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Homosexual Orientation in Males: Evolutionary and Ethological Aspects

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Abstract Evolutionary theory proposes that adaptive traits are reproduced more successfully than maladaptive traits. Accordingly, natural selection should favor heterosexuality as it facilitates reproduction and the propagation of genes. However, the question becomes, what has maintained homosexuality in a small but consistent percentage of the human population? Research into the evolutionary and hormonal factors associated with a homosexual orientation have yielded provocative but inconsistent results. It also suggests that human sexual orientation, and in particular homosexual orientation, is too complex to be described by one simple model or a single research discipline. The current paper treads a new path and emphasizes an integrative approach for the understanding of homosexuality. The authors examine the combined effects of evolutionary factors and neurohormonal processes on the development of a homosexual orientation. It is suggested that research into the topic could benefit from an examination of and change in some of the assumptions upon which much past research has been based.

Introduction

Sexual orientation, usually categorized as heterosexual, homosexual, and bisexual, is perhaps the most compelling, yet least understood, component of human sexuality. The contemporary scientific paradigm is based upon the assumption that heterosexual orientation is the norm. Thus, deviations from this, particularly homosexual orientation – erotic and emotional attraction to the same gender – have been considered abnormal and have required explanation. Homosexuality has been persistently studied by various disciplines such as biology, psychology, sociology, and anthropology with the goal of finding – and presumably eliminating – its cause.

The changes in society's and science's conceptualization of homosexuality and its 'treatment' reflect the changes in the prevailing paradigms over time of the causes of human behavior. For much of the 20th century psychoanalytic theory exerted significant influence on thinking about human behavior. Not surprisingly, until the 1960s, it was commonly believed that homosexuality resulted primarily from pathogenic influences in childhood such as an over involved mother and under involved father. The treatment was psychoanalysis, and it was found to be unsuccessful [1]. By the middle of the 20th century a considerable amount of research in human sexuality focused on the role of hormones [2]. Thus, the causes of homosexuality were assumed to be related to hormonal imbalances at different levels of development. Treatment of homosexuality with hormones was as unsuccessful as psychoanalysis [3].

Most recently, there has been a shift to the study of genes and their influences on various aspects of the human condition. Gene therapy is already in use for certain medical conditions, but the likelihood for behavioral changes through genetic manipulation remains unknown. Nesse [4] writes of '*Darwinian Medicine*'. In this light, he tries to understand why the human body is not better designed and why therefore, diseases exist at all. The genetic/Darwinian paradigm has extended its influence to the social sciences, and the influence is most clearly seen in the emergence of the new discipline of evolutionary psychology. Evolutionary psychology holds that human behavior can be understood in terms of its adaptive value. Behaviors commonly exhibited by humans can be expected to have contributed to survival and reproduction in the evolutionary past, thus perpetuating the genes that influenced the behaviors. In light of the increased visibility and influence of the evolutionary paradigm, it seems only natural to extend it to the study of homosexuality. However, it is clear that, historically, homosexuality has not been amenable to explanation by a single model. This is undoubtedly due to the complexity of the factors influencing its development. Thus, we are taking a more integrative approach in this paper. We will first present recent theory on the evolution of homosexual behavior and then try to integrate it with research and theory from the field of (neuro-)endocrinology.

Evolution and homosexual behavior

The study of homosexual behavior has been impeded by a lack of reliability for the term 'homosexual' [5, 6]. Furthermore, there is poor construct validity for the concept of sexual orientation [7, 8]. Muehlenhard [9] has pointed out that many categories (e.g., homosexual/heterosexual) used as variables in sexuality research are social constructions lacking in real meaning and thus pose serious methodological problems. Not surprisingly, in view of the serious psychometric problems involved, all psychological theories of sexual orientation development are lacking in empirical support [10].

The first and most widely recognized evolutionary theory of homosexuality is that of E. O. Wilson [11, 12] and is based on the concept of kin-selection (i.e., a sociobiological explanation for the evolution of altruistic behaviors). This theory holds that during the course of human evolution homosexual individuals may have helped family members, through direct or indirect provision of resources, to reproduce more successfully than they would have otherwise. Thus, genes for homosexual behavior would have been propagated indirectly through relatives. The theory has been criticized for a variety of reasons including reliance on a number of false assumptions [13, 14] and a lack of supporting evidence [15, 16, 17, 18]. Consequently, it has been rejected as an explanatory model [6].

The general consensus of writers in the field of evolutionary psychology has been that homosexual behavior in humans does not have adaptive value. Some authors consider homosexual behavior to be biologically maladaptive because, they argue, it has no association with potential reproductive success [19, 20, 21, 22]. In most cases, it has been considered best explained as a by-product of the plasticity of the human brain and the resultant variability of human sexuality [16, 18, 23, 24].

Miller [25] has suggested that male homosexuality is a by-product of variable brain feminization associated with personality traits (e.g., empathy) that make males attractive to females and better fathers. In this theory, sexual orientation is conceptualized as a polygenetic trait, i.e. it is influenced by a number of genes. Some of these genes might shift male brain development, and thus behavior, into the female direction. Although some feminization contributes to male reproductive success, too much would have deleteri-

ous effects. Due to normal genetic variation, a small percentage of men would be over-feminized and thus, show more feminine brains, behavior, and perhaps even bodies [25]. However, there is no scientific evidence supporting this speculated linear association between brain development, behavior, and morphology in homosexual men.

Recently, a new evolutionary perspective on homosexual behavior has begun to emerge. Ross and Wells [26] have argued that evolutionary explanations of homosexuality have been based upon homosexual expression in contemporary Western societies. They state that these environments do not reflect the ancestral environments in which the behavior would have evolved nor do they contain the same ecological conditions, which would have affected their expression. Further, Ross and Wells [26] propose that homosexual behavior is an 'exaptation' of homosocial behavior. An exaptation is not a direct product of natural selection but a neutral variation of a behavior, which with time demonstrates some fitness enhancing quality. As a result, natural selection acts upon it. According to Ross and Wells [26], male homosocial behavior could have contributed to male survival through increased social support and access to resources. Homosexual behavior would have reinforced homosocial bonds and thus would have been acted upon by natural selection. Vasey [27] has also proposed that some aspects of homosexual behavior in primates may have developed as an exaptation. Further, it has been argued that male homosociality is conducive to increased homosexual behavior [28].

Kirkpatrick [5] and Muscarella [29] argue that the evolutionary study of the topic should be behavior based, focusing on homosexual behavior and not on the unreliable concept of homosexuality. They review much cross-cultural and historical evidence and argue that for most of our species, and for most of our history, bisexual behavior was the norm. They also argue that most homosexual behavior has been exhibited by people who do not considered themselves homosexual.

This evolutionary perspective on homosexual behavior posits adaptive value for the behavior itself in humans. Kirkpatrick and Muscarella speculate that during the course of human evolution homosexual behavior may have reinforced same-sex alliances, which contributed directly to survival [5, 6, 29] and indirectly to reproduction [29]. Kirkpatrick [5] argues that homosexual behavior comes from individual selection for reciprocal altruism, which would have contributed to resource exchange and a reduction in inter-male aggression. In a similar vein, Muscarella [29] argues that adolescent and young adult hominids were probably socially peripheralized and that the capacity to engage in homosexual behavior reinforced alliances, which contributed directly to survival. Further, the alliances benefited the unique reproductive needs of each sex. Same-sex allies helped males climb the social hierarchy more effectively, giving access to females and reproductive opportunities. Same-sex allies amongst females helped them move to the safer and resource richer center of the group, which increased their chances of raising their offspring successfully.

The theories put forth by Kirkpatrick [5] and Muscarella [5, 29] do not address sexual orientation *per se*. Rather, they address the selection of a behavioral response. It is assumed that this has a genetic basis, which varies among individuals such that some would have a much greater disposition than others. The ranges of dispositions to engage in the behavior would interact with a range of personal experiences, ecological conditions, and psychological processes resulting in a general sexual orientation.

Hormones and homosexual behavior

Hormone research on sexual orientation has focused on testosterone and estrogen. A common hypothesis has been that homosexual men have more elevated levels of estrogen and depressed levels of testosterone than heterosexual men [e.g., 30, 31, 32, 33, 34]. However, the results of these studies have been inconsistent (see for review [35]). The fact that sexual behavior in rodents [36] and primates [37] can be altered by early exposure to sex hormones has raised the possibility that variation in exposure to hormones might be the basis for variation in sexual orientation also in humans [38]. Clinical studies of the sexuality of individuals who experienced biological conditions which alter the usual prenatal hormonal processes (e.g., congenital adrenal hyperplasia) strongly suggest that some aspects of human sexual orientation and behavior are due to hormonal mechanisms [39].

From this perspective, male homosexuality is considered as only one expression of sexual behavior from a continuum of sexual variation that may be significantly influenced by hormonal changes. Male sexual preference may be dictated by testosterone action on the brain, which begins in the prenatal period and continues during a critical postnatal period [40, 41]. For example, Robinson and Manning [42] present evidence suggesting that exposure to high levels of prenatal testosterone contributes to homosexual and bisexual orientations. They measured the 2^{nd} to 4^{th} digit ratios of heterosexual, homosexual and bisexual men. This ratio is believed to be affected by prenatal exposure to testosterone and is set early in prenatal development. There is also an established sex difference in the ratio with men showing less of a ratio than women [43].

Robinson and Manning [42] found that, among men, the ratio was greatest in heterosexual men, less in homosexual men, and least in bisexual men. They indicate that this suggests greater exposure to prenatal testosterone for homosexual and bisexual men. Robinson and Manning argue that this could be interpreted as an alternative explanation to some adaptive value associated with homosexuality. In the male fetus there may be strong selection for high testosterone for sexual differentiation of systems associated with effective male survival and reproduction. The cost of this may be that some males are exposed to over-optimal levels of testosterone. This contributes to deviation from a heterosexual orientation and to a variety of other biologically deleterious effects. However, their finding that bisexual males may have had greater exposure to prenatal testosterone than homosexual males does appear to be inconsistent with their own interpretation. They imply that with increasing exposure to testosterone there is increasing deviation from a heterosexual orientation. If this were true, the increasing testosterone-heterosexual deviation pattern should be as follows: heterosexual, bisexual, and homosexual.

Robinson and Manning's argument that a homosexual orientation results from exposure to too much testosterone suggests that a homosexual orientation is due to an over-masculinized brain. The conclusion is contradictory to Miller's [25] work suggesting that it is due to a feminized brain. However, Rahman and Wilson [44] have suggested that homosexual preferences may be due to high levels of unbinded testosterone during prenatal development that results from a lack of receptors at particular brain sites. From this perspective, the brain could be feminized while other features of the developing fetus, for example 2nd to 4th digit ratio, could be over-masculinized. Two major neurohormonal theories of sexual orientation development hold that prenatal hormonal effects upon brain differentiation actually involve complex patterns of masculinization, unmasculinization, feminization, and defeminization associated with particular patterns of sexual orientation [45, 46].

Feierman [47] has extended the neurohormonal theory for the development of sexual orientation. He states that patterns of sexual differentiation of the brain can be associated with particular patterns of preferred partner characteristics based on evaluation of features of the target relative to self. For example, he suggests that a masculinized and defeminized brain leads to attraction to targets that are younger and more feminine than the self. In this category would fall, heterosexual adult men, but also, heterosexual and homosexual pedophiles, men attracted to adolescent females, and men attracted to adolescent males. On the other hand, he speculates that brains which are masculinized and feminized direct attraction to targets younger and more masculine than the self, and homosexual men would fall in this category. There is some evidence that gay men are strongly attracted to masculine looking men [48] and to men slightly more masculine than themselves [49].

A speculated genetic-endocrine basis for homosexual behavior

In an attempt to explain a genetic-endocrine basis for selection for homosexual behavior, Rahman and Wilson [44] have proposed the following scenario. They believe that during human evolution intrasexual aggression constituted an adaptive problem because it led to reduced individual survival and infanticide [50, 51]. Rahman and Wilson [44] speculate that there were genetic mutations that took advantage of evolutionarily based neuroendocrine plasticity. By plasticity they mean a mechanism conserved among vertebrates, upon which selection can act and generate variation in sexual phenotypes.

Rahman and Wilson [44] base their theorizing on Grober's [52] work with teleost fish, which exhibit a variety of sexual phenotypes. Specifically, according to Rahman (personal communication), there are shifts in the sex of the fish (i.e. sexually active males and females regularly transform into an alternative reproductive morph) with accompanying changes in sexual behavior. The neuroendocrine mechanism, which permits this is plastic in its ability to change structure and function (see also [53]) and involves changes in the hormones produced by the hypothalamic-pituitary-adrenal (HPA) axis and the hypothalamic-pituitary-gonadal (HPG) axis. Rahman (pers. comm.) speculates that social cues affect the neural substrates, which change the level of sex hormones through the feedback loops associated with each neural axis. Indeed, Grober and Sunobe [54] demonstrated that socially mediated serial sex change in the marine goby (*Trimma okinawae*) involves significant and reversible changes in the size of arginine vasotocin-producing forebrain cells. Changes in these sex hormones cause structural and functional changes in neural structures associated with sexual behavior such as the preoptic area of the hypothalamus and the supra-chiasmatic nucleus. These are the same areas that are believed to be associated with sexual orientation in mammals, including humans.

Brain differentiation as an evolutionary adaptation

Rahman and Wilson [44] agree in principal with the idea that homosexual behavior may have been adaptive because it contributed to alliance formation.

However, they disagree that humans are essentially bisexual and argue that evidence supports a bimodal male sexual orientation and possibly trimodal female sexual orientation. They also point out that Kirkpatrick [5] and Muscarella [6, 29] have failed to theorize on the genetic-endocrine basis for selection for homosexual behavior.

Based upon research on the sex shift of fish and Miller's [25] theory of selection for feminine traits in men, Rahman and Wilson [44] propose that variations in genotypes produced hominid males who were more feminine in behavioral traits and bisexual in sexual preferences. These characteristics contributed to same-sex affiliation and females were attracted to these traits because they were associated with decreased aggression and infanticide, and increased parenting behavior. Over time, females chose increasingly feminine traits in males, which led to the evolution of alleles associated with exclusive homosexual interest. The contribution of the feminine traits to parenting and the viability offspring offset the reproductively deleterious effects in males. In this way, alleles for bimodal homosexuality are maintained in a balanced polymorphism.

However, there appears to be a significant inconsistency in the argument made by Rahman and Wilson [44]. They speculate that particular genotypes present among hominids made males more feminine in behavioral traits and bisexual in sexual preferences. Thus, bisexuality was a successful survival and reproductive strategy for ancestral males, and there was selection for it. If this were the case, then the majority of human males would be expected to be bisexual or at least have the potential for bisexuality under certain conditions. This is what both Kirkpatrick [5] and Muscarella [6, 29] have argued. However, Rahman and Wilson [44] disagree with the contention that human males are essentially bisexual. It is not at all clear how a population of human males would have evolved to be essentially heterosexual when selection was for bisexual traits. According to a recent U. S. survey, only .8% of men were categorized as bisexual and 96.9% were categorized as heterosexual [55]. It does seem reasonable that a small percentage of men could be genetically predisposed to an exclusively homosexual orientation due to normal variation in the genotype regulating same sex preferences. However, it is not clear how a genotype for sexual preference theorized to be the most adaptive would disappear during the course of human evolution leaving genotypes for the less adaptive alternatives.

It is possible that although contemporary surveys show a bimodal distribution of sexual orientation this reflects the effects of cultural constraints and not actual genotypic variation. For example, a dictum of evolutionary psychology is that males evolved to be sexually promiscuous (e.g., [56]), but the majority of married American men remain faithful to their wives [55] appearing essentially monogamous. Most ethological observers would agree that this apparent monogamy is best explained as the result of culture constraints upon evolutionary predispositions. In a similar light, it would be scientifically reckless to assume that the incidence of a behavior as complex and poorly understood as human sexual orientation reflected genotypic variation devoid of cultural and societal influences. From this perspective, Rahman and Wilson's [44] theory of selection for bisexual traits in human evolution may be more similar than it appears to that proposed by Kirkpatrick [5] and Muscarella [6, 29].

Conclusion

The minds of scientists, and the questions they ask, are shaped by the cultures in which they live. Contemporary Western culture has been shaped by Judeo-Christian beliefs, foremost among which has been that the purpose of sex is procreation. This driving assumption is the reason that, historically, the study of the cause of homosexuality has generated such a preponderance of research in the area of human sexuality [1]. Twentieth century advances in research technology have not altered the underlying assumption. Thus, sophisticated methods for identifying and measuring hormones and genes are still used to try to answer the question what causes homosexuality? There are also more nefarious implications to this search because the identification of a cause implies the existence of an intervention, which will allow successful elimination of the behavior. Thus, the scientific quest for the cause of homosexuality continues to have compelling implications for those men and women whose sexual orientation has been deemed by society as requiring explanation. Even evolutionary psychology, which promised different insights into human nature, relied heavily upon unquestioned assumptions about homosexual behavior [6].

Past evolutionary theories tried to explain how homosexual behavior was either maladaptive or a biologically irrelevant by-product of the plasticity of the human brain. A recently emerging view in evolutionary psychology is that some homosexual behavior was adaptive during the course of human evolution, and there was selection for it. However, there appear to be two major perspectives regarding this. One emphasizes that homosexual behavior itself reinforced same-sex alliances, which contributed directly to survival and indirectly to reproduction [5, 26, 29]. These theorists fail to explain underlying genetic and neuroendocrine mechanisms regulating the behav-

ior. The other perspective also holds that homosexual behavior may have been adaptive. It tries to explain the possibility of a neuroendocrine basis by emphasizing the feminization of the male brain, especially the brains associated with a homosexual orientation [25, 44]. At this time, it is unclear if this is a productive theoretical framework or if it is excessively burdened with the cultural and continuing scientific stereotype that men with a homosexual orientation are somehow less masculine and more feminine than heterosexual men.

Research in neuroendocrinology strongly suggests that prenatal, and perhaps some postnatal, hormonal effects may shape the development of sexual orientation (e.g., [57]). Although the evidence indicating trends is clear, research trying to show persistent differences between heterosexual and homosexual men has been inconsistent [35]. It is possible that this research is also burdened by the cultural stereotype that a homosexual orientation in men can be clearly equated to femininity. It appears that the thrust of the neuroendocrine research has been to show that men with a homosexual orientation exhibit hormonal and neuroendocrine functioning more similar to that of women than to that of men.

Clearly, a single theoretical model cannot explain a phenomenon as complex as human sexual orientation. We present an integrated model. Increasing evidence suggests that there may have been adaptive value for some homosexual behavior under certain conditions during human evolution. This is why genes for the behavior remain in the population. Neuroendocrine and hormonal factors are undoubtedly involved in homosexual behavior since they are involved in many aspects of sexual behavior for most species. We entertain the possibility that in our evolutionary past there was selection for more 'feminine' and thus bisexual traits in males. However, it is not yet clear that this is the best explanation. For example, Ross and Wells [26] speculate that homosociality was a pre-adaptation for homosexuality, and Kirkpatrick [5] theorizes that selection was for reciprocal altruism. These approaches do not require a statement on the selection of feminine traits for the interpretation of human sexual orientation.

Homosexual behavior may represent a form of sexual flexibility not unlike the behavioral scaling exhibited in many behaviors by many species [58]. For example, during the mating season male sea lions cannot tolerate each other and fight ferociously. After the mating season, they loll together quite affectionately on the beach. Similarly, roaming pairs of adult male lions are formidably aggressive, but also known to engage in frequent homosexual behavior with each other [59]. The behavior of these animals is not explained in terms of excessive feminization but rather simple behavioral scaling. Accordingly, human males may have evolved to exhibit some degree of bisexual behavior under certain conditions. The predominantly homosexual orientation exhibited by a very small percentage of men may be due to a greater genetic predisposition, the result of genetic variation, in conjunction with social and cultural factors that allow its manifestation.

The inconsistencies found in the neuroendocrine research may be due the fact that the research is based on a faulty assumption: sexual orientation is reliably dichotomous. Genetically based characteristics tend to be continuous [60], thus the expression of genetically mediated homosexual behavior could similarly be expected to be continuous. The measures of sexual orientation reflecting a bimodal distribution of heterosexual/homosexual, at least in Western countries, may not accurately reflect actual genotypic variation and its accompanying neuroendocrine variation.

Most studies use volunteers self-labeled as 'homosexual' and 'heterosexual'. There are strong countervailing social pressures associated with an open acknowledgement of a homosexual orientation. Thus, it is reasonable to speculate that the homosexual group is stringently self-selected and reliably homosexual in psychology and the neuroendocrinology, which underlies this. However, assuming that the genotype for homosexual behavior is continuous, there is arguably much more variation in the heterosexual group. Much of the variation in overt sexual behavior that could be generated by the corresponding genotypic variation is only likely to be seen under environmental conditions more conducive to homosexual behavior. This may explain the universally high rate of homosexual behavior in self-identified heterosexual males with limited access to opposite sex partners (cf., [61]).

A change in the scientific paradigm and the assumptions which guide the search for the cause of homosexual behavior and orientation in humans may allow a better understanding of human sexual orientation in general. Bancroft [61] has stated "….it soon becomes apparent that many of our widely held assumptions about the origins of homosexuality are a product of our social values rather than an objective appraisal of the evidence" (p. 300). Homosexual orientation is no longer considered a psychopathology by psychiatry and psychology, and society has become increasingly tolerant and accepting of those with a homosexual orientation [62]. Future researchers, shaped by a more tolerant society, may ask different questions about the origins of homosexuality and find unexpected answers.

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