

Understanding heterosexual women's erotic flexibility: the role of attention in sexual evaluations and neural responses to sexual stimuli

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Abstract

Many women experience desires, arousal and behavior that run counter to their sexual orientation (orientation inconsistent, 'OI'). Are such OI sexual experiences cognitively and neurobiologically distinct from those that are consistent with one's sexual orientation (orientation consistent, 'OC')? To address this question, we employed a mindful attention intervention—aimed at reducing judgment and enhancing somatosensory attention—to examine the underlying attentional and neurobiological processes of OC and OI sexual stimuli among predominantly heterosexual women. Women exhibited greater neural activity in response to OC, compared to OI, sexual stimuli in regions associated with implicit visual processing, volitional appraisal and attention. In contrast, women exhibited greater neural activity to OI, relative to OC, sexual stimuli in regions associated with complex visual processing and attentional shifting. Mindfully attending to OC sexual stimuli reduced distraction, amplified women's evaluations of OC stimuli as sexually arousing and deactivated the superior cerebellum. In contrast, mindfully attending to OI sexual stimuli amplified distraction, decreased women's evaluations of OI stimuli as sexually arousing and augmented parietal and temporo-occipital activity. Results of the current study constrain hypotheses of female erotic flexibility, suggesting that sexual orientation may be maintained by differences in attentional processing that cannot be voluntarily altered.

Key words: sexual arousal; sexual orientation; fMRI; women; mindfulness; attention

Despite advances in understanding women's sexuality, the ways in which sexual orientation—the overall pattern of attractions, desires and behaviors directed toward the same gender, other gender(s) or mixed genders—guides women's sexual processing remains elusive. Women's sexuality has proven 'fluid,' such that many women have the capacity to experience attractions, desires and behavior that run counter to their sexual orientation (e.g. Diamond, 2003, 2007, 2008, 2012; Chivers et al., 2004). Women

also show flexibility in their autonomic and subjective arousal. For example, heterosexual women, including those who report zero sexual attraction toward women, show comparable genital arousal to both male (consistent with their orientation consistent, or 'OC') and female (inconsistent with their orientation inconsistent, or 'OI') sexual stimuli (Chivers et al., 2007; Chivers and Timmers, 2012). Although heterosexual women's autonomic response exhibits a gender non-specific pattern, women

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evaluate and experience OC and OI sexual stimuli differently. The current study sought to understand women's erotic flexibility by examining how women attended to, sexually evaluated and neurally responded to OC and OI sexual stimuli. Further, we investigated whether an intervention designed to enhance women's attention to OI stimuli would change their subjective and neurobiological responses.

Understanding the sexual response informs potential differences in women's attention to and evaluation of OC and OI stimuli

Overview of the sexual response

The sexual response involves attending to sexual stimuli, experiencing autonomic and subjective arousal and culminates in sexual desire. The processes involved in the sexual response are associated with specific patterns of neurobiological activity (for a review, see Stoléru et al., 2012; see Table 1). Table 1 lists brain regions relevant to sexual stimuli, describes the general and sexual-specific functions and hypothesizes differences between OC and OI stimuli.

The information processing model (IPM; Janssen et al., 2000) describes two pathways of processing sexual stimuli. The first pathway describes the sexual response as a 'go system' that, without inhibition, automatically unfolds in the presence of a sexual stimulus (Spiering et al., 2004). In absence of a sexual stimulus, continuous inhibitory control of the sexual response occurs, resulting from tonic activity in the lateral temporal cortex (see Table 1; Stoléru et al., 2012). The presence of a sexual stimulus alleviates such inhibition, which leads to the unfolding of the sexual response (Stoléru et al., 2012). First, sexual stimuli are implicitly detected by drawing preconscious attention to the sexual elements. Implicit attention recruits the thalamus, locus coeruleus (Posner and Rothbart, 2007), and low-level visual areas (Sundaram et al., 2010) and triggers autonomic arousal. The hypothalamus incites autonomic arousal (Pfaus, 2009) and transmits visceral information to brain regions associated with autonomic processing and implicit appraisal (see Table 1).

Conscious awareness comes online during the second pathway, characterized by explicit attention and appraisal. Specifically, women orient their attention toward the sexual elements of the stimulus (associated with the frontoparietal network; Posner and Rothbart, 2007). The relevance of these sexual cues becomes encoded in the hippocampus and evaluated based on salience and reward value in the medial orbitofrontal cortex (OFC). Attention and appraisal feedback onto autonomic arousal and trigger further attentional processing to help sustain attention on the stimulus.

Whereas appraising the stimulus as sexual and rewarding augments autonomic sexual responses, negative appraisals or judgments deter further sexual processing. Negative judgments detract attention away from the sexual elements and direct women's attention towards the non-sexual elements of the stimulus (Spiering et al., 2007; Anderson and Hamilton, 2014) or away from the stimulus, altogether. Such distraction directly blocks subjective sexual responses (de Jong, 2009). The cognitive processes involved in distraction and judgment activate a specific pattern of neural activity associated with attentional shifting, mentalizing, inhibition and negative evaluation (see Table 1).

Following attention to and appraisal of stimuli as sexual and rewarding, somatosensory awareness ensues. Somatosensory awareness integrates emotional, cognitive and visceral experiences in the insula, and gives rise to the subjective experience of arousal—a physiological state of readiness for sexual activity.

These peripheral and central neural events culminate in a cognitively mediated state that motivates individuals to pursue sexual rewards, known as sexual desire.

OC and OI sexual responses

The implicit pathway of the IPM may respond to both OC and OI stimuli. Indeed, the gender non-specific pattern of heterosexual women's sexual responses to OC and OI stimuli has been evidenced across autonomic and genital arousal, early visual attention, and implicit processing of sexual cues (e.g. Sylva et al., 2013; Dawson and Chivers, 2016; Dawson et al., 2017). In contrast, explicit attentional and appraisal processing that characterize the explicit pathway of the IPM align with women's self-described sexual orientation (e.g. see Israel and Strassberg, 2009; Dawson et al., 2017; Chivers, 2017). However, results across studies vary. For example, some researchers have found that women show comparable levels of explicit attention to (Lippa et al., 2010), sexual appraisal of (Snowden and Gray, 2013) and subjective sexual arousal in response to (Bossio et al., 2014) both OC and OI stimuli and others have found that women implicitly process OC and OI stimuli differently (Sawatsky et al., 2018).

Given the mixed findings, differences between OC and OI sexual processing may depend on the interplay of implicit and explicit pathways. According to the IPM, explicit attention to sexual elements of the stimulus creates a positive feedback loop, heightening implicit sexual processing, whereas attention to non-sexual elements deters further sexual processing. Indeed, when heterosexual women view photographs void of non-sexual elements (i.e. penises, vulvas) women show greater genital and subjective arousal to OC stimuli (Spape et al., 2014). When women view stimuli that is less sexually explicit, such as nude photographs of male and female bodies, women's neurobiological response does not differ between OC and OI stimuli. Yet, when women view stimuli that is more sexually explicit (videos depicting sexual activity), they show greater neural activity to OC sexual stimuli across both implicit and explicit pathways, including implicit visual attention, somatosensory experiencing and sexual imagery (Safron et al., 2018). Hence, OC sexual stimuli facilitates positive feedback of the sexual response. In contrast, OI stimuli may capture attention and initiate the cascade of sexual processing, but may not be attended to or evaluated in a way that results in positive feedback between implicit and explicit pathways. Without positive feedback, women would not subjectively experience sexual arousal or desire.

Why might OC and OI sexual processing differ?

By definition, OC sexual experiences are more common and more relevant to women's romantic and sexual lives. Hence, women may be more likely to attend to and appraise OC stimuli as sexual and rewarding and interpret their physiology as sexually arousing. This is consistent with research demonstrating that women more quickly attend, maintain attention longer and report greater subjective sexual arousal for OC stimuli (Chivers et al., 2004; Israel and Strassberg, 2009). In contrast, OI sexual experiences are experienced as unexpected (Diamond, 2008) and may be less salient, given the inherent inconsistency with women's overall romantic and sexual interests. This is consistent with research demonstrating that heterosexual women interpret OI desires differently, describing them as less motivating and stemming from the 'heart,' rather than the 'gut' (Diamond, 2005; Thompson and Morgan, 2008). The inconsistency inherent to OI sexual experiences and the social stigma surrounding same-gender sexuality may lead heterosexual women

Table 1. Hypothesized regions associated with OI and OC sexual responses, listed by lobes of the brain

Region	General findings	Sexuality findings	OI > OC?
Limbic areas Thalamus	Has reciprocal connections to cortex, relaying sensory and motor information, necessary for conscious awareness (Llinás et al., 1998); involved in alerting attention (Posner and Rothbart, 2007); plays a role in general arousal, affective behavior, memory, emotion processing (Metzger et al., 2013), and predicting and selecting actions associated with reward (Lane et al., 1997; Doya, 2008; Knutson and Greer, 2008)	Responds to erotic stimuli (see Stoléru et al., 2012; Sylva et al., 2013); involved in emotional arousal associated with sexual stimuli (Karama et al., 2002; Metzger et al., 2010; Walter et al., 2008a; Walter et al., 2008b) and attentional processes in sexual arousal (Metzger et al., 2013); associated with perception of male genital arousal (Moulier et al., 2006; Redoute et al., 2000); activated in early stage of male sexual arousal (Sundaram et al., 2010); greater activity among sexually functional women vs women with sexual dysfunction (Woodard et al., 2013); inhibited among women with desire disorders (Cacioppo, 2017); greater activation during OC vs OI erotic photographs (Paul et al., 2008; Sylva et al., 2013)	OC > OI
Hypothalamus	Relays information and controls autonomic nervous system activity (Hull et al., 2006; Pfaff et al., 2006), releases hormones; controls basic bodily processes such as temperature, hunger, thirst, sleep (e.g. Sawchenko and Swanson, 1981); directly involved in the process of motivation and sexual motivation (Mathews and Edwards, 1977; Balthazard and Ball, 2007; Graham and Pfaus, 2012)	Lesions abolish sexual behavior in animals (Pfaff and Sakuma, 1979) and humans (Baird et al., 2007); activation is specific to processing of sexual intensity of erotic stimuli (Walter et al., 2008a); one of the first regions activated in male sexual arousal (Sundaram et al., 2010); inhibited among women with desire disorders (Cacioppo, 2017); greater activation in men than women (Hamann et al., 2004); activation in response to olfactory OC, but not OI stimuli (Savic et al., 2001); greater activation during OC vs OI erotic photographs (Sylva et al., 2013)	OC > OI
Hippocampus	Encodes and consolidates declarative memories (e.g. Olton and Paras, 1979) and modulates emotional memories (Phelps, 2004)	Responds to erotic stimuli (see Sylva et al., 2013); hypothesized to encode sexual stimuli in explicit memory and match prior sexual experiences with current situation (Spiering and Everaerd, 2007); initial activation associated with later recognition of stimuli (Hamann et al., 1999); activated during middle stages of male sexual arousal (Sundaram et al., 2010); responds to sexual stimuli among post-menopausal women, but only if they have been treated with testosterone (Archer et al., 2006); activated among normally functional women, but not among women with sexual desire and arousal disorders (Arnouw et al., 2009; Bianchi-Demicheli et al., 2011; Woodard et al., 2013)	OC > OI
Amygdala	Receives multimodal sensory inputs and relays information to limbic areas and prefrontal cortex (Stoléru et al., 2012), encodes in emotional implicit memory and modulates hippocampal activity associated with emotional memory consolidation (Labar and Cabeza, 2006), responds to stimuli that elicits fear, disgust and anger (Davidson and Irwin, 1999; Davis and Whalen, 2001) evaluation of emotional content, and responds to positive emotions (Breiter et al., 1996; O'Doherty et al., 2001a, 2001b), works with OFC to process emotional aspects of decisions associated with reward (Murray, 2007)	Responds to erotic stimuli, although evidence is mixed (Stoléru et al., 2012); responds to emotional nature of sexual stimuli and involved in the evaluation of complex emotional content associated with erotic stimuli (Ferretti et al., 2005; Walter et al., 2008a); specific amygdalar lesions impair ability sexual functioning in rodents (Mascó and Carrer, 1980; Hull and Dominguez, 2007) and cause hypersexuality in humans (Kluver and Bucy, 1939; Baird et al., 2004); deactivated in male sexual arousal (Georgiadis and Holstege, 2005); activated in later stages of male sexual arousal (Sundaram et al., 2010); greater activation among women with sexual dysfunction in some studies (Woodard et al., 2013), but other studies show amygdala activation among sexually functioning women (Arnouw et al., 2009) inhibited among women with desire disorders (Cacioppo, 2017)	OI > OC

Continued.

Table 1. Continued

Region	General findings	Sexuality findings	OC > OI?
Occipital lobe Middle occipital gyri	Basic visual processing	Correlated with subjective arousal in women (Arnow et al., 2009); activated early in sexual arousal (Sundaram et al., 2010a) and precedes erectile response in men (Arnow et al., 2002); related to sexually arousing character of sexual stimuli (Stoléru et al., 2012), normal functioning women show greater activation than women with sexual dysfunction (Arnow et al., 2009; Woodard et al., 2013); responds to sexual stimuli corresponding to one's sexual orientation (Ponseti et al., 2006)	OC > OI
Extrastriate cortex (BA17, 18, 19)	Higher order visual processing; has reciprocal connections to amygdala (Amaral et al., 1992); involved in emotional responses evoked by visual stimuli (Phan et al., 2002); visual perception of human body (Downing et al., 2001); modulates top-down attention (Corbetta et al., 1991; Stoléru et al., 1999)	Responds to erotic stimuli (Park et al., 2001); correlated with erection in men (Arnow et al., 2002); modulates interaction of sexual intensity and emotional valence of sexual stimuli (Valter et al., 2008a); activated during photos of genitals, regardless of orientation (Ponseti et al., 2006); activation among women with desire and arousal disorders (Cacioppo, 2017); no difference in OC and OI photographic stimuli (Sylva et al., 2013)	OI = OC
Temporal lobe Fusiform gyri (occipitotemporal) (BA37)	Processes visual information, object recognition and face and body perception (Yovel et al., 2008; Harris and Aguirre, 2010; Van Den Hurk et al., 2011)	Related to perception of sexual stimuli (Stoléru et al., 2012), correlated with subjective sexual arousal (Arnow et al., 2009); activated in response to visual sexual stimuli and odorous compounds of the preferred sex (Savic et al., 2001; Paul et al., 2008); activation greater in sexually functional women than women with desire and arousal disorders (Woodard et al., 2013); greater activation during OC vs OI erotic photographs (Sylva et al., 2013)	OC > OI
Lateral temporal cortex	Involved in language processing (Saygin et al., 2010); involved in memory encoding and shows inhibition in verbal processes; inhibitory neuronal activity occurs prior to initiation of output (Ojemann et al., 2009); involved in conceptual processing and mediates representations of motion features of action-related stimuli (Kable et al., 2005)	Believed to exert tonic inhibition over sexual arousal (Stoléru et al., 2012), deactivation in response to visual sexual stimuli (Maturilla and Yang, 2008), deactivation in response to tactile stimulation (Georgiadis et al., 2009); greater activity in women with low sexual desire compared to women without low sexual desire (Arnow et al., 2009)	OI > OC
Parietal lobe Inferior temporal-parietal junction/angular gyrus (BA39)	Higher level visual and language processing; part of the default mode network (Fox and Raichle, 2007); activated in evaluative processes of guilt (Berthoz et al., 2002; Takahashi et al., 2004); responds to novel stimuli, distractions and shifting attention (Posner and Rothbart, 2007)	Evidence is mixed. Responds to erotic stimuli (Stoléru et al., 2012; Wehrum-Osinsky et al., 2014); other studies show deactivated during erotic stimuli (Mouras et al., 2003) and manual stimulation (Georgiadis and Holsteg, 2005); lesions associated with hypersexuality (Klüver and Bucy, 1939; Devinsky et al., 2009); inhibited among women with desire and arousal disorders (Cacioppo, 2017); may have tonic inhibition over development of sexual arousal (Stoléru et al., 2012)	OI > OC
Inferior parietal lobe/supramarginal gyrus (BA40)	Visual attention, responding to new information and maintain attention (Posner and Rothbart, 2007), responds to desired actions (Lynch et al., 1977); alerts and integrates somatosensory attention (Singh-Curry and Husain, 2009)	Erotic stimuli (Stoléru et al., 2012; Wehrum-Osinsky et al., 2008); greater code for autonomic correlates of actions (Mouras et al., 2008); greater activation in response to masculinized faces among heterosexual women in the follicular phase (Rupp et al., 2009); greater activation among sexually functional women than women with desire and arousal disorders (Arnow et al., 2009); greater activation during OC vs OI erotic photographs (Sylva et al., 2013)	OC > OI

Continued.

Table 1. Continued

Region	General findings	Sexuality findings	OC > OI?
Superior parietal lobe (BA5 and 7)	Orients attention to sensory information and selects responses based on information (Wolpert et al., 1998; Fan et al., 2005; Posner and Rothbart, 2007); activates in response to distractors (Corbetta et al., 1995)	Responds to sexual desire (Georgiadis, 2012; Wehrum-Osinsky et al., 2014); differentiates sexual stimuli as pleasurable (Borg et al., 2014); greater activation during OC visual stimuli among men (Ponsetti et al., 2006; Hu et al., 2008); greater activation among sexually functional women than women with desire and arousal disorders (Bianchi-Demicheli et al., 2011)	OC > OI
Precuneus (BA7)	Episodic memory (Lundstrom et al., 2003; Lundstrom et al., 2005); involved in imagery, self-consciousness, reflective self-awareness (Lou et al., 2004) and default mode network (Fox and Raichle, 2007)	Activated during erotic stimuli (Stoleru et al., 2012), greater activation during the menstrual phase than ovulation (Georgiadis et al., 2009); greater activation among women with desire and arousal disorders than sexually functional women (Woodard et al., 2013)	OI > OC
Primary somatosensory cortex (BA1, 2, 3) Insula (joins parietal, frontal, temporal cortices)	Corresponds to the homunculus, somatosensory integration, and representation Visceral sensory processing, somatosensory awareness; representation of internal milieu; involved in consciousness and attention; integrates somatosensory, cognitive and emotional experiences (Critchley et al., 2001; Critchley, 2004; Critchley et al., 2004; Craig, 2009; Menon and Uddin, 2010; Critchley and Harrison, 2013; Simmons et al., 2013)	Responds to erotic stimuli (Stoleru et al., 2012), associated with tactile stimulation in men (Georgiadis, 2012), but not well understood in women Responds to erotic stimuli (Diamond and Dickenson, 2012); receives and sends genital sensory information (Moulier et al., 2006; Mouras et al., 2008; Stoleru et al., 2012); activation is hormonally mediated by testosterone (Banczerowski et al., 2001); greater activation among sexually functional women than women with desire and arousal disorders (Woodard et al., 2013)	OC = OI
Frontal lobe			
Dorsal ACC (BA 25, 32)	Involved in top-down attention; responds to initiation of goal-directed behavior; detects and monitors conflict and distractions (Bush et al., 2000; Fan et al., 2005; Posner and Rothbart, 2007)	Correlated with subjective sexual arousal in women; initiates erection in men (Robinson and Mishkin, 1968); thought to process sexual stimuli and associated in resolving conflict (e.g., see Stoleru et al., 2012); greater activation among sexually functional women than women with desire and arousal disorders (Bianchi-Demicheli et al., 2011); greater activation during OC vs OI erotic photographs (Sylva et al., 2013)	OC > OI
Rostral ACC (BA24, 25, 33)	Activated by emotional processing and biological drives (Denton et al., 1999); involved in emotion regulation and lesions mute emotions (Damasio and Van Hoesen, 1983; Whalen et al., 1998)	Responds to sexual stimuli (Hamann et al., 2004; Walter, et al., 2008b); implicated in conscious attempts to regulate arousal (Beauregard et al., 2001); assesses salience of emotional and motivation information to sexual stimuli (Ferretti et al., 2005); correlated with how much individuals feel they associated with sexual stimuli (Heinzzel et al., 2006); associated with level of sexual desire irrespective of the category or object of that desire (Kawabata and Zeki, 2008); greater activation among women with desire and arousal disorders than sexually functional women (Woodard et al., 2013)	OI > OC
Medial OFC or right lateral OFC (BA 10, 11, and 14)	Monitors reward value of stimuli and codes received reward (O'Doherty et al., 2001a, 2001b); adjusts future motivation and behavioral responses to rewards (Elliott et al., 1997; Moulier et al., 2006); integrates reward values and emotional arousal (O'Doherty, 2007)	Responds to sexual stimuli (Karama et al., 2002); activation is testosterone-dependent (Redouté et al., 2005); corresponds to rewarding aspect of sexual stimuli (Kim et al., 2006) and erection (Mouras et al., 2008); responds to attractive OC faces (Aharon et al., 2001; Kranz and Ishai, 2006; Ishai, 2007). Deactivated among women with desire disorders (Cacioppo, 2017). Greater activation during OC vs OI erotic photographs (Sylva et al., 2013)	OC > OI

Continued.

Table 1. Continued

Region	General findings	Sexuality findings	OC > OI?
Left Lateral OFC & gyrus rectus (BA47 and 12)	Activated by tasks requiring moral judgment (Möll et al., 2002); lesions result in lack of social restraint (Miller et al., 1986); involved in suppressing reward responses (Elliott et al., 2000; Arana et al., 2003; Kringsbach and Rolls, 2004; Zald et al., 2014)	Deactivated during sexual arousal (Stoléru et al., 2012); deactivation of lateral OFC depends on testosterone (Redouté et al., 2005); activated when instructed to inhibit emotional reaction to visual sexual stimuli (Redouté et al., 2000) and among individuals with desire arousals disorders (Arnow et al., 2009; Bianchi-Demicheli et al., 2011)	OI > OC
Medial PFC (BA8, 9 and 10)	Involved in the default mode network (Fox and Raichle, 2007), self-referential thought and higher-order processing of socially relevant stimuli (Gusnard et al., 2001)	Responds to erotic stimuli; negatively correlated with subjective and physiological arousal in men (Bocher et al., 2001; Moulier et al., 2006; Tsujimura et al., 2006); greater activation among women with desire and arousal disorders than sexually functional women (Arnow et al., 2009; Woodard et al., 2013)	OI > OC
Dorsomedial PFC (BA 8)	Involved in attentional control and switching attention and higher-order social processing (Fan et al., 2005; Menon and Uddin, 2010)	Responds to erotic stimuli; responds to emotional and sexual intensity of sexual stimuli (Walter et al., 2008a); increases attention to sexual and emotional stimuli (Walter et al., 2009); greater activation among naturally cycling women than women not using hormonal contraceptives (Abler et al., 2013)	OC > OI
Striatum/brain stem striatum (Putamen/caudate)	Involved in motor responses; involved in motivation and reward processing and executive attention (Posner and Rothbart, 2007)	Responds to erotic stimuli and induces erection in male primates (Stoléru et al., 2012); Greater activation during OC vs OI erotic photographs (Sylva et al., 2013); inhibited among women with desire disorders (Cacioppo, 2017)	OC > OI
Midbrain/ventral tegmental area	Contains dopamine-releasing neurons, responds to stimuli predicting future reward and signals unexpected reward (Schultz, 1986; Schultz and Romo, 1990; Schultz et al., 1997)	Responds to erotic stimuli (Borg et al., 2014); correlates with erection (Bocher et al., 2001); interrupts dopamine transmission inhibits copulation in rodents (Hull et al., 1995); associated with romantic love (e.g. see Diamond and Dickenson, 2012)	OC > OI
Basal forebrain/nucleus accumbens	Central component of reward system (Salamone et al., 2003); activated by expected or actual rewards and correlates with the salience of reward (Breiter et al., 2001)	Responds to erotic stimuli (Borg et al., 2014); responds to subliminal sexual stimuli (Oei et al., 2012); activation is unique to sexual processing of sexual stimuli (Walter et al., 2008a); greater activation among sexually functional women than women with desire and arousal disorders (Arnow et al., 2009); greater activation among OC desires for men, but not for women (Sylva et al., 2013)	OC > OI
Cerebellum	Involved in motor control, cognitive control and motivational processes (Schmahmann and Caplan, 2006)	Responds to erotic stimuli; may be associated with a 'feeling' experience associated with sexual arousal (Stoléru et al., 2012)	OC = OI

to negatively evaluate their OI sexual processing, maintain tonic inhibition or attend to non-sexual elements. If OI sexual processing is more prone to judgment and distraction, then enhancing non-judgmental attention to women's sexual experience might change the way women process OI stimuli.

Can mindful attention change the way women process OC and OI stimuli?

Mindfulness—paying attention to one's present-moment experience on purpose and non-judgmentally (Kabat-Zinn, 1994)—involves acknowledging one's emotional, visceral and cognitive responses with compassion and non-judgment. Mindfulness helps people to acknowledge and disengage from detrimental (Farb et al., 2010; Gard et al., 2011) and distracting appraisals (Frewen et al., 2008; Füstös et al., 2013). Mindfulness also disinhibits subtle evaluations suppressed from awareness (Garland et al., 2011), mindful attending to sexual stimuli may decrease negative judgments and augment conscious awareness of subtle sexual responses.

Mindfulness acts on the same cognitive processes triggered by the sexual responses. For example, mindful attention enhances orienting attention (Jha et al., 2007; Moore et al., 2012) through frontoparietal network activity (e.g. Ivanovski and Malhi, 2007; Lutz et al., 2008; Dickenson et al., 2013). Mindful attention facilitates the ability to sustain attention on the object of mindfulness and detect and disengage from distractions (Maclean et al., 2010; Malinowski, 2013), by activating the executive attention network and deactivating mind-wandering activity (Brewer et al., 2011; Hasenkamp et al., 2012; Dickenson et al., 2013). Mindful attention augments somatosensory awareness (Lane et al., 1998; Farb et al., 2012) through insula activity (Brefczynski-Lewis et al., 2007; Taylor et al., 2011; Dickenson et al., 2013). As such, mindful attention may mediate non-judgmental attention to sexual cues and may enhance positive feedback between explicit and implicit pathways of sexual response.

Indeed, mindfulness enhances sexual desire, subjective arousal, and alignment between subjective and autonomic arousal (Silverstein et al., 2011; Sommers, 2013). Mindfulness-based sex therapies show promise in treating sexual desire and/or arousal concerns (e.g. Brotto et al., 2008). Women with desire and/or arousal concerns show comparable levels of genital arousal as women without desire and/or arousal difficulties (Brotto et al., 2016) but explicitly attend to and appraise sexual stimuli differently, with greater distractibility and more negative judgments (De Jong, 2009; Nelson and Purdon, 2011; Fromberger et al., 2012). These women report benefiting from mindfulness-based therapies, reporting that mindfulness reduces worries and distractions, cultivates awareness of subtle sexual sensations, and facilitates their ability to maintain present-moment awareness of their sexual response (Brotto and Heiman, 2007).

Could mindfulness have a similar impact on attending to and evaluating OI stimuli as sexually arousing, which, on some level, might mirror the degree of distraction, judgment or subtlety of sensations? 'Participation,' being fully immersed in an activity, is a byproduct of mindful attention and women are better able to fully 'participate' in OC, compared to OI, stimuli (Bossio et al., 2013). If OI sexual experiences differ from OC sexual experiences in their explicit attentional processing as prior research indicates, then mindful attention might facilitate 'participation' to OI sexual stimuli, allowing women to attend to and evaluate OI stimuli as more sexually arousing.

The current study

The current study sought to understand women's erotic flexibility by assessing women's sexual evaluations (the degree to which women found OC and OI stimuli sexually arousing). This assessment allows women to evaluate sexual stimuli while also reflecting on their visceral, cognitive and/or emotional sexual experiences when viewing sexual stimuli. Because attentional processing directly impacts subjective sexual processing (Beck et al., 1983; De Jong, 2009), we also examined women's subjective distractibility to OC and OI stimuli. We compared differences in subjective evaluations and neural responses to OC and OI neutral and sexual stimuli and investigated how such patterns were affected when women consciously amplified mindful attention.

We hypothesized that OC stimuli would exhibit stronger interplay of the explicit and implicit pathways, as manifested by greater activity associated with implicit attention and autonomic arousal (primary visual areas, thalamus, brainstem, hypothalamus), orienting attention (frontoparietal network: inferior parietal lobule/supramarginal gyrus, superior parietal lobule, primary somatosensory cortex, dorsomedial prefrontal cortex), executive attention (executive attention network: dorsal anterior cingulate cortex, basal ganglia, dorsolateral prefrontal cortex), suppression of default mode network (the precuneus, angular gyrus, and medial prefrontal cortex), enhanced appraisal of stimuli as sexual and rewarding (medial OFC, hippocampus), suppression of negative appraisals (lateral OFC, amygdala) and enhanced somatosensory awareness (insula). We hypothesized that OI stimuli would exhibit more distraction and greater judgment (default mode network, left lateral OFC, amygdala). Mindful attention was expected to reduce distraction, increase subjective sexual evaluations of stimuli and change women's processing of OI stimuli through heightening attention and reducing negative appraisals, thereby attenuating the neurobiological differences between OC and OI stimuli.

Materials and methods

Participants

Participants were 29 single, heterosexually identified women aged 18–35, who reported a previous same-gender attraction and that no more than 30% of their overall pattern of attractions were directed toward women (see Table 2 and Supplementary materials). Because the menstrual cycle phase is a known moderator of sexual functioning and brain activity (e.g. Dreher et al., 2007; Rupp et al., 2009), all women had normal, natural menstrual cycles and completed the assessment near their ovulatory window. All women reported they were right-handed (Knecht et al., 2000) and had no neuropsychiatric conditions nor were taking medications that affect sexual functioning. This study was approved by the University of Utah Institutional Review Board.

Materials

Stimuli. Given the lack of standardized erotic stimuli and that female-centered pornography elicits greater sexual responses among women (Woodard et al., 2008), clips were derived from a feminist pornography website (Naughty, 2015), depicting 'real' people of varying degrees of attractiveness and body shape. To ensure that neurobiological differences were exclusively related to gender and limited confounding contextual factors associated with the type of sexual activity, sexual videos depicted men and

Table 2. Demographics of the sample

Variable	M (SD) n (%)
Ethnicity	
Caucasian	22 (75.9%)
Hispanic/Latino	3 (10.3%)
Asian or Pacific Islander	2 (6.9%)
Black or other	2 (6.9%)
Education	
GED or equivalent	3 (10.3%)
Some college	16 (55.2%)
Bachelor's or RN	6 (20.7%)
Some graduate school or higher	4 (13.8%)
Income	
Less than \$16 000	5 (17.2%)
\$16 000–\$35 000	11 (37.9%)
\$35 000–\$55 000	6 (20.7%)
\$55 000–\$75 000	3 (10.3%)
More than \$75 000	4 (13.8%)
Age	24.71 (4.86)
Body mass index	26.55 (5.63)
Previous experience practicing mindfulness ^a	9 (31.0%)
Number of lifetime male sexual partners ^b	27.36 (23.05)
Prior sexual contact with a woman ^b	15 (51.7%)

^an denotes the sample size for those who had practiced mindfulness 'never' to 'several' times (compared with those who had practiced mindfulness 'many times').

^bSexual activity is defined as any genital sexual contact (e.g. oral, manual, penetration).

women masturbating using their hands. In neuroimaging studies, differences in lighting, color, movement, cinematography and audio introduce significant confounds. Thus, videos were carefully chosen to ensure the similarity of such features. Neutral videos depicted the same individuals engaging in neutral activity shown in the non-sexual portion of the sexual imagery film (e.g. reading a book, talking during an interview).

To obtain the sufficient number of trials while mitigating imaging drift, 12 erotic and 12 neutral 30-s film clips, presented without sound, were organized into two 16-min 'runs' (E-Prime 2.0, Psychology Software Tools, Sharpsburg, PA), comprised of six blocks that specified the attentional tasks. Each block randomly presented four videos, one of each type of stimuli: male actor masturbating, female actor masturbating, male actor engaging in non-sexual activity and female actor engaging in non-sexual activity. Stimuli were presented in random order within and across blocks to mitigate any order effects and avoid confounds between a specific stimulus and condition type.

Subjective evaluations. To assess subjective evaluations to OC and OI stimuli (dependent variables for behavioral analyses), participants answered two questions after each video using a button box: 'To what extent did you find the stimulus sexually arousing?' and 'To what extent did you feel distracted?' on a 1 (not at all) to 4 (extremely) scale.

Procedure

Participants provided informed consent prior to completing an initial questionnaire. Starting on day 7 of their next menstrual cycle, participants performed ovulation tests. Those who received a positive test (34.5%) underwent the fMRI assessment within 48 h. The number of women who ovulated during the

study is consistent with prior research indicating variability in ovulatory cycles (e.g. Wilcox *et al.*, 2000). Those who never received a positive test completed the assessment during the standard ovulation window, days 14–16. Four of the 29 participants were imaged outside of this window due to scheduling difficulties.

At the imaging center, participants were oriented to the tasks and engaged in a practice run outside of the scanner, where they were trained in mindful attention, adapted from previous studies (Brotto *et al.*, 2016). Participants were instructed to non-judgmentally tune into the moment-by-moment experience of their bodies. The control task instructed participants to view the stimuli as they normally would, without shifting or monitoring their attention (see Supplementary materials).

After being situated in the scanner, participants engaged in two runs. First, participants completed two control task blocks (to ensure a baseline measure uninfluenced by toggling between attentional tasks), followed by two mindful attention blocks, one control task and one mindful attention block. The second run reversed this order. Each block consisted of visual instructions (7 s duration), followed by a set of four 30-s videos and ratings of their subjective responses following each video displayed for 5 s each (see Supplementary Figure S1). Three participants did not complete the second run, due to power outage and image reconstruction failure. Participants were debriefed and reimbursed for their time.

fMRI data acquisition

Scans were performed on a Siemens Prisma 3 Tesla scanner with a 64-channel head coil (Siemens). Functional data were acquired with a susceptibility weighted gradient echo EPI sequence (field-of-view 22 cm, spatial resolution 2.0 × 2.0 × 2.0 mm, TR = 1230 ms, TE = 33.2 ms, slice thickness 2 mm, flip angle 52°, multiband factor of 3). Each repetition acquired 72 oblique-axial slices. Resolution, echo time and slice angulation of ~30 degrees were chosen to minimize signal dropout in the OFC (Deichmann *et al.*, 2003). The first 10 image volumes were discarded to ensure signal equilibrium. Anatomic T1-weighted images were acquired using an MP2RAGE sequence (field-of-view 25.6 cm, spatial resolution 1.0 × 1.0 × 1.0 mm, TR = 5 s, TE = 2.93 ms, slice thickness 1 mm, flip angle 4°).

Analysis

Behavioral analysis. To assess how mindful attention affected participants' subjective responses, we ran a multilevel model (employed with HLM 7.0 software; Bryk and Raudenbush, 2002), where observations were nested within persons. To test the overall within-person association between sexual response ratings and each of the conditions, we ran an unconditional model, which estimated the within-person effects (OC vs OI stimuli, neutral vs sexual stimuli and control vs mindful tasks) and their interactions, controlling for time (trial number). Each condition type was effect coded so that the intercept represents the average rating across all conditions during the first trial.

Imaging analysis. Imaging data were analyzed using Statistical Parametric Mapping 12 (SPM12; Wellcome Trust, London). Motion correction of BOLD images was performed with a realign and reslice procedure. Anatomic images were coregistered to BOLD images and normalized onto a Montreal Neurobiological Institute (MNI) standard stereotactic space template brain. BOLD

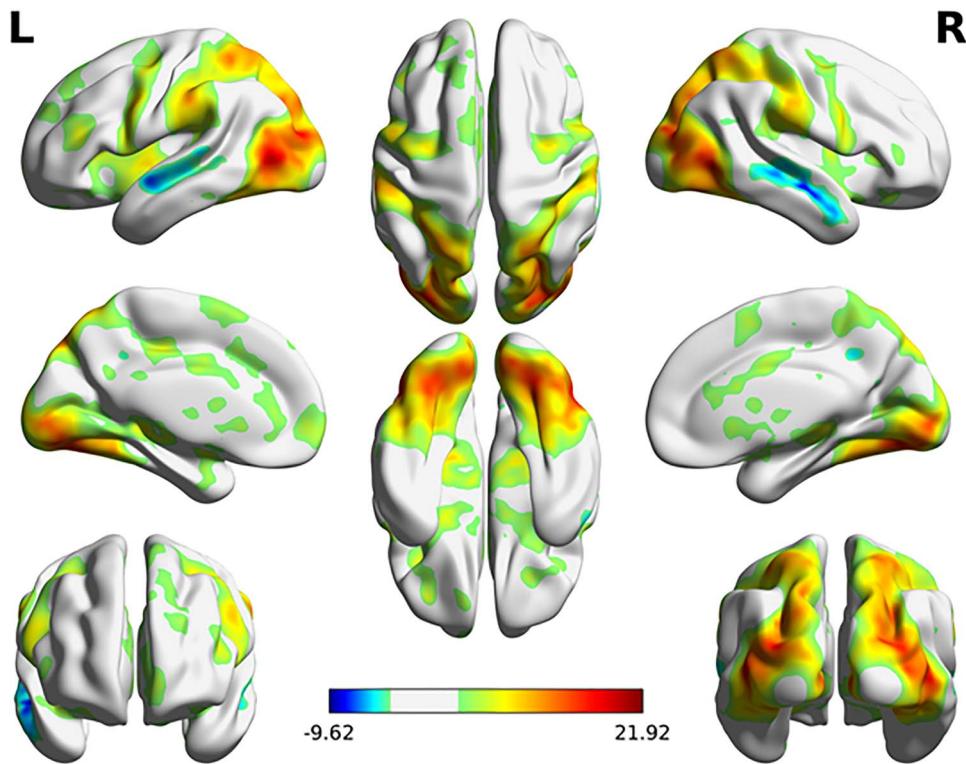


Fig. 1. Brain activation associated with erotic stimuli in predominantly heterosexual women. Color scale represents t-statistic for greater activation for sexual (positive values) vs non-sexual (negative values) stimuli. Results were thresholded for display at $P < 0.001$, uncorrected. Bottom images are shown from an anterior view.

images were smoothed using a 6 mm kernel. The model used a 2 (neutral/sexual) \times 2 (OI/OC) \times 2 (mindful attention/control task) within-subjects factorial design. Planned comparisons contrasted sexual vs neutral stimuli, OC vs OI sexual stimuli, OC mindful vs control sexual stimuli, OI mindful vs control sexual stimuli, OC vs OI for mindful and for control task sexual stimuli. Research using similar within-subject factorial designs suggests that a sample size of 30 provides sufficient power to detect the effects of interest (Desmond and Glover, 2002). Head motion parameters were included as regressors. Second level random-effect analysis across subjects was performed using a general linear model. A whole-brain analysis was conducted, using a cluster-defining threshold of $P < 0.001$ and a familywise error cluster correction of $P < 0.05$. Labels of regions were identified using the SPM Anatomy toolbox and corroborated using [neurosynth.org](#).

Results

Brain activation associated with the perception of sexual, compared to neutral, stimuli were dominated by the dorsal attention network (bilateral intraparietal sulcus, frontal eye fields), bilateral thalamus and hippocampus, and bilateral secondary visual cortex. Neutral, relative to sexual, stimuli elicited greater activity in the bilateral superior temporal sulcus (Figure 1; Supplementary Table S1). OC, relative to OI, sexual stimuli induced greater activation in the bilateral thalamus, right parietal cortex, bilateral OFC, bilateral primary visual cortex and left primary somatosensory cortex (Figure 2; Supplementary Table S2). In contrast, OI, relative to OC, sexual stimuli elicited greater activation in the lateral occipital cortex

bilaterally, left superior parietal lobe and left fusiform cortex (Figure 2; Supplementary Table S2).

Behavioral analyses of women's subjective sexual evaluations and distraction ratings (Table 3) revealed a significant interaction between orientation-consistency and task type ($\beta_6 = -0.14$, $SE = 0.07$, $T = -2.0$, $P = 0.046$). Simple slopes test revealed that women's sexual evaluations significantly increased ($\chi^2(2, N = 29) = 322.96$, $P < 0.0001$) when engaging in mindful attention, relative to the control task during OC stimuli ($b_{control} = 1.7$, $SE_{control} = 0.09$; $b_{mindful} = 1.79$, $SE_{mindful} = 0.10$), such that they found OC stimuli 'somewhat' arousing (i.e. nearly a 2 on the four-point scale). In contrast, engaging in mindful attention decreased women's sexual evaluations of OI stimuli ($\chi^2(2, N = 29) = 276.26$, $P < 0.0001$; $b_{control} = 1.58$, $SE_{control} = 0.10$; $b_{mindful} = 1.52$, $SE_{mindful} = 0.11$), such that women found OI sexual stimuli minimally arousing (i.e. 1.5 on the four-point scale).

With regard to distraction ratings (Figure 3; Table 3), we found a significant three-way interaction ($\beta_8 = 0.27$, $SE = 0.14$, $T = 1.98$, $P = 0.048$). Simple slopes (Figure 3B) revealed that women's distraction levels differed across OC for neutral ($\chi^2(2, N = 29) = 473.83$, $P < 0.0001$) and sexual stimuli ($\chi^2(2, N = 29) = 218.83$, $P < 0.0001$). Women were less distracted when engaging in mindful attention for OC neutral stimuli ($b_{control} = 1.85$, $SE_{control} = 0.09$; $b_{mindful} = 1.78$, $SE_{mindful} = 0.12$), OC sexual stimuli, ($b_{control} = 2.08$, $SE_{control} = 0.10$, $b_{mindful} = 1.96$, $SE_{mindful} = 0.11$) and OI neutral stimuli ($b_{control} = 1.69$, $SE_{control} = 0.12$; $b_{mindful} = 1.57$, $SE_{mindful} = 0.12$). Yet, women became more distracted when they mindfully attended to OI sexual stimuli ($\chi^2(2, N = 29) = 261.6$, $P < 0.0001$; $b_{control} = 1.57$, $SE_{control} = 0.10$; $b_{mindful} = 1.66$, $SE_{mindful} = 0.12$). Thus, mindful attention shifted reduced distraction and augmented sexual evaluations for OC stimuli but worsened distraction and weakened sexual evaluations for OI stimuli.

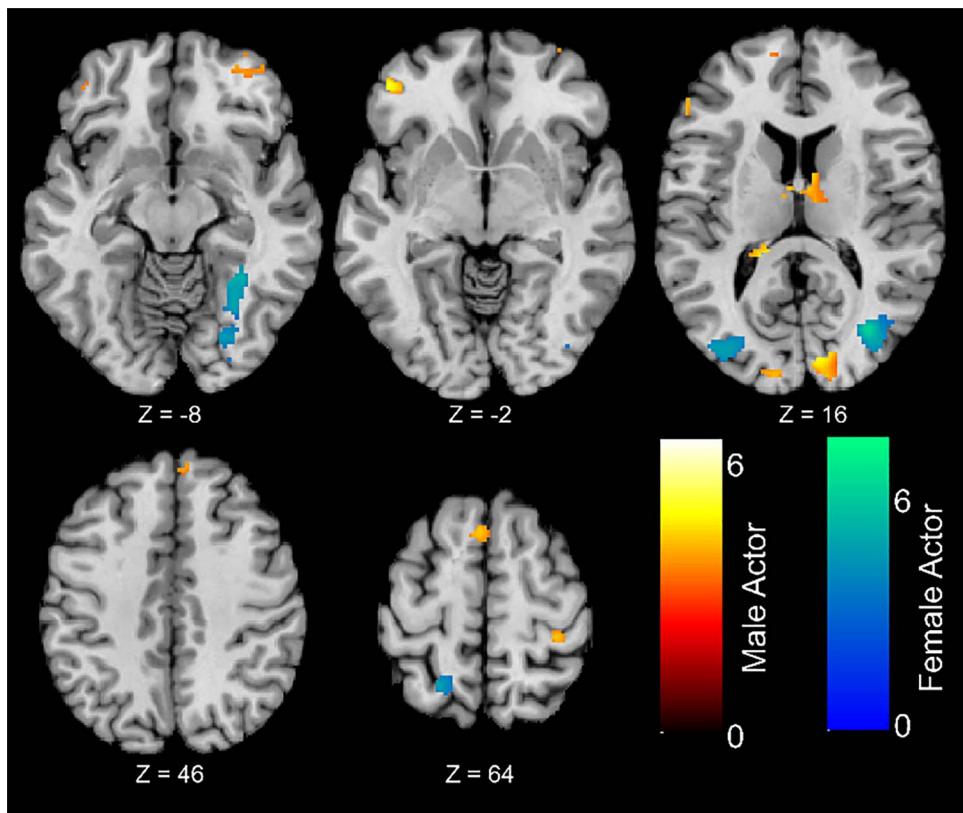


Fig. 2. Brain activation greater during OC vs OI stimuli (warm colors) and greater during OI vs OC (cool colors) stimuli. The color scale represents t-statistics. Slice z-coordinates below the images represent MNI space slice locations. Images are in neurological format with the left hemisphere on the left of the image. Images were thresholded for display at $P < 0.001$, uncorrected.

Table 3. Multilevel models assessing subjective arousal and distraction ratings across conditions

Model term	Coefficient	Standard error	95% CI	T	P-value	Random effect
DV: Arousal ratings						
Intercept	1.65	-0.09	1.61; 1.69	18.50	<0.001	0.236 (0.486)*
Trial number	0.00	0.00	-0.00; -0.00	-0.11	0.911	
Stimulus type (Sexual = 1)	0.75	-0.09	0.75; 0.75	8.35	<0.001	
Condition (OI = 1)	-0.20	-0.08	-0.20; -0.19	-2.41	0.016	
Task type (Mindful = 1)	0.02	-0.03	0.02; 0.02	0.69	0.492	
Stimulus type*condition	-0.06	-0.11	-0.06; -0.05	-0.56	0.574	
Stimulus type*task type	-0.08	-0.05	-0.09; -0.08	-1.60	0.110	
Condition*task type	-0.14	-0.07	-0.14; -0.13	-2.00	0.046	
Stimulus type*condition* task type	-0.18	-0.09	-0.18; -0.17	-1.88	0.060	
DV: Distraction ratings						
Intercept	1.77	0.09	1.73; 1.81	18.97	<0.001	0.221 (0.470)*
Trial number	0.01	0.00	0.01; 0.01	3.40	0.002	0.000
Stimulus type (Sexual = 1)	-0.29	0.05	-0.30; -0.29	-5.72	<0.001	
Condition (OI = 1)	0.10	0.05	0.10; 0.10	1.87	0.061	
Task type (Mindful = 1)	-0.05	0.05	-0.06; -0.05	-0.99	0.321	
Stimulus type*condition	-0.22	0.07	-0.22; -0.21	-2.92	0.004	
Stimulus type*task type	0.08	0.06	0.08; 0.08	1.39	0.165	
Condition*task type	0.08	0.08	0.07; 0.08	0.99	0.323	
Stimulus type*condition* task type	0.27	0.14	0.26; 0.28	1.98	0.048	

Notes: All effects were dummy coded such that for condition, OI received a value of 1; for stimulus type, sexual stimuli received a value of 1; and for task type, mindful attention received a value of 1. The name of the effect received a value of 1. The random effect of time was dropped from the model if not significant. * $p < .05$

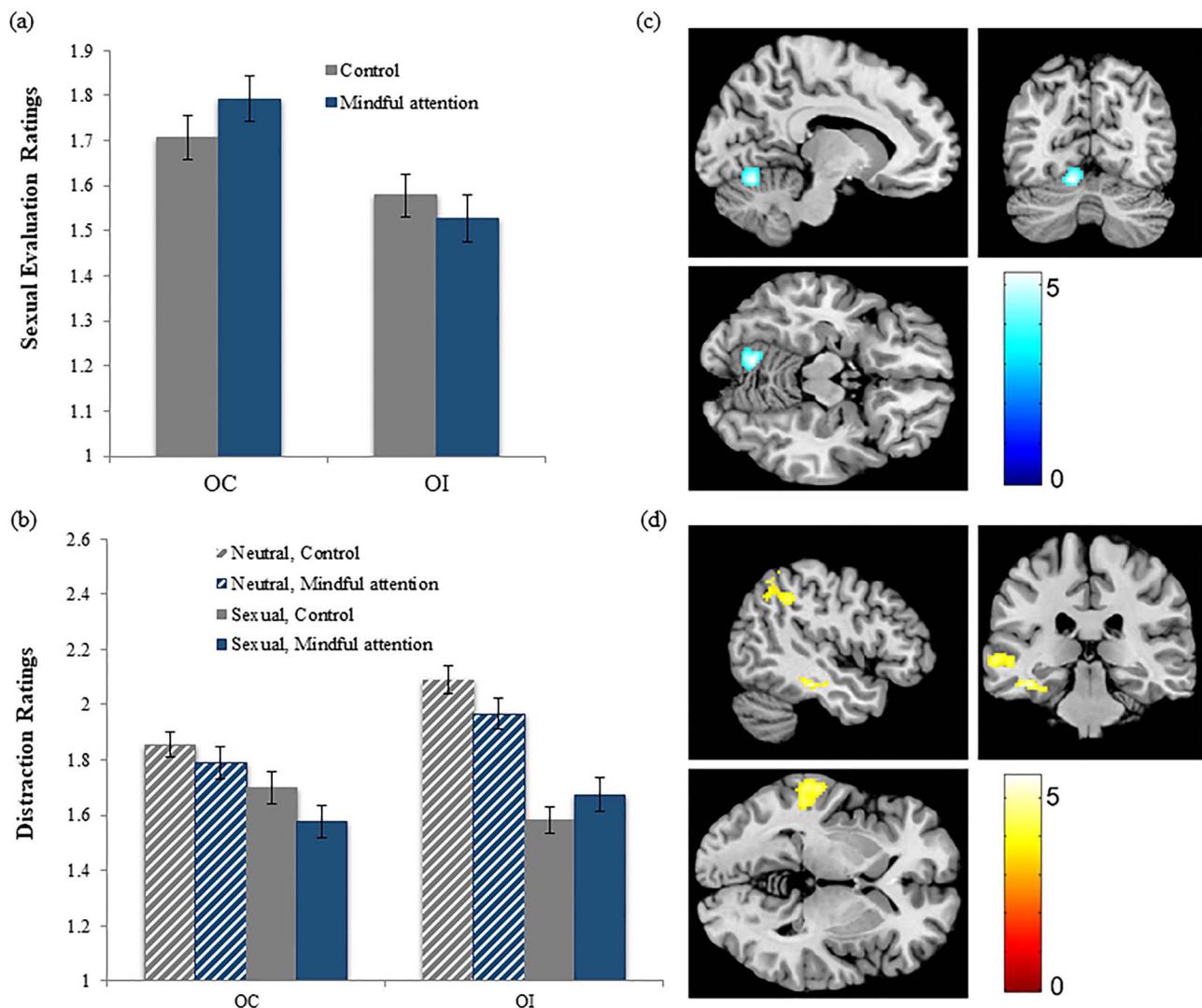


Fig. 3. Effect of mindful attention on (a) arousal ratings and (b) distraction ratings and neural activation comparing mindful attention to the control task during (c) OC sexual stimuli and (d) OI sexual stimuli. Regions of activation that are greater during mindful attention than control task (mindful attention > control task) are shown in warm colors and regions of activation that are greater during the control task compared to mindful attention (control task > mindful attention) are shown in cool colors, displayed at $P < 0.001$, uncorrected. Sexual evaluations and distraction levels were rated on a 1–4 scale from not at all to extremely. Error bars represent standard errors.

We also compared brain activity across mindful attention and control tasks for OC and OI sexual stimuli (Supplementary Table S3; Figure 3). Across OC sexual stimuli, mindful attention (relative to the control task) was not associated with any increases in BOLD signal, but showed deactivation of a cluster encompassing a portion of the left lingual gyrus and superior cerebellum (Supplementary Table S3; Figure 3C). Across OI sexual stimuli, mindful attention (relative to the control task) was associated with greater neural activity in the superior parietal lobule, intraparietal sulcus, supramarginal gyrus, and angular gyrus, and the middle and inferior temporal lobes (Supplementary Table S3; Figure 3D).

Finally, we explored differences between OC and OI sexual stimuli across the mindful attention task alone. Greater neural activity during OI, compared to OC, sexual stimuli remained the same in the mindful attention task as when we compared OI > OC sexual stimuli across both mindful attention and control tasks (compare Figure 2 with Supplementary Figure S3). Whereas we found various regions that were more active in

response to OC sexual stimuli, compared to OI sexual stimuli across both attentional tasks (mindful attention and control task), these differences disappeared when examining only the blocks of mindful attention. That is, no brain regions showed heightened activity when participants mindfully attended to OC (compared to OI) sexual stimuli (see Supplementary Figure S3 and Figure 2).

Results did not differ when we covaried degree of same-sex attraction, the timing of the assessment relative to the day of their cycle, or obtaining a positive ovulation test prior to the assessment.

Discussion

We found that OC, relative to OI, sexual stimuli elicited greater activity in brain regions involved in automatic visual processing, executive attention and appraisal whereas OI, relative to OC, sexual stimuli elicited greater activity in brain regions involved

in complex visual processing and shifting attention. In contrast to our hypothesis that mindful attention would enhance the sexual processing of OI stimuli, results suggest that mindful attention augments women's natural-occurring responses—increasing sexual evaluations of OC sexual stimuli but decreasing sexual evaluation of OI sexual stimuli.

Consistent with prior neuroimaging research on men's processing of sexual stimuli (see Table 1), women's neural responses to sexual, relative to neutral, stimuli activated regions associated with autonomic processing (midbrain, periaqueductal gray, posterior insula), attention (frontoparietal network, thalamus, anterior cingulate cortex, middle prefrontal cortex and lateral prefrontal cortex), appraisal (OFC, hippocampus), somatosensory awareness (anterior insula), motor imagery (cerebellum, premotor cortex) and deactivated areas involved in inhibition and devaluation (lateral temporal cortex, amygdala). These findings provide neurobiological support for the information processing model of the sexual response (e.g. see also Janssen et al., 2000; Chivers, 2017) and corroborate existing neurobiological models of sexual arousal (see Stoléru et al., 2012).

Differences across women's OC and OI sexual processing

Importantly, women showed greater neural activity in the primary and secondary visual cortices and the thalamus. Primary and secondary visual areas are the first areas to receive visual input and the thalamus serves as a relay station to transmit relevant motor and sensory information to the cortex necessary for conscious awareness. These areas have been implicated in preconscious attention, precipitate male erectile responses, and are related to perceptions of arousal (see Table 1). Together, these findings suggest that women process OC stimuli on a more implicit level, marked by basic visual processing and implicit attention.

According to the IPM, preconscious visual attention serves to draw one's attention to the sexual properties of the stimuli and trigger autonomic arousal and implicit appraisal. Although women showed greater neural activity associated with autonomic arousal in response to sexual, compared to neutral stimuli, these regions responded similarly to OC and OI sexual stimuli. On a neural level, women hold similar representations of autonomic or visceral responses across OC and OI sexual stimuli. This pattern of results indicates that women's sexual orientation is more likely constrained by early implicit attention than by autonomic arousal or visceral sensations.

Predominantly heterosexual women showed greater processing in the explicit pathway. Women evaluated OC stimuli as more sexual and less distracting and women's self-report mirrored the pattern of neural activity. When women viewed OC sexual stimuli, their brain showed greater activity in regions associated with volitional attention (e.g. dorsolateral and dorsomedial prefrontal cortex) and explicit appraisal (orbitofrontal areas, which evaluates and encodes reward value of punishers and integrates reward with emotional arousal), but not somatosensory awareness. Situating these findings in the context of the IPM suggests that women explicitly appraise OC stimuli as more sexual and more rewarding and better sustain volitional attention to OC, compared to OI, sexual stimuli, but are not any less aware of their sexual sensations toward OI sexual stimuli than they are for OC sexual stimuli. Hence, women may be just as aware of their somatosensory response to OI stimuli as they are to OC stimuli, suggesting that women's erotic flexibility is not related to differences in or a lack of somatosensory awareness. Rather,

differences between OC and OI sexual stimuli appear to be driven by attentional processing.

Additionally, OC stimuli elicited heightened activity in regions associated with sexual imagery and, unexpectedly, speech production and language processing. One possibility is that OC stimuli elicited self-referential mentalizing in the default mode network and Broca's and Wernicke's areas represent associated 'self-talk' (Raichle et al., 2001). Alternatively, the angular gyrus, premotor cortex, Broca's area, somatosensory cortex and inferior temporal areas comprise the extended mirror neuron system (Caspers et al., 2010). The greater self-relevance of OC stimuli may facilitate the linkage between women's observations of male masturbation and their own experience in response to this behavior. Future research should investigate how mentalizing, sexual imagery and self-referential processes contribute to OC sexual responses.

OI sexuality is not related to inhibition or judgment. In contrast to the hypothesis that women would be more likely to judge and negatively evaluate OI sexual stimuli, neural responses to OI, relative to OC, sexual stimuli showed no neural differences associated with judgment or negative evaluation. Rather, women responded to OI sexual stimuli with greater activity in higher order visual association areas, such as the fusiform gyri, involved in body and face perception, modulation of volitional attention and responses to genitalia and attractive faces, regardless of sexual orientation (see Table 1). As well, women showed greater activity in the superior parietal lobe (which acts in orienting attention, responding to distractors, and rearranging information to modify perspectives; Van Assche et al., 2014) and the posterior angular gyrus (involved in decoding symbolism and serves as a linking hub to transform visual input into associations; Caspers et al., 2012). Whereas predominantly heterosexual women visually process OC stimuli implicitly and automatically, OI visual processing is more elaborative, emphasizing face and bodily perception and modulating shifts in attention, meaning and perspective. Hence, OI stimuli might require more active symbolic interpretation that prompts predominantly heterosexual women to shift their perspective. This attentional and perspective shifting corroborates the very nature of OI stimuli—an inconsistency with women's orientation.

The relative impact of mindful attention

Mindfully attending to OC stimuli enhanced women's evaluations of OC stimuli as more sexually arousing and suppressed neural activity. Specifically, deactivation in superior cerebellum/lingual gyrus (involved in the visual processing of faces and complex visual processing) suggests that mindful attention operates by suppressing complex visual or facial processing. This is consistent with prior research demonstrating that mindfulness may operate by acting as an enhanced recovery phase that suppresses, rather than activates, neurobiological activity associated with general arousal (Dickenson et al., 2019).

Mindfully attending to OI sexual stimuli reduced women's evaluations of OI stimuli as sexually arousing, but heightened activation in regions associated with complex visual processing and attention. The angular gyrus and superior parietal lobule work together to detect novel stimuli, distractions and to shift attention (Corbetta et al., 2008). These results extend findings concerning the role of distraction in inhibiting sexual responses (e.g. De Jong, 2009). Specifically, neural responses to OI stimuli are marked by attentional shifting, which is further enhanced by mindful attention, and ultimately weakens subjective sexual

attention and evaluation. Importantly, these results indicate that the direction of one's subjective sexual processing cannot be changed by volitionally altering attention or appraisal. Hence, the underlying mechanism that guides sexual orientation and deviations in sexual responses is distinct from explicit attentional and appraisal processes.

Within the specific direction of one's sexual processing, mindful attention can impact the magnitude of evaluating sexual stimuli as arousing. That is, mindful attention facilitates sexual evaluations of genders that women typically find arousing (OC) and impedes sexual evaluations of genders that women find less arousing (OI). Women felt less distracted when viewing OI in a sexual, relative to a neutral, context and mindful attention improved women's attentional focus toward OI neutral stimuli. However, mindful attention exacerbated women's distraction toward OI sexual stimuli. This pattern of results suggests that women were not feeling distracted by OI stimuli until they were asked to attend their bodies in a sexual context. Such pattern of findings also suggests that women were similarly subjectively responsive to the sexual content in the absence of mindful attention to their bodily sensations. Perhaps results were due to the specific attentional processes altered, such that greater explicit monitoring (e.g. monitoring non-judgment and bodily sensations) may have overridden women's implicit enjoyment of OI sexual stimuli. An important avenue for future research is to investigate the pathways by which specific forms of attention may impede or enhance compassion and sexual pleasure.

Specifically, mindful attention can shift attention either by heightening a detached, observational stance, attending to a stimulus as a third-party observer, or by heighten one's ability to fully immerse oneself within an activity. Previous research has found that immersive attention increases subjective arousal, whereas more observational forms of attention reduce women's subjective arousal (Both et al., 2011). Women are more likely to employ immersive attention to OC stimuli and employ detached, observation to OI stimuli (Bossio et al., 2013). Moreover, immersive participation has been associated with a lack of frontal lobe activation (Dietrich, 2003). Hence, mindful attention may have reduced effortful attention, through suppressing complex visual processing in OC stimuli. In contrast, mindful attention may increase detached observation to OI stimuli, which should then increase effortful attentional shifts, thereby decreasing arousal. Although we did not measure immersive or observatory attention, results suggest that sexual processing may be enhanced or attenuated based on the specific form of attention mindfulness augments. Investigating the pathways by which specific forms of attention account for the ways in which mindful attending to OC and OI stimuli impact sexual responses could explain the diversity of effects across mindfulness-based therapies for sexual desire and arousal concerns (Brotto et al., 2012). Our findings suggest that sexual orientation, rather than erotic flexibility, guides women's sexual processing and attempting to change attentional processing only magnifies the effect of sexual orientation on women's sexual processing.

Limitations and future directions

Inferring function from brain activation cannot serve as a proof of function. Nonetheless, identifying relevant brain regions helps to narrow the range of processes potentially involved. Additionally, our single-item measure of sexual response was limited to evaluating the stimulus as sexually arousing and does not reflect a specific aspect of sexual response. These limitations are also

strengths, in that we were able to test our specific hypotheses because we engaged in careful inference of brain function and because our measure of sexual evaluation was not limited to a specific aspect of sexual response.

Although prior research indicates that one training session is sufficient to induce emotional regulation benefits (Arch and Craske, 2006), we know little about how many instances of mindful attention training are required to elicit changes in the processing of sexual stimuli. Although we were unable to determine how effectively participants were able to toggle between mindful attention and control tasks within the short epochs or assess for demand characteristics related to OC and OI stimuli, women's self-reported level of distraction did, in fact, decrease as a result of the mindful attention task for OC and OI neutral stimuli. Future research should explore how these factors influence the degree to which participants are able to direct their attention to present-moment sensations to OC and OI desires, attractions, and arousal with compassion and non-judgment.

The current sample included predominantly heterosexual cisgender women who were willing to undergo brain scans while watching erotic films. Moreover, the sample mirrored the racial demographics of the state in which this study was conducted (mostly white). Among these women, we found that attempting to change attentional processing only magnified the effect of sexual orientation on women's sexual processing. A critical direction for future research is to investigate subjective and neurobiological differences between OC and OI desires among women of various orientations, genders (including transgender and gender non-binary individuals) and ethnicities/races. A particularly intriguing direction is to examine differences between the same and other gender(s) desires of bisexual women (who rarely report that their desires for all genders are absolutely equivalent in frequency and intensity) and pansexual women (who report attraction toward a person, rather than a specific sex/gender).

Conclusion

The current study contributes to a growing body of research examining the specificity of neural response to OC and OI sexual stimuli. Imaging and behavioral results suggest that sexual processing of OI stimuli is not inhibited as a result of negative evaluation, but require shifting attention and perspectives and that OI sexual responses are more prone to distraction due to attending to non-sexual visual elements of the stimulus. In contrast, OC stimuli were processed in a more automatic way and associated with greater volitional attention and appraisal processes. Mindfulness exacerbated women's tendency to evaluate OI stimuli as less sexually arousing. Yet, mindfulness enhanced women's evaluations of OC stimuli as sexually arousing, by reducing brain activity (suppressing extrastriate/cerebellar areas). Such findings hint that automaticity may be more essential than explicit attention and appraisal in directing predominantly heterosexual women's sexuality. Sexual orientation, rather than erotic flexibility, guides how women sexually respond to various genders, and such variation appears to be maintained by differences in visual and attentional processing that cannot be voluntarily altered. The current study constrains hypotheses of female erotic flexibility, suggesting that flexibility or changes in sexual orientation should not be conflated with volition or control.

Supplementary data

Supplementary data are available at SCAN online.

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Conflict of interest

Declaration of interest: None.

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