



Four Additional Questions for the Preparation Hypothesis

Kirstin Clephane¹ · Anneliis Sartin-Tarm^{1,2} · Tierney K. Lorenz^{1,2} 

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As Lalumière, Sawatsky, Dawson, and Suschinsky (2020) note in the discussion of their Target Article, the preparation hypothesis has been remarkably successful in launching a wide variety of research projects attempting to understand the nature of the relative cue non-specificity seen in women's genital arousal.¹ They do an excellent job reviewing this wide literature with an eye to balancing evidence for and against the preparation hypothesis; however, there are still some outstanding questions about the preparation hypothesis that we did not see fully explored, and which may also lead to fruitful new avenues for research on sexual arousal. Here, we describe four remaining questions with implications for future research: Is there evidence of sufficient selection pressure to warrant developing an adaptation to overcome that pressure? Is this truly a sex/gender-specific effect? How does a history of sexual trauma influence women's perceptions of sexual cues, and does this alter preparatory genital responses? And finally, are there other ways in which non-specific genital arousal may contribute to women's reproductive fitness?

Claiming an Evolutionary Adaptation Implies Selection Pressures, Universality Across Cultures, and Specificity to Fertile Individuals

Throughout their review, Lalumière et al. (2020) hold an assumption: automatic genital responses that are elicited by sexual stimuli are both necessary and sufficient to protect

the vaginal lumen during penetration. However, there is a dearth of research documenting the extent to which damage from penetration actually impairs fertility sufficiently to warrant an adaptation, let alone whether the vasocongestion and lubrication elicited by non-preferred stimuli are sufficiently protective to prevent such impairments. For a behavior to be considered an evolutionary adaptation, there must be evidence of both selection pressure—some problem that impairs reproductive fitness—and evidence that behavior overcomes this pressure. There are aspects to both of these requirements that were not fully explicated in Lalumière et al.'s (2020) review, which we consider below.

The assumption that genital injury from penetration would be sufficient enough to impair fertility requires examination. There is no consensus as to whether penetration of an unaroused vagina causes sufficiently more damage than penetration of a moderately aroused vagina or that it differentially impairs fertility to the extent that the owner of the former would produce fewer babies than the owner of the latter. Evolution does not care about injury if those injuries do not impair actual fertility. A few studies in large samples suggest that number of children is unrelated to either women's positive arousal function or arousal concerns (Avis et al., 2009; Witting et al., 2008), although these studies used only self-reported arousal measures. Thus, research is needed that directly examines fecundity and fertility among people with varying levels of vaginal arousal.

A great deal more research is needed regarding the existence, let alone the nature, of lubrication responses that correlate with the blood flow responses. Much of the research supporting the preparation hypothesis has used vaginal photoplethysmography (VPP). Though not without problems, VPP is a gold-standard method to reliably measure vasocongestion, that is, vaginal blood flow in response to sexual stimuli (Chivers, Rieger, Latty, & Bailey, 2004;

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✉ Tierney K. Lorenz
tierney.lorenz@unl.edu

¹ Center for Brain, Biology and Behavior, University of Nebraska-Lincoln, Stadium East C66, Lincoln, NE 68588-0156, USA

² Department of Psychology, University of Nebraska-Lincoln, Lincoln, NE, USA

¹ We recognize the fact that not every owner of a vagina is a woman, and not all women have vaginas. However, the majority of prior research on the preparatory hypothesis has examined cis-gendered women (with a few notable exceptions) and in keeping with the review of this literature, unless otherwise noted, we here we reference “women” as shorthand for “person with a vagina.”

Chivers & Bailey, 2005; Geer, Morokoff, & Greenwood, 1974). While vasocongestion may be a reliable indicator of sexual arousal, it is likely only one piece of the protection puzzle. Certainly, increased vasocongestion promotes increased elasticity within the vaginal tissue, which decreases the likelihood of injury (Levin, 2003; Masters & Johnson, 1966). However, vasocongestion is not thought to be solely responsible for the proposed lumen protection, as lubrication is also critical (Levin, 2003; Masters & Johnson, 1966). As Lalumière et al. (2020) outline, for VPP research to be considered evidence for the preparation hypothesis, we must also assume that vasocongestion consistently precedes vaginal lubrication, that the degree of vasocongestion is directly associated with degree of lubrication, and that the very moderate amount of vasocongestion observed during automatic arousal produces lubrication sufficient to be protective of the lumen. Setting aside the fact that introital lubrication may not follow the same patterns of cue non-specificity as vasocongestion (Sawatsky, Dawson, & Lalumière, 2018), the question of threshold needs to be answered. What degree of vasocongestion and lubrication is required to protect the vaginal lumen from fertility-impairing injury?

However, insofar as lubrication protects against tissue damage and/or STIs, the question may go beyond simply the amount, but also the quality, of the lubrication provided. The microbial immunology and composition of vaginal mucus can provide a better understanding of the extent of protection. Though the link between sexual psychophysiology and immune responses has only relatively recently been documented, it is possible that the automatic genital response to sexual stimuli serves to alter the activity of the immune system (Huang & Vita, 2006; Lorenz, 2019b). While the length of time required for immune factors to be called into action—specifically within vaginal mucosa—has yet to be determined, it is possible arousal serves as a cue to the immune system to allocate appropriate resources in preparation for possible tissue damage, a phenomenon known as immunoredistribution (Braude, Tang-Martinez, & Taylor, 1999). For example, sexual arousal may redirect secretion of antibodies and cytokines (immune signaling molecules) from the general circulation toward mucosal sites (Lorenz, Demas, & Heiman, 2015)—in particular, toward vaginal mucosa (Lorenz, 2019a). Further investigation into the psychoneuroimmunology of this seemingly automatic, non-specific genital response is warranted to develop a better understanding of protective adaptations.

Finally, the evolutionary basis of the preparation hypothesis implies that automatic, non-specific genital responses should be relatively independent of culture. While there has been some research comparing East Asian and Euro-Canadian women's genital responses, there seems to be a lack of cross-cultural representation of the automatic genital

response phenomenon (Yule, Woo, & Brotto, 2010). Though it is anticipated to remain stable across cultures, demonstration that this response happens on a global scale would strengthen the argument for the evolutionary basis of the preparatory hypothesis. While such data could prove difficult to attain owing to ethical or even legal concerns for sex research in many cultures, a possible first step could be to begin researching this phenomenon in industrialized, non-Western settings.

Male Genital Responses in Non-Consensual Situations Raise Questions About the Sex/Gender Specificity of the Preparatory Response

While laboratory studies have established the reliability of male subjective and genital response as highly concordant, this research overlooks reports of real-life subjective and genital responses that males experience in non-consensual sexual situations. Much of the research leading to the preparatory hypothesis is founded on the idea that female-bodied people and children make up the majority of those subjected to non-consensual sexual activity and would thus benefit from an automatic arousal response. However, this assumption leaves a large gap in understanding the experiences of male survivors.

Male genital response has been established as reliably responsive to preferred stimuli (Chivers, 2010; Chivers & Bailey, 2005; Seto, 2001). It is assumed that this specificity to preferred stimuli would translate to lack of automatic arousal to assault stimuli. However, the caveats to this research are that males rarely—if ever—are exposed to stimuli that depict a male as the target of assault (and thus, the need for a preparatory arousal response). Perhaps male genital responses would be different given a stimulus in which they perceived themselves as targets. Alternatively, if we extend our research beyond the laboratory, we find many males have physiologic responses that do not match what we would expect to see using laboratory-based phallometry. Many male rape survivors report “involuntary arousal” during an assault, which one could argue is an automatic response to non-preferred stimuli (Bullock & Beckson, 2011; Groth & Burgess, 1980). Involuntary arousal leaves many male victims confused and ashamed because subjectively they were terrified, but physiologically their bodies responded in a way that is narrowly viewed as conveying interest and consent (Bullock & Beckson, 2011; Groth & Burgess, 1980). Does this experience qualify as an automatic, non-specific genital response, paralleling that seen in women and cited as evidence of the preparatory hypothesis? If so, is there evidence that male genitalia are harmed during sexual assault? And if not, what

are the boundaries around what is and is not considered a “preparatory” response?

Sexual Trauma Alters How Women Perceive Sexual Cues, Which Would Reduce Preparatory Arousal in Future Sexual Assaults

A major assumption of the preparation hypothesis is that vaginal arousal occurs to any cue encoded as sexual—and importantly, not to non-sexual cues. According to the information processing model of sexual responding, initial stages of genital arousal do not depend upon appraisal as preferred or non-preferred, only as sexual (Janssen, Everaerd, Spiering, & Janssen, 2000). As Lalumière et al. (2020) discussed, vaginal responses are elicited to some degree by any sexual stimuli, even if these responses are ultimately weakened by negative affect (Brauer, ter Kuile, & Laan, 2009).

This selectively indiscriminate responding is cited as evidence that the vagina is preparing for penetration, even in the context of sexual assault. But do we have evidence that during sexual assault, women attend to and appraise sexual cues as sexual, and not as threatening? Moreover, are sexual stimuli the most salient and attention-commanding during sexual assault? Threatening stimuli tend to direct attention away from sexual stimuli and toward situational or contextual cues. Specifically, women visually attend toward more contextual cues and more readily inhibit sexual responding than men, theoretically through attention to context (Bangasser, Eck, & Ordoñez Sanchez, 2019; Rupp & Wallen, 2008). If women perceive non-consensual stimuli as threatening and thus direct attention toward non-sexual cues, their genitals may respond to a lesser degree. However, empirical evidence may be inherently limited by its reliance on in-laboratory tests of genital responding, which cannot completely replicate the contextually rich setting of sexual violence. The interplay between contextual information and related emotions during sexual violence may be fundamentally impossible to replicate in lab; however, we may begin to tease apart this question with tests of divided or masked attention.

Affect is also likely to contribute to attentional biases in the sexual violence context. Though there is wide inter-individual variability, women frequently report feeling strong disgust and fear during sexual violence (Badour, Ojserkis, McKay, & Flender, 2014; Kunst, Winkel, Bogaerts, 2011; Rizvi, Kaysen, Gutner, Griffin, & Resick, 2008). These basic emotions serve important evolutionary purposes, by orienting attention toward salient stimuli and motivating avoidance of potential threat (Al-Shawaf, Conroy-Beam, Asao, & Buss, 2016). In the sexual context, these emotions differentially interact with sexual responding. For example, disgust—but not fear or anxiety—has been shown to inhibit genital arousal

(Bradford & Meston, 2006; Fleischman, Hamilton, Fessler, & Meston, 2015). Thus, there is a need for more research examining the nature of attention to sexual versus threat aspects of a stimulus while experiencing extreme anxiety and/or disgust, as would be experienced during sexual violence.

Moreover, research suggests that among sexual trauma survivors, encoding of sexual stimuli shifts such that these stimuli are implicitly associated with threat rather than eroticism (Rellini, Ing, & Meston, 2011). Affective and physiological cascades can strengthen conditioned fear or disgust responding with trauma-related stimuli, which for sexual trauma survivors would include sexual stimuli (Yehuda & LeDoux, 2007). Several studies have suggested that some women who have experienced sexual assault develop conditioned threat bias, both within and outside of the context of sex (Marx & Sloan, 2005; van Berlo & Ensink, 2000; Zoldbrod, 2015). For many, conditioned emotional responses to trauma-related sexual cues do not extinguish, resulting in learned threat bias and subsequent decreased sexual arousal (Chapman et al., 2012; Walsh, Galea, & Koenen, & 2012). In other words, insofar as preparatory responses are dependent on encoding stimuli as (primarily) sexual, we may expect to see significantly fewer such responses among survivors of sexual violence.

Some data also suggest that genital arousal occurs in response to violent, non-sexual cues, suggesting that women may perceive associations between violent, non-sexual cues and violent sexual cues (Suschinsky & Lalumière, 2011). Because sexual violence and non-sexual violence frequently occur together, these data may support the idea that genital preparation serves as an energy-efficient protective mechanism in response to sexual and non-sexual violence. Indeed, in the evolutionary context of unwanted sex, attentional biases in women may be especially advantageous for detecting sexual and non-sexual threat cues (Dawson & Chivers, 2016).

Given the evidence suggesting a robust role of prior sexual trauma on sexual arousal processes, more studies examining associations between physiological and subjective sexual arousal should explicitly account for participants’ prior sexual violence exposure. The argument for the universally adaptive nature of the preparation hypothesis in protecting reproductive processes would be strengthened if applied among women who have experienced sexual trauma—who may exhibit different conditioned responses in the context of sexual threat—using stimuli varying in sexual reward and threat. Future research would benefit from assessing (1) whether preparatory arousal responses consistently occur in sexual trauma survivors, (2) how attentional processes (such as negative emotion) in trauma survivors interact with preparatory arousal responses, (3) how sexual violence experiences may alter encoding of non-preferred sexual stimuli as sexual, and (4) whether preparatory arousal response to

violent, nonsexual stimuli is conditioned, and if so, is this conditioning stronger among survivors of sexual violence?

Cue Non-Specificity May Serve Other Adaptive Functions Beyond Preparing the Vagina for Penetration

Finally, let us consider how the observed phenomenon—automatic, moderate, and non-specific vaginal vasocongestion to a range of sexual cues—may procure indirect benefits that impact reproductive fitness, above and beyond a role in preventing tissue injury per se.

In addition to preventing injury during penetration (and presumably also reducing pain and discomfort), vaginal arousal is a positive and powerful reinforcer for future sexual behavior (Pfaus et al., 2012). Improving the balance of pain to pleasure may reinforce women's sexual approach behaviors and reduce avoidance. This is not an argument against the preparation hypothesis, but rather a proposal for an additional cognitive–affective mechanism involving an easily engaged arousal response which may improve reproductive fitness by changing the likelihood women will want to approach sexual cues and engage in sexual activity. The balance of reward and punishment may be particularly important for human females, whose sexual approach and avoidance are not strictly tied to fertile windows and thus may be relatively more governed by reinforcement schedules. For humans, who have evolved extended sexuality, experiences of pain and pleasure may play a more significant role in determining future sexual behavior and thus chances of reproducing. Although women with sexual pain do not show lesser preparatory arousal responses, as reviewed in Lalumière et al. (2020), they do show markedly higher avoidance of sexual activity through higher sexual disgust (Borg, de Jong, & Schultz, 2010), which in turn leads to having fewer children (Witting et al., 2008).

Lastly, it is possible that the non-specificity of female sexual arousal may benefit reproductive fitness by increasing the chances of female polysexuality (that is, attraction to partners of multiple genders). Highly social primate species use sex as a form of communication and the means to cement social bonds—including bonds with same-sex conspecifics (Enomoto, 1990; Manson, Perry, & Parish, 1997). These sociosexual ties are critical to survival of the individual and can provide additional caretaking resources that improve survival rates in offspring as well (Parish, 1996). Polysexuality, then, may be particularly adaptive for the sex that provides relatively more care—and indeed, we do see higher rates of polysexuality among women than men (Copen, Chandra, Febo-Vazquez, 2016; Lippa, 2007). In other words, female sexual engagement with other females

may open up additional social resources at relatively low cost.

We are not arguing that arousal is orientation—the former is a physiologic process and the latter, a complex construct including but not limited to identity and role performance. But, non-specific and flexible arousability to a variety of cues may permit the development of polysexual behavior patterns at higher rates in women (Diamond, 2007). If a female primate is arousable to female sexual cues—even if that arousal is low relative to her arousal to male cues—it subtly increases the chances that she will be reinforced by orienting toward those cues. This, in turn, may make her slightly more receptive (or even proceptive) to engaging in same-sex behaviors, particularly if those behaviors gain her allies and alloparents. This idea is underscored by the research showing low cue specificity even in neural correlates of arousal as referenced by Lalumière et al. (2020)—surely, the female body is not preparing the brain for risk of injury. Direct tests of this hypothesis in modern humans would be confounded by the enormous social and political discrimination faced by queer mothers, which would presumably counteract some of the benefits of sociosexual alliances and shared caretaking. Nevertheless, this hypothesis would explain why so much of the phenomenon of cue non-specificity is due to women's arousal to other females (for review, see Chivers, 2017)—even though other females are unlikely to injure them through penetration.

In conclusion, we applaud Lalumière et al. (2020) for their thoughtful and thought-provoking review of the preparatory hypothesis. We have presented here a variety of additional considerations and questions for the next generation of research to be launched by this venerable hypothesis. The research it will take to answer these questions will span a variety of areas, from the cognitive and affective bases of sexual arousal, to the psychosexual sequelae of trauma survivorship, to the evolution of human social behavior. As such, we can heartily agree with Lalumière et al.'s ultimate conclusion that the preparatory hypothesis has been a remarkably useful tool for furthering our understanding of sexuality, and we look forward to its continued success.

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Compliance with Ethical Standards

Conflict of interest The authors declare no conflicts of interest.

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