https://doi.org/10.1038/s41559-023-02273-9

A broader cultural view is necessary to study the evolution of sexual orientation

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The causation of sexual orientation is likely to be complex and influenced by multiple factors. We advocate incorporating a broader cultural view into evolutionary and genetic studies to account for differences in how sexual orientation is experienced, expressed and understood in both humans and nonhuman animals.

The data currently available to scientists who study sexual orientation are astounding in their breadth, complexity and specificity. For example, in humans, sequenced genomes and surveys from hundreds of thousands of individuals are available, as are decades of observations from brain scans, eye tracking, recordings of genital arousal and daily digital diaries. If there were a single, simple explanation for differences in sexual orientation, it would probably have been discovered by now. The fact that it has not been suggests that core assumptions about what causes variation in sexual orientation (for example, occurrence, function, representation, genetic underpinning, stability and gender) need to be revisited. Sexual orientation is likely to be shaped by a complex interplay of various factors[1]. In this context, we will concentrate on the causes that contribute to variations in phenotype. Additionally, an area of research that remains relatively unexplored pertains to the reasons behind and consequences of aversion to same-sex sexuality, both at the individual and societal levels. Here we discuss these historic assumptions, the research that has overcome them and possible directions for the future.

Homosexual behaviour is rare (assumption 1)

Although homosexual behaviour has historically been described as rare or deviant[2], homosexual expression is widespread in many animals and relatively common in some, which demands mechanistic and evolutionary explanations[3,4]. Homosexual behaviour has also been described as a 'Darwinian paradox', because – intuitively – a genetically influenced focus on non-reproductive sex to the detriment of reproductive sex should eventually lead to extinction. Breakthroughs have been made that illustrate the diversity of causation across the animal kingdom. For example, in insects, same-sex sexual behaviour may stem from indiscriminate sex recognition. In fruit flies, male courtship behaviour is controlled by one simple pathway[5], and a glial amino-acid transporter known as genderblind controls whether *Drosophila melanogaster* males will attempt to mate with other males[6]. In others (such as termites), however, same-sex sexual behaviour is observed as a result of flexible same-sex pairing with accurate sex discrimination[7]. In mice, the gut microbiome affects sociosexual behaviour (including same sex) and can be manipulated using antibiotics[8].

Homosexual behaviour is not adaptive (assumption 2)

Exclusive homosexuality has not been described in nonhuman primates, but bisexuality occurs in some species. The latter can be adaptive (for example, fostering alliances in rhesus macaques[9]) or neutral, with no concomitant decrease in reproduction. Female Japanese macaques who behave bisexually routinely choose same-sex partners even when motivated, opposite-sex mates are available[10]. Bisexuality is also expressed in humans[11], although in men exclusive homosexuality is more common and decreases reproduction[1]. However, more research is needed to characterize same-sex sociosexual behaviour in animals to dissect both genetic and environmental influences on its expression. For example, it is still unknown how rhesus macaques – our closest relative that is routinely used in biomedical research – vary in sexual orientation over time (that is, plasticity).

WEIRD societies are representative (assumption 3)

Most research on sexual orientation in humans has been conducted in WEIRD ('Western, educated, industrialized, rich and democratic') societies; little is known in other cultures and the data that are available provide conflicting results. A survey of cultures in the *Human Relations Area Files* (an internationally recognized resource for cultural anthropology curated at Yale University) found data on male homosexuality only in 52 of 135 cultures and almost no data on female homosexuality. In these data, homosexuality was either unknown or ignored in 8%; acceptable or well-accepted in 44%; and condemned in 48% of cultures[12]. One study found that variation in social stratification may have a role, as a positive relationship was observed between the level of social stratification and the probability of observing homosexual orientation in a given society[13]. Social stratification might relate to operational sex ratios (for example, via polyandry or polygyny, or even wealth), which in turn might affect attitudes to homosexuality. Social stratification refers to the hierarchical arrangement of individuals within a society based on factors such as income, education and social status. The operational sex ratio, on the other hand, refers to the ratio of sexually active men to women in a population. For instance, if an operational sex ratio became male-biased one might predict greater acceptance of male homosexuality, and vice versa. Similar arguments have been proposed in birds such as the Laysan albatross, in which operational sex ratio variation is associated with the expression of same-sex behaviour[14]. The question remains of what causal factors drive differences in the aversion or acceptance of homosexuality and/or bisexuality across cultures worldwide. Developing more realistic models (for example, multi-loci, societies with some degree of social inequality and including variation of the extent to which different social norms are followed) combined with genomic analyses from distinct populations could eventually provide some clues to this question.

There is a gene for sexual orientation (assumption 4)

Although this assumption has a long and sometimes difficult history, it has received no empirical support. Twin studies have shown that sexual orientation in humans is heritable, with heritability estimates of about 30%. In 2019, Ganna et al.[1] published a well-powered genome-wide association study that investigated the genetic causes of homosexual behaviour in 470,000 men and women. In line with other complex traits, the genetic architecture of homosexual behaviour is highly complex and is influenced by many variants with small individual effect sizes. These only partially overlapped between male and female individuals. The genetic correlation between male and female individuals is 0.63, which is lower than that observed in most other complex behavioural traits (such as educational attainment and risk-taking behaviour)[15]. Further, the genes that differentiate between exclusively heterosexual individuals and those who have engaged in any kind of same-sex behaviour are not the same as the genes that differentiate between individuals who engage in bisexual versus exclusively same-sex behaviour. Such findings — alongside anthropological and sociological evidence for culture- and context-dependent expressions of same-sex desire and behaviour — indicate that linear measures such as the Kinsey scale may not adequately capture the full range of phenotypes related to sexual orientation. Future studies should investigate the multivalent nature of sexual orientation by assessing levels of attraction, identity and behaviour separately for male versus female partners.

Evolutionary maintenance of sexual orientation is stable through time (assumption 5)

A recent large-scale genetics study in humans[16] tested a theory that may explain the maintenance of homosexual orientation despite apparent selection — namely, antagonistic pleiotropy[17]. The hypothesis proposes that genetic variants associated with homosexuality in one sex may be associated with a mating advantage in the other. Using data from individuals, genetic effects associated with homosexual behaviour were found to predict a greater number of opposite-sex partners in exclusive heterosexual individuals[16] — although with the advent of contraception, the fitness relationship between number of sex partners and number of children is disappearing, reversing the genetic correlation with same-sex sexual behaviour[18]. Finally, substantial evidence points to the important role of epigenetic factors in homosexuality[19,20]. One idea is based on epigenetic marks laid down in response to the XX versus XY karyotype in embryonic stem cells in humans[19,21]. These marks boost sensitivity to testosterone in XY fetuses and lower it in XX fetuses and thereby canalize sexual development. If a subset of these canalizing epigenetic marks carry over across generations, they may lead to mosaicism for sexual development in opposite-sex offspring and a homosexual phenotype[19,21]. Despite the availability of technology to empirically evaluate this hypothesis (as suggested by Rice et al.[21]), such tests have yet to be conducted. How biological versus social context, especially epigenetics, affects the nature of sexual orientation remains unclear.

Sex does not matter (assumption 6)

Future research that tests evolutionary hypotheses for the evolution of human sexual orientation must keep in mind the robust sex differences that have been observed in the expression of (and social constraints on) sexual orientation[22,23]. Consequently, different explanations may be needed to account for the development and evolution of male versus female sexual orientation. Indeed, the vast majority of research on sexual orientation (particularly within a biological and evolutionary framework) has been conducted with men, and studies increasingly suggest that the phenotypes and causal pathways for same-sex sexuality in women may be markedly different from those of men. Yet, this does not mean that comparing samples of women and men lacks value: rather, determining which phenotypes (and causal pathways) are sexually dimorphic versus shared should be a priority. The evidence suggests this approach will yield compelling new insights about the evolution of human sexual behaviour. For example, men are usually genitally aroused to one preferred sex, whereas most women — including heterosexual women — show some degree of genital arousal to both sexes (often outside of conscious awareness)[22]. Cross-species comparisons offer promising possibilities for studying the ultimate and proximate mechanisms that underlie sex differences in sexual orientation.

Future studies of sexual orientation

Homosexuality is illegal in 65 countries and is punishable by death in 12. Aversion to same-sex sexuality results from a blend of genetic and environmental influences, the latter of which are primarily cultural: a twin study showed that variation in homophobia could be explained by additive genetic (36%), shared environmental (18%) and unique environmental (46%) factors[24]. Applying a conservative estimate of 10%[25] of the world population being gay, lesbian or bisexual, this percentage translates into 800 million individuals who may directly suffer humans' vociferous and violent aversion to this form of sexuality. It is noteworthy that such aversion might even be self-defeating. First, genetic variants linked to homosexuality may have a beneficial pleiotropic effect for closely related, opposite-sex-attracted kin by increasing their number of opposite-sex sexual partners[16]. In theory, reducing the frequency of these genes could, in turn, result in diminished fecundity. Second, in some populations, homosexuality may provide further advantages through kin selection. For example, in Samoan and Istmo Zapotec populations, it has been documented that same-sex-attracted, third-gender male individuals known as *fa'afafine* and *muxe* invest more in their nieces and nephews than do heterosexual men[26,27]. Third, one might expect that in societies in which same-sex behaviour is punished and shamed, individuals who desire such behaviour will instead pursue traditional marriage and childrearing and thereby maintain (or increase) the prevalence of these variants in the local population. Therefore, we advocate for incorporating the scientific study of aversion to same-sex sexuality into studies of sexual orientation, so that we can promote greater acceptance of sexual diversity.

Homosexual behaviour probably involves many different factors (especially cultural ones). Animal models and human studies can complement each other in this quest. For example, unlike *Drosophila* (in which a simple molecular pathway for courtship and homosexual behaviour has been identified[5,6]), the development of sexual orientation, identity and expression of behaviour in humans is most certainly much more complex and remains largely unknown. Further research on these fundamental processes would be of lasting importance for understanding heterosexual, bisexual and homosexual orientations alike.

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Published online: 08 January 2024

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Acknowledgements

We thank the participants of a Royal Society–Theo Murphy scientific meeting on 'Genetics and evolution of sexual orientation' (27–28 March 2023) for the lively discussion that initiated this Comment; G. Rieger and P. Vasey for comments on the manuscript; and the Royal Society, the American Institute of Bisexuality and the Evolution Education Trust for funding. For the purpose of open access, the corresponding author has applied a 'Creative Commons Attribution' (CC BY) licence to any Author Accepted Manuscript version arising.

Competing interests

The authors declare no competing interests.

Additional information

Peer review information *Nature Ecology & Evolution* thanks Thomas Dickins and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.