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COMMENTARY

Specificity of Women's Sexual Response: Proximate Mechanisms and Ultimate Causes

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Chivers' (2017) review on the psychophysiology of women's sexual arousal provides a broad synthesis between experimental evidence and theoretical approaches. Chivers concludes that androphilic (sexually attracted to adult males) women's early stimulus processing, genital response, autonomic responses, and responsive solitary sexual desire are "gender-nonspecific." In contrast, androphilic women's later stimulus processing, affective, and subjective responses are "more gender-specific."

Arousal to Gender or Sex?

Problematically, Chivers (2017) does not define the key term *gender*, which results in ambiguity regarding the actual signals to which subjects respond. Are they responding to the gender or the sex of the target stimuli? Chivers implicitly seems to use *gender* to mean *sex*, as is typically done to avoid confusing biological sex with sexual activity. *Sex* refers to an individual's biological, evolved features as male or female, including sexually dimorphic external genitalia and secondary sexual characteristics that develop at puberty. *Gender*, on the other hand, refers to behaviors, attitudes, or traits associated in a particular culture and time with the roles or characteristics considered more typical of and appropriate for men or women (Rosario & Schrimshaw, 2014). Although it is not necessary for there to be a

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biological link or correspondence between sex and various manifestations of gender, such a link often exists across cultures and, interestingly, even across species (Alexander & Hines, 2002; Lonsdorf, 2017; Rosario & Schrimshaw, 2014). It is beyond the scope of this commentary to review the extent to which biological sex influences gender manifestations and vice versa; instead, we direct interested readers to more comprehensive discussions on the topic (Hyde, 2014; Meredith, 2015; Wood & Eagly, 2012). What is more important, when shown photographs or videos of nude women, it is probable that subjects assess features of sex, not gender: The former become accentuated, while the latter are more difficult to convey in such material. Nevertheless, it is possible to construe a situation in which variations in *gender* become salient features of women's arousal. If women are presented with sexually explicit audiovisual stimuli that include two femme lesbians, their responses might be different from being presented with two butch lesbians, which might again vary from observing a butch–femme pair. In these three scenarios, the sex of the target individuals is constant, but their gender/sex manifestations likely vary in several ways. van Anders (2015) proposed that using the umbrella term *gender/sex* is preferable in contexts where gender and sex cannot be disentangled. It seems reasonable to infer that in the majority of the data that Chivers (2017) reports, gender and sex *can* be disentangled: The independent variable in most of the reported data is ostensibly sex, not gender. This is not mere semantic pedantry, but can advance our understanding of which features of sexual stimulus trigger sexual arousal in women. Using precise language to communicate findings will increase the impact of the sexual arousal research program.

Evaluating Hypothesis 7: In Utero Neurohormonal Events Affect Response Specificity

Subsequent to the review of the existing literature on women's sexual arousal, Chivers (2017) discussed ten hypotheses that could explain why androphilic women become aroused by a broader

range of stimuli than gynephilic women and men. Without discussing the other hypotheses in greater detail, we note that there is a wealth of evidence supporting Hypothesis 7, the theory that prenatal sex hormone exposure has organizational effects on the determination of sexual orientation in women and men (reviewed by Bao & Swaab, 2011; Breedlove, 2017; Rosario & Schrimshaw, 2014). In contrast, Chivers' Hypothesis 9 emphasizes the idea that socialization may be a factor causing less specificity in androphilic women's sexual response. Testing Hypothesis 9 could, according to Chivers, be a fruitful line of enquiry, given that "disentangling the effects of early neurohormonal events from later socializing influences is near to impossible (in humans)." We contest this view by noting that several biomarkers and behavioral studies have been advantageously used to do just that—to disentangle whether women's predisposition for gynephilic preferences arises through biological processes or through socialization (Bao & Swaab, 2011; Breedlove, 2017). There are several lines of enquiry that provide support for the hypothesis that prenatal neurohormonal processes are associated with an increased likelihood of female gynephilia and gender-atypical behavior. These include sexually dimorphic traits such as digit ratio (Grimbos, Dawood, Burriss, Zucker, & Puts, 2010; Zheng & Cohn, 2011), click-evoked otoacoustic emissions (McFadden & Pasanen, 1998), and long bone growth (Martin & Nguyen, 2004), which are masculinized in gynephilic women. In this context, we can only provide a glimpse into the divergent lines of evidence accrued from human and nonhuman animal studies which indicate that prenatal sex steroid exposure is an important determinant of nonheterosexual preferences in females. We offer it as a corrective to Chivers' claim about the difficulty to disentangle socializing influences from neurohormonal ones.

We believe that the evidence summarized above indicates that Chivers' (2017) Hypothesis 7 constitutes the most plausible explanation—not to the question why androphilic women's sexual responses are less sex specific—but rather to the question how do they develop that way. Explanations for the evolution of a trait or a behavior are typically given on two different, complementary levels: What is the proximate mechanism underlying the trait and why did the trait evolve (Laland, Sterelny, Odling-Smee, Hoppitt, & Uller, 2011). The organizational effect of the prenatal neurohormonal environment pertains to the proximate question of how a trait such as sex specificity of sexual arousal develops during ontogeny. A female brain is the default mode in fetal development; for a male brain to develop, in utero androgenization is required (Bao & Swaab, 2011). As Chivers' review indicates, the "default brain"—that is, the brain of the androphilic female—seems to be capable of invoking sexual arousal by reacting to sexual stimuli of both sexes. The androgenization of the brain, therefore, seems to be the mechanism that eliminates arousal to male sexual signals, as observed in gynephilic men and women. Although it may appear that the existence of androphilic men negates this hypothesis due to their being masculinized yet showing arousal to male sexual signals, empirical evidence suggests that the brains of androphilic men are in fact significantly less masculine than those of gynephilic men. The corpus

callosum (Witelson et al., 2008), the anterior commissure (Allen & Gorski, 1992), and the INAH3 region of the anterior hypothalamus (LeVay, 1991) of androphilic men are more similar to androphilic women's brain morphology than that of gynephilic men, giving indirect support to the hypothesis that androgenization of the brain eliminates arousal to male sexual signals.

Nevertheless, this explanation fails to specifically address the ultimate question of why sex-nonspecific sexual response evolved in phylogeny, that is, what benefit does it confer to the genotype that induces it? The above discussion suggests that it is evolutionarily and psychophysiologically parsimonious to equip the "default brain" with a capacity to be aroused by both sexes. The androgenization of the brain subsequently eliminates one pathway to arousal. This suggests—but does not conclusively demonstrate—that due to lower brain androgenization, androphilic men have retained the "default capacity" to become sexually aroused by men. The crucial question that follows is this: If prenatal androgenization eliminates sexual arousal to men in gynephilic men and gynephilic women, how does arousal to females become eliminated in androphilic men?

Hypothesis 11: Nutritional Rewards

To tackle these questions from a novel perspective, we suggest another hypothesis that flows from the premises of the Incentive Motivation Model (IMM) outlined by Toates (2009). According to the IMM, organisms become motivated by rewards in the environment and form preferential associations with sources that provide them. Neuroscientific evidence shows that the brain networks, reward anticipation, and consummation involved in the sexual response cycle are remarkably similar to the pleasure cycles associated with food consumption (Georgiadis & Kringelbach, 2012). Nutritional rewards precede sexual ones both phylogenetically and ontogenetically, utilizing similar reward pathways and associative mechanisms. Evolution tinkers with existing mechanisms when increasing organismal complexity, and so it is possible that the female body becomes hedonically incentivized to neonates due to repeated associations with nutritional rewards. This association occurs not only directly during lactation, but also indirectly throughout ontogeny as the mother provides food to her child.

More generally, it has been suggested that the perception of stimuli from homogenous classes (in the present case: female bodies) that share common configurations is based on the features of a template representation that is used as a reference point to perceive other exemplars. The exemplars that are more similar to the template representation have higher hedonic valence (Kirsch, Urgesi, & Cross, 2016; Valentine, Darling, & Donnelly, 2004). The degree of attention devoted to male and female bodies may therefore be an index of the overall hedonic quality associated with such bodies (cf. Dawson, Fretz, & Chivers, 2017; Spiering, Everaerd, Karsdorp, Both, & Brauer, 2006), which could explain a "spillover effect" from nutritional rewards to sexual ones (cf. Garcia & Ramirez, 2005; Morehouse, Nakazawa, Booher, Jeyasingh, & Hall, 2010).

Developing a psychophysiological aversion to same-sex bodies is significantly costlier for women than it is for men, since women's bodies offer a more tangible and more constant source of nutrition for human infants than men's bodies do. Men do use their bodies to harvest energy from the environment to promote the fitness of their offspring, but, *ceteris paribus*, women's bodies are more directly incentivized for human infants than men's bodies due to internal gestation, lactation, and the greater parental care that women typically provide for infants (Morehouse et al., 2010). The reason why the majority of men do not become sexually aroused by same-sex bodies would, according to the nutritional rewards hypothesis, be that same-sex bodies have not been similarly incentivized for men as a nutritional source through ontogeny as female bodies have. It could even be that there are costs associated with men who become sexually aroused by other men's bodies, such as suffering from direct aggression were they to act on their androphilic desires with some gynephilic men. Foregoing heterosexual mating opportunities, which are asymmetrically distributed between men and women due to the abundance and "cheapness" of sperm, constitutes a greater cost for men than for women. These costs are less severe for women than for men for two reasons: (1) Female aggression is less fatal than male aggression (e.g., Campbell, 1999) and (2) parental investment theory predicts that women have more mating opportunities than men do (Trivers, 1972) and so foregoing some heterosexual mating opportunities due to same-sex arousal poses significantly smaller costs to women. The selection pressures against same-sex body incentivization are therefore higher for men than they are for women, while the selection pressures *for* same-sex body incentivization are higher for women than they are for men due to the female body's association with nutritional rewards. The nutritional rewards hypothesis is falsifiable by analyzing the sexual responses of women who have been raised without a female caregiver and seeing whether they exhibit similar sexual arousal to female stimuli as do women who were raised with a female caregiver.

Hypothesis 12: Alloparenting

The alloparenting hypothesis of female sexual fluidity predicts that female gynephilia could be an adaptive response to environmental conditions (Kuhle & Radtke, 2013), much like male androphilia is when analyzed via an inclusive fitness model (VanderLaan & Vasey, 2014). Forming stable pair bonds with other women may be adaptive if a woman is impregnated by a man who provides little or no parental care (including, but not limited to, rape). In such a situation, it may be doubly beneficial for a woman to form a pair bond with another woman, since stepfathers could be more liable than stepmothers to abuse the existing offspring (cf. Daly & Wilson, 1998). Apart from the nutritional rewards hypothesis, alloparenting would further reduce the selection pressures against women's sexual arousal to same-sex individuals. Theoretically speaking, it could be beneficial for a mother to become aroused by same-sex sexual signals and engage in homosexual behavior if it encouraged other women to allocate bioenergetic resources, including parental effort, to her offspring.

Future Directions

Hypotheses 11 and 12 provide additional directions for explaining why all women and most men are sexually aroused by female bodies. The question with which they leave us is this: Why are androphilic men incentivized more by male than by female bodies? The nutritional rewards hypothesis—if assessed *in isolation* from other theories of how sexual orientations emerge—would make the seemingly implausible prediction that androphilic men have experienced more frequent food-related rewards in association with *male* rather than female bodies. This prediction is not only implausible but also easily falsifiable, and while we have discussed other factors that play a greater and more extensively documented role in shaping sexual arousal patterns in both men and women (see "Evaluating Hypothesis 7"), we nevertheless propose the nutritional rewards and alloparenting hypotheses to be added to the ten hypotheses provided by Chivers (2017). The nutritional rewards hypothesis has some existing (albeit indirect) theoretical support (Lassek & Gaulin, 2008; Morehouse, 2014; Sakaluk, 2000; Vahed, 2007) and can therefore make a valuable addition to a pluralistic explanatory framework within the sexual arousal research program.

Further research could, for example, manipulate the signals that female subjects observe under experimental conditions. Are women's sexual responses equal when presented with visual stimuli of females in the following categories: (1) nulliparous, (2) parturient, (3) parous, (4) postmenopausal, (5) having gender/sex-typical versus gender/sex-*a*typical physical appearance (e.g., femme vs. butch), (6) having underdeveloped sex-typical secondary sexual signals (e.g., due to low adiposity), versus well-developed ones, (7) having sex-*a*typical secondary sexual signals, such as a conspicuously muscular body (e.g., due to an exercise regime and diet that promote muscle growth), or (8) having body morphology that resembles versus does not resemble that of the subject's primary caregiver? These types of experimental manipulations would help determine what are the salient features of same-sex stimuli that induce sexual arousal in women, thus increasing the experimental evidence with which to evaluate the existing hypotheses—or to create novel ones. What we wish to highlight is that the hypotheses should distinguish causation occurring both at the proximate and at the ultimate levels, ideally making connections between the two to better inform syntheses between various research programs.

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