*
18	Homo	−1.40	0.82	3.020	8.35**	4.210	4.30*
19	Homo	−1.20	1.54	0.440	0.40	0.220	0.06
21	Homo	−0.90	0.73	2.100	7.54**	2.020	1.35
22	Homo	−1.39	1.39	4.430	68.20***	5.140	51.20***
23	Homo	−0.67	1.18	5.020	63.70***	6.990	31.20***
24	Homo	−2.00	1.93	2.030	9.75***	1.940	8.54**

Note. General linear testing was performed for neural responsiveness to specific stimulus types for individual participants. The LC[0] term indicates the estimated differential evoked neural activity, and the *F* statistic indicates the significance of this measure (*F* statistics without asterisks are not significant). Negative LC[0] terms correspond to greater evoked activity for the second stimulus set, and positive scores correspond to greater activity for the first stimulus set.
* $p < .05$. ** $p < .01$. *** $p < .001$.

Table 6
Analyses of Variance Testing for Category-Specific Activity in Response to Preferred and Nonpreferred Stimulus Types and Whether This Varied as a Function of Sexual Orientation

	Preferred − Nonpreferred		Strongly liked preferred − Strongly disliked nonpreferred	
Regions	Stimulus, $F(20, 1)$	Stimulus × Orientation, $F(20, 1)$	Stimulus, $F(20, 1)$	Stimulus × Orientation, $F(20, 1)$
AC (BA 24/32)	15.20***	2.870	16.50**	1.210
Amy	7.81**	5.670*	4.61*	3.180
Hip	20.60***	1.540	36.50***	0.662
Hyp	6.12*	0.446	10.30***	0.064
MDTN	13.20**	0.232	15.30***	0.149
Midbrain	10.50**	0.861	5.18*	1.180
mOFC	5.86*	0.860	7.22*	1.490
NAc	13.00**	0.169	22.70***	0.203
SLEA	13.00**	0.748	22.90***	0.459
Visual (BA 17/18)	41.20***	0.184	46.30***	0.283

Note. All regions exhibited greater activity for preferred than for nonpreferred stimuli. *F* statistics without asterisks are not significant. AC = rostral anterior cingulate; BA = Brodmann area; Amy = basolateral/medial amygdala; Hip = hippocampal complex; Hyp = hypothalamus; MDTN = medial dorsal thalamic nucleus; mOFC = medial orbitofrontal cortex; NAc = nucleus accumbens/subcallosal cortex; SLEA = sublenticular extended amygdala.
* $p < .05$. ** $p < .01$. *** $p < .001$.

types of self report. It is interesting that the single participant whose self-reported orientation did not match his pattern of brain activation provided unusually positive ratings to nonpreferred stimuli. A recent study showed that a majority of bisexually identified men have a pattern of genital sexual arousal similar to that of homosexual men (Rieger, Chivers, & Bailey, 2005). For this participant, too, self-identified sexual orientation may reflect something other than relative degrees of arousal to male and female stimuli.

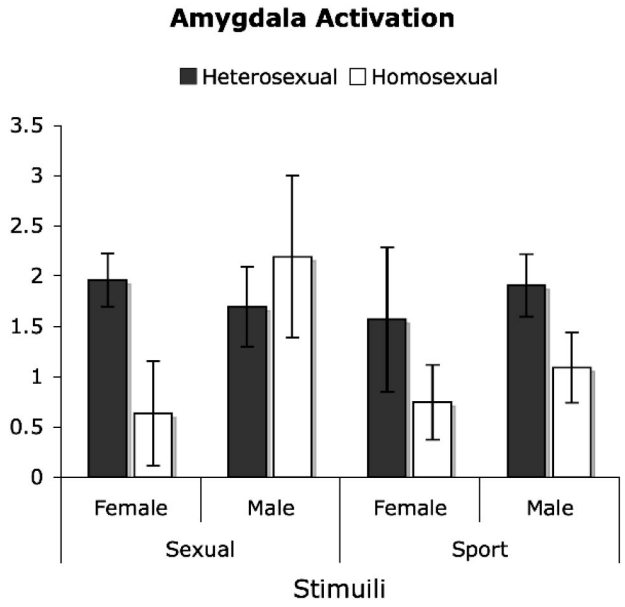

Figure 4. Average amygdala activation (± *SE*) to male versus female stimuli, separately by stimulus type, for homosexual and heterosexual participants.

Because psychophysiological responses to sexual stimuli begin in the brain, neurological activity may be a more effective way to assess the basis of the arousal state than peripheral measures. The "gold standard" measure of sexual arousal in men has been the penile plethysmograph, but this measure has the substantial limitation that approximately one third of men do not have sufficient erections for valid measurement (e.g., Chivers et al., 2004). Our results suggest that fMRI can be a useful psychophysiological measure of sexual arousal. A relatively imprecise method of a priori ROIs drawn on an average brain achieved a degree of sensitivity and specificity comparable with that obtained by other physiological measures of arousal (Blanchard, Klassen, Dickey, Kuban, & Blak, 2001). These results indicate that neurological measures may provide a useful means of assessing populations in which erectile measures are not an option and may have potential clinical applications in the diagnosis of sexual dysfunctions and the evaluation of treatment efficacy.

Predictive power may be improved in future fMRI studies. For example, a block design using either sexual pictures with longer stimulus onsets or video erotica may be more effective at producing robust arousal responses. Furthermore, functional ROIs from studies using similar preferred versus nonpreferred sexual stimuli could be used to choose regions of greatest sensitivity and thus provide more precise estimates of arousal responses.

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Received November 30, 2005
Revision received October 31, 2006
Accepted December 7, 2006 ■