LEARNED BUT NOT CHOSEN: A REWARD COMPETITION FEEDBACK MODEL FOR THE ORIGINS OF SEXUAL PREFERENCES AND ORIENTATIONS

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Abstract: Is sexual orientation an evolutionary adaptation or social construct? With respect to sexual preferences, to what extent are we “born that way” and to what extent does learning matter? This chapter discusses how nature and nurture may interact to shape sexual motivation by reviewing existing literature on sexual preferences and orientations, as well as by considering sex/gender differences in erotic plasticity, sexual fluidity, and the specificity of sexual arousal. We describe how these phenomena might be accounted for by processes in which mind-body feedback loops amplify some sexual responses over others on multiple levels, which we refer to as the Reward Competition Feedback (RCF) model. With respect to sex/gender differences, we describe how these positive feedback processes might be amplified in men compared with women, potentially substantially driven by differences in the constraints and affordances of female and male anatomy. More specifically, we argue that the well-known female-male difference in the concordance of genital and subjective arousal may contribute to well-known differences in sexual specificity and plasticity/fluidity. We further provide convergent support for RCF by reviewing preexisting theories of sexual learning. Finally, we consider some of the

ethical implications of models in which sexual orientation might be shaped by experiences over the course of development.

Key words: sexual preference, sexual orientation, sex, gender, development, learning

INTRODUCTION: SEXUAL MOTIVATION: NATURE AND NURTURE

Evolutionarily speaking, one would predict that most women would prefer to have sex with men, and most men would prefer to have sex with women. Though the underlying mechanisms remain unclear, this is precisely what is observed: most individuals report primarily heterosexual orientations, but a substantial minority of individuals also report homosexual and bisexual attractions and orientations (Chandra et al., 2011; Santtila et al., 2008). Although the term sexual orientation is sometimes used to indicate individuals' self-defined sexual identities, *sexual orientation* is herein defined as an *enduring pattern of sexual desire, which is often (but not necessarily) motivated by sexual arousal* (Bailey, 2009; Diamond, 2003a; Laumann et al., 1994; Reiter, 1989). *Sexual preference*, in contrast, is defined as *motivation for particular types of sexual experiences*, regardless of whether this motivation is driven by sexual desire, and irrespective of duration or stability. In this view, sexual orientation can be viewed as a special case of sexual preference, and the potential origins of both these phenomena will be explored within this chapter.

Many attempts have been made to explain the origins of these phenomena, as well as the variability found within and between individuals and cultures (Lippa, 2005, 2009). The primary difference between these models is the degree to which they emphasize learned or innately predetermined factors. From the *nativist* perspective (Pinker, 2002) that has been historically characteristic of the fields of ethology and biology, most animals are genetically programmed to

be attracted to features of the opposite sex, and humans are no exception. From the *empiricist* perspective that has been historically characteristic of the fields of sociology and cultural anthropology—i.e., the “standard social science model” (Wright, 1995)—all humans are born with an unbound capacity for experiencing sexual pleasure, but are shaped to have different patterns of attraction and aversion on the basis of their different social roles and personal histories. Debate continues regarding the extent to which innate and learned factors shape human sexuality (Vasey & Lalumière, 2012).

To the extent that sexuality is influenced by evolution, adaptations are thought to depend on the relative “feminizing” and “masculinizing” effects of hormones on the developing brain (LeVay, 2010; Savic et al., 2010; Swaab, 2008). More specifically, hormones are believed to be necessary mediators for shaping nervous systems to respond in particular ways toward physical and behavioral characteristics typical of male and female organisms (Conway et al., 2010; Viveros et al., 2012). According to this model, non-heterosexual attraction results from these processes of developmental masculinization and feminization proceeding in ways that are sex-“atypical” (Muscarella, 2002; Muscarella et al., 2004; Paus, 2010).

Although genetic effects on sexuality have been observed, among identical twins where at least one sibling reports homosexual preferences, the probability of the other sibling reporting homosexuality has consistently been estimated as less than 50% (Bailey, Dunne, et al., 2000; Bailey & Pillard, 1991; Burri et al., 2011; Hu et al., 1995; Mustanski et al., 2005; Rice et al., 1999). This limited heritability demonstrates that orientation cannot be completely determined by genetic factors. Rather, developmental programs may be genetically specified, but the underlying processes could be altered by a variety of environmental factors (e.g. hormonal and immunological), especially prenatally (Blanchard et al., 2006; Blanchard, 2008; M L Lalumière

et al., 2000). In this way, there can be innate influences on sexuality that are biologically determined without being genetically specified.

Alternatively, the intensely pleasurable nature of sexual activity implies that reward learning can have profound impacts on sexuality (Hoffmann & Safron, 2012). Indeed, some have argued that classical and operant conditioning may be the central means by which adult sexual preferences are established in humans as well as other species (Coria-Avila, 2012; Hoffmann, 2012, 2017; Pfaus et al., 2012; Woodson, 2012; Wunsch, 2010). These proposals have been generally dismissed on the grounds that reproduction is central to evolutionary fitness, and so natural selection must have evolved specific and robust mechanisms for ensuring adaptive (i.e., reproductive) behavior.

However, experience-focused models are increasingly plausible as general learning processes are discovered to be more powerful than previously recognized (Flusberg et al., 2010; Gentner, 2010; Lakoff & Johnson, 1999; Pezzulo et al., 2011; Tenenbaum et al., 2011; Tomasello, 2001). In these empiricist accounts, organisms learn complex world models through experience, rather than merely tracking “simple” correlations between stimuli, actions, and outcomes. By utilizing these learned models, organisms are capable of maximizing evolutionary fitness more effectively than would be the case if they relied upon genetically determined responses. Indeed, learning processes may be capable of explaining evidence commonly interpreted as supporting innate neural mechanisms. For example, an aspect of psychology can be nearly universally observed in humans because of convergent learning on the levels of individuals and cultures (Bell, 2010; Bell et al., 2009; Laland, 2008). Or, a phenomenon could be observed in very young children and still result from learning that occurs shortly after birth (Gómez & Gerken, 2000), or even prenatally (DeCasper et al., 1994; Mehler et al., 1988). Even for behaviors as fundamental to survival as

drinking or eating, experience is required for newborn rats to learn the association between approaching water and obtaining hydration when thirsty, or between approaching food and obtaining nutrition when hungry (Changizi et al., 2002; Hall et al., 2000).

Although learning may play a surprisingly powerful role in shaping sexuality, potential innate shaping is suggested by intriguing correlations between sexual preferences and sexually differentiated brain structures (Berglund et al., 2006; Byne et al., 2000, 2001; Kinnunen et al., 2004; Safron et al., 2007; Savic et al., 2005, 2010, 2010; Savic & Lindström, 2008; Swaab, 2008). For example, inspired by work in which male rodents exhibited female-typical sexual behavior (e.g. lordotic back arching to expose the anogenital region) with disruption of prenatal hormonal surges, LeVay (1991) conducted postmortem analyses of the brains of homosexual men compared with heterosexual men and women. The third interstitial nucleus of the anterior hypothalamus (INAH-3) was approximately twice as large in heterosexual men than it was in heterosexual women and homosexual men. A later study replicated the gender differences in INAH-3, but only found a non-significant trend for smaller volumes in homosexual men, with no differences in the number of neurons (Byne et al., 2000, 2001). Additionally, Garcia-Falgueras and Swaab (2008) found that the INAH-3 volume of male-to-female transsexuals was similar to control females. Perhaps most compellingly, female-typical characteristics of preoptic/anterior hypothalamic nuclei have been found to correspond with male rams exclusively mounting other males (Roselli & Stormshak, 2009a, 2009b). However, it is difficult to know how to reconcile this homosexual mounting behavior with the “feminized” behavior observed in the rodent literature. These neurological differences remain poorly understood, particularly the means by which they impact behavior. Theoretically, genetically and hormonally differentiated neural systems may indirectly influence what developing organisms learn as they interact with their

environments. That is, evolved developmental programs may produce more or less female-typical or male-typical response patterns via modulating factors that are causally upstream, such as pain sensitivity or thresholds for psychomotor activity (Chakrabarti et al., 2010; Dewing et al., 2006). However, these differences could also result from brain plasticity—the brain’s ability to change itself through experience—rather than being caused by organizational effects of sex hormones (Doidge, 2007; Remedios et al., 2017).

This theoretical review attempts to account for factors contributing to the development of orientations, with the overall goal of parsimoniously integrating findings from sexology with models emphasizing reward learning. To this end, this chapter is divided into three main sections. First, we review existing literature on sexual preferences and orientations, describing gender differences in the specificity and flexibility of sexual responses, as well as their potential functional significances. Then, we attempt to account for these sex/gender differences in orienting by providing an integrative model in which a variety of feedback processes contribute to the amplification of particular patterns of desire on multiple levels. Finally, after laying out a proposal for the reward-driven shaping of sexuality, we describe how convergent support for these models may be found in independently developed theories for the origins of sexual preferences and orientations.

SEXUAL PREFERENCES AND ORIENTATIONS

GENDER DIFFERENCES IN EROTIC PLASTICITY

Baumeister (2000) controversially proposed that women are more malleable than men in terms of the effects of sociocultural and situational factors on sexuality. Three lines of evidence were presented in support of this model of greater female erotic plasticity:

- 1) Women show larger effects of social and cultural factors on sexual attitudes, desire, and behavior.
- 2) Sexual attitude-behavior consistency is lower in women than in men.
- 3) Women exhibit more intra-individual variability in sexual behavior.

A variety of non-mutually exclusive explanations were suggested for the origins of these gender differences. First, Baumeister suggested that men have had greater power than women throughout history, with some of this dominance continuing into the present day; on account of this power differential, men were able to influence women by encouraging a more flexible sexual response. Second, he speculated that change is an inherent part of the female role in sex in that when sex happens, it is usually because “the woman has changed her vote from no to yes” (Baumeister, 2000, p. 367). While one could argue that it is just as necessary for men to be able to transition from no to yes, men (on average) seem more likely to have a default response of “yes” (Bailey et al., 1994; Bailey, Kirk, et al., 2000; Buss & Schmitt, 1993; Gangestad & Simpson, 2000; Symons, 1981). Finally, he argued that women have a weaker sex drive than men, and as such, it should be easier to transform desire if the initial configuration is less strongly directed. This last proposition was supported by evidence from gender differences in self-reported spontaneous thoughts about sex, frequency and variety of fantasies, desired frequency of intercourse, desired number of partners, masturbation, liking for various sexual practices, willingness to forego sex, initiating versus refusing sex, making sacrifices for sex, and other measures (Baumeister et al., 2001). However, he further noted that this gender difference should not be generalized to other constructs such as sexual capacity, enjoyment, or extrinsic motivation.

Baumeister's proposal was controversial when it was first introduced (Andersen et al., 2000), and would likely be even more controversial if it were openly discussed today. A substantial proportion of such controversies may arise from failures to distinguish between descriptive and normative statements. That is, just because a sex/gender difference is observed (on average), that in no way speaks to the desirability of associated behaviors. Ethical considerations notwithstanding, while researchers have provided alternative explanations for these phenomena as well as opposing results (Benuto & Meana, 2008; Hyde, 2005; Hyde & Durik, 2000; Petersen & Hyde, 2010), the overall volume of findings suggests a substantial gender difference in sexual flexibility, with men exhibiting relatively less plasticity compared with women (Beckstead, 2012; Kinnish et al., 2005; Savin-Williams et al., 2012; Vrangalova & Savin-Williams, 2012).

SEXUAL FLUIDITY: THE DYNAMIC SYSTEMS PERSPECTIVE

In considering these gender differences in erotic plasticity, Diamond's (2008b) seminal research provided a particularly rich source of data by collecting detailed interviews over extended periods of time. In a prospective study involving 89 women with same-sex attractions, a surprising amount of "sexual fluidity" was observed with respect to partner choices, feelings, and identities (Diamond, 1998, 2003b, 2008a). Two thirds of women changed identity labels at least once during a 10-year period, with one third changing labels two or more times, and with the most commonly adopted identity being "unlabeled." Notably, although unlabeled and bisexual women exhibited greater variability than did homosexual women, these identities did not represent a "transitional stage" on the way to homosexuality or heterosexuality. More women adopted bisexual and unlabeled identities than relinquished them, and very few women ultimately identified monosexually. Furthermore, all of these non-heterosexual women reported an increased ratio of other-sex to same-sex behavior over time, suggesting a potential continuity

between female homosexuality and bisexuality. Although one could question the representativeness of this sample for heterosexually identified women (Mock & Eibach, 2011), these findings provide additional support for the hypothesis that sexual motivation may be more complexly determined (on average) in women than in men (Carvalheira et al., 2010; Carvalho & Nobre, 2010, 2011; Rupp & Wallen, 2008).

Based on this evidence, Diamond (2007, 2012) argues that a dynamical systems approach is necessary for conceptualizing the development, expressions, and transformations of female same-sex sexuality over life courses. In her longitudinal research, women exhibited discontinuities in attractions, behaviors, and identities, characterized by abrupt emergence of novel erotic feelings and experiences in specific contexts, as well as periodic episodes of reorganization in sexual self-concept. Diamond contends that these observations are best explained using dynamical systems models, which emphasize non-linearly changing, bidirectional person-environment interactions. From this perspective, the sexual identity transformations experienced by these women would correspond to “phase shifts” in which old patterns of interactions break down and a system fundamentally reorganizes.

According to Diamond (2012), in contrast to the regularity suggested by “essentialist, organismic” (p. 78) models of sexual orientation, the dynamical approach anticipates that developmental pathways will be complexly determined through interactive processes, and thus are necessarily idiosyncratic. More specifically, situations and patterns of interaction influencing sexual identities change over time, as experiences shape patterns of behavior that shape further experiences. Further, dynamical systems exhibit “equifinality” in that similar outcomes (in this case, sexual identities) can be achieved through different routes, as well as “multifinality” in that radically different developmental trajectories can emerge from similar initial conditions,

depending on unique aspects of life histories. Despite this inherent variability, Diamond (2012) clarifies that stability in identities may “reliably [emerge] as new patterns of thought and behavior are repeated and reinforced via internal feedback mechanisms” (p. 78). While this emergent stability of sexual identities is necessarily dynamic with respect to changing contexts, she notes that some patterns are more or less prone to reorganization in response to internal or external events. The relative stability or instability of an aspect of sexuality is determined by the precise configurations of parameters that influence the person as a system, such as biological predispositions, early sexual experiences, sex drive, cultural norms, or other factors. However, when a parameter or combination of parameters varies outside of typical ranges, it may trigger the sort of non-linear “phase shifts” observed in the sexualities of non-heterosexual women.

Diamond suggests that the relative variability of sexual identities can be modeled in terms of the influences on the development of “chaotic attractors.” She defines these attractors as “coordinated patterns of thought and behavior that tend to ‘pull’ subsequent thoughts and behaviors toward them, producing consistency and regularity in experience over time” (Diamond, 2007, p. 155). In a particularly informative visualization, she describes a metaphor in which rivulets of water gradually carve out a ditch through a flower garden with each rainfall; water running into a shallow ditch might easily run out again, but water is less likely to escape from deep ditches. While a broad ditch might capture raindrops from far away in the garden, narrow ditches will only capture raindrops that fall immediately around it. With respect to these attractors, breadth determines the range of influence, and depth determines the degree of “attractive force.” She goes on to describe how heterosexuality could be represented by having a strong other-sex attractor, but a same-sex attractor “so weak as to be potentially nonexistent” (Diamond, 2007, p. 156). However, she also notes that attractors can have different “basins” that

vary as a function of biological and cultural factors, as well as idiosyncratic sexual histories of opportunities and experiences. Diamond also defines “degree of fluidity” as the capacity to respond to different opportunities once available. All these factors might influence an individual with a predominantly heterosexual attractor to develop a “competing same-sex attractor.” For example, periodic same-sex intimate contact could result in a single emotional bond, but this desire for homosexual intimate contact may not generalize to individuals outside of that particular connection. In this case, those experiences “triggered the initial formation of a same sex-attractor, albeit a shallow and narrow one” (Diamond, 2007, p. 156). If this bond persists over time or results in the woman being more open to homosexual relationships, then “the same-sex attractor can be expected to grow deeper and broader, making it progressively more likely that she will pursue such relationships in the future” (Diamond, 2007, p. 156). Alternatively, Diamond describes “broad but shallow” attractors, corresponding to desire being stimulated by a wide range of experiences, but only weakly and “readily displaced by competing other-sex attractions and relationships” (Diamond, 2007, p. 156).

Diamond (2007, 2012) further proposes a research program for defining and characterizing the multiple parameters influencing variations in women’s same-sex and other-sex sexualities. Although non-deterministic, these models could yield “probabilistic predictions about conditions promoting stability and change” in sexual attraction, behavior, and identity (Diamond, 2007, p. 156). By analyzing sexual variability in these terms, it may be possible to systematically account for coexisting biological, cultural, and situational influences, as well as for additional complexities such as the fact that shifts can take place suddenly and unpredictably, and can be precipitated by a variety of factors over extended periods of time. (Hypothetically, support for these kinds of dynamical system views may potentially be evidenced if changes in patterns of

attraction are predicted by the widespread phenomenon of “critical slowing” (Carhart-Harris & Friston, 2019; Friston et al., 2012), in which systems with attracting states at boundaries between modes of organization show longer periods of time in returning to equilibrium after perturbations.)

Although Diamond focuses on female sexuality, this sort of ecological thinking can be applied to many psychobiological phenomena. Thus, to the extent that there are average differences in sexuality between women and men, they may arise from different manifestations of fundamentally similar processes. More specifically, both women and men’s preferences can be modeled as attractor networks, but different configurations of parameters may influence dynamics in different groups of individuals. The greater the number and variety of attractors that influence sexual dynamics—rather than systems being dominated by fewer, deeper attractor basins—the more likely it is that non-linear patterns will result, as Diamond (1998, 2003b, 2008a) observed in non-heterosexual women. In this way, although all biological systems are dynamical, qualitatively different emergent properties might characterize female and male sexuality. While this manuscript particularly focuses on Diamond’s work as illustrating the ways that sexuality can dynamically change over time, for interested readers, we also recommend Fausto-Sterling’s (2019) embodied dynamic systems perspective as being particularly emblematic of the kind of thinking that motivates this chapter.

SEXUAL AROUSAL, PREFERENCES, AND ORIENTATIONS

Bailey (2009) has offered an additional explanation for gender differences in erotic plasticity and sexual fluidity; namely, he argues that orientation is best conceived of as a sexual arousal pattern capable of driving behavior, and that this mechanism may be present in most men, but not most

women. Thus, female sexuality could be particularly changeable because of the absence of specifically directional sexual desire, which should be distinguished from the proposal of an attenuated sex drive described above (Baumeister, 2000; Baumeister et al., 2001). In claiming that sexual orientation is a sexual arousal pattern, Bailey (2009) distinguishes orientation from other phenomena such as behavior patterns, private identities, public identities, and preferences. These other aspects of sexuality do not necessarily match each other, and preferences are distinct from orientation in that a person may prefer to have sex with people who they do not find sexually desirable. Unlike sexual orientation, these other factors are considered to be malleable, potentially complexly determined, and not necessarily driven by feelings of desire that are specifically sexual in nature. Orientation is commonly described in terms of desire, fantasy, and attraction, but physiological arousal is the only aspect that can be directly measured independent of self-report.

Although it may seem as if this conceptualization of orientation in terms of arousal is methodologically motivated, Bailey (2009) argues for this operationalization on theoretical grounds. That is, he views sexual orientation as an evolutionary adaptation for ensuring reproductive fitness, where directed arousal patterns constitute the underlying proximate mechanism. Specifically, sexual arousal is rewarding, and if a given kind of stimulation reliably generates arousal, then organisms will engage in behaviors to maximize that stimulation pattern. If evolutionary ancestors innately varied in the stimuli that they found to be sexually arousing, then the greatest reproductive success would have been achieved by individuals who found characteristics of the opposite sex to be arousing, and hence rewarding. Thus, if genes existed that were capable of shaping brains to respond to cues indicating fitness, then these genes would eventually predominate in the species.

In men, patterns of genital arousal are consistent with this evolutionary account in that heterosexual men exhibit patterns of sexual arousal that are *category specific* in being specifically directed towards women, but in women, the situation is more complex (Blanchard et al., 2012; Chivers et al., 2004, 2007, 2010; Chivers & Bailey, 2005; Suschinsky et al., 2009). Using genital assessment, previous research has demonstrated that women's patterns of sexual arousal do not closely correspond with their self-reported orientations. Compared with men, homosexual and heterosexual women tend to have a more bisexual pattern of sexual arousal in the laboratory, with more similar levels of genital arousal to male and female erotic stimuli. Notably, relative to men, women also show a larger degree of subjective arousal to their less preferred sex. Men, however, tend to show a high degree of correspondence (or *concordance*) between self-reported orientation and their category-specific genital arousal patterns. That is, homosexual and heterosexual men show substantially higher arousal to the gender category that they prefer—i.e., men for homosexual subjects and women for heterosexual subjects—compared with their nonpreferred gender category. Most women, on the other hand, do not show this pattern. Interestingly, homosexual women show a greater degree of category specificity than do heterosexual women, in that they have relatively elevated genital and subjective arousal to stimuli depicting their preferred sex (Chivers et al., 2004, 2007). Notably, relatively greater erotic specificity in homosexual women has also been observed in neuroimaging investigations focusing on the ventral striatum (Safron et al., 2018), a dopamine-sensitive area of the brain of central importance for reward learning and action selection (Mannella et al., 2013). However, homosexual women also exhibit substantial arousal to their nonpreferred sex (on average), suggesting a relatively bisexual pattern compared with the results for homosexual and heterosexual men. Bailey (2009) speculates that the brains of homosexual women may have been

masculinized to some degree and that this could potentially account for a more male-typical (i.e., category-specific) arousal pattern.

When non-concordance occurs in men, it is frequently because they fail to show erectile activity to stimuli that are subjectively arousing, which happens with approximately 1/3rd of men in plethysmography experiments (Bailey, 2009). An additional form of non-concordance was observed in a study of bisexual men, where although relatively bisexual subjective arousal patterns were reported, genital arousal patterns were indistinguishable from those of homosexual and heterosexual men (Rieger et al., 2005). However, by using more stringent inclusion criteria, a later investigation by Rosenthal and colleagues (2011, 2012) succeeded in finding distinctly bisexual arousal patterns in bisexually identified men. In subsequent work, these bisexual arousal patterns were also found to be reflected in brain activations in the ventral striatum (Safron et al., 2017). Most recently, by aggregating data across prior studies (474 to 588 individuals, depending on analyses), it was unambiguously demonstrated that bisexual men show greater levels of non-specific arousal as assessed by genital measures (Jabbour et al., 2020).

While neuroimaging investigations involving men have shown clear correspondences with the genital arousal literature (Safron et al., 2007, 2017), patterns in women remain inconclusive. An early study by Ponseti (2006) and colleagues showed category-specific patterns of arousal in both homosexual and heterosexual women, including in the ventral striatum. However, interpretations of this study are unclear due to the stimuli being comprised of close-up pictures of female and male genitalia. That is, while it could be the case that functional neuroimaging has greater sensitivity than genital measures—and so is able to observe more subtle affective reactions—it could also be the case that women tend to respond with appreciable arousal for any stimulus indicating a possible sexual encounter (Rupp & Wallen, 2008; Spape et al., 2014). With

respect to this particular study, women may tend to show erotic responses to either a) context-rich stimuli (with a potential for non-specific arousal patterns), or b) context-poor stimuli with which they have had actual sexual experiences (resulting in category-specific patterns). Some notable evidence for non-specific arousal in women was observed by Sylva and colleagues (Sylva et al., 2013), although not within brain areas for which clear valence could be inferred, such as the ventral striatum (Stark et al., 2005; Walter et al., 2008). That is, while elevated activity in sensory or motor regions could indicate increased sensitivity and preparation to engage with desired sexual stimuli, it could also reflect a more general kind of salience (e.g. novelty, or even negative reaction) that does not reflect sexual preferences. Interpretations of this study and subsequent investigations (Safron et al., 2018) are also challenged by generally low subjective stimulus ratings, thus making it unclear whether non-specific arousal in women reflects actual bisexual attraction or merely a lack of interest in stimuli with uncertain ecological validity. Careful stimulus selection will be of paramount importance for future research (Safron & Hoffmann, 2017).

Despite observations of bisexual arousal patterns in the laboratory, most women do not behave or identify bisexually (Chandra et al., 2011; Kinnish et al., 2005; LeVay, 2010; McCabe et al., 2011; Mock & Eibach, 2011; Savin-Williams et al., 2012). In light of this disconnect between arousal and behavior/identity, Bailey (2009) considers three different options for conceiving of sexual orientation in heterosexual women. The first option is that most women have bisexual—or perhaps more broadly non-specific or “pansexual”—orientations, but that this has little to do with their sexual identities and preferences. Alternatively, female arousal patterns could be thought of as category specific in the case that female genital arousal patterns are misleading and do not actually reflect the way in which sexual arousal is experienced subjectively. Finally,

women could be oriented towards certain targets and not others, but factors other than arousal shape behavior; by this account, men and women both have orientations, but while men seem to be driven by sexual arousal patterns, women would be driven by factors other than sexual arousal. After considering these three alternatives, Bailey concludes that the term “sexual orientation” is most productively conceptualized as a specific phenomenon of arousal directing sexual desires, fantasies, and attraction. However, based on the discrepancy between psychophysiology and behavior/identity, he proposes that a “compass”-like mechanism for directing sexuality may be an adaptation that exists in most men, but not most women. Women clearly have sexual preferences and desires, but on average, they may not have orientations of the same sort that drive male sexual behavior.

Although intuitively compelling, the proposal that sexual orientation is a compass-like mechanism is difficult to reconcile with the prevailing theory that male homosexuality is best explained in terms of either “incomplete masculinization” or partial “feminization” of a brain shaped by activational and organizational effects from sex hormones and genes (LeVay, 2010; Lippa, 2005, 2009). More specifically, if sexual preferences in women are determined by factors other than arousal, this suggests that a female-typical arousal pattern in homosexual men would correspond to a bisexual arousal pattern, rather than category-specificity with respect to other men. During a meeting of researchers studying the origins of sexual orientation (Vasey & Lalumière, 2012), Bailey noted that the intensity of sexual motivation could interact with innate arousal patterns in shaping desire and behavior. Under the two-factor arousal-pattern orienting hypothesis, rather than lacking biases towards sex-specific cues, an attenuated sex drive in women could result in smaller differences in the magnitudes of the underlying vectors (i.e., the length of the compass needle pointing in a given direction) biasing arousal toward one sex or the

other. This dual-factor model incorporating both the magnitude and direction of orienting may more effectively reconcile partial sexual differentiation theory with observations of non-specific patterns in women and category-specific patterns in homosexual men. That is, homosexual men could potentially have a female-typical directing mechanism towards male features, and a male-typical sex drive. Relative degree of heterosexuality, homosexuality, or bisexuality would depend on the extent to which different aspects of these putative mechanisms were masculinized or feminized over the course of development.

In these ways, it may be the case that women have adaptive biases that are only physiologically measurable when they are also experiencing relatively greater motivation towards sexual reward. The finding of category-specific brain activation patterns in women provides indirect evidence for this hypothesis, since theoretically, functional neuroimaging could be more sensitive than genital assessment (Ponseti et al., 2006; Savic et al., 2001; Savic & Berglund, 2010). Also consistent with conditionally active sexual orientations, periods of increased fertility and desire are associated with more male-centered fantasies in heterosexual women (Dawson et al., 2012). Additionally, greater interest in highly masculinized men has been observed near ovulation (Rupp et al., 2009a), as well as in women with relatively high scores on measures of sociosexuality (Provost et al., 2006). However, evidence is lacking for the claim that women experience increased category-specific physiological arousal during the periovulatory window, despite increased responsiveness to sexual rewards (Slob et al., 1996; Wallen & Rupp, 2010).

Considering that an initially similar body plan can be differentiated into male-typical or female-typical anatomies depending on which genes are expressed (LeVay, 2010), the partially-atypical sexual differentiation scenarios described above are not biologically implausible. However, it is more challenging to explain an innate basis for paraphilias, where individuals are motivated by

sexual arousal patterns involving unusual objects, activities, or situations that would be unlikely to contribute to reproductive success in the environment of evolutionary adaptation (Rowland & Incrocci, 2008). However, some paraphilias are more common than others (Scorolli et al., 2007), and it has been suggested that many of these alternative sexualities could arise from the malfunctioning of mechanisms that were adaptive in other contexts (Quinsey, 2012). Yet, it is difficult to think of a neurologically realistic causal pathway that would not rely on a substantial degree of learning, especially considering instances of sexual arousal centering on imagining oneself as an amputee (Money & Simcoe, 1984), feeding one's partner to the point of obesity (Terry et al., 2012), desiring to transform into a cartoon dog (Freund & Blanchard, 1993), or numerous other scenarios. Anecdotally, individuals often report formative childhood experiences that were instrumental in shaping these atypical arousal patterns (Johnson, 1973; Pfaus et al., 2012), which can be considered to be 'orientations' to the extent that they strongly and stably drive sexuality over time. The fact that individuals often act on these atypical desires in spite of social disapproval, or even imprisonment, provides evidence that at least some paraphilias can be considered to be orientations in the sense previously discussed (Bailey, 2009; Seto, 2012). When paraphilias are considered according to the two-factor model of orienting, degree of sexual motivation would need to be 'male typical' in order to be capable of producing arousal strong enough to drive behavior. The fact that paraphilias are far more common in men than women is consistent with this hypothesis (Cantor, 2012). However, even if only a rare exception, paraphilias for which innate origins are a priori implausible—e.g. arousal responses to party balloons or bicycles (Scorolli et al., 2007)—represent a proof-of-concept that childhood experiences can result in robust patterns of arousal that continue into adulthood. Moreover,

experiences of arousal must interact with learning processes in order to explain how specific aspects of preferences change with time.

If sexual orientations can arise without innate biases in at least some instances, then parsimony demands that we consider whether this could be the case more generally, as will be explored below. Regardless of the extent of mediation by learning processes, if stable arousal patterns are reliably associated with orienting sexuality, then they could instantiate a proximate mechanism by which natural selection directed sexual behavior in human males, but possibly not females. In the view presented here, sexual orientations could still be considered to be evolutionary adaptations, even if they lack significant inborn neurological biases towards specific stimuli.

ON THE SIGNIFICANCE OF NON-SPECIFIC AROUSAL PATTERNS IN WOMEN AND MEN

Genital arousal is part of a coordinated set of emotional and physiological changes that both result from and contribute to the psychological experience of sexual arousal (Janssen et al., 2000). In both men and women, vasocongestion and engorgement of reproductive tissue sometimes occurs spontaneously without any clear psychological cause, but in the context of an experiment where participants are viewing erotic stimuli, reliable genital responses to one stimulus type versus another suggests some degree of psychological causation (Basson, 2002; Chivers et al., 2010; Lawrence et al., 2005; Rupp & Wallen, 2008; Suschinsky et al., 2009). Similar results have also been obtained with non-genital measures such as looking time (Lippa, 2012). Yet the nature of these psychological processes is unclear, especially when one considers the phenomenon of women showing significant genital—but not subjective—arousal to videos of Bonobo apes copulating, while men do not exhibit signs of arousal to these stimuli (Chivers et

al., 2007; Chivers & Bailey, 2005). While these were smaller magnitude effects compared to more typical erotic stimuli, they are nonetheless notable in that the videos only depicted brief encounters lasting a few seconds; theoretically, more extended sexual acts could have induced even stronger responses (if the Bonobos could be motivated to comply for the sake of advancing scientific research). Based on such findings, Chivers and colleagues have suggested that there may be innate psychological mechanisms in women for genitally responding to any sort of sexual stimulus, and that this adaptation may serve a protective function in preventing physiological damage from non-lubricated intercourse (Chivers et al., 2007; Lalumière et al., 2020; Suschinsky & Lalumière, 2010). This model is consistent with the finding that presence or absence of sexual activity in an image is more strongly associated with female genital responses than the sex of the person being depicted (Chivers et al., 2007); indeed, women in this particular study exhibited greater responses to pictures of sexual encounters featuring their “nonpreferred sex” compared with pictures of their “preferred sex” exercising in the nude.

Alternatively, conditioned learning processes could explain the non-specific genital arousal patterns of women (Hatch, 1981; Hoffmann, 2012, 2017; Hoffmann et al., 2004; Slob et al., 1996). More specifically, experiences of aroused and lubricated intercourse are more likely to be pleasurable and rewarding, and experiences of intercourse without arousal are more likely to be painful and punishing. In this way, variability in reward associated with a woman’s sexual experience may depend more on the extent to which vaginal lubrication takes place, regardless of how much attraction is felt towards that particular partner. If the contingencies of reinforcement and punishment for genital vasocongestion are primarily dependent upon the imminence of a sexual encounter, then genital arousal patterns may primarily be driven by the presence of sexual activity, even if it does not necessarily indicate subjective preferences.

These two hypotheses assume that female genital arousal does not necessarily reflect desire for the conditions that evoke it. Indeed, physical arousal patterns may not necessarily reflect desire for the activities being depicted, as genital arousal can occur even in cases where people are experiencing substantial negative affect (Suschinsky & Lalumière, 2010). In the previously discussed studies, it is possible that the erotic stimuli depict people and situations that female participants would on some level want to engage with sexually. Or, women may automatically “mirror” with the depicted individuals and thus experience vicarious arousal (Mouras et al., 2008; Rupp & Wallen, 2008). Or, considering that female sexual autonomy may be treated with ambivalence by cultures and individuals (Eagly et al., 2004), implicit—and sometimes explicit—sociocultural messages about sexuality could lead women to experience their sexualities in a more reactive fashion.

These alternative interpretations do not exclude the possibility that non-specific genital arousal also reflects the sexual fluidity observed in non-heterosexually identified women (Diamond, 1998, 2003b, 2008a), as well as the non-exclusivity of desire that has been documented in many heterosexual women (Chandra et al., 2011; Chivers & Timmers, 2012; Dawson et al., 2012; McCabe et al., 2011; Savin-Williams et al., 2012; Vrangalova & Savin-Williams, 2012). Further, although there is relatively low concordance between genital and subjective measures in women, self-reported sexual arousal for “nonpreferred” stimuli is also greater in women than in men. Thus, considering that feelings are not necessarily an all-or-nothing affair, it seems reasonable to conclude that non-specific genital arousal patterns indicate at least some degree of greater flexibility in the conditions capable of inducing desire.

Below, we will propose an additional, non-mutually exclusive hypothesis for understanding the significance of genital arousal patterns: *gender differences in the degree of sexual arousal*

specificity may contribute to gender differences in the degree of concordance between genital and subjective arousal. That is, strong correspondences between genital and subjective arousal in men (on average) may contribute to the acquisition of strongly directed arousal patterns during critical periods (i.e., the development of sexual orientations). Further, a more fluid relationship between genital and subjective arousal in women (on average) may contribute to the development of more fluid and plastic sexual preferences, rather than enduring orientations.

THE DEVELOPMENT OF SEXUAL PREFERENCES AND ORIENTATIONS THROUGH REWARD, COMPETITION, AND FEEDBACK

PHYSIOLOGICAL AROUSAL, LEARNING, AND THE DEVELOPMENT OF SEXUAL ORIENTATIONS: THE REWARD COMPETITION FEEDBACK (RCF) MODEL

Sexual arousal is a composite psychological state constituted by arousing (and often rewarding) mind-body feedback loops of a sexual nature, which are typically (but not always) facilitated by either perceiving or imagining patterns of stimulation that contribute to this state (Basson, 2001; Damasio, 2000, 2003; James, 1894; Lang, 1994). More specifically, mind-body feedback loops are created by attending to arousing sensations (i.e., genital engorgement), which can be perceived as viscerally pleasurable, and so result in the further enhancement of the physiological processes that produce these sensations. This feedback can occur both within and between physiological and psychological levels, where interactions can be mutually excitatory (e.g., awareness of arousal contributing to further arousal) or inhibitory (e.g., the types of dynamics associated with sexual dysfunction) (Janssen & Bancroft, 2007). If high arousal states are experienced as pleasurable (Hoffmann, 2012, 2017; Pfaus et al., 2012; Toates, 2009), then

associated stimuli will become reinforcing, thereby strengthening underlying neuronal connections for actions—potentially including the mental ‘acts’ of attending and thinking—that tend to result in those kinds of perceptions. Because these associations occur in the context of particular psychophysiological conditions, the appetitive behaviors potentiated by these stimuli will be of a specifically sexual nature (Hall et al., 2000).

These experiences of feedback-amplified arousal may cause sensitization to the conditions that result in their initiation and enhancement, so directing both attention and behavior in ways that further these dynamics through additional reward learning (Hoffmann, 2012, 2017; Pfaus et al., 2012). In this way, in addition to mind-body loops underlying particular sexual experiences, feedback processes may unfold on longer timescales as conditioning shapes behavior, shaping further conditioning experiences, and so on (Safron, 2015; Toates, 2014). An initial sexual experience may be only mildly arousing at first, or even neutral or possibly unpleasant, but with further experience it could become an ‘acquired taste.’ Importantly, unpleasant and punishing experiences may disrupt positive feedback cycles that amplify sexual arousal (Janssen & Bancroft, 2007; Safron, 2018), and may even produce negative affective associations, potentially leading to both mental and behavioral avoidance. Also importantly, it may not be necessary for these reinforcing or punishing experiences to be grounded in overt sexual behavior. Rather, affective associations can result from experiences with observed behaviors, or imagined scenarios, or even highly idiosyncratic fantasies with no clear basis in probable modes of sexual expression (e.g., transforming into a cartoon dog) (Freund & Blanchard, 1993).

Over time, accumulated conditioning could produce relatively stable preferences (Safron, 2018, 2019), depending on the strength of the feedback processes involved with respect to particular reinforcers, as well as individual experiential histories. In this process of differential

amplification of affective responses via iterated action selection and reinforcement learning, different types of action tendencies (and evoking stimuli) can be viewed as competing (and cooperating) in shaping the overall development of the organism. We refer to this integrative perspective as the *Reward Competition Feedback (RCF) model*, which we believe offers a unifying perspective for the development of preferences and orientations. RCF can be considered to be a combination of the dynamic systems perspective described above (Diamond, 2007), the “Incentive Motivation Model” wherein sexual reward value is learned through experiences (Toates, 2009), as well as the “Dual Control Model” that emphasizes the importance of both positive and negative feedback processes in regulating sexuality (Janssen & Bancroft, 2007). Notably, this account does not preclude the existence of innate orienting mechanisms, but describes how the maturation of such biasing processes into robustly enduring patterns of arousal and motivation is necessarily mediated by experience. Thus, RCF provides a general model for describing the development of goal-oriented behavior, applying not just to sexuality, but with potential application to all preferences and motivations.

SEX DIFFERENCES IN AROUSAL AND DYNAMICS OF REWARD COMPETITION FEEDBACK

Although the distinctions between female and male genital arousal may seem obvious, it is important to consider the physiological characteristics of each (Basson, 2001; Pfaus & Scepkowski, 2005), as these provide somatic markers that direct attention and thus determine the nature of the mind-body loops underlying the ‘feelings’ that ground emotions. More specifically, penile erection results in visually noticeable expansion in thickness and length, tactilely noticeable stretching and pressure sensations, and indirect proprioceptive information due to either gravity- or contact-induced torqueing forces. In women, on the other hand, the markers of

genital arousal are subtler. Engorgement of the vaginal walls results in lubrication, of the clitoris results in increased turgidity, and of the labia results in swelling and temperature increases (Kukkonen et al., 2007, 2010). Although these physiological changes can be noticed, the relative parametric correspondences between percent changes in engorgement and gross changes in volume are such that genital arousal may be more obvious in men than it is in women (Laan & Janssen, 2007). While a woman may experience substantial genital arousal without realizing it, it is difficult to ignore an erect penis—even if only partially aroused, depending on the extent of arousal and situational context—as most men learn during adolescence. Furthermore, due to the physical characteristics of expanding cylinders described above, differences in erection allow for a dose-dependent (although not necessarily linear) relationship between degree of engorgement and degree of noticeable physiological sensations. In women, this sort of dose-dependent relationship is likely more difficult to ascertain due to the more complex and subtle geometric properties of female genitalia, relative to those that are manifestly observable for the hydraulically expandable/collapsible quasi-cylindrical objects that constitute male genitalia.

As a result of this difference in the availability of information pertaining to the degree of sexual arousal, one should expect a difference in the degree to which the previously-discussed positive feedback processes take place. Enhancement of positive feedback processes in men would be even greater considering that conditioning most readily occurs when a precise temporal conjunction exists between clearly discernable behaviors and outcomes (Pickens & Holland, 2004). In this case, not only are physiological—and thereby hedonic (Laan & Janssen, 2007)—outcomes more readily discernable for men, but erectile activity changes can be monitored on a moment-to-moment basis. Thus, any behavioral changes, including shifts in attention and imagination, can be correlated with the amount of arousal and pleasure experienced. The process

of finding correspondences between behaviors and outcomes has been characterized as a “credit assignment problem” in reinforcement learning (Fu & Anderson, 2008), and with respect to genital arousal, this problem has been greatly simplified for men. Speculatively, the period of young men’s lives where they are confronted with the challenge of reconciling erectile activity with social appropriateness may play a significant role in consolidating a specific relationship between genital and subjective arousal; theoretically, this sort of social learning could potentially result in the development of default inhibitory processes that further contribute to category specificity.

Indeed, greater parametric detectability of genital changes may allow arousal patterns to more readily drive orienting in men by making them consciously accessible to a greater degree, thus contributing to awareness-based amplification of physiological arousal (Safron, 2016, 2020). With respect to the feedback processes described above, the strength of excitation (or inhibition) may increase as individuals facilitate rewarding (or punishing) patterns of stimulation and attending to particularly pleasurable (or unpleasant) aspects of experience. Further, the temporal specificity of moment-to-moment changes in the arousal state may allow particular stimuli to become associated with sexual arousal, and thereby facilitate integration into erotic schemas and scripts (Pfaus et al., 2012). On the basis of this history of reinforcement, stimuli associated with arousal may be able to more readily capture attention when encountered and—depending on the extent of learning at that point in time—outcompete other stimuli for access to limited attentional resources. When a sufficient degree of conditioning has taken place, these stimuli may drive habitual thought patterns, fantasies, and eventually behaviors, all of which may produce additional experiences of reinforcement. And due to differences in genital arousal dynamics

described above, men may be more likely to experience this ‘critical mass’ of conditioning within critical windows of developmental plasticity (Safron, 2018).

In these ways, experiential intensity may both contribute to and result from arousal amplification, so shaping competitive reinforcement (or punishment), with accumulated conditioning shaping behavior and thought in ways that may further contribute to additional reinforcing and punishing experiences. Thus, although these processes operate on different timescales, they interact synergistically in that they are both affected by and capable of influencing the degree of arousal experienced in response to different stimuli under different circumstances. Feedback amplification occurs in women as well, but these processes may be sufficiently stronger in men such that a difference of degree creates a difference of kind, thus resulting in the emergent phenomena of specific arousal patterns capable of directing behavior (i.e., orientations), and potentially restricted sexual fluidity.

ADDITIONAL FACTORS INFLUENCING RCF DYNAMICS

Numerous and varied phenomena could synergistically contribute to differential rates of sexual learning in women and men. First, for the reasons described above, male anatomy may support mind-body feedback loops of higher intensity and specificity. Considering that the relationship between arousal-facilitating stimuli and genital pleasure may be more tightly coupled in men, they may begin masturbating at an earlier age than women. Indeed, not only is this the case, but men are also likely to masturbate more frequently once they begin to do so (Baumeister et al., 2001; Leitenberg et al., 1993). Although masturbation practices are clearly influenced by social pressures, considering the intensity of reward associated with direct genital stimulation and orgasm (Safron, 2016), age of initiation for sexual self-stimulation and specific masturbation

practices could deeply influence the developing mind. Initial schemas and scripts set the stage for later developments (Pfaus et al., 2012), and thus the conditions surrounding early sexual experiences are more likely to have this ‘first-mover’ advantage in shaping erotic development. Furthermore, the sooner a learning process begins in development (Safron, 2019), the more time it has to operate and thus accumulate a more extensive history of conditioning. Moreover, early experiences can take advantage of the greater plasticity of young brains, which are still in a period of dynamic alteration due to factors such as changing hormones, progressive myelination, and ongoing neuronal and synaptic pruning (Gogtay et al., 2004; Kuhn et al., 2010; Sisk & Foster, 2004; Teicher et al., 1995; Vigil et al., 2011).

Diverse factors are capable of influencing reward-driven learning through highly variable pathways. With respect to biology, in males, elevations in testosterone around puberty could interact with reinforcement processes more generally (Arnedo et al., 2000, 2002; Cunningham et al., 2009; Hermans et al., 2010; Pfaus, 2010; Redouté et al., 2005; Rupp & Wallen, 2007; Schober et al., 2005), and thereby enhance the feedback dynamics described above. Sex-specific epigenetic modifications could also influence reward-learning processes, and non-hormonally mediated genetic effects are also possible, such as have been observed for the male-determining Sry gene in impacting dopamine-producing neurons of the substantia nigra (Dewing et al., 2006). With respect to social influences, boys seem to be exposed to a greater degree of homophobia than are girls (Thurlow, 2001), and thus they may be less open to homosexual experience. Or, Baumeister’s (2000) previously mentioned explanations of patriarchy or female behavioral restraint—specific causal pathways notwithstanding—could inhibit arousal processes in young women, thus making it less likely that a ‘critical mass’ of rewarding experiences will trigger

sufficient positive feedback amplification to learn strongly directed arousal patterns within developmental windows associated with elevated plasticity.

Group differences in sexual reward-driven feedback could be further attenuated by the fact that compared with men, women are generally more sensitive to social context and less sensitive to physiological states in interpreting emotions and drives (Roberts & Pennebaker, 1995). However, although men are generally more sensitive to interoceptive signals such as heart rate and respiration, degree of sexual concordance in women is not correlated with awareness of these signals (Suschinsky & Lalumière, 2012). These results suggest that genital arousal may be particularly important in shaping human sexuality. However, while explicit conscious awareness of somatic states and their functional significances should be expected to enhance dynamics of feedback amplification, differences in genital morphology could impact sexuality in non-human animals as well. For example, while both male and female Bonobos initiate sexual interactions, males do so more frequently, and are also more likely to begin courtship behaviors at greater distances of separation (Furuichi & Hashimoto, 2004); females, on the other hand, require close proximity to males before engaging in sexual approach. Theoretically, these sex differences in non-human primates could be partially accounted for by the kinds of differential perceptual characteristics for female and male genitalia previously described (for humans). That is, most mammals have more prominent genital arousal in males than in females, which could potentially form a phenotypic basis for the development of heterosexual reproductive behavior. We might expect relatively greater category specific sexuality in females with more pronounced genital arousal, although such experiments might be confounded if greater neural androgenization (Fenstermaker et al., 1999) contributes to bisexual behavior through overall increases in sexual motivation.

While RCF emphasizes learning processes, all of this evidence is consistent with a model in which sexual orientation is most validly understood as an evolutionary adaptation whereby specific arousal patterns shape motivation and drive behavior, and that this adaptation may be present in most men, but not in most women (Bailey, 2009). The reward-driven learning model described above does not address the existence of innate preferences for specific stimulus characteristics. Rather, it stipulates a proximate mechanism by which genital arousal acts as a powerful and reliable conditioning stimulus that amplifies preferences such that they may become enduring orientations.

While innate contributions to sexual orientations clearly exist, these may potentially operate in an indirect fashion that is substantially mediated by experience. For example, evidence of behavioral and (neuro)physiological sex-atypicality associated with homosexual orientations may be taken as evidence for overall differences in feminization and masculinization, including with respect to evolutionarily-selected neural systems governing reproductive behavior.

However, such findings are also compatible with models in which initial differences in femininity and masculinity contribute to different modes of interaction with the environment, and so differences in reward learning (Figure 1) (Safron, 2018). Perhaps the best known (and widely contested) proposal along these lines is the “Exotic Becomes Erotic” theory described below (Bem, 1996). Yet, a range of models could provide a causal (rather than merely correlational) role for behavioral sex/gender-typicality in the development of sexual orientations. For example, a highly feminine boy may find himself identifying to a greater degree with more female-typical social scripts in culture and media, or may find himself more likely to internalize the affective reactions (including expressed attraction) of female peers. However, such an account would fail to address the development of homosexual attractions in largely gender-

“typical” individuals, for which we might expect more idiosyncratic experiences to play a formative role in shaping patterns of desire.

Two models of the development of sex-atypical characteristics and sexual orientation

Fig. 1 Two models of the development of sex-atypical characteristics and sexual orientation

(reprinted with permission from Safron, 2018): (A) Standard models assume that sex-

atypicality in orientations (i.e., homosexuality) and more general sex-atypical characteristics

(e.g., gender non-conformity) both result from a common process of sex-atypical

neurodevelopment. (B) However, the same evidence is also consistent with a model in which the

relationship between sex-atypical neurodevelopment and sexual orientations is mediated by sex-

atypical characteristics and environmental interactions. Note: An experience-dependent causal

pathway should not be taken to imply that sexual orientations are arbitrarily malleable, perhaps

especially as plasticity decreases as development proceeds in time.

Although the standard explanation of an innate neural module for orienting seems simplest, the experience-mediated causal pathways described above appeal to empirically demonstrated phenomena, and avoid appealing to poorly-evidenced neurological mechanisms. When viewed as an adaptation, the genital-reward feedback model described above could be considered an ‘innate’ mechanism in the sense that the human body-plan is genetically specified, as is the sensory innervation that makes genital stimulation pleasurable. Yet, in the process of creating category-specific arousal patterns, this mechanism is nearly completely mediated by experience, thus problematizing an innate/learned distinction. The evolutionary psychological explanation of sexual orientation is probably correct with respect to its ultimate cause as a means of ensuring successful reproductive behavior in men, as well as for the psychological-level proximate details of arousal patterns being essential for strongly directing sexual behavior. Nonetheless, it may be the case that sexual orientation is not strongly determined by inborn neural mechanisms of a domain-specific nature.

Independently of their mechanistic origins, greater female erotic plasticity may have been adaptive in light of the reproductive challenges that men and women likely encountered in our evolutionary history (Bailey et al., 1994; Bailey, Kirk, et al., 2000; Buss & Schmitt, 1993; Gangestad & Simpson, 2000; Symons, 1981). More specifically, from an “adaptationist” perspective (Dawkins, 1976; Dennett, 1996), a strongly directed arousal pattern could represent a liability in women, considering differences in minimum obligate investment for successful reproduction (i.e., months of incubation and years of nursing, in contrast to mere minutes of energy expenditure on the part of men who avoid parental investment). That is, because the stakes of a sexual encounter are necessarily much higher for women, evolutionary fitness would be maximized by taking into account other higher-level factors, such as a tendency towards

parental investment and status in potential mates. Theoretically, lack of a specific orienting mechanism in women could help to ensure that reproductive behavior is driven by complex considerations, which would require experience and time in order to be discovered by general-purpose learning mechanisms. Conversely, in men, sexual arousal may be such a powerful driver of behavior that more complex factors are less capable of shaping preferences. In this way, while category-specific genital arousal patterns may act as the primary source of reward that orient most men towards preferred sexual stimuli, sexual preferences may be determined by a greater number of more complicated factors in women.

A study of sexual decision making in women exemplifies ways in which erotic motivation may be influenced by considerations of expected value that integrate multiple forms of utility (Rupp et al., 2009b). Rupp and colleagues (2009b) compared fMRI activations in response to male faces described as either frequently engaging in high-risk sexual practices (e.g., unprotected sex), or as being sexually cautious. Low-risk men were reported as more sexually desirable, and elicited stronger activations in areas associated with reward processes. However, executive control areas positively correlated with subjective evaluations of sex likelihood and response times during evaluation of high- but not low-risk men, which possibly reflected processing of conflicting motivations. Based on these findings, the authors concluded that for sexual decision-making, women utilize similar neural systems to those involved in nonsexual decision-making. These findings and interpretations are highly consistent with the evolutionary model described here.

Thus, sexuality may have highly different values for reproductive success based on women (relative to men) having a potentially greater burden in terms of obligate parental investment. Even with something as fundamental to evolution as ensuring adaptive mating behaviors in

humans, genes may have achieved this ‘goal’ through highly indirect means. More specifically, natural selection could have achieved nearly optimal adaptive behavior by specifying details of male and female body plans such that stimulation of reproductive organs differentially contribute to feedback amplification of experienced arousal and reward. By increasing the intensity of positive feedback processes in men, natural selection may have been able to produce qualitatively greater degrees of incentive motivation (Toates, 2009) towards stimulus characteristics associated with sexual arousal. Alternatively, by attenuating these processes in women, natural selection may have made it less likely that low-level stimulus features would dominate action selection (Safron, 2019), thereby allowing more abstract, complex, and context-sensitive reinforcers to be more heavily weighted in influencing behavior.

MULTI-LEVEL EVOLUTION AND THE DEVELOPMENT OF ADAPTIVE REPRODUCTIVE BEHAVIOR

In addition to the kinds of reward learning described above, animals may use social learning in addition to direct experience in inferring which behaviors are likely to be rewarding. This learning may be evolutionarily adaptive if cultures and other individuals (who may be potentially older and/or more experienced) are likely to encode successful patterns of behavior, which may be further enhanced in species wherein natural selection robustly occurs on the level of groups (Caldwell & Millen, 2009; Castro & Toro, 2004; Hyde & Durik, 2000; Molenberghs et al., 2009; Tomasello, 2001; Whiten et al., 2009). More specifically, pervasive and enduring selective pressures may allow aspects of life management to extend into culture, so providing a form of “sociocultural homeostasis” (Damasio, 2012), such as the practice of training children how to hunt. Indeed, it is increasingly appreciated that the rapidity and flexibility of cultural evolution may be responsible for more aspects of behavior than has been previously recognized (Henrich,

2017). Perhaps along these lines, with respect to sexual reproduction, norms supporting heterosexual interaction—or at least discouraging exclusively same-sex sexual activity (Safron, 2018; Savolainen & Hodgson, 2016)—could increase fitness both for individuals and groups.

Thus, in light of the ability of natural selection to occur across multiple levels, evolutionarily adaptive behavior need not depend on complex innate factors. Further, associated mechanisms are more likely to become vestigial if selective pressures are reliably satisfied by other means, whether via individually experienced rewards or through social learning. For example, the pheromonal system became vestigial in primates approximately 50 million years ago (Pfaus et al., 2019; Safron, 2018; Zhang & Webb, 2003), potentially due to the ability of general purpose learning systems to reliably infer which patterns of behavior are likely to enhance the positive affective states associated with reproductive success. If natural selection could depend on learning to meet this evolutionary imperative, then stabilizing selection for other adaptations (e.g., the vomeronasal system by which pheromones are detected) will have less influence on determining variability in differential rates of reproduction. In this way, every selective pressure may be understood as competing and cooperating with every other selective pressure in shaping populations of organisms across time.

Notably, we should expect similar dynamics to be observable not just across organisms in populations, but also internally to organisms and their nervous systems (Figures 2, 3, and 4) (Safron, 2018). This expectation is justified in that the multi-scale learning processes underlying affective orienting in action selection and the developments of sexual orientations can both be modelled as kinds of generalized evolution (Badcock et al., 2019; Campbell, 2016; Ramstead et al., 2017; Safron, 2019). More specifically, just as with selective pressures in phylogeny, RCF proposes that every preference competes and cooperates with every other preference in shaping

both moment-to-moment action selection (i.e., orientation as proximate mechanism), as well as the overall developmental trajectory of an individual over the course of ontogeny (i.e., orientation as evolutionary adaptation and life history strategy).

Mechanistic causes of orienting

Fig. 2 Mechanistic causes of orienting (reprinted with permission from Safron, 2018):

Mechanistically, orienting emerges from a process of sensation being assessed for affective value, so resulting in differential selection of neurophysiological dynamics (e.g., patterns of neural activity, autonomic and neuroendocrine changes). These affective assessments contribute to the selection of global organismic modes, which in turn bias perception in a circular process of affective construction (i.e., emotions/feelings). The sum total of this dynamic processing shapes overall neuronal activity selection, which may contribute to orienting sexual behavior, so influencing likely future experiences. However, incentive motivation of sufficient strength to influence actions will only be likely to occur if sufficiently robust orienting is present.

Developmental causes of orienting

Fig. 3 Developmental causes of orienting (reprinted with permission from Safron, 2018):

Developmentally, orientations emerge from a process of ontogenic programs shaping plastic phenotypes and likely affective experiences, so resulting in differential learning (i.e., selection of neural connections). These affective experiences contribute to the shaping of different preferences, which in turn bias future likely experiences in a circular process of niche construction for individuals (i.e., the ways in which organisms both adapt themselves to their environments and adapt their environments to themselves). The sum total of this experience-dependent affective learning shapes overall preferences, which may result in enduring orientations, so influencing the overall unfolding of a life history. However, preferences of sufficient strength and robustness to be considered to be orientations may only develop if sufficiently robust reward learning occurs during sensitive periods of development.

Phylogenetic causes of orienting

Fig. 4 Phylogenetic causes of orienting (reprinted with permission from Safron, 2018):

Phylogenetically, changes in population characteristics emerge from a process of members of a population interacting with each other and the broader environment, so resulting in differential survival and reproduction (i.e., natural and sexual selection). The consequences of these interactions define operative selective pressures, which in turn bias the conditions of selection in a circular process of population-level niche construction. The sum total of these pressures shapes the overall direction of selection, which may result in appreciable fitness consequences for different phenotypes, so influencing future population characteristics over phylogenetic history. However, selection of sufficient strength and robustness to produce appreciable fitness consequences (sometimes yielding novel adaptations) may only develop if sufficiently robust selective pressures are present for multiple generations.

In these ways, RCF demonstrates how seemingly incompatible “nativist” and “empiricist” perspectives on sexuality can be reconciled. Notably, this experience-dependent framework is

not only mechanistically parsimonious, but is also capable of explaining previously mysterious gender differences. In the following sections, we discuss independently-developed theories for explaining sexual behavior, and consider the extent to which they provide convergent validity and refinement of the models described above.

ADDITIONAL THEORIES OF SEXUAL LEARNING

The theories presented below are not meant to constitute an exhaustive review. For further discussion of many of the ideas contained in this portion of the chapter, we recommend that the reader turns to Toates's (2014) excellent book, "How Sexual Desire Works: The Enigmatic Urge." A review is also provided in Safron (2015).

EXOTIC BECOMES EROTIC; FAMILIAR BECOMES BORING

Other proposals for the establishment of gender differences in category specificity involve both innate predispositions and learning processes. In Bem's (1996) "Exotic Becomes Erotic" theory of orientation development, association with gender-segregated peer groups leads to non-sexual arousal when people outside of the more familiar group are encountered (Bem, 1998, 2000; Krisel, 2001; Nicolosi & Byrd, 2002; Peplau et al., 1998). This general arousal is then "misattributed" in sexual contexts emerging spontaneously around puberty, and thus biases the development of orientation in one direction or the other, depending on whether individuals have more exposure to same-sex or other-sex peer groups. Based on this theory, Baumeister (2000) suggested that more mixed-gender social groups in childhood could result in less discrimination between males and females with respect to sexual arousal, thereby contributing to more general erotic plasticity.

While compelling in some respects, the Exotic Becomes Erotic theory underspecifies the means by which general arousal could influence the development of sexual preferences (Bem, 1996). Based on the kinds of differential feedback amplification between boys and girls described above, one would expect differential eroticization of the exotic to be more likely to result in category-specific arousal patterns in boys than in girls, even with identical peer group gender ratios. Additionally, Bem overlooked the relatively obvious mechanism of habituation (Rankin et al., 2009), wherein familiar stimuli become less psychologically impactful. Habituation may provide a mechanism capable of not only explaining reduced preferences for the familiar peer group, but also much of incest avoidance (Erickson, 1993; Leavitt, 1990; Lieberman et al., 2003). More-specifically, as familiarity with a peer group increases, increasingly predictable stimulus characteristics will produce smaller magnitude reward responses (Schultz, 1998); perhaps intuitively, rewards are processed relative to expectations, such that an otherwise rewarding stimulus may be nonetheless negatively experienced if it is less impactful than anticipated, and where only rewards greater than predicted are capable of producing strong affective reactions. This differential habituation would cause the more familiar peer group to become relatively boring compared with the unfamiliar peer group. Although not mutually exclusive with the exotic becoming erotic, this hypothesis of the familiar becoming boring may be sufficient for explaining the same phenomena. RCF may be further amplified if the inherently messy nature of sexual activities produces a default disgust reaction without successful eroticization (Fleischman et al., 2015). Regardless of whether the allure of the exotic or the lull of the familiar is more powerful, when differential arousal for familiar compared with unfamiliar peer groups is combined with reward-driven learning amplification, these models are potentially sufficient for explaining the developmental origins of sexual preferences and orientations.

THE EMERGENCE OF HETEROSEXUAL REPRODUCTIVE BEHAVIOR VIA PARTIAL INSTINCTS AND CULTURAL EVOLUTION

Wunsch (2010) proposed a parsimonious model of sexual orienting, whereby stimulation of erogenous zones may be the only primary reinforcer needed for reward-learning processes to sufficiently explain mating behavior in primates. Drawing upon a dynamical systems perspective, Wunsch suggests that there may be no inborn central programming of motor sequences for reproduction, but rather a learning process wherein simpler bodily responses are combined to produce adaptive sexual behavior. He refers to these adaptations as “partial instincts” in that an incomplete set of innate elements are combined via associations with reliably predictable environmental circumstances. More specifically, heterosexual reproductive behavior is proposed to reliably emerge from the combination of 1) the innately pleasurable stimulation of “hairy skin,” and 2) complimentary gonadal structures and body postures in females and males. With these basic elements, general-purpose learning mechanisms may be capable of discovering that pleasure is reliably achieved via vaginal-penile coitus, which animals come to prefer relative to forms of stimulation that tend to be less rewarding, on average.

In addition to the numerous sources of evidence identified by Wunsch, research on the development of sexual behavior in rhesus monkeys provides further support for this model (Wallen, 2001). Wallen (2001) found that male monkeys mount other males and females in equal proportions as juveniles, but switch to exclusively heterosexual mounting after puberty. Intromissions with other males do occur, but they are more likely to ejaculate with females. Notably, the timing of this transition was most strongly predicted by having ejaculated with a female and was less strongly correlated with increases in pubertal testosterone. Furthermore, the time-course of this transition was most strongly predicted by the number of ejaculations with

females. The later removal of testosterone in adulthood reduced male sexual motivation, but it did not eliminate capacity for sex, nor did it change which sex was preferred. Although not definitive, these data suggest that copulatory experience was a necessary mediator for directed heterosexual mating behavior to develop. At least in rhesus monkeys, evolutionary pressures for successful reproduction could be subserved by general-purpose reward-learning mechanisms and their interactions with the affordances and constraints of their embodiments and environments.

OLFACTION, INNATE ORIENTATIONS, AND SEXUAL LEARNING

Kohl (2001) has proposed another parsimonious learning model where olfactory cues are the sole primary reinforcer involved in the development of a wide variety of phylogenetically significant behaviors, including those for reproduction (Kohl, 2007; Kohl et al., 2001, 2001). According to this theory, stimulus characteristics become “sexual” only because of conditioned associations with olfactory stimuli. Although strong links between smell and emotion have been clearly established (Barwich, 2020; Herz, 2008), Kohl’s claims remain controversial in light of his insistence that innate affective responses for complex visual stimuli do not exist, as well as his claim that human pheromones do exist.

Kohl is indeed correct that unambiguous evidence is lacking for inborn responses to complex visual stimuli in mammals. However, ambiguous evidence is plentiful, as well as commonly cited as constituting strong evidence. As we discuss below, such mechanisms may be biologically implausible and possibly un-evolvable. Attractive features such as anatomical symmetry or sexually dimorphic physiology can be universal, but that does not necessarily imply an innate basis. If these attractive stimuli are correlated with other features of interest (e.g., strength, robustness, immunity, fertility), then organisms can reliably learn these associations

either through individual experience or cultural evolution. Speculatively, to the extent that uncertainty is inherently punishing, or if a common cortical process reinforces successful prediction (Friston & Kiebel, 2009; George & Hawkins, 2009), then the enhanced predictability of symmetrical structures could potentially act as a primary reinforcer.

However, the claim that humans are responsive to pheromones seems unlikely in light of the deterioration of the vomeronasal organ and accessory olfactory bulb in humans and other Old World primates (Brennan & Zufall, 2006; Yang & Schank, 2006; Zhang & Webb, 2003). This system is usually responsible for sensing phylogenetically-relevant classes of olfactory compounds from other organisms, and then triggering species-specific fixed action patterns through connections to structures such as the medial amygdala, and then the hypothalamus and brainstem. Although primates have shown phylogenetically relevant affective reactions to such odorants (Ferris et al., 2001, 2004), the lack of functionality of the accessory olfactory system and prior relevant experiences suggest that these responses may be learned (Ferris et al., 2004), and as such it may be misleading to describe these compounds as acting as ‘pheromones,’ per se. Finally, it is notable that, experience-dependence has been observed even for mammalian responses to pheromones (Hosokawa & Chiba, 2005), and even with respect to the mating behavior of fruit flies (Zhao et al., 2020).

Nonetheless, smell is a unique sense in several respects (Croy et al., 2012; Shepherd, 2004; Yeshurun et al., 2009). First, compared with other stimulus modalities, smell is a priori more likely to be capable of influencing phylogenetically significant behaviors due to closer proximity of olfactory inputs to core structures for emotion selection, neurophysiological regulation, and memory encoding. Although these areas receive extensive projections from other sensory modalities, these connections are achieved through pathways with a far greater number of

intervening synapses through a dynamically self-organizing cortex. Second, a large number of genes specifically code for odor receptors, which are sensitive to specific compounds. Although only 350-450 of our 1000 odor-receptor specific genes remain functional—compared with 1,100 out of 1300 for mice, suggesting weaker selective pressures for olfaction in humans—the number of permutations of gene-expression profiles is still enormous. Thus, it is not unreasonable to suggest that evolution was able to use the olfactory system to adaptively shape behavior.

The amygdala complex is probably the most likely mechanism for mediating innate affective biases to particular odorants. This system receives extensive olfactory inputs, has been implicated in emotional learning and responses for appetitive and aversive stimuli, and has been shown to regulate sexual behaviors in a variety of animals (Maras & Petrulis, 2010; Pradhan et al., 1998; Winston et al., 2005). In both humans and non-human animals, the amygdala has high concentrations of sex hormone receptors (B. M. Cooke & Woolley, 2005; Fowler et al., 2008; van Wingen et al., 2010), as well as sexually differentiated anatomical features (Giedd et al., 1997; Goldstein et al., 2001). In neuroimaging studies, sex differences in amygdala responses have been observed for emotional processing (Cahill et al., 2004; Kilpatrick et al., 2006), as well as sexual processing (Hamann et al., 2004), with some evidence suggesting differences on the basis of sexual orientation (Safron et al., 2007).

However, although the amygdala receives multi-modal inputs, complex visual stimuli are unlikely to produce specific innate responses via cortex, given the dependencies of cortical development on idiosyncratic experiences of individual organisms (Cadieu et al., 2014; Held & Hein, 1963; Roe et al., 1992). Theoretically, the superior colliculus could provide this input using connections that are simpler and more predictable than a cortical pathway. However, although it receives a substantial portion of projections from the retina, receptive field properties

of colliculus neurons are not sensitive to shape or color (Redgrave et al., 2008), and thus it is extremely unlikely that specific connections could form the basis of some sort of innate visual stimulus detector. However, if the relationship between the degree of smell-induced arousal and reward is characterized by an “inverted U” function—that is, too weak being unnoticeable, and too strong being aversive (Yerkes & Dodson, 1908)—increasing or decreasing the sensitivities of the innate olfactory system could provide an elegant means of ensuring that different smells will be likely to have different affective associations (Haddad et al., 2010). Although, at the present moment, evidence is lacking for innate valence specificity being achieved via this sort of mechanism.

Kohl’s model of primary olfactory conditioning is supported by evidence that attraction can be influenced by cross-modal associations with emotionally salient odors, as in a study where medial orbitofrontal cortex (implicated in appetitive responses) activated for neutral faces paired with positive odors, and lateral orbitofrontal cortex (implicated in aversive responses) activated for faces paired with negative odors (Gottfried et al., 2002). However, attractive and sexually arousing visual stimuli can also act as unconditioned rewards that engender affective associations with conditioned stimuli (Bray & O’Doherty, 2007; Klucken et al., 2009), as in Hoffmann et al. (2012) demonstrating that neutral smells facilitate arousal after pairing with sexual activity. This potential bidirectional conditioning between olfactory and non-olfactory stimuli suggests that caution is appropriate in interpreting studies of reward or arousal in response to sexually dimorphic smells. For instance, studies using androgen and estrogen related olfactory compounds have demonstrated both differential activations in heterosexual women and men, as well as sex-atypical activations in homosexual women and men (Savic et al., 2001, 2005; Savic & Arver, 2011; Savic & Berglund, 2010). Notably, these differential responses were not

reflected in subjective reports, suggesting that these affective processes could operate unconsciously. Misleadingly, these studies were invariably reported as suggesting innate bases for preferences, but this sort of inference cannot be made from non-longitudinal observations of adults already shaped by a lifetime of experiences with male and/or female sexual partners.

Additional evidence is required to establish whether sexually dimorphic olfactory compounds contribute to sexual preferences. Longitudinal studies in children would be particularly promising, and given the non-explicitly sexual nature of many sex-specific odorants, such experiments could be conducted with minimal ethical concerns. Male children reporting gender dysphoria may be particularly informative, as nearly 75% of them go on to identify as homosexual men in adulthood (LeVay, 2010). Theoretically, these gender-atypical male children would be more likely to exhibit preferential brain responses to male-specific odorants, or they may have different expression profiles for relevant receptors. Some intriguing evidence exists along these lines, with pre-pubertal children who experience gender dysphoria showing gender-atypical responses to the male steroid-related chemo-signal, androstadienone (Burke et al., 2014).

REWARD LEARNING AND FLEXIBLE CRITICAL (OR SENSITIVE) PERIODS

On the basis of numerous lines of evidence, Pfaus (2001, 2003, 2012) has argued that salient features from early sexual experiences come to be preferred in subsequent partners through reward-driven learning. By this view, a sexual orientation represents a “constraint on learning, biasing the subsequent development of sexual preferences toward the preferred gender” (Pfaus et al., 2012, p.53). This process unfolds over a series of critical periods where preceding stages influence which emergent properties are likely to arise in subsequent stages of development.

Pfaus et al. (2012) outline five “developmental epochs,” which they map onto neo-Piagetian stages in which sexual behavior is molded by experience. The 1st epoch is an initial period of “sexual differentiation” where perinatal hormones shape the brain and body, commencing prenatally and extending into the sensorimotor stage (i.e., birth-2 years; simple reflexes to internalization of schemas). The 2nd epoch is characterized by a period of “gender differentiation” wherein individuals identify themselves as female or male, beginning during the sensorimotor stage, and then extending into preoperational stages (i.e., 2-7 years; symbolic function, intuitive thought). The 3rd epoch is characterized by a period of “social/emotional attraction and bonding,” beginning during the preoperational phase, and then extending into the concrete operational phase (i.e., 7-11 years; logical reasoning, context dependency). During this period, genital arousal is increasingly recognized as caused by external circumstances, and becomes subject to classical and operant conditioning based on the reward-contingencies encountered by the learner. However, genital arousal is not explicitly linked to external causes until the 4th epoch, which begins during the concrete operational phase, and then extends into the formal operational phase (i.e., 11 years-adulthood; integrated cognitive theory, values, abstract reasoning, hypothetical-deductive reasoning). Pfaus believes that sexual orientation derives from the first two epochs, but is not explicitly recognized by an individual as a sexual identity until the 4th epoch, or possibly as late as his 5th and final epoch. It is during this final period where sexual behavior and sexual reward begin to take a stable form as the adolescent/learner begins to experience the powerful reinforcements of masturbation and sexual interaction.

In this reward-based developmental trajectory, sexual and gender differentiation creates an initial foundation for early social interactions and bonding, which then interacts with developing awareness of genital arousal, and is finally consolidated by the powerful reinforcement of sexual

stimulation. Sexually preferred features also move along a temporally unfolding continuum that ranges from more pre-potent (e.g., gender) to flexible (e.g., hair type). These preferences arise in the context of the development of sexual “gestalts” and “scripts” shaped by early experiences that “feed forward to create desire for distal, proximal, and interactive features that predict the reward state” (Pfaus et al., 2012, p. 54). The particular unfoldings of these dynamic processes will be unique in each individual, but commonalities occur due to species-specific behavior or stimulation patterns, or as features of culture-specific attractiveness. Yet, according to Pfaus, “there are as many sexual preferences as there are people,” and “every desired feature is to some extent a ‘fetish’ that is sought after in the people we find attractive” (Pfaus et al., 2012, p. 55).

Pfaus’s model is grounded in animal literatures, and in particular his extensive studies of rat sexuality in terms of behavior, neural mechanisms, and learning (Pfaus et al., 2003, 2012). Pfaus and colleagues have demonstrated that numerous aspects of mating behavior can be shaped by experience, and that initially non-sexual stimuli can become sexually rewarding through conditioning. Examples of sexual conditioning range from rats with “fetishes” for the velcro-jackets they wore during early sexual experiences, to rats that desire the smell of the initially unconditionally aversive odor of cadaverine. These mechanisms of sexual imprinting have been observed in numerous other species as well. As potential examples of the enduring results of imprinting (Bolhuis, 1999), adult male mice and geese both mate preferentially with females that have attributes similar to those of the females that nursed them early in life (F. Cooke & McNally, 1975; Yamazaki et al., 1988). Even more intriguingly, through cross-fostering, male and female goats and sheep were able to develop cross-species partner preferences (Kendrick et al., 1998). Notable evidence has also been observed for sexual imprinting in humans (Bereczkei et al., 2004), albeit with more subtle effects relative to those reported in animal studies.

As a neural basis for sexual learning, Pfaus (2012) proposes that odorants are processed within the olfactory tubercle and piriform cortex, and that sexual reward depends on the posterior dorsal nucleus of the medial amygdala and hypothalamic nuclei. These two pathways converge upon a third mesolimbic dopamine system that integrates both conditioned olfactory cues as well as rewarding sexual outcomes. Although the studies supporting this model used methods that are too invasive for human experimentation, other evidence suggests these neural mechanisms may support sexual learning in mammals more generally. Using olfactory cues that had been conditioned with sexual activity in rats (Kippin et al., 2003), neural activity markers were detected in rat brain areas similar to those activated in fMRI studies of human reactions to visual sexual stimuli. On the basis of previously observed activations in these regions in response to both unconditioned olfactory and genitosensory stimulation associated with copulation, Pfaus speculates that conditioned odors may activate representations of the unconditioned rewards with which they are associated through experience. Moreover, considering that these conditioned rewards produce common activations with neural responses to stimuli predicting cocaine and heroin cues (Childress et al., 2008), as well as maternal bonding (Young & Wang, 2004), he goes on to suggest that these regions “function together as a general system for appetitive arousal and desire related to reward” (Pfaus et al., 2012, p. 48).

Two notable neuroimaging studies of male marmoset monkeys provide supporting evidence that Pfaus’s rodent olfactory studies may have identified evolutionarily conserved neural mechanisms for sexual reward (Kippin et al., 2003). When activation patterns were compared in response to the scents of a novel receptive female (periovulatory) compared with ovariectomized females, Ferris and colleagues found enhanced signal intensity in the preoptic area and anterior hypothalamus (Ferris et al., 2001). In an additional study by the same group (Ferris et al., 2004),

periovulatory odors produced similar activation patterns to those observed in humans for visual stimuli (Georgiadis & Kringelbach, 2012; Kühn & Gallinat, 2011; Stoléro et al., 2012), suggesting that important aspects of sexual functioning may be similar across mammalian species. In addition to these responses to female sexual odors, male marmoset monkeys also exhibit increases in serum testosterone (Snowdon et al., 2011), potentially suggesting pheromone-like properties. However, after Snowdon et al. (2011) paired sexual cues with an arbitrarily chosen lemon odor, these novel olfactory associations were capable of stimulating erections, as well as increased exploration of locations where they previously experienced a receptive female. In addition to suggesting that cortical expansion may have produced novel dynamics with respect to reinforcement learning, this study demonstrates that learned olfactory associations could produce pheromone-like effects without relying on specific receptor mechanisms.

CONCLUSION

The models discussed above are based on divergent empirical and theoretical considerations, but each account converges on general-purpose learning mechanisms as the primary means of producing adaptive behavior from diverse experiences. Although learning-based models such as RCF (Reward Competition Feedback) combine explanatory power with theoretical parsimony, further evidence could be obtained from cross-cultural, cross-species, and cross-sectional (or better yet, longitudinal) research. Such investigations have the potential to overthrow the currently dominant paradigm for understanding human sexuality in terms of inborn preferences. The scientific consensus about sexual orientation has been one in which individuals are “born that way.”

The strong nativist model of sexual orientation has been politically expedient in terms of appealing to people's notions of fairness, in an argument that goes roughly as follows:

1. Sexual orientation is based on innately determined orientations.
2. Thus, people are unable to substantially control these preferences.
3. Therefore, as long as no one is harmed, people should be free to fulfill their desires, particularly if those desires overlap with matters as central to human happiness as romantic love.

Proposition 3 is so incontrovertible as to require no further elaboration. However, proposition 1 may end up being empirically unsupported, and conditional relations between these claims are based on unsound reasoning. More specifically, sexual orientations could be entirely learned, but individuals may still be unable to control their preferences in childhood, adolescence, and adulthood. The converse is also problematic, in that sexual orientations could be inborn, yet only weakly constraining, so allowing for substantial degrees of choice with respect to the expression and shaping of initial preferences via reward-related learning. However, given that brains lose plasticity with age, preferences may become similarly rigid and difficult to modify with time. Alternatively, on even longer timescales, changing life experiences and hormonal states may cause preferences to become plastic yet again. It is also possible that erotic plasticity may be present in the majority of women for most of their lives—and so proposition 2 might not hold—which is a consideration that is often omitted from these discussions. Finally, propositions 2 and 3 are logically independent in that the connection between choice and permissibility seems to derive from an inappropriate extension of legalistic standards to social norms. Indeed, it is common practice to reduce punishments for violations where intentional choice is obstructed. But it is nonsensical to consider a harmless interaction between consenting adults as some sort of

violation. If no one is violated, then the situation cannot rationally be construed as a legitimate penal matter, and all such quasi-legal reasoning is inapt. Conversely, there are some cases where choice is limited, yet social regulation is still applied due to negative consequences. But again, these types of considerations do not apply to harmless interactions between consenting adults.

While learning-based models of sexual preferences have implications that are potentially enormous for science, these implications are also probably miniscule for ethics. Yet, all of these considerations are irrelevant with respect to the accuracy of hypotheses, which in ideal scientific practice, rise and fall on the basis of evidence, and nothing else. Finally, no matter which models end up being supported by existing and future data, there is at least one conclusion about which we can be confident: sexuality is central to the human condition in countless ways, and with relation to our varying sexualities, our flourishing requires us to relate to others (and ourselves) with respect and compassion.

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