Sexual Orientation and Human Sexuality

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Synonyms

Bisexuality; Heterosexuality; Homosexuality; Same-sex sexuality; Sexual attraction; Sexual minorities; Sexual preference

Definition

Sexual orientation refers to a psychological mechanism directing one's sexuality towards individuals based on their apparent sex. Individuals form a continuum between extreme point of exclusive heterosexuals, i.e., oriented exclusively towards individuals of the opposite sex, and exclusive homosexuals, i.e., oriented exclusively towards individuals of the same sex, with bisexuals being similarly attracted to both sexes and other individuals being attracted to both sexes in various degrees (e.g., predominantly heterosexual with some potential to same-sex attraction). Sexual orientation refers more to attraction or desire than behavior or identity, because orientation is not necessarily manifested by overt sexual behavior, associated with self-identification of sexual orientation label, or aligned with affectional bonding (love).

Introduction

The majority of males and females predominantly prefer opposite-sex sexual and/or romantic partners. Such sexuality has been accepted as a standard default, possibly because it is easier to see its biological/evolutionary relevance. Indeed, in sexually reproducing species, preference for and sexual activities with opposite-sex partners evolved as a mechanism for combining genomes through complementary gametes gaining genetic variability and direct fitness. Thus, scholars have argued that homosexuality is an evolutionary puzzle because it impedes the reproductive success of their owners. However, on the phylogenetic level, evolutionary fitness is more than direct fitness, and on the ontogenetic level, sexuality is more than fertile heterosexual penile-vaginal intercourse. Although direct reproduction is the ultimate evolutionary force behind most sexual activities, sexuality in general gained many other proximate functions during its evolution, e.g., as a social and pair bonding mechanism or means of resource acquisition. Such functions are intermediate goals to achieve direct reproduction, e.g., by means of survival and alliance formation and/or indirect reproduction by helping kin, also known

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as inclusive fitness. Therefore, many forms of sexuality, such as oral or anal sex, masturbation, sexual preferences for different species, preferences of same-sex individuals, or individuals outside of reproductive age, cannot per se offer direct reproductive success of the individual, but still these nonfertile forms of sexuality can offer other adaptive sociosexual functions (e.g., pair bonding, alliance formation, resource acquisition, well-being, etc.) that might indirectly foster future reproduction, regardless of sexual orientation. It is important to note that personal motivations for sexual activities, homosexual or heterosexual ones, are quite different from their possible sociosexual functions or possible evolutionary adaptive values. Sexual relations are mostly motivated by pleasure, love, self-esteem/revenge, and/or obtaining resources. Such personal motivations triggering homo/heterosexual behavior should not be confused with the socioecological or evolutionary reasons that maintain sexual activity in the population.

Further, sexual orientation is a psychological mechanism that generates a continuous array of individual variation and not a dichotomous psychological trait (e.g., Kinsey et al. 1948; Petterson et al. 2015). In this sense, exclusive homosexuality and exclusive heterosexuality present the extreme opposite poles of the continuum, while the majority of individuals fall in between, although closer to the heterosexual extreme. Following this line, homosexuality or nonheterosexuality (including bisexuals) is more than exclusive homosexuality, and sexual orientation does not equal homosexuality. One possibility would be to focus on the adaptive value of the mechanism itself (i.e., sexual orientation); the other would be to explore the possible adaptive value of one of its manifestations (e.g., exclusive homosexuality). The adaptiveness of the mechanism itself is usually not the focus of the debate. The debate is mostly centered on whether and how the individual differences generated by this mechanism are adaptive. A mistake would be to extrapolate a possible nonadaptiveness of an extreme point within the continuum (exclusive homosexuality) to the other variations along the whole continuum of sexual orientation (e.g.,

predominantly heterosexual, bisexual, predominantly homosexual, etc.). Similarly, a severe clinical depression or severe forms of autism are most probably not adaptive; they are not only neutral but rather maladaptive. However, they both are extremes on a continuum of adaptive variation, such as the capacity of sadness and systemizing abilities, respectively (for an overview about adaptive individual differences see, Buss and Greiling 1999). In the same line, bisexuality or some degree of homosexual tendencies among predominantly heterosexual individuals as well as some heterosexual tendencies among predominantly homosexual individuals could be viewed as adaptive variation of sexual orientation. From this perspective, even if exclusive homosexuality does not have any possible adaptive value, it would be a mistake to assume that the same is true for the whole continuum of sexual orientation.

Evolutionary Theories of Sexual Orientation

Sexual orientation has been described as a mechanism navigating or directing sexuality towards individuals of the opposite sex, same sex, or in varying degrees to both sexes (Bailey 2009; Bailey et al. 2016; Savin-Williams 2016; Vrangalova and Savin-Williams 2012). Similar to some heterosexual practices (e.g., extra-pair affairs), attitudes toward same-sex sexuality can vary greatly between cultures. In some cultures, same-sex sexuality constitutes an integral part of the sociocultural system; in others such sexuality is criminalized and persecuted (for review see, Bailey et al. 2016). For these reasons, individuals can vary in their overt manifestation of sexual preference, from a tendency hidden from public or even self to open preferences and behaviors. There are also other motives why sexual preferences, behaviors, and identities do not need to be aligned. Nonpreferred sexual behavior can be manifested, for example, under conditions without access to preferred sexual partners; it can be done for financial motives or simply to satisfy one's partner. Similarly, romantic affection can be largely disconnected from sexual desires (Diamond 2003). For example, a person can repeatedly fall in love only with individuals of the same sex, but prefer and actively seek sexual partners of both sexes. Thus, sexual orientation refers to sexual desires, attraction, and preferences rather than to overt sexual behavior, identity, or affective feelings.

Sexual orientation has a genetic component that explains approximately one third of the variation between individuals (e.g., Zietsch et al. 2012; for review, see Bailey et al. 2016). This suggests that sexual orientation is a complex trait that is influenced by genetic and environmental factors. Sex hormones are one of the environmental factors that influence the development of sexual orientation. According to the organizational hypothesis, the neural system of homosexual individuals is influenced by sex-atypical hormone levels during early developmental phases. Systematic differences in neuroanatomy between homosexual and heterosexual individuals suggest that compared to their heterosexual counterparts homosexual men were, on average, less androgenized and homosexual women more androgenized during early, probably prenatal, development (for review, see Bailey et al. 2016; LeVay 2010; Wilson and Rahman 2005). Neither genetic nor hormonal influences suggest that sexual orientation is necessarily fixed and rigid over the lifespan. Sexual orientation develops during ontogeny whereas sexual identity can change over time, particularly among women (Diamond 2008). Such a fluidity of sexual orientation does not equal to a conscious choice of different sexual desires and attractions (Diamond 2008). Thus, sexual orientation is not a choice nor a cultural invention; it has genetic and neurohormonal underpinnings and is not necessarily immutable. Furthermore, occasional same-sex behavior and stable same-sex preferences have been documented along a number of nonhuman animal species (Sommer and Vasey 2006). Thus, a variation on the sexual orientation continuum is not a human specific and has its phylogenetic roots.

Moreover, it is commonly accepted that homosexuals do not have any reproductive success. Although it has been shown that reproductive success of transgendered male homosexuals (males who adopt female look and behavior) is close to zero (Vasey et al. 2014), this does not need to apply to other forms of nonheterosexual individuals. In one study, 32.8 % of men and 65.4 % of women reported a potential for homosexual response, suggesting that a huge percentage of predominantly heterosexual people do have a propensity to experience same-sex sexual attraction and/or interaction (Santtila et al. 2008). In this study, the potential for homosexual response was based on responses (quite impossible, very unlikely, quite unlikely, not likely, not unlikely, relatively likely, very likely) on the following question: "If a, in your opinion, handsome man [to male participants]/beautiful woman [to female participants], whom you like, suggested sexual interaction with you, how likely would you be able to do it (if you could define the nature of the interaction and nobody else would know about it)?". In line with this finding, a large-scale study demonstrated that almost 10 % of heterosexually identified men reported that they have engaged in same-sex sexual activities (Pathela et al. 2006). This applies even more to non-Western populations, such as Samoa, where the majority of predominantly heterosexual men engage in sex with both women and transgender males called Fa'afafine (Petterson et al. 2015). Further, 20 % of homosexually identified white American men reported having been married to a woman at some point in their life, and 50 % of homosexual men reported having produced at least one child (Bell and Weinberg 1978). According to the more recent demographic data (2013) of the USA, 37 % of LGBT-identified individuals report having at least one child. Keeping in mind these assumptions, we can outline some of the empirically supported evolutionary theories explaining the adaptiveness of human homosexuality and nonheterosexuality.

 Homosexuality as an adaptation: Kin selection theory

One of the oldest and partly supported theories of homosexuality as an adaptation was postulated by E. O. Wilson (1978), inspired by Hamilton's kin selection theory. Homosexual individuals, who do not invest into their own exclusive reproduction, may propagate their genes indirectly by supporting reproduction of close relatives, with whom he/she shares own genes. Studies conducted in the USA, Great Britain, or Japan did not support the theory (for review, see Bailey et al. 2016), which can be explained by persisting relatively negative attitudes toward homosexual individuals in these countries. On the other hand, systematic investigations of Fa'afafine, who are officially recognized as "third gender" or a transgender type of male homosexuals (individuals who are biologically males but have feminine characteristics and adopt feminine gender roles) among the population of Samoa, supported the theory of kin selection. In particular, Fa'afafine show higher avuncular tendencies (support of nieces and nephews) compared to men who prefer women as sexual partners, which supposedly their fitness increases (e.g., Vasey and VanderLaan 2010).

Samoan Fa'afafine fit a specific subgroup of homosexual men, the transgender type of male homosexuals that is a specific although still heterogeneous group. This subgroup of transgender individuals whose sexuality is aimed at individuals of the same biological sex is frequent in many other societies, such as India (Hijra), Thailand (Kathoey), or native North American tribes (Berdache). The transgendered homosexuals mostly prefer same-sex relationships, although usually with cisgender (i.e., biological sex aligned with gender role) men. Sexual and/or romantic relations between partners of different gender roles are documented in numerous populations around the world (Crapo 1995). Furthermore, age stratified type of same-sex relationships (i.e., one of the partners is much younger than the other) has been documented across populations, such as ancient Greece, Middle Ages Japan, or contemporary New Guinea (Crapo 1995). Such relationships, as opposed to gender-stratified ones, do not need to imply one transgendered and one cisgender partner, rather both of them are cisgender but of different age categories, although such interactions can be temporary and do not need to imply predominant same-sex

preferences of none of the partners. Both age-stratified and gender-stratified styles of same-sex relationships exist in the modern Western culture, although the most frequent style of relationships is egalitarian between two individuals who identify as homosexuals and are of similar gender role, status, education, and age. This latter style of same-sex relationships seems to be specific for contemporary Western populations. On the other hand, the other two styles of samesex relationships appear in populations that share more common sociocultural characteristics with human ancestral populations (e.g., geographical connectedness of the kin and strong familiar bonds), and the evolutionary strategy can thus still be adaptive in the present as it could have been advantageous in the ancestral environment (VanderLaan et al. 2014). Importantly, evolutionary strategy of transgender homosexuals can differ from the one adopted by cisgender homosexuals or nonheterosexuals. In other words, some evolutionary hypotheses (e.g., kin selection) can be supported in one specific subgroup of homosexual individuals (e.g., in transgender homosexual men) in specific society contexts (e.g., large families, close kin bonds, geographical proximity) but not in others (e.g., in cisgender homosexual men in big anonymous cities with prevalent homophobia).

2. Homosexuality as a by-product of sex-atypicality

Miller (2000) suggested that male homosexuality per se is not adaptive, but rather it is a by-product of another adaptation. He proposed that some characteristics that are, on average, more typical for women than men, such as lower aggressiveness, higher cooperation, and social skills in general, became adaptive also in men during the changes in social structure of relatively recent human evolution. Futher, more feminine characteristics in men can be typical for slow life history of men who invest more in relationship commitment and parental care than in mating success (Jeffery 2015). Thus, men who have more feminine and fewer masculine characteristics can thrive better in а more complex and

predominantly monogamous society, including having relatively higher reproductive success.In this scheme, male homosexuality would thus be an extreme nonadaptive by-product of a general adaptive male shift to feminization. Gender nonconformity (lower masculinity in men) has a strong genetic component (for review, see Bailey et al. 2016), and women find femininity in men attractive (Perrett et al. 1998). Furthermore, numerous studies indicate that nonheterosexual men are, in comparison to heterosexuals, more feminine (for review, see Bailey et al. 2016). Homosexual men would thus form an extreme point on a continuum between male masculinity and male femininity, while relatively feminine heterosexual men would have some adaptive advantages, at least in urban, middle class Western groups.In line with the kin selection theory outlined above, this theory also aims to explain the existence and maintenance of feminine male homosexuals in the population. This theory, nonetheless, does not apply to masculine male homosexuals and other nonheterosexuals nor to female homosexuals. Rice et al. (2013) suggested that homosexual orientation is a by-product of sex-atypical epigenetic marks that feminize males and masculinize females during embryonic development. Thus, the opposite logic of the theory could also be applied to explain masculine female homosexuals who would represent an extreme pole of a general female masculinization. This might have been adaptive for some women during the evolutionary past, for example, by concentrating more social and physical power, leading to higher independence, better self-defense and defense of their kin, and higher resource acquisition. Such characteristics might have been advantageous in the ancestral and also recent society, where mortality in men has been relatively higher than in women.

3. Predominant homosexuality as an adaptation: Sneaking and conditional sexual strategy

Following the previous line of reasoning, predominant homosexuality in feminine males can be also understood as a sneaking sexual strategy (Jeffery 2015). In humans, it has been suggested that the most frequent strategy would be exclusive or at least predominant heterosexuality with males of rather masculine characteristics, while bisexuality and predominant homosexuality linked to increased femininity in men would represent a sneaking sexual strategy. From this point of view, feminine men who have some potential for opposite-sex activities can be successful in opportunistic heterosexual activities and secure direct reproductive success. This can happen in particularly because feminine characteristics were shown to be attractive to women (e.g., Perrett et al. 1998), at least under certain conditions. At the same time, more feminine bisexual or predominantly homosexual men can be perceived as weak rivals to more masculine exclusively or predominantly heterosexual men and can thus reduce intrasexual male-male competition. Consequently, feminine predominantly homosexual men can be accepted more as friends of heterosexual men's female partners, thus offering opportunities to sneak copulations. High numbers of predominantly homosexual individuals reporting some opposite-sex attraction, behavior, and also biological offspring (see above) would tend to support this theory. The theory thus does not attempt to explain exclusive homosexuality or transgender homosexual men who do not have any interest in sexual encounters with opposite-sex partners. It rather shows that various degrees of bisexuality and predominant homosexuality can serve as an alternative and successful reproductive strategy. This theory need not apply only to men because bisexual and predominantly homosexual women can also show some opposite-sex attraction and behavior, as well as some reproductive success. On average, lesbian women are more masculine than heterosexual women (Bailey and Zucker 1995), and masculine heterosexual women report higher sociosexuality (tendency for uncommitted sexual variety) than feminine women (Mikach and Bailey 1999). We can thus speculate that masculine predominantly homosexual women can secure direct reproductive success without the necessity of creating and maintaining long-term bonds with men but rather with other women.Compared to predominant female homosexuality or bisexuality, a fluid sexual orientation might have helped

ancestral women secure resources and care for their offspring under conditions without a primary male partner by receiving parental investment from other women (Kuhle and Radtke 2013). According to this theory, fluidity of female sexual orientation can be understood as a conditional sexual strategy, meaning that variations between opposite-sex and same-sex sexuality can be adaptive in different conditions, such as different age or life phases.

4. Nonheterosexuality as an adaptation: Samesex alliance formation

This theory holds that various degrees of sexual feelings and behaviors aimed toward both males and females offer an individual advantage over an exclusive orientation toward only one sex (Kirkpatrick 2000). The main reason towards nonheterosexual interactions would be formation and maintenance of same-sex alliances that are crucial in many other primates and in particular in the human evolutionary past. The author shows anthropological and primatological evidence supporting the view that strong and emotional same-sex alliances can offer a reproductive advantage to the individual. More specifically, same-sex alliances reduce competition and increase cooperation between members of the same sex, while maintained access to partners of the opposite sex ensures potential reproductive success. In this perspective, heterosexual sex among stable partners outside the fertile period (i.e., outside the fertile window within the female menstrual cycle and after menopause) or any sexual activities that do not lead to fertilization (e.g., oral or anal sex) serve the same function, i.e., reducing disputes, increasing cooperation, and thus maintaining the stable dyad (Bártová and Valentová 2012). The question is whether nonheterosexual behavior was originally selected for alliance formation or whether alliance formation is rather a newly acquired sociosexual function of same-sex sexual behavior. In this sense, nonheterosexuality would serve proximate sociosexual functions for which nonprocreative sexuality in general was co-opted, such as alliance formation, dyad maintenance, lowering stress,

peacemaking and reconciliation, or resource gains.

5. Homosexuality as a by-product: Overdominance and sexually antagonistic gene hypothesis

Both behavioral and molecular genetic studies have shown that the male homosexuality is linked, among others, to the X chromosome and is thus inherited from the maternal lineage (Sanders et al. 2014). Further, female relatives of male homosexuals have more children and grandchildren than control group of women with no homosexual individuals among relatives (e.g., Ciani and Pellizzari 2012; for review, see Bailey et al. 2016). It is thus suggested that greater fecundity and fertility of female relatives of homosexual men can explain the persistence of a nonadaptive form of male sexuality through sexually antagonistic selection (e.g., Ciani and Pellizzari 2012; Zietsch et al. 2008). In other words, sexually antagonistic genes can bring advantages for one sex (e.g., higher fecundity in women) but can be principally disadvantageous for the other sex (e.g., can cause exclusive homosexuality in men). However, as shown by recent models, the frequency of only female carriers cannot explain a stable proportion of exclusive male homosexuals in the population but a large proportion of both nonhomosexual female and male carriers can (Chaladze 2016). Based on behavioral genetic studies, a considerable proportion of men carrying the homosexual genes are not exclusively or predominantly homosexual. It was suggested that homosexual phenotype can only be expressed in a homozygous form of the underlying alleles, while individuals with a heterozygous form (only one allele of the gene) carry the phenotype but the phenotype is not expressed (for review, see McKnight 1997). Such heterozygous carriers are supposed to possess some advantageous characteristics that can increase reproductive success of their owners. So far, this theory was supported by a study showing that heterosexual twins of homosexual men, who most probably share the genetic component of homosexuality although not homosexual orientation, report

higher number of female sexual partners than heterosexual men with a heterosexual twin (Zietsch et al. 2008). Thus, heterosexual men who carry the homosexuality-linked genetic component, potentially in a heterozygous form, do have higher mating success (considered a proxy of a reproductive success) than the control group of heterosexual men, which can explain its relatively stable prevalence in the population.

The theories of by-product thus focus more on explanation of the extreme exclusive form of male homosexuality, rather than the rest of the nonheterosexual continuum. The theories can apply to other forms of nonheterosexuals, though, because they can also be carriers of the homosexual genotype. It has been shown that a potential for homosexual response has a stronger genetic component than homosexual behavior or selflabeled identification (Santtila et al. 2008). Thus, any degree of nonheterosexual tendencies might be more suitable for genetic analyses than exclusive heterosexual homosexuality with no potential.

Furthermore, the theories of homosexuality as a by-product originally did not apply to women, although in principle they can work similarly, since genetic component has been documented also in female sexual orientation (for review, see Bailey et al. 2016), and the potential to homosexual response is even more frequent in women than men (Santtila et al. 2008). Thus, exclusive male and female homosexuality indeed can be a by-product of otherwise adaptive variation of sexual orientation.

Conclusion

During the last century, human and other animal (vertebrates and invertebrates) sexual orientation has been extensively studied within many scientific areas. Despite important findings in the areas of psychology, anthropology, medicine, neuroscience, genetics, endocrinology, and development, evolutionary reasoning has suffered numerous conceptual and terminology issues. These misconceptions have led to the view that homosexuality can only be exclusive and thus an evolutionary paradox. However, when essentialist categorical thinking is discarded, it might become clearer that the majority of variation on the continuum of sexual orientation can offer adaptive advantages for their carriers. This view can be supported by changing the perspective of sexuality equaling only with reproduction, and by acknowledging the fact that at least some homosexual and nonheterosexual individuals within the whole spectrum of sexual orientation do reproduce and raise their offspring.

Most outlined theories present adaptive reasons for the evolution of nonheterosexual orientations, either by stressing indirect reproduction via kin selection or direct reproduction via sneak copulations or same-sex alliance formation that can increase survival and future direct reproductive capacity. Even by-product theories offer plausible evolutionary reasoning for the origins and maintenance of nonheterosexual orientations. In this sense, nonheterosexual orientations would have been passed on throughout generations together with the adaptive trait of sex-atypicality, advantages of an increased fertility in the other-sex kin, or in carriers who do not express the homosexual phenotype. These theories are not mutually exclusive, and together they can explain a bigger proportion of the sexual orientation continuum. Moreover, these theories offer a stronger case against the argument that it is impossible for any form of homosexuality to have evolved.

Finally, it is important to realize that the outlined theories are not *just-so-stories* nor naïve panadaptationism as critics often portrait it. The theories offer specific hypotheses with predictions that can be empirically tested. We attempted to provide the existing empirical support for each theory, although we realize that more research using a variety of sources of evidence and methods is still needed. Only convergent evidence of numerous empirical tests can give decisive support and scientific credibility to a particular adaptive hypothesis.

Sexual orientation is a complex psychological mechanism that can profit from analysis within an evolutionary framework, where otherwise heterosexuality might be taken for granted. Future studies should pay more attention to female nonheterosexuality, to sex-typical nonheterosexuals, bisexuals, integration and empirical confrontation of the existing theories, and to empirical testing of the theories in Western as well as non-Western populations with varying concepts of same-sex sexuality.

Cross-References

- ▶ Homosexuality
- ► Kin Selection
- ► Mate Preferences
- Sexual Strategies

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