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TARGET ARTICLE

The Specificity of Women's Sexual Response and Its Relationship with Sexual Orientations: A Review and Ten Hypotheses

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Abstract Category-specific sexual response describes a pattern wherein the individual shows significantly greater responses to preferred versus nonpreferred categories of sexual stimuli; this pattern is described as gender specific for sexual orientation to gender, or gender nonspecific if lacking response differentiation by gender cues. Research on the gender specificity of women's sexual response has consistently produced sexual orientation effects, such that androphilic women (sexually attracted to adult males) typically show gender-nonspecific patterns of genital response and gynephilic women (sexually attracted to adult females) show more gender-specific responses. As research on the category specificity of sexual response has grown, this pattern has also been observed for other measures of sexual response. In this review, I use the Incentive Motivation and Information Processing Models as complementary frameworks to organize the empirical literature examining the gender specificity of women's sexual response at each stage of sexual stimulus processing and response. Collectively, these data disconfirm models of sexual orientation that equate androphilic women's sexual attractions with their sexual responses to sexual stimuli. I then discuss 10 hypotheses that might explain variability in the specificity of sexual response among androphilic and gynephilic women, and conclude with recommendations for future research on the (non)specificity of sexual response.

Keywords Women · Sexual arousal · Sexual desire · Sexual psychophysiology · Genital response · Sexual orientation

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Introduction

Over a decade ago, I led an article describing a gender difference in the specificity of genital sexual response (Chivers, Rieger, Latty, & Bailey, 2004), coining the term "category-specific" to describe a pattern of sexual response that differentiates between preferred and nonpreferred categories of sexual stimuli. For the 2004 studies, gender was the category of interest: Briefly, men showed a gender-specific pattern, with gynephilic men (sexually attracted to adult females) responding more to sexual stimuli depicting females, and androphilic men (sexually attracted to adult males) showed the inverse pattern. In contrast, both androphilic and gynephilic women showed a gender-nonspecific pattern, responding similarly to stimuli depicting men or women.

Prior to this article, the dominant thinking regarding women's sexual orientation (the direction of sexual attractions) was mostly informed by models of men's sexual orientation (Chivers, 2005, 2010) wherein sexual attractions, sexual identities, and sexual responses are highly correlated and generally stable over time (Mustanski, Chivers, & Bailey, 2002). The sexual psychophysiology and sexual orientation literature was predominantly focused on assessment of male sexual interests, particularly those of clinical or forensic relevance (e.g., pedophilia) because patterns of genital response in the laboratory are among the strongest predictors of future sexual behavior (Seto, 2008).

Before 2004, only a handful of studies had examined the relationships among sexual attractions, sexual response, and sexual orientation in women (Steinman, Wincze, Sakheim, Barlow, & Mavissakalian, 1981; Wilson & Lawson, 1978; Wincze & Qualls, 1984). These studies reported gender differences in response specificity as well, with women generally showing more nonspecific genital responses. These findings were, however, relatively ignored, possibly because they did not fit the dominant models of sexual response and sexual orientation (Mustanski et al., 2002). Then Laan and her research team presented data at the 1995

International Academy of Sex Research meeting (Laan, Sonderman, & Janssen, 1995; later published as Peterson, Janssen, & Laan, 2010) showing nonspecific genital responses in lesbian and heterosexual women to audiovisual stimuli (heterosexual and lesbian couples engaged in sex) and a combination of audiovisual and tactile stimulation. These data inspired my line of research examining the effects of gender cues on women's sexual response, started at Northwestern University, continued at the University of Toronto, and now at Queen's University.

Since Chivers et al. (2004), research on the specificity of sexual response has exploded, with multiple research teams examining the gender specificity of different aspects of sexual response to sexual stimuli. Originally shown using genital and self-report measures of sexual response, the scope of this research has broadened to include cognitive measures, visual attention, pupil dilation, and neural responses. Across these measures, the pattern is strikingly similar: Men usually show gender-specific responses, whereas androphilic women's are nonspecific, showing significant and similar sexual responses to both female and male sexual stimuli. Coupled with evidence for significant fluidity in women's attractions, identity, and behavior over time (see Diamond, 2013), an altogether different model of female sexual orientation is being built. In this model, women's sexual identities are not synonymous with their sexual attractions, and neither of these aspects of women's sexuality is highly correlated with patterns of sexual response and behavior.

More broadly, the gender difference in the specificity of sexual response also highlights how existing models have not defined the nature of sexually competent stimuli (Janssen, Everaerd, Spiering, & Janssen, 2000), that is, stimuli capable of evoking a sexual response. The underlying assumption in these models is that only those stimuli matching sexual experience or preference are sufficient to activate sexual response. Data from women have highlighted how the relationship between stimulus and response is more nuanced, with a range of nonpreferred sexual cues activating female sexual response. Indeed, there are many lessons to be gleaned from research on specificity of sexual response. Most important to this review, however, are the opportunities to closely examine how sexual attractions/orientations and arousal intersect at each stage of a sexual response. Doing so brings us to a deeper conceptualization of how sexual orientation manifests, of what is being oriented (Diamond, 2003), and expectations for concordance across aspects of sexuality (van Anders, 2015). It also structures inquiry regarding how stimuli become sexually competent, reinforced, and capable of eliciting automatic recruitment of psychophysiological resources.

By integrating two major contemporary models of sexual response as an organizing theoretical framework, I will review the specificity of sexual response research that is relevant to each component of these models, with a specific focus on female sexual psychophysiology and sexual orientation. I will then review additional evidence, predominantly collected using genital sexual psychophysiology, examining women's sexual responses to other categories of incentivized cues, and discuss their relevance for understanding the specificity women's sexual response. Next, I will discuss ten hypotheses aimed at explicating gender differences, and within-gender variation in the specificity of women's sexual response. Last, I will discuss how these data inform our understanding of the nature of sexual cues capable of activating sexual response in women.

The Gender Specificity of Women's Sexual Response

Throughout what follows, I will describe experimental studies that have used a specificity paradigm, whereby the individual is exposed to both preferred and nonpreferred sexual stimuli and different aspects of sexual response are observed. A "preferred" stimulus, in this context, is one that corresponds with direction of self-reported sexual attractions, or what is most typically thought of as sexual orientation. A *gender-specific* pattern of response is one where responses to preferred gender stimuli are significantly greater than to nonpreferred gender stimuli. Note that responses to nonpreferred gender stimuli may, or may not, be significantly greater than to neutral stimuli. A *gender-nonspecific* pattern would evidence as response to both preferred and nonpreferred sexual stimuli that are significantly greater than to neutral stimuli; nonspecific response might also be characterized as significantly greater response to nonpreferred versus preferred stimuli. Sexual orientation with respect to gender will be described as gynephilia, ambiphilia, and androphilia where possible (e.g., when researchers have directly assessed the direction of sexual attractions with respect to gender). Where only self-identification or sexual identity was assessed, such as self-identification as heterosexual, bisexual, or lesbian, this is clearly noted.

Models of Sexual Response

Two contemporary models of sexual response provide a strong theoretical framework for understanding the specificity of sexual response among women. The first, the Incentive Motivation Model (IMM: Toates, 2009), frames sexual response as an interplay between central cognitive and affective processes, peripheral responses such as genital vasocongestion, and the reciprocal integration of central and peripheral phenomena (e.g., perception of genital response, feeling sexually aroused) to give rise to motivated sexual behavior (e.g., sexual desire). The sexual response system must have sensitivity to sexual stimuli, which can be influenced by hormonal factors (Diamond, 2007). One important component of the IMM with regard to specificity of sexual response is the nature of stimuli capable of activating sexual arousal and eliciting sexual motivation. Stimuli are described as excitatory (Toates, 2009), hedonically potent (Ågmo, 1999), and previously associated with sexual rewards or incentives (Ågmo, 2011).

The Information Processing Model (IPM: Janssen et al., 2000) provides more detail than the IMM regarding the initial stages of stimulus processing and evaluation, and their influences on central and peripheral manifestations of sexual response; integrating the IPM and the IMM therefore provides a fuller picture of early responses to sexual stimuli. The IPM describes two cognitive pathways for stimulus processing. The first is implicit processing: the pre-attentive and unconscious detection of sexual features, associated with automatic recruitment of autonomic events associated with genital responding. The second is explicit processing: the controlled, elaborative processing of sexual meaning, giving rise to the affective or subjective experience of sexual arousal, and modulating peripheral sexual response. Early visual attention to sexual stimuli is associated with implicit stimulus processing; orienting and fixating on a stimulus feature is automatic. Later visual attention is associated with explicit stimulus processing, the deliberate allocation of attention to a stimulus during which time cognitive elaboration and extraction of stimulus meaning ostensibly happens. According to the IPM, sexual cues that activate sexual response are "sexually competent", however, the IPM lacks a description of the features that render sexual stimuli competent.

In what follows, I will review the existing literature on the specificity of women's sexual response at each of the stages of the IMM and IPM. The structure follows the sequence of stages of sexual response as outlined by the IMM. Following Figure 2 of Toates (2009), sexual stimuli initiate the sexual response cycle with stimulus processing, comprised of two stages including early/initial visual attention and implicit processing, and later visual attention and explicit processing in this review. According to the IMM, this information directly links to autonomic and cognitive processes giving rise to sexual arousal, referred to as "affective processing," "genital and subjective sexual response," and "autonomic arousal." Sexual stimuli are elaboratively processed through comparisons with existing cognitive schemata and sexual memory, and through elicitation of incentive factors or evaluation of hedonic value associated with the stimulus, referred to as "reward assessment." Multiple pathways between cognitive, affective, reward assessment, and arousal components of sexual response highlight the capacity for these components to interact, producing the subjective state of feeling sexually aroused. Last, the product of these central and peripheral neural events undergoes arbitration, a decision about whether sexual arousal will be expressed as behavior, referred to as "sexual desire/sexual behavior."

Stimulus Processing

The first stage of sexual response is the pre-attentive detection of sexual stimuli followed by the implicit-to-explicit processing of attention to its features. In the past decade, a number of studies have investigated pre-attentive processing and visual attention to sexual stimuli, many employing gender specificity paradigms. For sexual orientation to manifest at this level of stimulus processing, we would expect preferred or incentivized (associated with reward) sexual stimuli to evoke greater responses than nonpreferred or nonincentivized stimuli. Features comprising the preferred sexual cues would capture attention more quickly, sustain attention for longer, and do so at both very early (e.g., implicit) and later (e.g., explicit) stages of processing of sexual stimuli.

Early/Initial Visual Attention

In general, predictions regarding gender specificity of women's early visual attention are not supported for androphilic women, whereas gender-specific effects are shown for both gynephilic and androphilic men and for gynephilic women. We recently used eye tracking to assess early visual attention to sexually preferred and nonpreferred cues, operationalized as time to first fixation, in a sample of androphilic women and gynephilic men (Dawson & Chivers, 2016); results supported predictions from the IPM regarding gendered processing of sexual stimuli in men and women; men's initial attention patterns were gender specific, whereas androphilic women's responses were nonspecific. These results replicated Nummenmaa, Hietanan, Santtila, and Hyönä (2012) who showed gender-nonspecific first visual fixations among androphilic women to nude and clothed female and male stimuli. Dawson, Fretz, and Chivers (2016) further examined visual attention phenomena among women, demonstrating gender-specific latency to first fixations among ambiphilic (sexually attracted to both women and men) and gynephilic women, and replicating nonspecific initial visual attention among androphilic women.

The Dawson and Chivers (2016) and Dawson et al. (2016) studies were coupled with a task demand to evaluate the hedonic value of the stimuli by rating one's sexual attraction to the presented images. The task demand could bias results by influencing the manner in which stimuli are scrutinized. In a free-viewing task, Bradley, Costa, and Lang (2015) presented (presumably) heterosexual women and men (sexual orientation of neither group was specified) with images of nude females or males alongside a neutral stimulus; visual attention was assessed via eye tracking throughout a 3-s interval. During the first 1000 ms (which would capture both early and later visual attention), women showed gender-nonspecific visual fixations on sexual versus neutral stimuli, whereas men showed a gender-specific pattern, similar to Dawson and Chivers (2016).

Functional neuroimaging of cortical responses during very early stages of stimulus processing of visual sexual cues produces similar results. Assessed using electroencephalography (EEG) measuring event-related potentials (ERP; specifically, occipitotemporal N170 amplitude) to images of (headless) nude females and males, exclusively androphilic women showed a gender-nonspecific pattern, with significant ERP to both female and male stimuli (Hietanen & Nummenmaa, 2011). This same research team (Alho, Salminen, Sams, Hietanen & Nummenmaa, 2015) also examined early cortical processing of sexual cues using EEG and magnetoencephalography (MEG), producing data

that could speak to the affective-motivational salience of preferred and nonpreferred sexual stimuli. In a small sample of androphilic women, N170 amplitude was greater to female than male stimuli, and no stimulus effects were observed for MEG-dependent variables.

Implicit Cognitive Processing

Implicit cognitive processes show mixed, perhaps task-dependent, results with respect to gender-specific patterns of response. Using an implicit association task, Snowden and Gray (2013) found that associations between evaluations as sexually attractive/unattractive and pictures of female and male clothed targets were gender-nonspecific for self-identified heterosexual women and gender specific for self-identified lesbian women. Conversely, Jiang, Costello, Fang, Huang, and He (2006) showed gender-specific effects using an attentional paradigm whereby subliminal presentation of sexual stimuli depicting nude women or men would, hypothetically, bias attention and improve task performance when task items were presented on the same side as the preferred stimulus. Androphilic women showed better task performance when items were presented on the same side as male images, whereas predominantly gynephilic women were less discriminating, an atypical result that has not yet been replicated. Conversely, both female and male subliminal images of genitals augmented predominantly and exclusively androphilic women's genital response to a supraliminally presented target image depicting an opposite-sex couple engaged in sex acts in Ponseti and Bosinski (2009).

Later/Controlled Visual Attention

In eye tracking studies, later, controlled visual attention is assessed by measuring the proportion of time spent looking at stimuli, usually within regions of interest. When focal attention to specific features within a sexual scene is assessed (instead of total time spent looking at a picture, as in viewing time), a mix of gender-specific and gender-nonspecific patterns are found; androphilic women spend about the same amount of time looking at male and female individuals within a stimulus depicting an opposite-sex couple engaged in sex acts (Lykins, Meana, & Kambe, 2006; Lykins, Meana, & Strauss, 2008; Rupp & Wallen, 2009). Self-report measures of visual attention produce similar results; we found that self-reported attention to sexual cues was a stronger mediator of gender-specific genital and self-reported sexual arousal in men than androphilic or gynephilic women (Huberman, Maracle, & Chivers, 2014). Conversely, Dawson and Chivers (2016) reported gender-specific patterns of controlled visual attention to stimuli depicting nude women and men among androphilic women, operationalized as total fixation duration on these gendered visual targets. Others have reported gender-nonspecific controlled visual attention (total dwell times) among androphilic women using eye tracking to nude and clothed female and male stimuli (Nummenmaa et al., 2012). Similar to other studies such as Imhoff et al. (2010), however, Nummenmaa et al. also found gender-specific viewing times for face stimuli. The Bradley et al. (2015) study, discussed earlier, found that women avoided looking at both the female and male sexual stimuli, with greater proportion of visual fixations on the neutral stimuli. Looking times were related to sexual affect in that study; self-reported sexual disgust was negatively correlated with visual fixations on sexual stimuli, such that higher sexual disgust was associated with shorter viewing times, and this effect was only observed for women.

Explicit Cognitive Processing

Total time spent viewing a sexual stimulus (not just to focal regions of interest, as in eye-tracking studies) is another measure of explicit cognitive processing of sexual stimuli. Gender-specific patterns for explicit cognitive processing measures, like viewing time, are more variable and tend to show gender specificity, particularly for gynephilic women, albeit less robustly than typically reported for men. Androphilic women have shown both gender-nonspecific viewing times for sexual stimuli (Dawson, Suschinsky, & Lalumière, 2012; Ebsworth & Lalumière, 2012; Israel & Strassberg, 2009; Lippa, 2013; Lippa, Patterson, & Marelich, 2010; Rieger et al., 2015), or small effect gender-specific responses (e.g., Imhoff et al., 2010; Quinsey, Ketsetzis, Earls, & Karamanoukian, 1996), whereas gynephilic women more clearly show gender-specific viewing times (Ebsworth & Lalumière, 2012; Lippa, 2012; Rieger et al., 2015; Rullo, Strassberg, & Israel, 2010). Ambiphilic women show significantly less gender-specific pattern of viewing time than androphilic (Ebsworth & Lalumiere, 2012) and gynephilic women (Ebsworth & Lalumiere, 2012; Rullo, Strassberg, & Miner, 2014). In their investigation of mechanisms underlying viewing time effects, Imhoff et al. described a heuristic for prolonged response latencies to sexually attractive targets whereby stimuli are evaluated for relevant gender, age, and attractiveness cues. Women's viewing times were examined in a number of these studies, and curiously, gender-nonspecific viewing times were shown for both standard and restricted viewing times, but age preferences were detected; for women, age specificity was found (as greater response to adult versus child/adolescent stimuli) but gender nonspecificity effect remained. In a speeded task where women evaluated whether the image represented a potential sexual partner, androphilic women's response latencies were greatest for male sexual stimuli, with effect sizes ranging from medium to large. This gender-specific effect demonstrates how task demands can influence outcomes in viewing time experiments; Imhoff et al. thus proposed that response times in the speeded task might more accurately reflect sexual attractions. In a fourth experiment displaying women's and men's faces, clear gender specificity was shown in women's viewing times, an effect that was replicated in another study using a behavioral measure (a button-press task) to assess motivations to look at gendered facial stimuli (Hahn, Fisher, DeBruine, & Jones, 2015). These effects

underscore how stimulus content (e.g., showing bodies with primary and secondary sexual characteristics versus faces only) and task demand effects can have a substantial influence on women's sexual response, a consistent pattern that will be discussed in greater detail later in this review.

Other cognitive paradigms reveal similar patterns. Explicit processing of preferred and nonpreferred sexual stimuli also shows evidence of nonspecific cognitive interference effects in androphilic women. Schimmack and Derryberry (2005) showed that supraliminally presented same-gender sexual stimuli produced similar cognitive interference as opposite-gender stimuli in androphilic women, resulting in longer response times for math problems and a line judgment task. Gender-nonspecific cognitive interference effects have also been observed using choice reaction time (Wright & Adams, 1999). In this decision-making task, participants are required to locate a dot as quickly as possible; delays observed when dot placement corresponds with a preferred stimulus are thought to reflect attentional engagement and elaborative processing of the preferred sexual stimulus.

In summary, the data examining early visual attention and implicit processing of sexual cues generally shows gender-nonspecific effects for androphilic women and gender-specific effects for gynephilic women. The data on later visual attention and explicit processing of sexual cues are more variable in terms of gender nonspecificity among androphilic women; however, the few studies available generally report gender specificity for gynephilic women. Referring back to the IMM and IPM, gender features associated with preferred sexual cues do not differentially capture and sustain androphilic women's early visual attention, nor show consistently biased implicit and explicit cognitive processing; later stimulus processing is more gender specific. For gynephilic women, effects are more aligned with predictions regarding the differential potency of incentivized sexual stimuli in stimulus processing.

Affective Processing

From the IMM and IPM, we could predict that affective evaluation of sexual stimuli occurs relatively automatically, with preferred stimuli matching with incentivized representations in memory, activating positive affective responses, resulting in more positive appraisals than for nonpreferred sexual stimuli; presumably, negative appraisals such as disgust or anxiety would curtail further responding to nonpreferred sexual stimuli, possibly via attentional disengagement (Barlow, 1986). The data comparing affective responses to preferred and nonpreferred sexual stimuli are somewhat scant and mostly based on self-reported affect. Peterson et al. (2010) reported that self-identified heterosexual women's self-reported positive and negative affective responses to sexual stimuli (heterosexual and lesbian couples engaged in cunnilingus) were nonspecific; only self-identified lesbian women reported greater threatened affect in response to heterosexual cunnilingus stimuli across both studies. In a second study, using a different set of visual stimuli (films of heterosexual and lesbian couples engaged in penetrative sex, defined as vaginal-penile sex, and vaginal penetration with a dildo, respectively), preference-specific patterns emerged for positive affect in both heterosexual and lesbian women, and lesbian women reported greater anger and tense affect in response to heterosexual penetrative sex. Chivers and Timmers (2012) examined predominantly and exclusively androphilic women's affective responses to audio narratives describing sexual interactions with females and males. Although women reported more disgust after female narratives, and greater interest, happiness, and relaxation after hearing male narratives, women's patterns of affective response were generally more gender-specific than their genital and subjective sexual responses. Self-reported positive and negative affective responses therefore show significant variability among women, but are generally in the direction of more gender-specific patterns.

Genital and Subjective Sexual Arousal Responses

According to the IMM and IPM, sexual arousal responses, particularly genital responses, are activated in parallel with implicit and explicit cognitive and affective processing of sexual stimuli. Feedback from midbrain activation (e.g., hypothalamic and insular structures) and peripheral genital processes reenters the cognitive/affective processing loop, influencing further appraisals of sexual stimuli and self-reported sexual arousal. If one were looking for the most objective and unbiased means of assessing neural processes associated with categories of preferred sexual stimuli, it would make the most sense to focus on very early attention and processing events: Genital responses, in general, are slower processes that may be more influenced by cognitive events. Nonetheless, it was gendered variation in the specificity of genital sexual response that initiated research into the specificity of sexual response more generally.

The very first study published on the specificity of women's genital and subjective sexual responses examined this question within the frame of an alcohol expectancy study (Wilson & Lawson, 1978). Both heterosexual and lesbian couple films evoked significant increases in genital response for both predominantly and exclusively androphilic women; responses from the two groups were not compared. Subjective sexual responses were correlated with genital response but were not analyzed by stimulus category. This was soon followed by a pair of studies examining the gender specificity of sexual response published by Wincze and colleagues in the early 1980s. Steinman et al. (1981) compared self-identified heterosexual women's (predominantly/exclusively androphilic, based on Kinsey scores) and men's sexual response patterns to films of heterosexual, lesbian, and gay couples, as well as a group sex film depicting multiple men and women. Women's genital responses were greatest to heterosexual and group sex films than to other conditions, with no significant response (i.e., compared to responses to a sexually neutral film) to the lesbian or gay sex films reported in text, although substantial

genital responses to these stimulus categories can be seen in visual depictions of the data. Women's subjective arousal was nonspecific, with women reporting similar responses to heterosexual and lesbian films.

Wincze and Qualls (1984) reported on the companion study examining sexual responses in self-identified lesbian and gay men, and found lesbian women (predominantly/exclusively gynephilic, based on Kinsey scores) showed greatest genital response to lesbian and group sex films, with significant increase in genital response to other categories (heterosexual and gay sex) versus neutral; women's subjective response was not significantly gender specific. The Wincze et al. group concluded that sexual response was gender specific for both women and men, despite reporting somewhat gender-nonspecific patterns for women. Data from Laan's research group (Laan et al., 1995) contributed to this equivocal picture in the 1990s, showing gender-nonspecific genital and subjective sexual responses among self-identified lesbian and heterosexual women to films of lesbian and heterosexual oral and penetrative sex. In an ingenious manipulation, this group also amplified genital responding to these stimuli through the addition of hands-free genital vibration, and the same pattern emerged.

Our first set of studies following up on these results used videos depicting lesbian, heterosexual, and gay couples engaging in oral and penetrative sex acts. The rationale for this was entirely practical at first; we were concerned about potential floor effects in sexual response, and therefore we selected the most potent form of sexual stimulus—audiovisual depictions of sexual activity—to provoke female genital response (Heiman, 1980). The studies that focused on women's sexual response showed gender-nonspecific sexual response among predominantly androphilic and gynephilic women (Chivers et al., 2004; Chivers & Bailey, 2005). We replicated gender-nonspecific genital responding among predominantly and exclusively androphilic women using a different set of audiovisual stimuli (Suschinsky, Lalumière, & Chivers, 2009). In an important extension, we also found that genital responses to preferred and nonpreferred sexual stimuli were distinct from other emotional states that might activate significant autonomic activity, such as exhilaration or happiness (Suschinsky et al., 2009).

Chivers, Seto, and Blanchard (2007) tested the hypothesis that, perhaps, nonspecific genital response was related to the intensity of sexual stimuli; we reasoned that nonspecific response might represent a ceiling effect in women's genital responses obtained within the 2-min videos. By reducing the intensity of the sexual stimuli from couples engaging in sex acts to solitary people masturbating, and by including solitary images of nude males and females exercising and not engaged in any sexual activity, we could obtain a clearer picture of genital and subjective responses to gender cues. By reducing the intensity of sexual activity, we revealed that gynephilic women did have gender-specific genital and subjective sexual responses: Androphilic women continued to be a mystery, showing gender-nonspecific responses in both genital and subjective arousal, regardless of the intensity of sexual activity depicted. We have since accrued more data using the 2007 paradigm, facilitating a more nuanced examination of within-gender variation in women's sexual response as a function of sexual attractions (see Chivers, Bouchard, & Timmers, 2015). Replicated in two studies, we showed that only exclusively androphilic women show gender-nonspecific genital responses, whereas women reporting any degree of gynephilia, including women who are predominantly androphilic or ambiphilic (sexually attracted to both women and men; Bouchard, Timmers, & Chivers, 2015; Timmers, Bouchard, & Chivers, 2015), have greater genital responses to female sexual stimuli, in both audiovisual and narrative forms. With these results, the puzzle of women's gender-nonspecific sexual response gets even more fascinating, revealing numerous clues as to how sexual stimuli are processed, incentivized, and result in genital responding.

Stimulus Modality and Content Effects on Specificity of Sexual Response

The influence of stimulus modality and content has become an important wrinkle in the measurement of women's gender-specific sexual response, given the multitude of positive or negative associations that can be made with erotica. The bulk of commercially available films are produced for a male audience (see Laan, Everaerd, van Bellen, & Hanewald, 1994), including elements that might evoke negative affect, encourage attentional disengagement, or lead women to feel "turned off." Although women do show greater genital and subjective sexual response to visual versus narrative sexual stimuli (Heiman, 1980), using narrative stimuli might reveal specificity that is obscured by more potent stimuli, similar to the Chivers et al. (2007) study. Also, addressing the issue of women's gender-specific sexual response using narrative stimuli allows for a degree of stimulus control that we could never achieve using commercially available films. Despite these attempts to create the perfect conditions for gender specificity to emerge in androphilic women's genital responses, it did not (Chivers & Timmers, 2012); these women showed gender-nonspecific responding to narratives describing sex with women and men that varied by relationship context (describing sex with long-term partners, strangers, and close friends). To our surprise, relationship context was more relevant to women's genital response than were gender cues (discussed in more detail in the next section).

Cycle Phase Effects on Gender-Specific Sexual Response

A lingering concern regarding patterns of nonspecific sexual response among women is the frequent confound of hormones, such as oral contraceptives and related medications used for non-contraceptive reasons, and endogenous hormonal variations associated with menstrual cycle phase and fertility. Given the large body of literature documenting shifts in women's sexual interests as a function of cycle phase, specifically the *ovulatory shift hypothesis* (see Gildersleeve, Haselton, & Fales, 2014), it was reasonable to predict that similar effects might manifest in women's genital

response. But, like many a beautiful hypothesis slain by data, we did not find cycle-related effects on the gender specificity of women's genital or self-reported responses to the stimulus set used in the Chivers et al. (2007) study (Bossio, Suschinsky, Puts, & Chivers, 2014). Along similar lines, Dawson et al. (2012) found gender-nonspecific viewing times for androphilic women in both high- and low-fertility phases of the menstrual cycle.

In another analysis of the Bossio et al. (2014) data, seeking to test a related hypothesis regarding cycle phase effects on arousal to conceptive versus non conceptive sex acts, an intriguing effect was revealed (Suschinsky, Bossio, & Chivers, 2014) related to the cycle phase in which women first participated in the two-session study. Androphilic women who were in the fertile phase of their cycle when they first viewed the stimulus set showed significantly greater genital response to heterosexual penetrative versus oral sex, whereas women who began the study in the non-fertile, luteal, phase, did not. No interaction effects were observed depictions of gay and lesbian oral versus penetrative sex acts, and no cycle phase or order effects were found for subjective arousal (which was mostly gender-specific). Similar cycle phase by testing order effects have also been observed in two other studies using different dependent variables (labial temperature: Slob, Ernste, & van der Werff ten Bosch, 1991; viewing time: Wallen & Rupp, 2010), with greater response to sexual stimuli first viewed during the fertile phase. Collectively, these data suggest that any cycle phase-related influences on the specificity of sexual response may not be associated with incentivized gender features but incentivized sex acts.

Method of Assessing Women's Genital Response

A final concern regarding the validity of gender-nonspecific genital responding among women is the means by which genital measurements are obtained. Until very recently, all studies examining specificity of women's genital responses have used vaginal photoplethysmography. Some researchers have questioned the validity of this ubiquitous device, with the main concern focusing on the weaker correlations between subjective measures of sexual response and the VPP (Kukkonen, 2014). Instead, external and temperature-based measures are advocated as more valid measures of women's sexual response, based on studies showing higher sexual concordance (subjective/genital agreement) using these measures. In our 2010 meta-analysis of the sexual psychophysiology literature (Chivers, Seto, Lalumière, Laan, & Grimbos, 2010), we also reported that thermal measures of sexual response ($n = 97$, $k = 6$ studies) yielded higher sexual concordance ($r = .55$, 95% CI .28–.82) than VPP ($r = .33$, 95% CI .26–.40, $n = 1170$, $k = 56$ studies), on average. In that meta-analysis, however, we also reported that research designs employing greater variation in stimulus content and modality, thereby producing more variability in genital and subjective sexual responses, also produced VPP sexual concordance correlations in the same range typically obtained for temperature-based measures (average $r = .49$, 95% CI .35 to .63, $n = 208$, $k = 4$ studies). It is therefore unlikely that the device used to assess genital response is a problem. Instead, it is more likely that the concerns about construct validity might relate to the way VPP sexual concordance is assessed, typically using one stimulus (usually a film depicting heterosexual sex), resulting in a research design that does not allow for much variation in sexual response.

Fully addressing debates regarding best methodological approaches to studying women's sexual response is beyond the scope of this article. Nonspecific genital response among predominantly and exclusively androphilic women to films of solitary women and men masturbating has been reported using thermal imaging (Huberman & Chivers, 2015). Also, gender-specific genital response, assessed using VPP measurement of neovaginal vasocongestion, has also been shown among transgender women (Chivers et al., 2004). Coupled with the accumulating literature showing gender-nonspecific activation of the sexual response system in androphilic women at multiple levels of stimulus processing and response beyond the genitals, it is unlikely that gender nonspecificity effects in genital response are an artifact of how genital response is measured.

Activation of the Autonomic Nervous System

Extragenital autonomic nervous system activation is thought to occur in parallel with stimulus processing and genital response. Differential activation of the autonomic nervous system by preferred and nonpreferred sexual stimuli can be detected by assessing pupil dilation. Rieger and Savin-Williams (2012) and Rieger et al. (2015) have shown that androphilic women have a gender-nonspecific pattern of pupil dilation, versus the more gender-specific patterns observed for gynephilic women or for men. Notably, Rieger et al. also showed that genital responses to female sexual stimuli, assessed via VPP, were significantly associated with pupil dilation to female stimuli, and this effect was more pronounced for gynephilic women. Observing fMRI responses to still pictures of nude women and men and pictures of same- and opposite-sex couples having sex, Sylva et al. (2013) reported greater limbic response to nonpreferred stimuli in all women compared to men, despite mostly nonspecific activation to still pictures of nude females and males, and pictures of same-sex couples in other brain areas.

Reward Assessment

Reward assessment refers to the evaluation of the potential hedonic value associated with a sexual stimulus; this evaluation is, according to the IMM, dependent on learning. Operationalizing a behavioral measure of reward assessment of sexual stimuli is challenging when obvious candidates like visual attention for preferred and nonpreferred categories produces results that run counter to expectations, particularly for androphilic women. An ideal behavioral measure would be robust to nonspecificity effects and

demonstrate response differentiation for preferred and nonpreferred stimuli. The attractiveness of sexual stimuli could be one candidate feature, such that physical features associated with reproductive fitness might evoke greater sexual response. Reward associated with features like attractiveness may be more salient to women's sexual response than gender, thereby explaining gender-nonspecific responses, at least among androphilic women. For example, phenotypic features associated with genetic fitness and fecundity, such as facial symmetry, vocal pitch, and masculinized/feminized body shapes (Gangestad & Scheyd, 2005), are rated as more sexually attractive (Haselton & Gildersleeve, 2011; Puts, 2010), and cues signalling genetic fitness are appraised as more sexually attractive at times of high fertility (Gildersleeve et al., 2014). In the case of specificity of sexual response among women, we would predict greater response to attractive targets of their preferred gender.

Again, this was not the case for androphilic women; Richard Lippa reported that heterosexual women have similar patterns of viewing time to both female and male models, despite reporting greater sexual attraction to male models (Lippa et al., 2010). A second study found some specificity in viewing time among heterosexual and lesbian women (Lippa, 2012). What is consistent across Lippa's studies is that, for women, viewing time increased as a function of stimulus attractiveness for both preferred and non-preferred targets; Lippa interpreted this as "… high photo model attractiveness would "energize" heterosexual women's attractions to both sexes" (Lippa et al., 2010, p. 242). Another interpretation is that features of sexual attractiveness may be more relevant to (androphilic) women's sexual response than gender cues. Curiously, when the reward value of only faces is examined, with reward value operationalized as behavioral task assessing number of button-presses to reveal the face stimuli, gender-specific effects emerge and these effects were more pronounced for physically attractive preferred faces (Hahn et al., 2015).

Using fMRI to assess activation of brain regions associated with reward assessment (e.g., orbitofrontal cortex, dorsal lateral prefrontal cortex) has produced results congruent with predictions from the IMM regarding greater activation by preferred versus nonpreferred sexual stimuli. Using images of attractive nude women and men, Sylva et al. (2013) showed that androphilic and gynephilic women had more gender-specific response in the dorsal striatum and dorsal anterior cingulate, brain areas associated with reward and cognitive control, respectively. This activation was not, however, of the same magnitude as observed for gynephilic men; "women showed a stronger limbic response than men to nonpreferred-sex stimuli (relative to resting baseline). This occurred in the left amygdala (and extended amygdala), hippocampus, thalamus, and left midbrain. This suggests that the observed sex difference in category specificity may be partly due to women experiencing a stronger motivational reaction than men to nonpreferred-sex stimuli (relative to resting baseline)" (Sylva et al., 2013, p. 681). Similarly, using still images of torsos and sexually aroused genitals, Ponseti et al. (2006) obtained gender-specific patterns of ventral striatum, centromedial thalamic, and bilateral ventral premotor cortex activation in androphilic and gynephilic women. The authors interpreted these findings to suggest gender-specific activation in brain areas associated with reward salience and motor interactions with incentivized sexual stimuli, and anticipation of sexual reward (ventral striatum). These two studies represent some of the strongest evidence for using the IMM for understanding women's sexual attractions.

Sexual Desire/Behavior

According to the IMM, the sum activation of the multiple components of the sexual response system contributes to the experience of sexual desire, leading to a subjective state of wanting or craving sexual gratification, and, depending on circumstances and context, engagement in overt sexual behavior. Given gender-nonspecific activation of sexual response among androphilic women, we wondered whether sexual desire could also be activated by both preferred and nonpreferred sexual stimuli. Responsive sexual desire refers to sexual motivation arising from the experience of sexual arousal. Another term for responsive sexual desire is state sexual desire (Dawson & Chivers, 2014a), distinguishing it from trait sexual desire, a more stable personality like construct that characterizes an individual's sexual motivation. State sexual desire refers to the situation-specific sexual motivation activated by processing sexual cues. Gender differences in trait desire have been widely reported, whereas an emerging literature suggests that state sexual desire may be similar in magnitude for women and men (see Dawson & Chivers, 2014a). For example, Goldey and van Anders (2011) found no significant gender differences in the magnitude of self-reported solitary or partnered sexual desire in response to three modalities of preferred sexual stimuli (i.e., imagined sexual situation, sexual story, and sexual fantasy).

We examined this phenomenon of responsive sexual desire among gynephilic and androphilic women and men to preferred and nonpreferred sexual stimuli (Dawson & Chivers, 2014a). These data came from the larger study examining gender and sexual orientation effects on sexual responses to exercise, masturbation, and coupled sex stimuli (Chivers et al., 2007). Gynephilic and androphilic women and men reported the strength of their sexual desire by responding to items asking about desire to masturbate (solitary desire) and desire to engage in sex with a partner (dyadic desire), both before and after viewing sexual stimuli. Men and gynephilic women exhibited gender-specific patterns of solitary and dyadic responsive sexual desire, with effect sizes (Cohen's *d*) greater than .65. Androphilic women's dyadic desire, however, showed significantly less gender specificity, with *ds* ranging from .41 to .56 for male versus female stimuli, and gender-nonspecific solitary desire in response to masturbation ($d = .18$) and intercourse stimuli ($d = .16$). Curiously, solitary desire was significantly greater in response to female than male nude stimuli ($d = .51$).No gender differences in the magnitude of responsive

solitary and dyadic sexual desire were observed, highlighting that these patterns of response are not attributable to low responsive desire among androphilic women compared with men or gynephilic women. In a follow-up study of gynephilic men and androphilic women's responsive desire to narrative sexual stimuli (Chivers & Timmers, 2012), these gender-nonspecific patterns of responsive desire were replicated for androphilic women (Dawson & Chivers, 2014b). In the 1970s, Schmidt and his research team reported similar effects, with heterosexual women reporting gender-nonspecific responsive sexual desire—operationalized as engaging in solitary and/or partnered sexual activity in the 24 h following the laboratory session—in response to viewing films of women and men engaged in masturbation, whereas men showed gender-specific responsive desire (Schmidt, Sigusch, & Schäfer, 1973).

The difference in the gender specificity of androphilic women's responsive solitary and dyadic sexual desire reported by Dawson and Chivers (2014b) provides an intriguing clue regarding the nature of women's responsive sexual desire. Although nonpreferred sexual stimuli can energize the sexual response system and still evoke desire to masturbate, the depiction of a preferred sexual partner—an incentivized sexual stimulus—resulted in greater dyadic desire and a more differential response in terms of desiring sexual contact with a partner.

Specificity of Sexual Response to Other Categories of Sexual Cues

By now, it should be clear that sexual response is not directly related to androphilic women's sexual orientation to gender, whereas sexual response among gynephilic women is more gender-specific; the few studies of ambiphilic women suggest greater response to female sexual stimuli but results need to be independently replicated. One possible interpretation of these data is to suggest that women, specifically women who are exclusively androphilic, do not have a "sexual orientation," meaning that sexual stimuli depicting preferred gender partners do not differentially activate and direct the sexual response system (Bailey, 2009). This review makes clear that these effects are evident at multiple levels of sexual response beyond direct assessments of genital and subjective sexual arousal, the one notable exception being gender-specific activation of brain areas associated with sexual reward (Ponseti et al., 2006; Sylva et al., 2013). As tempting as this conclusion might be for some, there are additional data to consider showing that androphilic women's sexual response does vary meaningfully with sexual activity and with relationship context, albeit not in entirely expected ways.

If we expand the definition sexual orientation to encompass sexual activity preferences (Chivers, 2016), the alignment of androphilic women's directed sexual interest and sexual response begins to look more conventional, though data are scarce and, at this point, based only on one study conducted by my laboratory in collaboration with Seto (Chivers, Roy, Grimbos, Cantor, & Seto, 2014; see also Seto, 2016, for a discussion of multi-dimensional sexual orientations). In this examination of effects of gender and sexual activity cues on sexual response, we found that exclusively and predominantly androphilic women with no sexual interest in masochism showed significantly greater genital response, and reported greatest sexual response, to conventional sex acts versus pure masochism, and to conventional sex versus masochistic sex acts. Pure masochism stimuli described only dominance, submission, and pain, without any sexual cues, and masochistic sex acts described masochism along with oral sex, thereby allowing us to test hypotheses about activation of sexual response by conventional sex acts, like oral-genital stimulation, and less conventional sexual acts, like being spanked without direct genital contact. Women's pattern of response was remarkably similar to what was also observed among men with conventional sexual interests. Both women and men reporting sexual interest in masochism, however, showed little differentiation between conventional and masochism narratives in both their genital and self-reported sexual responses. In the study with women, we varied the gender of the person described in the sexual narratives to examine gender specificity and, remarkably, gender cues mattered little to either group of women with regard to genital responses.

Looking more closely at these findings, one feature of the response pattern was intriguing; women with conventional sexual interests did show some genital response to the pure masochism and masochism with sex narratives. Using an IPM approach, we could conceptualize masochism as part of a sexual memory network that has the capacity to evoke some genital response when activated by processing even aschematic information, like spanking. These cues may not match with previously incentivized sex acts or erotic fantasies, but might correspond to widely publicized information about mild sexual masochism associated with eroticism; for example, many women who did not have any strong interest in sexual masochism read and enjoyed *50 Shades of Grey*, with two-thirds finding the content sexually arousing in one study (Deller & Smith, 2013).

In further exploration of stimulus factors associated with women's sexual response, we designed a study that varied the relationship context within which sex acts with women and men were described. The original intent of this study was to examine gender specificity of sexual response evoked by a less potent stimulus modality. To our surprise, we observed no gender specificity among androphilic women (but see Chivers et al., 2015 for gender-specific responding to these stimuli among gynephilic women, and Bouchard, Timmers, and Chivers (2015) for responses of ambiphilic women), but we did find a relationship context effect that ran counter to predictions; women showed significantly lower genital response to the close friend stories than to long-term relationships or to strangers, while their subjective responses showed no relationship context effects. When this pattern of genital response to relationship context emerged in our Toronto sample, I was

skeptical and collected a second sample at Queen's University that replicated the pattern (Chivers & Timmers, 2012).

By administering the revised sociosexuality inventory (SOI-R; Penke & Asendorpf, 2008) to the Queen's University sample, we could examine sexual response in relation to another dimension of sexual interests, propensity to engage in sex as a function of relationship commitment, or *sociosexual orientation* (Timmers & Chivers, 2012). Individuals high in sociosexuality, or who have an unrestricted sociosexual orientation, are more likely to engage in casual sex, have one-time sexual encounters, and are more comfortable engaging in sex without love, commitment, or closeness. Individuals low in sociosexuality, or who have a restricted sociosexual orientation, prefer greater commitment and emotional closeness before having sex with romantic partners. Using self-reported and genital responses to the described relationship contexts, we computed indices of partner familiarity and relationship commitment and correlated these with factors on the SOI-R. The behavioral factor of the SOI-R, a subscale score of engagement in casual sex behavior, was significantly correlated with two indices of the effects of relationship context on sexual response. The first was partner familiarity, that is, sexual responses to known (friend, long-term romantic partner) versus unknown (stranger) narratives; women's genital responses on the partner familiarity were correlated, $r(24) = .50$, with the behavioral factor of the SOI-R. The second context was a relationship commitment index, contrasting sexual responses to committed (long-term partner) versus uncommitted (friend, stranger); this index was also correlated with SOI-R behavior subscale at $r(24) = .44$. Of note, these effects were seen only for the male sexual narratives; relationships with female sexual stimuli and with self-reported sexual response did not reveal this pattern. In this regard, we may be observing how the contextual elements of these sexual stimuli interact with gender cues to influence physiological sexual response.

The vast majority of sexual psychophysiology studies have examined sexual responses to dyadic sexual stimuli, typically depicting a heterosexual couple. Depictions of group sex as sexual stimuli are, by constrast, rare in recent years, although they were more frequently used in the 1970s and 1980s. In a handful of studies (Steinman et al., 1981; Wincze, Hoon, & Hoon, 1977; Wincze & Qualls, 1984), group sex stimuli were included in broader stimulus sets, but without any specific hypothesis guiding their inclusion described in these publications. The effects of group sex on genital response were fairly consistent; women and men tended to show as much genital response to group sex stimuli as to their preferred stimulus. Subjective response patterns to group sex were more variable, but generally showed greatest arousal to preferred stimuli and little to no response to group sex stimuli. From these studies, group sex stimuli do consistently evoke highest or equivalent levels of genital response, and this response is consistently discordant with subjective arousal. If this is a reliable effect, it would be interesting to know whether people with sexual activity preferences for group sex show greater response to these stimuli than to typical dyadic heterosexual films (Frank, 2013).

Another category of sexual cue that has yet to be explored in women is age preferences. The chronophilias (see Seto, 2016) are a relatively well-studied phenomenon in men, with data serving to inform clinical assessment and treatment of sexual offenders against minors, in particular men with atypical age preferences, such as pedophilia. The number of women self-describing as pedophilic, that is sexually attracted to sexually immature individuals, or who have been charged and convicted of sexual offenses against a minor is small (approximately 5%; Knack, Murphy, Ranger, Meston, & Federoff, 2015), and therefore little attention has been paid to the assessment of age preferences in women's sexual response research. The only published article is a case report of a self-described pedophilic woman undergoing laboratory assessment of genital and subjective sexual response to adult and child sexual stimuli (Cooper et al., 1990). Her genital responses did not discriminate between sexual stimuli depicting children or adults, nor between depictions of coercive and consensual sex.

As described earlier, Imhoff et al. (2010) reported that women's viewing times were gender nonspecific, but age preferences, for sexually mature versus immature individuals, were detected; Ebsworth and Lalumiere (2012) demonstrated similar effects. It could be that stimulus features relevant to age, including body size, body shape, and the presence of secondary sexual characteristics, modulate sexual response but are still insensitive to gender features. Knack et al. (2015) proposed that age preferences may be detectible in women's genital response patterns. Future research could also explore questions regarding age preferences in nonoffender populations of women.

Contextual elements of sexual stimuli also include the power dynamics depicted between actors, such as responses to consensual versus nonconsensual sex. Multiple studies have shown women experience significant increases in genital response to visual (Both et al., 2003; Laan et al., 1995; Suschinsky et al., 2009) or narrative (Stock, 1983) depictions of sexual coercion. In their study examining women's and men's sexual responses to auditory narratives varying by consent, violence, and sexual cues, Suschinsky and Lalumière (2011) reported similar effects; women showed similar genital responses to the consensual and nonconsensual sexual narratives, but reported greater arousal to consensual. Their design also included a consensual nonsexual violence category, similar to the Chivers et al. (2014) pure masochism stimuli, although not explicitly presented in the context of a dominant/submissive relationship; curiously, women's genital responses to this category were significantly greater than to the neutral condition, suggesting a sexual response even though no overt sexual cues were present. Automatic genital responses to these stimuli are, perhaps, related to the ubiquity of competent sexual features depicted in both coercive and consensual sex, such as body or activity cues. Responding to consensual nonsexual violence may also, however, reflect responding to descriptions of enjoyment and pleasure result-

ing from acts of violence, and speaks to the potential for these contextual cues to evoke genital sexual response.

Collectively, these data suggested that certain contextual elements of sexual stimuli are competent sexual cues for women's sexual response, both subjective and physiologically. We indirectly tested this hypothesis by assessing sexual responses to visual stimuli from which we subtracted as much sexual context as possible, building upon Ponseti et al. (2006) who used "core sexual stimuli" in their fMRI study and reported gender-specific brain activation among androphilic and gynephilic women and men. Would a gender-specific pattern of response emerge, especially among androphilic women who had, to this point, demonstrated a consistent potential for genital and subjective sexual responses to be partially independent (e.g., Chivers et al., 2010)?

In a straightforward gender specificity design, we exposed androphilic women to a series of slideshows depicting "prepotent sexual stimuli" (sexually aroused genitals: erect penises and visibly engorged and lubricated vulvas depicted with women's legs spread) and "nonprepotent genitals" (non-aroused genitals: flaccid penises and pubic triangle images that showed women's vulvas with legs closed) and sexually neutral images depicting solitary women and men clothed and engaging in nonsexual activities. To our surprise, androphilic women showed gender-specific subjective and genital sexual responses, with their greatest response to the prepotent male stimuli (Spape, Timmers, Yoon, Ponseti, & Chivers, 2014). Along similar lines, the Nummenmaa research group reported gender specificity for dwell times on the male versus female pelvic region among androphilic women (Nummenmaa et al., 2012). In a follow-up study, we observed gender-specific sexual responses among gynephilic women, albeit in a very small sample ($n = 4$; Timmers, Hildebrand, & Chivers, 2013). It is likely that gender-nonspecific responses to depictions of sexual activity trump gender cues. We have shown that the gender specificity of visual attention effects varies by stimulus modality, such that androphilic women's visual attention, assessed as total gaze time, is gender specific for still images, but gender nonspecific for video stimuli that depict sexual activity (Dawson, Fretz, & Chivers, 2015). Sexual activity cues may, therefore, draw attention to nonpreferred gender cues, activating gender-nonspecific sexual response.

Some investigators have proposed that extracting gender-specific genital responses from heterosexual (but not lesbian) women's data can be accomplished using complex spline modeling (see Pulverman, Hixon, & Meston, 2015). This statistical method, however, accounted for very little of the variance in specificity of sexual response among exclusively and predominantly androphilic women. Uncovering gender-specific sexual responding in cisgender androphilic women is, however, potentially as straightforward as subtracting the myriad contextual features in audiovisual and narrative sexual stimuli, such as sexual activity cues, that may also be associated with women's genital response. These latest studies suggest that we are only now beginning to understand the features associated with women's sexual response: Gender may not be irrelevant, but sexual responses to gender cues may be superseded by contextual features, depending on individual differences like sociosexuality, interest in masochism, and degree of gynephilia.

Discussion: Why Do Only Androphilic Women Show Gender-Nonspecific Sexual Response?

Across most, if not all, stages of sexual response outlined by the IMM and IPM, androphilic women show nonspecific responses to gender cues. The question that still remains is, why? Why do women who report little to no sexual interest in other women, no or few previous sex experiences with women, and few sexual fantasies involving women (relative to frequency of fantasizing about males; see Dawson et al., 2012) exhibit sexual responses to stimuli depicting women that are, in many cases, relatively equal to what they exhibit to male sexual stimuli? And why are gender specificity effects more variable among gyne- and ambiphilic women? In what follows, I will critically discuss 10 hypotheses for these findings.

Hypothesis 1 *Erotic plasticity*

The first hypothesis is that women demonstrate greater erotic plasticity than men, that is, women have a sexuality that is more malleable by external influences such as social, cultural, and other contextual factors (Baumeister, 2000). Greater responsivity to a broader range of sexual stimuli would be one manifestation of erotic plasticity. This is, however, a circular argument: Androphilic women show gender-nonspecific sexual response because women generally have greater erotic plasticity, and women have greater erotic plasticity in part because they respond to a broader range of sexual stimuli than do men. This argument fails to explain how or why nonincentivized sexual cues might serve as competent sexual stimuli capable of evoking significant sexual responses in androphilic women, but not to the same degree in gynephilic women or men.

Hypothesis 2 *Preparation hypothesis*

The preparation hypothesis (Suschinsky & Lalumière, 2011) posits that any sexual stimulus, preferred or not, provokes an automatic genital response that produces vaginal vasocongestion and genital lubrication as a protective mechanism (Laan & Everaerd, 1995), reducing pain (Bancroft & Graham, 2011) and/or injury (Chivers, 2005) during wanted or unwanted vaginal penetration. This explanation does not account for variation in genital responding, but instead proposes that any sexual stimulus could evoke a nonspecific vasocongestive response sufficient to produce vaginal transudate. Sawatsky, Dawson, and Lalumière (2016) have tested this hypothesis and shown category-specific introital lubrication (greater lubrication to the female–male sexual activity film) among androphilic women using a set of sexual stimuli similar to Chivers et al. (2007) in terms of variation in sexual activity and actor

gender. Of note, vaginal lubrication elicited by sexual stimuli other than the female–male sexual activity film was no greater than to a sexually neutral film. These results highlight the complex relationships between stimulus content and introital lubrication and suggest that a preparation hypothesis explanation for vaginal vasocongestion to nonpreferred stimuli is unsatisfactory.

Hypothesis 3 *Sexual objectification of women's bodies*

The third hypothesis is derived from objectification theory (Fredrickson & Roberts, 1997). From this perspective, women's bodies are ubiquitously eroticized and sexualized in popular media and therefore women may be doing the same when viewing sexual stimuli depicting women. Women objectifying and sexualizing women's bodies, particularly predominantly or exclusively androphilic women, could expand cognitive networks associated with sexual arousal and response and result in activation of the sexual response system by these nonpreferred, nonincentivized stimuli.

We examined self-reported objectification and identification with actors in sexual stimuli (what we called observational stance) as predictors of sexual responses to preferred and nonpreferred gender stimuli among andro- and gynephilic women and men (Bossio, Spape, Lykins, & Chivers, 2013). For women, observational stance did not predict genital response, but did predict self-reported arousal, with participant stance uniquely predicting self-reported arousal to all sexual stimuli; observer stance uniquely predicted self-reported arousal for heterosexual oral sex, lesbian penetrative sex, and gay oral and penetrative sex. Objectification theory may therefore not explain androphilic women's gender-nonspecific genital response, but it might explain some variation in women's subjective arousal to gendered sexual stimuli.

It is worth noting, however, that the Bossio et al. (2013) data were self-reported and observational, not experimental. Asking women to adopt objectifying versus nonsexual cognitive schemas when viewing preferred and nonpreferred sexual stimuli may provide a stronger test of an objectification theory account of androphilic women's sexual responses to nonpreferred sexual stimuli (see Middleton, Kuffel, & Heiman [2008] and Kuffel & Heiman [2006] for effects of schemas on genital and subjective sexual response). In a relevant study design, Both, Laan, and Everaerd (2011) demonstrated that cognitive strategies, adopting emotion-focused versus spectator-focused stance, could regulate self-reported feelings of absorption and sexual arousal, but not objectively assessed attention to sexual stimuli or genital response.

There are two additional predictions related to an objectification hypothesis for androphilic women's sexual response to nonpreferred sexual stimuli. The first is a capacity for observationally learned sexual associations with nonpreferred stimuli that have never once been directly paired with sexual reward. Women could, however, covertly reinforce sexual response to nonpreferred sexual stimuli through sexual fantasy and masturbation. For example, Dawson et al. (2012) reported high prevalence of same-gender fantasy among heterosexual women, with half of their androphilic women reporting some same-gender fantasy, albeit at a significantly lower frequency than opposite-gender fantasy. To date, however, no study has directly linked experience of same-gender fantasy or exposure to sexualized media objectifying women with gender-nonspecific sexual response among androphilic women. The second prediction is that observational learning of sexual objectification for nonpreferred sexual stimuli is unique to women; gay men are as exposed to sexualized imagery of women, but they do not demonstrate nonspecific sexual response patterns.

Hypothesis 4 *Identification with sexual pleasure*

A fourth hypothesis derived from simulation theory, or theory of mind, perspectives on social cognition (Gallese & Goldman, 1998; Gallese, Keysers, & Rizzolatti, 2004) is that observation of sexual activity, whether preferred or not, would activate neural representations of sexual response. From this perspective, gender-nonspecific sexual response reflects a gendered capacity for women, particularly androphilic women, to identify with the actors in a sexual stimulus. If they become sexually aroused by a nonpreferred stimulus, it is not because they are objectifying the women in the stimulus so much as identifying with her sexual pleasure (Money & Ehrhardt, 1972). As such, genital responding is not associated with the preferredness of the actors per se, but with identification with the sexual pleasure being depicted.

Evidence for the capacity for nonpreferred stimuli to provoke mirror neuron activity in the ventral premotor cortex, a brain region that is key to simulation theory, has not, however, been reported. Ponseti et al. (2006) reported gender-specific activation of the ventral premotor cortex in androphilic women when viewing stimuli depicting the torsos and sexually aroused genitals of males versus females. If these stimuli had been depictions of other women (or perhaps simply other people) experiencing sexual pleasure; however, we might predict, based on simulation theory, that androphilic women would experience a sexual response, regardless of the preferredness of the stimulus.

Hypothesis 5 *Fertility-dependent change in specificity of sexual response*

A fifth hypothesis derived from strategic pluralism theory (Gangestad & Simpson, 2000) proposes that gender-nonspecific sexual response may reflect reproductive-aged women's capacity for sexual receptivity, responsiveness, and arousability throughout the hormonal cycle (Diamond, 2007). At times of high fertility, proceptive sexuality might become strategically oriented toward preferred sexual partner. In terms of sexual response, this might be demonstrated by gender-specific sexual response. Using daily diary assessments of self-reported gendered sexual attractions throughout the menstrual cycle, Diamond and Wallen (2011) tested this compelling hypothesis for gynephilic and ambiphilic women. These women showed the expected ovulatory peak in same-gender attractions, though these effects were moderated by degree of fluidity of women's

sexual identities over time. Among androphilic women, the picture was somewhat more complex. Exclusively androphilic women showed a reduction in desire for sex with men at midcycle (which may relate to fear or anxiety about pregnancy) whereas predominantly androphilic women showed the expected increase in desire for sex with men (Diamond, 2015). As discussed earlier, however, gender-specific sexual response did not evidence at midcycle in one study of androphilic women (Bossio et al., 2014), but greater genital response to reproductively relevant sexual activities did emerge for women first tested in their fertile phase (Suschinsky et al., 2014). Future research might investigate fertility-related effects on other components of women's sexual response.

Hypothesis 6 *Magnitude of sexual response to preferred stimuli among androphilic women is, on average, lower than men's*

A sixth hypothesis is that sexual stimuli are capable of attracting attention and generating sexual response, but the magnitude of this response in women is relatively lower when compared with men's, therefore responses to preferred and nonpreferred stimuli may not be distinguishable. Sylva et al. (2013) proposed a similar hypothesis, suggesting that, "Heterosexual women may have experienced more extraneous mental processes and a relatively lower degree of attention and arousal in response to their preferred-sex stimuli compared with homosexual women, which would be consistent with findings from studies using genital arousal measures (Chivers et al., 2004, 2007)" (p. 682). If lower arousal or inattention to sexual cues leading to lower sexual response explains gender-nonspecific responding, then amplifying response through tactile stimulation might reveal different patterns; however, Peterson et al. (2010) found no such effects with a hands-free vibration device paired with visual sexual stimuli. Concurrent assessment of visual attention to sexual stimuli and genital responses could help determine whether reduced attention to gender cues is related to gender-nonspecific sexual responding among androphilic women.

Even when women and men report equivalent experience of sexual affect in response to sexual stimuli (e.g., Hamann, Herman, Nolan, & Wallen, 2004), gendered effects on neural processing of sexual stimuli persist. Measuring female and male genital response using an identical measure is very difficult, even with the same technology (e.g., thermography) because male and female bodies typically have different genitals that behave differently during sexual response; although we can measure genital vasocongestion and resulting temperature changes, these physiological effects occur on different scales (e.g., the temperature differential during penile vasocongestion is larger than for vulvar vasocongestion because the penis is more distal to the torso, see Huberman & Chivers, 2015). As such, only relative comparisons are possible unless we can measure identical structures, such as pelvic vasocongestion through anal photoplethysmography; even so, internal structures still differ between the sexes. But we must remind ourselves that nonspecific response patterns are mostly observed for androphilic women, perhaps only for exclusively androphilic women, and perhaps only for gendered stimuli. A hypothesis invoking distraction or reduced attention capture, or measurement differences, leading to lower sexual response among women, would therefore also need to explain sexual orientation and stimulus cue effects.

Hypothesis 7 *Early neurohormonal events affect response specificity in adulthood*

The hypotheses discussed to this point tend to overlook within-gender variation in the specificity of sexual response; they do not explain why androphilic women show gender-nonspecific responses, but gynephilic and ambiphilic women more often show gender-specific responses. As discussed earlier, we have recently produced data suggesting that only exclusively androphilic women have gender-nonspecific genital responses (Chivers et al., 2015), and this pattern has been replicated in measures of visual attention (Dawson et al., 2016). Neurohormonal hypotheses regarding women's same-sex attractions (Bailey et al., 2016; Mustanski et al., 2002) suppose that gynephilia among women may be associated with atypical androgen exposure during fetal gestation. Little attention has been given to understanding the neurohormonal events associated with androphilia among women.

Given the bulk of research showing an undifferentiated pattern of response to gender cues among androphilic women, a seventh hypothesis, an extension of the neurohormonal hypothesis for sexual orientation, is that prenatal androgen exposure is associated with differentiation of response patterns in the direction of preferred gender, and lack of androgen exposure results in no differentiation. In a fMRI study comparing brain responses of androphilic genetically female women, gynephilic genetically male, and androphilic genetic males with complete androgen insensitivity syndrome (CAIS) who were assigned a female gender at birth, and identify and live as women, showed gender-nonspecific brain responses among genetic females and CAIS women (Hamann et al., 2014). CAIS women lack functional androgen receptors, and therefor their prenatal neurohormonal environment is very similar to natal genetic women's. Indeed CAIS women showed less specificity in brain responses than genetic, androphilic females. Hamann et al. summarized these effects as, "…converging findings indicate that women with CAIS have brain responses to sexually arousing stimuli similar to those of control women, with whom they share female-typical socialization and predominantly estrogenic postnatal hormonal exposure" (p. 728). According to the neurohormonal hypothesis, gender-specific sexual responses, both genital and neural, are associated with the action of prenatal androgens. Genetic males with CAIS who identify as women show a pattern of sexual response typical of genetic females who identify as women, and counter to that of genetic males who identify as men, because they had no prenatal exposure to androgens. Both neurohormonal effects of prenatal androgens, postnatal estrogens (exogenous for CAIS women), and socialization as women, are therefore associated with gender-nonspecific responding among CAIS and genetic women.

Hypothesis 8 *Gender-specific sexual response reflects "masculine" sexual and nonsexual traits in gynephilic women*

Rieger, Savin-Williams, Chivers, and Bailey (2015) proposed that nonsexual masculinity among gynephilic women may relate to gender-specific sexual response and investigated in two studies whether women's levels of masculinity and femininity mediated or moderated the relationship between sexual orientation, operationalized using sexual identity labels (e.g., straight, mostly straight, bisexual leaning straight, bisexual, bisexual leaning lesbian, mostly lesbian, lesbian) and sexual response, assessed as vaginal photoplethysmography or pupil dilation. Neither mediation nor moderation was observed and we concluded, "Although both studies confirmed that lesbians were more male-typical in their sexual arousal and nonsexual characteristics, on average, there were no indications that these 2 patterns were in any way connected. Thus, women's sexual responses and nonsexual traits might be masculinized by independent factors" (p. 1).

Hypothesis 9 *Greater variability in sexual rewards among androphilic women*

The contributions of female-typical socialization to the specificity of sexual response may be among some of the more fruitful avenues to explore, given that disentangling the effects of early neurohormonal events from later socializing influences is near to impossible (in humans). The stereotypical heteronormative mating script (Jackson, 2006), where men pursue women sexually and women are "gatekeepers" for sexual activity may, for example, have a role to play in androphilic women's nonspecific sexual response. Although androphilic women may be sexually attracted to men, preferred gender cues may not be as strongly linked with prolonged reward-seeking behavior because of the commonly observed lower frequency of orgasm during partnered sex among androphilic women (Coleman, Hoon, & Hoon, 1983; Wade, Kremer, & Brown, 2005). Seeking and detecting mates based on distally perceived cues, like gender features, would pair these cues with reward-seeking behavior, anticipation of rewards, and consummation of sexual rewards (Ågmo, 1999). Among gynephilic women, by dint of a lower base rate of opportunity with other gynephilic women, finding a mate would entail more significant effort to seek, engage, and eventually consummate sexual desire; this process may reinforce and incentivize gender cues in a way that is not typically observed among androphilic women who may be more constrained by a heteronormative mating script. Variability in the consistency of reinforcement via orgasm has been reported for queer versus heterosexual women, with queer women more consistently prioritizing and experiencing orgasm during sexual encounters with other women (Goldey, Posh, Bell, & van Anders, 2016). More consistent reinforcement of female sexual cues could therefore shape future sexual responses such that queer women demonstrate greater sexual response to female than male cues. Heterosexual women's less consistent experience of orgasm would not, by contrast, selectively reinforce male sexual cues, and the result would be a nonspecific pattern of sexual response. Likewise, women who are less likely to follow a heteronormative mating script and engage in more proceptive sexual behaviors, such as among women higher in sociosexuality, may show more gender-specific sexual response patterns (e.g., Timmers & Chivers, 2012).

Hypothesis 10 *Nonsexual motivations to attend to sexual stimuli interact with stimulus prepotency to produce nonspecific response*

A tenth hypothesis is particularly promising in terms of integrating perspectives to explain gender-nonspecific response in androphilic women. A key component of sexual response is attention to sexual cues (Janssen et al., 2000). In this review, it is clear that androphilic women's early visual attention and neural responses to sexual cues are gender-nonspecific, mirroring their gender-nonspecific patterns of genital response. It is therefore possible that nonpreferred sexual cues may capture and sustain attention, and initiate a cascade of sexual responses that may not ultimately manifest as motivated sexual behavior with another woman. Attention to female sexual stimuli may, instead, reflect nonsexual motivations, such as intrasexual competition (e.g., Maner, Gailliot, & DeWall, 2007; Maner, Gailliot, Rouby, & Miller, 2007; Maner, Miller, Rouby, & Gailliot, 2009).

Intrasexual competition might manifest as intensive scrutiny of possible female competitors for male mates, and be reflected in visual attention to female sexual stimuli. Attention to female sexual cues motivated by intrasexual competition may be sufficient to activate sexual response at multiple levels of initial stimulus processing, resulting in gender-nonspecific genital responses. Alho et al. (2015) proposed a similar hypothesis; "…though reproduction requires an opposite-sex partner, sexual behavior may well be triggered by perception of a nude body regardless of the gender, for example, through [cognitive] associations (Amoruso, Couto, & Ibanez, 2011)." As preferred sexual cues are further elaborated upon, self-reported sexual arousal may be gender-specific and later visual attention may become more gender-specific (e.g., Dawson & Chivers, 2016). Given the majority of studies examining gender specificity of sexual response use very short sexual stimuli, nonspecific genital responding may reflect only the initial phase of sexual response. Indeed, Pulverman et al. (2015) have suggested that, at least among androphilic women, genital responses to nonpreferred stimuli are not sustained during a longer stimulus in the same manner as preferred stimuli are, resulting in a more category-specific pattern of sexual response as the stimulus continues (but see Huberman & Chivers [2015] for evidence of sustained gender-nonspecific response using thermography and VPP).

Limitations

Technological and psychometric constraints are among the limitations to consider when evaluating the literature on specificity of sexual response. For the majority of methodologies, good psychometric properties have been reported; however, for some cognitive methods, like IAT, concerns about validity have been raised (Babchishin, Nunes, & Hermann, 2013). Other methodological factors to consider include small sample sizes in psychophysiological studies, typically between 15 to 30 participants per group. Although sufficient to detect specificity effects among men, subtler interactions with individual differences among women may require greater power, and thus larger sample sizes. Pooling data from multiple studies using similar methodologies can reveal these subtler third variable effects, such as effects of masturbation experience on sexual response (e.g., Laan, 1994).

The external validity of these effects must also be considered, given some of these data are collected in a laboratory setting, using a self-selected sample of people willing to volunteer for sexuality studies, some involving genital response assessment. Ascertainment bias effects on sexual response suggest impression management is associated with a more constricted range of self-reported sexual responses (Huberman, Suschinsky, Lalumière, & Chivers, 2013). Greater sexual experience among participants in sexual psychophysiology research may, for example, bias response patterns toward a more generalized, undifferentiated pattern. Indirect tests for ascertainment bias effects have, however, not produced results suggesting systematic bias in gender-nonspecific sexual response among women (e.g., Chivers et al., 2004).

Another significant concern is that the majority of the *genital* sexual psychophysiology studies discussed in this review are from my laboratory, using the relatively small sample sizes typical of psychophysiological studies. Given that gender-nonspecific sexual response in androphilic women has been observed across a wide range of methodologies, however, from brain imaging to genital responses, implicit stimulus processing to visual fixations, I believe the gender nonspecificity effects are not artefacts. Regardless, independent replication is always desirable, particularly for the surprising findings regarding specificity of sexual response for sexual activity (Chivers et al., 2014), relationship context effects (Chivers & Timmers, 2012), cycle phase effects (Bossio et al., 2014; Suschinsky et al., 2014), and prepotent cue effects (Spape et al., 2014).

Conclusions

Returning to the precept of this review, to examine specificity of women's sexual response at each stage of the IMM/IPM, a significant puzzle is revealed. For gynephilic women, sexual responses are typically gender-specific at most stages of sexual response. For androphilic women, a more textured pattern is revealed. Androphilic women show gender nonspecificity in early stimulus processing, and more gender specificity in later stimulus processing. Mixed specificity effects have been observed for affective response. Specificity of genital and subjective sexual response follows from stimulus processing, with androphilic women showing gender-nonspecific genital response, similar to early stimulus processing effects, and more gender-specific subjective response, similar to later stimulus processing.

Patterns of genital and subjective sexual response are sensitive to stimulus cues and context, with sexual activities, relationship context, and power dynamics also influencing response, typically obscuring gender-specific genital response among androphilic women. Autonomic activation patterns are similarly gender-nonspecific for androphilic women. Reward effects, operationalized as response to attractiveness cues for the purposes of this review, produce a similar pattern, with androphilic women showing greater modulation of response by attractiveness versus gender cues. For fMRI assessment of reward area activation, specificity has been reported for all women. Sexual desire in response to preferred and nonpreferred sexual stimuli shows different effects for type of desire; for solitary desire, androphilic women report gender-nonspecific increases in desire to masturbate, but greater specificity for desire for sex with a partner. In sum, androphilic women's early stimulus processing, genital response, autonomic responses, and responsive solitary sexual desire is gender-nonspecific, whereas their later stimulus processing, affective, and subjective responses, reward area activation, and responsive partnered desire are more gender-specific. We can therefore conclude that the specificity of women's sexual response may be modulated by individual differences in sexual attractions and stimulus composition.

The growing body of research on the specificity of sexual response has opened the door to multiple lines of work investigating women's sexuality. Questions regarding the development and expression of sexual attractions, the nature of competent sexual cues, and the incentivization of sexual stimuli are areas in which we have only the most remedial understanding. I hope that other researchers curious about these aspects of sexual response will strongly consider examining their effects as a function of sexual attractions, that is describing degrees of androphilia and gynephilia, versus reliance on self-description of sexual identity which is, particularly among women, a less accurate indicator of gendered sexual attractions. Investigators studying heterosexual women's sexuality are encouraged to clearly define gendered sexual attractions in addition to sexual orientations and identities (e.g., exclusive versus predominant androphilia, identifying as heterosexual) and to report their effects as a function of these different classifications. For example, in two studies (Suschinsky, Dawson, & Chivers, 2016; Dawson et al., 2016), we examined sexual concordance and visual attention to sexual cues as a function of degrees of gynephilia or androphilia among women. Given the different effects observed for activity preferences, I welcome more

investigation into other dimensions of women's sexual orientations. Last, I would also encourage sexual response researchers, particularly those interested in understanding determinants of women's sexual functioning, to strongly consider adopting a specificity paradigm, that is, comparing responses to preferred and non-preferred stimuli, versus a paradigm where responses to only one, preferred, typically heterosexual/opposite-gender stimulus, are examined; introducing more variation in sexual response has great potential in terms of understanding the incentivization of sexual cues in relation to the multiple stages of sexual response. Doing so may bring us closer to a better understanding of the relationships between women's sexual attractions, sexual responses, and sexual orientations.

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Compliance with ethical standards

Conflict of Interest The author declares no conflicts of interest.

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