Subcortical BOLD responses during visual sexual stimulation vary as a function of implicit porn associations in women

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Lifetime experiences shape people’s attitudes toward sexual stimuli. Visual sexual stimulation (VSS), for instance, may be perceived as pleasurable by some, but as disgusting or ambiguous by others. VSS depicting explicit penile-vaginal penetration (PEN) is relevant in this respect, because the act of penetration is a core sexual activity. In this study, 20 women without sexual complaints participated. We used functional magnetic resonance imaging and a single-target implicit association task to investigate how brain responses to PEN were modulated by the initial associations in memory (PEN-hot vs PEN-disgust) with such hardcore pornographic stimuli. Many brain areas responded to PEN in the same way they responded to disgust stimuli, and PEN-induced brain activity was prone to modulation by subjective disgust ratings toward PEN stimuli. The relative implicit PEN-disgust (relative to PEN-hot) associations exclusively modulated PEN-induced brain responses: comparatively negative (PEN-disgust) implicit associations with pornography predicted the strongest PEN-related responses in the basal forebrain (including nucleus accumbens and bed nucleus of stria terminalis), midbrain and amygdala. Since these areas are often implicated in visual sexual processing, the present findings should be taken as a warning: apparently their involvement may also indicate a negative or ambivalent attitude toward sexual stimuli.

Keywords: visual sexual stimulation; pornography; sexual penetration; disgust; single-target implicit association task; midbrain; basal forebrain; bed nucleus of stria terminalis

INTRODUCTION

Visual sexual stimulation (VSS) is a powerful route into the brain’s core emotional circuitry. A recent review of VSS brain imaging experiments led to the identification of a sexual interest or saliency network that seems to primarily support fast and early processing of VSS, that is, before objective or subjective sexual arousal becomes obvious (Georgiadis and Kringelbach, 2012). The core elements of this ‘early’ sexual network are amygdala, ventral striatum, anterior insula, posterior orbitofrontal cortex and perigenual anterior cingulate cortex (Hamann et al., 2004; Ferretti et al., 2005; Ponseti et al., 2006; Safron et al., 2007; Childress et al., 2008; Walter et al., 2008; Sescousse et al., 2010; Gillath and Canterberry, 2012; Oei et al., 2012). In men and women alike, activity of (components of) the sexual saliency network varies as a function of expectation, contingency awareness (Klucken et al., 2009), prediction error and hedonic value (Sescousse et al., 2010), which is at least suggestive of the possibility that prior experiences with sexual stimuli play an important modulatory role in shaping VSS-induced brain responses (Georgiadis and Kringelbach, 2012; Georgiadis et al., 2012).

Sexual activity is under strong social control, and expressions of sexuality (e.g. responses to VSS) are at least partly determined by social beliefs and group norms. Thus, one might expect people to vary in their attitudes toward sex, including the way they perceive and respond to VSS. The observation that people may have both negative as well as positive affective judgments about VSS should therefore not be surprising (Laan et al., 1995). Even though positive affect generally facilitates subjectively reported sexual arousal (Heiman, 1980; Laan et al., 1994; Janssen et al., 2000), people sometimes report ambivalent emotions (i.e. co-occurring negative and positive affective judgments) toward VSS, and this ambivalence does not exclude the occurrence of subjective sexual arousal (Peterson and Janssen, 2007). For example, when experiencing pleasure by watching pornography, people may at the same time feel guilty or disgusted with their behavior (Mosher and Maclan, 1994). Thus far, it is largely unclear whether the VSS-induced brain activation is most closely associated with the more positive or with the more negative components of people’s subjective evaluation of VSS. Germane to this, previous brain imaging studies on the relationship between sex and disgust have shown substantial overlap in VSS- and disgust-induced activation maps (Stark et al., 2005; Walter et al., 2008; Karama et al., 2011). This overlap is seen in occipitotemporal cortex, superior parietal lobule, amygdala, ventral pallidum and thalamus, and is generally attributed to general arousal and/ or attention phenomena (Walter et al., 2008). Yet, it may also reflect that the VSS-elicted negative affective associations. Therefore, in the present study we included the subjective VSS evaluations and investigated to what extent individual variability in VSS-induced brain activity could be explained by the participants’ positive and negative appraisals.

Research on people’s attitudes toward VSS up until now predominantly focused on explicit attitudes that can be indexed by self-report measures. However, current ‘dual process models’ emphasize the importance to differentiate between these explicit (deliberate) affective evaluations and more automatic (implicit) associations (Gawronski and Bodenhausen, 2006). Implicit attitudes are assumed to follow from the initial activation of simple associations in memory and to be involved in the more spontaneous, reflexive type of behavior (like...
genital responses in the case of sex); whereas, the explicit evaluations are thought to be the outcome of validation processes, and to be more closely linked to reflective behavior. Interestingly, people’s explicit reports are not necessarily concordant with their implicit associations. In the case of VSS, it may be that autonomous genital responses occur when negative affective evaluations (e.g. aversion) are reported, and this specific discordance is most typical of women (Laan et al., 1994; Laan and Everaerd, 1995a; Spiering et al., 2003). It is unknown whether VSS first (automatically) elicits positive affective associations followed by a negative appraisal, or whether the reverse order is true. Alternatively, both attitudes may initially act in concert, and discordance develops in the validation process.

Direct, automatic, associations may be indexed by performance measures, such as the implicit association task (IAT). Previously, the IAT has been used to test participants’ implicit attitudes toward PEN (hardcore pornography focusing on penile–vaginal penetration) and revealed a relatively strong automatic association between PEN and disgust in women with penetration disorder (Borg et al., 2010). This is interesting, because the act of penetration lies at the very core of sexual activity, and therefore might be conceived to carry considerable sexual incentive value. However, VSS including PEN may also be perceived as immoral and degrading to women (Padgett et al., 1989; McKenzie-Mohr and Zanna, 1990). Indeed, women had more negative sexual implicit associations than their male counterparts (as indicated by the IAT), especially when the words used in the task were of a more socially unacceptable nature (Geer and Robertson, 2005).

Our major aim was therefore to identify where in the brain, areas are particularly sensitive to individual variations in implicit PEN-disgust relative to PEN-‘hot’ associations. Such areas might conceivably be relevant in negotiating the automatic sexual pleasure or disgust response toward VSS, at least when it comes to PEN stimuli. We expect that individual IAT scores are most likely to modulate subcortical activity. First, this would be in line with a previous study connecting functional MRI (fMRI) and IAT, albeit in a completely different emotional context (Phelps et al., 2000). Second, deep brain areas are known to be most critical in fast, automatic processing of VSS (Childress et al., 2008; Oei et al., 2012). In addition, any cortical area known to respond robustly to briefly presented VSS (anterior insula, orbitofrontal cortex and perigenual anterior cingulate cortex) might be conceived to undergo such modulation.

All in all, the present study was designed to comprehensively assess how explicit and implicit attitudes toward PEN stimuli (a putative VSS subcategory) relate to PEN-induced brain activity.

MATERIALS AND METHODS

Participants

Twenty-one healthy women with a mean age of 22 years (s.d. = 2.1) participated in this study against modest reimbursement. One volunteer was excluded from evaluation because of excessive head motion and poor compliance. All participants provided written informed consent. The experiment was approved by the local Medical Ethical Committee, and all procedures were conducted in accordance with its standard.

The participants were scanned in the first half of their menstrual cycle and never during menstruation. From our sample, 20% did not make use any form of contraceptives, while 80% used oral contraceptives. Participants had to be in a heterosexual relationship for a minimum of 6 months to be eligible for participation. In this study, 35% reported being in a relationship of >2 year-long, 20% in a >1 year-long and <2 year-long relationship, and 45% of our sample were in a <1 year-long relationship. Women with a history of neurological or psychiatric problems, severe head trauma, drug abuse and/or prescribed psychotropic medications were excluded. All participants reported moderate alcohol and nicotine consumption at most. Participants self-reported as healthy controls in an on-going study about cognitive processes in women with sexual pain disorders. They were then screened over the phone and only those who have experienced sexual intercourse, and were free of sexual complaints could participate. Apart from two participants who were predominantly left handed, all participants were exclusively right handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). Participants were exclusively (75%) or predominantly (25%) heterosexual based on the Kinsey’s Heterosexual-Homosexual Rating Scale (Kinsey, 1998).

fMRI paradigm and procedure

For the broader study on sexual pain disorders that we are currently conducting in our laboratory, the stimuli consisted of 36 colored photographs representing six emotional categories: ‘Neutral objects’ (NEU), ‘Fear’, ‘Core disgust (DIS)’ (e.g. a person vomiting, feces), ‘Animal-Reminder disgust (e.g. mutilation), ‘Sexual Penetration’ (PEN) and ‘Neutral bodies’ (BOD). For this particular study, we focused on PEN, NEU, BOD and DIS stimuli. PEN depicted hardcore coital interaction, with explicit focus on PEN. The contextual information was limited and faces were not shown. BOD comprised interacting, minimally clothed male and female bodies without sexual connotations (e.g. sports). DIS was used because it represents the most primal disgust category (which compares to the primal nature of PEN) and because it induces similar arousal as PEN, but with negative valence (Rozin et al., 2000, Borg et al., 2013). Also for DIS and BOD, faces were not shown. Stimuli chosen from the International Affective Picture System (IAPS) (Lang et al., 1999) included: 7010 and 5520 (NEU). Selection of non-IAPS pictures was done in a pre-structured process. Initially more than 200 photographs were collected by the researchers. Based on characteristics agreed on a priori the research team selected 50 photographs. These characteristics included: no focus on faces, Caucasian heterosexual couples, easily recognizable features and very limited context. Selected pictures were then sent for further validation conducted with 40 females via an online survey (www.esurveyspro.com). This was done over and above the researchers’ team selection to make sure that each stimulus from the relevant category elicited significantly more the intended emotion than the other categories. For example, the DIS stimuli had to elicit significantly more disgust than the other categories. The research team matched the scenes for physical features such as complexity, brightness, contrasts and color. Apart from content-based validation, the stimuli were also validated with respect to color. No significant differences were found on the RBG color distribution ($P > 0.2$).

Stimuli were presented in a block design, with each block consisting of 10 pictures representing the same category. Each photograph was presented for 1.4 s, with a 1-s interval between consecutive stimuli. Six blocks (split by 16 s inter-block intervals), corresponding to the six stimulus categories, were run in a pseudo-randomized sequence. Six of these functional runs were acquired for each participant, separated by 30 s intervals, adding up to a total duration of the fMRI experiment of 1458 s. A psychotoolbox (http://psychtoolbox.org) application was developed for presentation of the experimental design.

Preceding the experiment, a training task was done inside the scanner. Participants were instructed to look at the pictures presented and melt with their emotions. Given the passive nature of the design participants were asked to respond (i.e. press a button) to an ‘*’ that was over-imposed on a (fixed) randomly selected number of photographs. These responses were recorded, but were not used in the analysis. After scanning, participants conducted a single-target (st) IAT and a Visual Analogue Scale (VAS), followed by a debriefing session.
The stIAT is a computerized reaction time (RT) task that measures to what extent a single-target category is associated with two attribute categories. In this study, the stIAT was used to measure the relative automatic associations with PEN. Pictures with PEN content formed the (single) target in the task, and the attributes consisted of negative/disgust vs positive/'hot' words. Participants were instructed to categorize words of the three categories that appeared in the middle of a computer screen by means of two response buttons. In one test phase 'sex' and 'disgust' were mapped on a single response key, and 'hot' on the other. The idea is that the task becomes easier when two pairings that are strongly associated, share the same response key. Consequently, the difference in RT between both test phases is assumed to reflect whether sex is associated more strongly with either attribute category. RTs were analyzed using the now widely used D4-measure scoring algorithm (Greenwald et al., 2003). In this article, we report the D4 measure (Table 1). Here, negative stIAT effects (i.e. negative D4 measure) indicate relatively fast responses when sex shared the response key with disgust. Hence, in this stIAT, negative D4 measure means stronger PEN-disgust associations (see Supplementary data for details). We included VASs to also rate the subjective appraisal of all the stimuli presented on the dimensions of disgust, pleasure and arousal. The VASs ranged from 0 (not at all) to 100 (very much). All stimuli were rated subjectively on the dimension of general arousal post hoc from an independent sample of 25 women that did not differ in other demographic data. This was done post hoc due to connotations to sexual and positive arousal for the Dutch word ('opwinding') that we used in the experiment (Table 2).

fMRI

Image acquisition

Images were acquired on a Philips Intera 3T MRI scanner. A sense eight-channel head coil was used for radio frequency reception. A series of echo-planar imaging (EPI) volumes were acquired to measure the blood oxygen level-dependent (BOLD) effect, which entailed a $T_2^\ast$-weighted gradient-echo sequence with a repetition time (TR) of 2000 ms and an echo time of 30 ms. Flip angle was 70° using whole-brain acquisition (matrix size $64 \times 64$ voxels) and interleaved slice acquisition order, with an inter-slice gap of 0 mm and plane thickness of 3 mm. EPIs were acquired at $3 \times 3$ mm in-plane resolution. The (axial) images (volumes) were acquired parallel to the anterior–posterior commissure plane. In total 740 volumes were obtained per participant. A $T_2^\ast$-weighted anatomical MRI (TR = 9 ms, TE = 3.5 ms, matrix size $256 \times 256$ voxels) and two diffusion tensor imaging volumes of 55 slices each of 620 ms duration (with scan resolution of $96 \times 96$, flip angle 70°) were acquired after the EPI runs. The diffusion tensor imaging measurements were not used in this article.

Image pre-processing

For image pre-processing and analysis, we used Statistical Parametric Mapping software SPM8 (University College London, UK; http://www.fil.ion.ucl.ac.uk). For each participant, all EPI volumes were realigned to the first volume acquired, and a mean EPI image was created. The realignment parameters were inspected and if movements exceeded 2 mm in any direction the participant was excluded from further analysis. The anatomical ($T_1$) scan was manually co-registered to the mean EPI image, and subsequently all EPI images and the $T_1$ image were spatially normalized to MNI (Montreal Neurological Institute) standard stereotactic space (Friston et al., 1995). Data were re-sampled to $2 \times 2 \times 2$ mm ($8\,\text{mm}^3$) isotropic voxels. All volumes were smoothed with an isotropic Gaussian kernel of $8\,\text{mm}$ full-width at half-maximum.

### Table 1

<table>
<thead>
<tr>
<th>stIAT Measurement</th>
<th>Participants</th>
</tr>
</thead>
<tbody>
<tr>
<td>RT</td>
<td>M (s.d.)</td>
</tr>
<tr>
<td>RT PEN-disgust (negative)</td>
<td>638 (75)</td>
</tr>
<tr>
<td>RT PEN-'hot' (positive)</td>
<td>628 (59)</td>
</tr>
<tr>
<td>D4</td>
<td>0.03 (0.79)</td>
</tr>
</tbody>
</table>

RT PEN-disgust is the reaction time with the pairings PEN-disgust, which here are negative associations and RT PEN-hot is the reaction time for the pairings PEN-hot, which here are positive associations. Overall, the RTs for both pairings were very similar within this cohort (Borg et al., 2010); D4 is the IAT effect typically referred to as the D measure (see Supplementary data for a detailed description).

### Table 2

<table>
<thead>
<tr>
<th>Emotion</th>
<th>DIS M (s.d.)</th>
<th>PEN M (s.d.)</th>
<th>BOD M (s.d.)</th>
<th>NEU M (s.d.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Disgust</td>
<td>79.3 (13.2)*</td>
<td>27.0 (24.7)*</td>
<td>1.6 (2.3)*</td>
<td>0.60 (0.7)*</td>
</tr>
<tr>
<td>Pleasure</td>
<td>5.3 (6.7)*</td>
<td>40.0 (24.2)*</td>
<td>56.4 (11.7)*</td>
<td>29.3 (25.3)*</td>
</tr>
<tr>
<td>Arousal</td>
<td>36.28 (18.4)</td>
<td>39.01 (22.7)</td>
<td>10.03 (10.2)</td>
<td>5.08 (8.7)</td>
</tr>
</tbody>
</table>

The subjective evaluation of each stimulus type (DIS, PEN, BOD and NEU) on the two dimensions, namely, disgust and pleasure. Different letters in superscript (a/b/c/d) indicate significant difference between stimulus categories within a dimension (P < 0.012). For instance, the ‘a’ on DIS and the ‘b’ on PEN elicits on the first row indicates that they do differ significantly from each other on the dimension of disgust. The second letter (x, y) applies to relevant comparisons across columns. For instance, the ‘z’ of the dimension of disgust with the ‘x’ on the dimension of pleasure indicates that the stimulus material PEN did not differ significantly on these two dimensions (P = 0.19).

All stimuli were rated subjectively on the dimension of general arousal post hoc due to connotations to positive arousal for the Dutch word ('opwinding') that we used in the experiment (see Materials and Methods section).

### Statistical analysis

After pre-processing, analyses were performed using the general linear model and random effects models for second-level analysis (Friston et al., 1995). First, we computed a general linear model for each participant, which included regressors for the six conditions (including conditions of no interest) and also one for the inter-run instructions, convolved with a canonical hemodynamic response function. Rotational and translational head movements were added as nuisance variables (six covariates). For each voxels, a high-pass filter (cut-off 128 s) was applied to remove low-frequency noise from the fMRI time series. In addition to the standard procedure of excluding low-intensity voxels (implicit masking), a binarized version of the standard gray matter mask provided by SPM8 was used as explicit mask. The following contrasts were computed: PEN > NEU, BOD > NEU and DIS > NEU. To assess hemodynamic changes at the group level, the results of these weighted contrasts (contrast images) were entered into a second-level flexible factorial model. We specified one factor (‘Contrast’, independence ‘no’; variance ‘equal’) with three levels representing the three contrast images. As covariates, we entered individual stIAT scores and subjective ratings for PEN stimuli. Because of multicollinearity between regressors, VAS-disgust ratings were orthogonalized with respect to stIAT scores. We specified one main effect (contrast) and three interaction effects (stIAT x contrast, VAS-disgust x contrast, VAS-pleasure x contrast).

Main contrasts and conjunctions between contrasts were thresholded at P < 0.05, family-wise error (FWE) corrected for multiple comparisons. Conjunction analysis was performed to investigate the overlap of PEN- and DIS-related brain activity following the more stringent ‘conjunction null hypothesis’ method. Correlations between contrasts and VAS and stIAT scores were initially thresholded at P < 0.001, uncorrected. In this instance, clusters were considered
significant if their peak voxel reached \( P < 0.05 \), FWE corrected for multiple comparisons. For the stIAT, we expected effects to occur in a rather circumscribed set of areas, and we therefore also accepted clusters that reached \( P < 0.05 \), corrected for a reduced search space. In the case of VAS ratings, we had no clear expectations on where brain activity would be sensitive to such ratings and we therefore adjusted the critical alpha for the fact that we included VAS ratings for two dimensions; rendering areas significant if they reached a FWE corrected \( P < 0.025 \). The mask that served as reduced search space for stIAT-related brain effects (8846 voxels) was designed to comprise all deep brain nuclei as well as cortical areas thought to mediate sexual interest (anterior insula, perigenual cingulate cortex and orbitofrontal cortex). A region-of-interest (ROI) representing bilateral anterior (agranular and dysgranular) insula was hand drawn on a brain template following the anatomical description in Nanetti et al. (2009). A ROI representing bilateral perigenual ACC was also hand drawn, following the description in Palomero-Gallagher et al. (2008). Caudate, putamen, accumbens, amygdala, hypothalamus, thalamus and pallidum ROIs were taken from the Harvard–Oxford Subcortical Atlas (http://www.cma.mgh.harvard.edu/), while basal forebrain and brainstem ROIs were hand drawn. Because of susceptibility artifact, the orbitofrontal cortex was not included in the mask.

RESULTS

Subjective evaluation of the still stimuli

Table 2 illustrates the subjective evaluation of each stimulus type on the dimensions of disgust, pleasure and (post hoc) general arousal. Participants’ picture ratings were subjected to a four picture (BOD, NEU, PEN and DIS) \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \times \time
modulated PEN-related activity. DIS- or BOD-related brain activity showed no relationship with stIAT scores. The nature of the interaction between individual stIAT and PEN-related brain activity was such that stronger negative PEN associations correlated with enhanced BOLD activity. Such modulation was significant in a limited number of areas: the right superior parietal lobule, the midbrain, the rostral basal forebrain and the right amygdala. The midbrain cluster was on the right side, centered ventrolaterally to the periaqueductal gray matter. The basal forebrain cluster was centered on the left bed nucleus of stria terminalis (BNST), but radiated medially to include the lateral septal nuclei (LS) and the same structures on the right side. Additionally, this cluster included the caudal-most part of the nucleus accumbens on both sides (Mai et al., 2003). Note that the cluster clearly stays dorsal and rostral to the anterior commissure (Figure 2), excluding the possibility that the hypothalamus was involved. Also note that for midbrain, basal forebrain and amygdala significance was obtained after correction for a reduced search space (see Materials and Methods section), which was justified because of our a priori expectation that deep brain areas would be most sensitive to modulation by the stIAT. Table 5 lists these effects, while in Figure 2 both their anatomical location as well as the relationship between BOLD activity and individual stIAT is depicted. There were no areas in the individual PEN > NEU maps where activity could be explained by increasing positivity of stIAT-PEN associations.

DISCUSSION

To our knowledge, this study is the first to examine the modulatory position of implicit PEN-disgust relative to PEN-'hot' associations in central VSS processing. The present findings first revealed that many parts of the brain responded to pornography (PEN) in the same way they responded to highly disgusting (DIS) stimuli. This was supported by the finding that the elicited disgust to PEN explained much more variance in PEN-induced brain activity than the elicited pleasure toward the same stimuli. Second, women with relatively negative (i.e. disgust-related) implicit PEN associations had the strongest PEN-related brain responses. However, this modulation applied to a limited set of mainly primordial brain areas (Figure 2). Furthermore, this relationship was specific for PEN: brain responses elicited by BOD or DIS were not modulated by PEN associations as measured on the stIAT, which supports the validity of this finding that it is not reflecting a general difference in stimulus processing. These findings delve into the complexity of processing VSS, and unveil the important modulatory role of disgust to these specific penetration stimuli, at least in women.

In this study, we meticulously controlled for phase of menstrual cycle, relationship status and type of anti-conception use. Moreover, the PEN stimuli we used were of a much more explicit nature than the erotica commonly used in sexual neuroimaging studies. Furthermore, we included an arousing but aversive control condition (DIS) to test the specificity of the findings. Indeed, a statistical test for shared brain activity in PEN- and DIS-related activation maps demonstrated substantial overlap between the two stimulus categories, which is in line with recent insights on central visual emotion processing that emotionally very distinct sexual and disgust stimuli bring out very similar brain activity (Stark et al., 2005; Walter et al., 2008; Karama et al., 2011). This overlap particularly pertains to deep brain structures like the amygdala, ventral pallidum, thalamus and midbrain, as well as neocortical areas like the Ventral Occipital Temporal (vOT) and Superior Parietal Lobule (SPL). At least some of this overlap (e.g. amygdala, thalamus, vOT and SPL) may be explained by the considerably heightened general arousal and attention that invariably accompany disgusting and erotic images (Walter et al., 2008).

Valence probably played a less significant role, if any: BOD was rated highest on 'pleasure', but PEN nevertheless induced much stronger activity in many brain areas (Figure 1). It could very well be that the BOD stimuli were relatively more pleasant due to their mildness, contrasting with the harsh edge of the PEN stimuli. PEN, on the other hand, was remarkable for eliciting moderate subjective disgust as well as pleasure, rendering it the most ambivalent among the present stimuli (Peterson and Janssen, 2007).

When we connected individual stIAT scores to brain activity, these scores selectively modulated the PEN activation maps, even when DIS activation maps were very similar (Figure 2). In line with a previous fMRI study that included IAT scores (Phelps et al., 2000), and with other fMRI studies on subliminal brain responses to VSS (Childress et al., 2008; Oei et al., 2012), this coupling predominantly involved deep brain areas. Specifically, stIAT-PEN scores modulated activity in the rostral basal forebrain the midbrain and the right amygdala (Figure 2). The only other area exhibiting this correlation was the right superior parietal lobule. This modulation in these areas turned out to be of a negative nature, namely, stronger PEN-disgust relative to PEN-'hot', implicit associations gave stronger activity (Figure 2). Women’s subjective reports of disgust toward PEN also correlated with midbrain and amygdala, whereas such a correlation was absent for pleasure ratings. Superior parietal lobule activity was connected to both VAS-disgust and VAS-pleasure, which corresponds to the idea that activity of this area reflects heightened attention to—or emotional capture by—bodies (Kret et al., 2011). Interestingly, SPL consistently activates in response to VSS (Georgiadis and Kringelbach, 2012), except when subjects begin to show signs of sexual arousal, e.g. penile erection (Cera et al., 2012; Georgiadis and Kringelbach, 2012). This could be taken to support that it is the initial heightened attention related to the processing of a highly emotional stimulus, and not the valence per se, that is reflected in the activation of this area. The finding that VAS-disgust explained more variance in PEN-induced brain activity than did the PEN-disgust stIAT is supported by similar observations for supraliminal vs subliminal processing of VSS (Gillath and Canterberry, 2012). This could be related to the stIAT being a very specific (and relative) measurement of two constructs (i.e. PEN-disgust vs PEN-'hot') whereas subjective appreciation includes a more comprehensive validation approach.

Intriguingly, some of the areas that showed a relationship with stIAT modulation (PEN-disgust vs PEN-'hot'), such as the basal forebrain/ nucleus accumbens, amygdala and the midbrain (Table 5; Figure 2), have in other studies tracked the positive hedonic value of VSS (Walter et al., 2008; Sescousse et al., 2010). This apparent inconsistency may be explained by the different types of VSS used across studies. The VSS presented in the earlier studies employed relatively soft stimuli such as single nudes (Childress et al., 2008; Sescousse et al., 2010), whereas the stimuli used in the present study are hardcore pornographic stimuli. Alternatively, some subcortical areas (amygdala and nucleus accumbens) are particularly well suited to mediate interactions between aversive and appetitive processing (Leknes and Tracey, 2008). The amygdala, for instance, houses different neuron populations that encode the hedonic value of conditioned visual reward and punishment cues at least in non-human primates (Paton et al., 2006). Such findings explain why an area may be found active under very different emotional circumstances. At any rate, within the confines of our study there was substantial overlap between the subjective appreciation and the more implicit associations toward PEN in their modulation of PEN-induced brain activity. The current findings thus suggest that even when a similar network of areas may be responsive to a wide range of VSS, such involvement does not necessarily reflect a positive affect.
Fig. 1 Main contrasts. A baseline emotional category of NEU was subtracted from a condition consisting of neutral male–female bodily interactions (BOD, A) and from a condition consisting of hardcore pornographic images focusing on PEN (B). PEN is clearly superior with respect to the BOLD activity it induces relative to NEU. However, most of these areas showed the same response to highly aversive DIS stimuli, as shown by a conjunction analysis on PEN > NEU and DIS > NEU activation maps (C). Activation maps were thresholded at $P < 0.001$, uncorrected for display purposes.

Fig. 2 Implicit associations with explicit pornography modulate subcortical responses to PEN. Implicit associations with explicit pornography modulate subcortical responses to PEN. The top half of the figure highlights two of the areas where activity is modulated by individual stIAT scores: the midbrain (right, green) and basal forebrain including BNST, LS and nucleus accumbens (left, red). The right amygdala involvement is also visible in the basal forebrain section. In the bottom part of the figure activity in these areas is plotted against individual stIAT scores. Mean activity from these areas was extracted with MarsBar, which used the PEN > FIX (fixation cross) contrast to ensure that effects were driven by the PEN condition. Note that activity in these areas clearly tracks with the relative negativity of stIAT scores (i.e. relative PEN-disgust associations). $P < 0.005$, uncorrected for display purposes (top half of figure).
The stITAT tapped in the more imprinted value attached to PEN. Such associations in memory tend to be more stable compared to the more deliberate attitudes, and their central signature accordingly was inclined toward the subcortical level in the present study. The question is how we can understand that these areas primarily reflected the negative implicit association with PEN stimuli. We have already seen that the amygdala may be capable of both appetitive and aversive processing (Leknes and Tracey, 2008), and that this relates to associative learning (Paton et al., 2006). The amygdala has been connected to implicit associations with race (Phelps et al., 2000), which is interesting because both race and sexuality have very strong moral connotations and associations with them and thus are likely to be influenced by cultural forces and social learning.

Unlike amygdala and midbrain, the basal forebrain did not show significant activation in the main PEN-contrast, or a significant association with subjective ratings. Thus we may conclude that its activity is particularly relevant to the workings of implicit associations (as measured by the stITAT). The cluster was centered on the left BNST, but included the LS and (part of) the nucleus accumbens. The BNST/LS has strong functional and anatomical ties with the midbrain and especially amygdala (Alheid et al., 1988). A recent review argued that BNST/LS is instrumental in producing a behaviorally appropriate response to a social stimulus, sexual incentives transmitted by a conspecific being a typical example (O’Connell and Hofmann, 2011). In male rats, their BNST/LS has indeed been connected to processing airborne sex odors (Powers et al., 1987). Likewise in men, clusters reported as ‘ventral striatum’ or ‘nucleus accumbens’, but located so medially that the BNST/LS likely contributed to the signal change, seem particularly responsive to VSS (Walter et al., 2008; Klucken et al., 2009; Sescousse et al., 2010). Thus, it seems reasonable to assume that human BNST/LS function has relevance for processing sexual signals. A different literature proposes that the BNST is most relevant in the elaboration of sustained anxiety states, whereas midbrain and amygdala activity is implicated in transient fear and conditioned fear responses (Walker et al., 2003; Duvarci et al., 2010; Somerville et al., 2013). Interestingly,

### Table 3 Contrasts of interest

<table>
<thead>
<tr>
<th>k</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Z-score</th>
</tr>
</thead>
<tbody>
<tr>
<td>PEN &gt; DIS</td>
<td>Mid temp gyr/occ temp c</td>
<td>3585</td>
<td>48</td>
<td>74</td>
</tr>
<tr>
<td>Right</td>
<td>(including contrastal struct)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PEN &gt; NEU</td>
<td>Mid temp gyr/occ temp c</td>
<td>12028</td>
<td>48</td>
<td>72</td>
</tr>
<tr>
<td>Right</td>
<td>(incl contrastal struct)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PEN &gt; NEU</td>
<td>Superior par lob</td>
<td>3584</td>
<td>44</td>
<td>28</td>
</tr>
<tr>
<td>Left</td>
<td>Inferior frontal gyrus</td>
<td>3629</td>
<td>10</td>
<td>26</td>
</tr>
<tr>
<td>PEN &gt; DIS</td>
<td>Midbrain/thalamus and post</td>
<td>21</td>
<td>4</td>
<td>28</td>
</tr>
<tr>
<td>PEN &gt; NEU</td>
<td>Ventral pallidum/amygdala</td>
<td>76</td>
<td>16</td>
<td>2</td>
</tr>
<tr>
<td>PEN &gt; DIS</td>
<td>Precentral gyrus</td>
<td>20</td>
<td>36</td>
<td>50</td>
</tr>
<tr>
<td>PEN &gt; DIS</td>
<td>Cerebellum</td>
<td>26</td>
<td>8</td>
<td>14</td>
</tr>
<tr>
<td>PEN &gt; DIS</td>
<td>Middle frontal gyrus</td>
<td>68</td>
<td>26</td>
<td>50</td>
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<tr>
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<td>40</td>
<td>30</td>
<td>5.43</td>
</tr>
<tr>
<td>PEN &gt; DIS</td>
<td>Anterior insula</td>
<td>7</td>
<td>16</td>
<td>4.84</td>
</tr>
<tr>
<td>PEN &gt; DIS</td>
<td>Hypothalamus/ventral pallidum</td>
<td>5</td>
<td>8</td>
<td>10</td>
</tr>
</tbody>
</table>

The results from the following contrasts are listed: BD0 > NEU, i.e. between images depicting neutral bodily male-female interaction and a neutral condition of inanimate objects; PEN > NEU, i.e. between hardcore pornography focused on PEN and the same inanimate objects; comparisons between PEN > NEU and DIS > NEU activation maps including a conjunction analysis showing the shared activity between them. Stimuli in the DIS condition depicted highly aversive DIS stimuli. All clusters listed reached P < 0.05, FWE corrected. The reverse contrasts (i.e. deactivations) did not yield significant clusters. Clusters are listed with coordinates (x, y, z) of the peak voxel in MNI standard space, and size (k-voxels). The peak Z-scores are provided. Inf = infinite; gyr = gyrus; mid = middle; occ = occipital; inf = inferior; par = parietal; lob = lobule; sup = superior; temp = temporal; post = posterior; c = cortex; contrastal struct = contrastal structures; incl = including.

### Table 4 Modulation of PEN-induced brain activity by subjective elicited affect

<table>
<thead>
<tr>
<th>VAS-disgust × (PEN &gt; NEU)</th>
<th>k</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Z-score</th>
</tr>
</thead>
<tbody>
<tr>
<td>Right</td>
<td>Calcarine gyr/mid occ gyr</td>
<td>242</td>
<td>26</td>
<td>76</td>
<td>10</td>
</tr>
<tr>
<td>PEN &gt; NEU</td>
<td>Inf occ gyr/occ temp c</td>
<td>11921</td>
<td>50</td>
<td>68</td>
<td>14</td>
</tr>
<tr>
<td>Right</td>
<td>Inf occ gyr/occ temp c</td>
<td>242</td>
<td>26</td>
<td>76</td>
<td>10</td>
</tr>
</tbody>
</table>

Individual PEN > NEU activation maps were correlated against subjective elicited disgust and subjective elicited pleasure as reported on the VAS. Interaction maps were thresholded at P < 0.001, uncorrected, but only clusters that reached P < 0.025, FWE corrected for multiple comparisons, are listed (because of two VAS scales tested, see Materials and Methods section). Clusters are listed with coordinates (x, y, z) of the peak voxel in MNI standard space, and size (k-voxels). The peak Z-scores are given along with corrected P-values. Gyr = gyrus; mid = middle; occ = occipital; inf = inferior; par = parietal; lob = lobule; sup = superior; temp = temporal; post = posterior; cing = cingulate; c = cortex; hipp = hippocampus; corr = corrected.

### Table 5 Modulation of PEN-induced brain activity by implicit PEN associations

<table>
<thead>
<tr>
<th>stITAT × (PEN &gt; NEU)</th>
<th>k</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Z-score</th>
</tr>
</thead>
<tbody>
<tr>
<td>Right</td>
<td>Sup occ gyr/sup par lob</td>
<td>172</td>
<td>28</td>
<td>76</td>
<td>42</td>
</tr>
<tr>
<td>PEN &gt; NEU</td>
<td>Midbrain</td>
<td>234</td>
<td>8</td>
<td>24</td>
<td>16</td>
</tr>
<tr>
<td>Right</td>
<td>Amygdala</td>
<td>72</td>
<td>28</td>
<td>6</td>
<td>20</td>
</tr>
</tbody>
</table>

Individual PEN > NEU activation maps were correlated against individual scores on the stITAT (with PEN-like stimuli as targets). Interaction maps were thresholded at P < 0.001, uncorrected, but only clusters that reached P < 0.025, FWE corrected for multiple comparisons, are listed. The basal forebrain cluster included left BNST, LS and part of the nucleus accumbens on both sides (see Results section for a detailed anatomical description). Clusters are listed with coordinates (x, y, z) of the peak voxel in MNI standard space, and size (k-voxels). The peak Z-scores are given along with corrected P-values. Gyr = gyrus; occ = occipital; sup = superior; par = parietal; lob = lobule; corr = corrected; *P < 0.05 FWE, for reduced search space (see Materials and Methods section for further details).
BOLD responses during visual sexual stimulation

BNST function is regarded as a reliable predictor of inter-individual differences in anxiety, (Duvarci et al., 2010; Somerville et al., 2013), which fits with the present finding that PEN-induced BNST/LS activity was sensitive to inter-individual variability in the way women connected implicitly to PEN. Translating this information to the present results, one might propose that BNST activity primarily reflected the tension between the social context and the sustained negative association with PEN. Midbrain and amygdala activity could then underlie the associated transient negative feeling of bewilderment.

Obviously, VSS carry high relevance for our social behavior: if preferred, such stimuli may make us want to approach. On the other hand, social learning mechanisms can alter the value attached to these stimuli in various directions, depending on elements like context and mnemonic associations. Whether the stIAT-related brain effects would be predictive of behavioral inhibition in real-life sexual situations remains to be investigated.

Several comments are in order here. First, we did not directly assess sexual desire or arousal, so it cannot be excluded that PEN-induced brain activation would also be related to subjective sexual desire, arousal or lust. Genital responses were not measured, and it can thus not be ruled out that these women did in fact show physiological sexual arousal in spite of their inclination toward negative appreciation of PEN (Laan and Everaerd, 1995b; Rellini et al., 2005; Both et al., 2011; Laan and Both, 2011). Additionally, based on the used design (which lacks an obvious positive valence stimulus category) it cannot be ruled out that the same modulatory effect of stIAT on brain activity would not also be observed in relation to a positive appreciation toward emotional stimuli. Second, the PEN stimuli were of a very explicit type, and both stIAT effects and stIAT-related modulations of brain activity may prove to be different with milder erotic stimuli. Third, the design of this study cannot resolve whether effects were due to implicit brain processes (like e.g. in a paradigm where pictures are presented subliminally), even when significant correlations between individual stIAT scores and BOLD activity were restricted almost exclusively to a subset of sub-cortical areas. This is relevant because similar activations have been found rather consistently in fMRI paradigms with on-magnet subliminal presentations of VSS (Childress et al., 2008; Gillath and Canterberry, 2012; Oei et al., 2012). Also, relevant is the point that although the IAT (interference) effects are assumed to be caused by participants’ implicit attitudes toward the target (e.g. PEN) stimuli (Greenwald et al., 1998), people do need to explicitly process the PEN stimuli in order to make the proper choices, even if participants are asked to do this categorization as fast as possible. In view of this, the link between stIAT and BOLD response may then reveal the shared component of the automatically activated affective (PEN-disgust) associations with explicitly processed sexual stimuli. As a final point, the spatial resolution of the present fMRI study makes it difficult to pinpoint activity to anatomical areas with relatively minor size, such as the BNST or LS.

CONCLUSION

The dependence of reproduction on sexual behavior often leads people into assuming that sexual cues have a fixed value and that associations with such stimuli are positive. However, human sexual behavior is flexible and complex. Over the course of our life there may be many experiences, circumstances, and cultural influences that shape the way we connect to particular sexual stimuli and consequently the attitudes we hold toward them. Our findings indicate brain activity that reflects an apparent negative appreciation toward pornography. This could be explained by attitudes toward porn imposed by social sexual morale, the lack of positive exposure and associations with porn or the mere difficulty to actually integrate the new learning with previous experiences toward a more positive appraisal. Psychological mechanisms like this may more frequently affect women (Widmer et al., 1998). In any case, our findings raise doubt whether all brain activity induced by such stimuli can safely be assumed to be a signature of a positive sexual incentive value, which is nevertheless the dominant sentiment in VSS neuroimaging studies. It seems more plausible that processes involved in assessing the meaning or significance of a possible sexual incentive in relation to associations in memory, experiences, context, and other elements, are major leads of brain activity. Future studies should try to dissect different routes for ambivalent, positive and negative sexual associations and to investigate how they influence subsequent behavior.

SUPPLEMENTARY DATA

Supplementary data are available at SCAN online.

Conflict of Interest

None declared.

REFERENCES

Karama, S., Armony, J., Bearegad, M. (2011). Film excerpts shown to specifically elicit various affects lead to overlapping activation foci in a large set of symmetrical brain regions in males. PLoS ONE, 6, e22343.


