

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 factors¹. 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 human and non-human animals.

The data currently available to scientists studying sexual orientation are astounding in their breadth, complexity, and specificity. For example, in humans, sequenced genomes and surveys are available from hundreds of thousands of individuals, as well as 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 likely have been discovered by now. The fact that it has not suggests that core assumptions about what causes variation in sexual orientation (e.g., 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. 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.

Assumption 1: Homosexual behaviour is rare

While, historically, homosexual behaviour has been described as rare or deviant², homosexual expression is widespread in many animals and relatively common in some, demanding 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 pathway⁵, and a glial amino-acid transporter genderblind controls whether *Drosophila melanogaster* males will attempt to mate with other males⁶. In others such as termites,

however, same-sex sexual behaviour is observed as a result of flexible same-sex pairing with accurate sex discrimination⁷. In mice, the gut microbiome affects socio-sexual behaviour (including same-sex) and can be manipulated using antibiotics⁸.

Assumption 2: Homosexual behaviour is not adaptive

In non-human primates, exclusive homosexuality has not been described, but bisexuality occurs in some species. The latter can be adaptive, fostering alliances in rhesus macaques⁹, 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 available¹⁰. Bisexuality is also expressed in humans¹¹, though in men, exclusive homosexuality is more common and decreases reproduction¹. However, more research is needed to characterise same-sex sociosexual behaviour in animals. For example, it is still unknown how rhesus macaques, our closest relative routinely used in biomedical research, vary in sexual orientation over time (i.e., plasticity), to dissect both genetic and environmental influences on its expression.

Assumption 3: WEIRD societies are representative

In humans, most research on sexual orientation has been conducted in WEIRD ('Western', educated, industrialised, rich, and democratic) societies; little is known in other cultures, and data that are available provide conflicting results. A survey of cultures in the *Human Relations Area Files*, an internationally recognised 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 cultures¹². One study found that variation in social stratification may play a role, with a positive relationship observed between the level of social stratification and the probability of observing homosexual orientation in a given society¹³. Social stratification might relate to operational sex ratios (e.g. via polyandry or polygyny, or even wealth), which in turn might affect tolerance to homosexuality. Social stratification refers to the hierarchical arrangement of individuals within a society based on factors like income, education, and social status. Operational sex ratios, 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 tolerance of male homosexuality, and vice-versa. Similar arguments have been proposed in birds such as Laysan albatross, in which operational sex ratio variation is associated with the expression of same-sex behaviour¹⁴. What are the causal factors driving differences in aversion/acceptance of homo/bisexuality across cultures worldwide? Developing more realistic models (e.g., 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.

Assumption 4: There is a gene for sexual orientation

Although this assumption has a long and sometimes difficult history, the evidence is unequivocal that it has received no empirical support. Twin studies have shown that sexual orientation in humans is heritable, with heritability estimates of ~30%. In 2019, Ganna et al.¹ published a well-powered genome-wide association study investigating the genetic causes of homosexual behaviour in 470,000 men and women. In line with other complex traits, its genetic architecture is highly complex, influenced by many variants with small individual effect sizes. These only partially overlapped between males and females. The genetic correlation between males and females is 0.63, lower than that observed in most other complex behavioural traits such as educational attainment and risk-taking behaviour¹⁵. Further, the genes differentiating between exclusively heterosexual individuals and those who have engaged in any kind of same-sex behaviour are not the same as the genes which differentiate

between individuals engaging 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/behaviour separately for male versus female partners.

Assumption 5: Evolutionary maintenance of sexual orientation is stable through time

A recent large-scale genetics study in humans¹⁶ tested a theory that may explain the maintenance of homosexual orientation, despite apparent selection, namely antagonistic pleiotropy¹⁷. 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 heterosexuals¹⁶, 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 behaviour¹⁸. 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 vs. 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, thereby canalising sexual development. If a subset of these canalising 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, affect the nature of sexual orientation remains unclear.

Assumption 6: Sex doesn't matter

Future research testing 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 strikingly different from that of men. Yet this does not mean 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 awareness²². Cross-species comparisons offer promising possibilities for studying the ultimate and proximate mechanisms underlying sex differences in sexual orientation.

Future studies of sexual orientation

Homosexuality is illegal in 65 countries, punishable by death in 12 (<https://www.humandignitytrust.org/>), most recently including Uganda. Aversion to same-sex sexuality results from a blend of genetic and environmental influences, the latter primarily cultural: a twin study showed that variation in homophobia could be explained by additive genetic (36%), shared environmental (18%) and unique environmental factors (46%)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. Noteworthy, such aversion might even be self-defeating. Firstly, genetic variants linked to homosexuality may have beneficial pleiotropic effect for closely related opposite-sex attracted kin by increasing their number opposite-sex sexual partners¹⁶. In theory, reducing the frequency of those genes could, in turn, result in diminished fecundity. Secondly, 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 males known as *fa'afafine* and *muxe* invest more in their nieces and nephews than heterosexual men^{26,27}. Thirdly, one might expect that in societies where same-sex behaviour is punished and shamed, individuals desiring such behaviour will instead pursue traditional marriage and childrearing, thereby maintaining (or increasing) their prevalence 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 tolerance of sexual diversity.

Homosexual behaviour likely involves many different factors, especially cultural. Animal models and human studies can complement each other in this quest. For example, unlike *Drosophila* where 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 have lasting significance for understanding heterosexual, bisexual and homosexual orientation alike.

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Competing interests

The authors declare no competing interests

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