

Further Reading

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Shari Thurer

genetics and the development of human sexual orientation

Sexual orientation describes what is erotically attractive to an individual and is usually consistent with *sexual identity*, which refers to an individual's labeling of self as heterosexual, homosexual, or bisexual; both are typically not consolidated until adolescence or later.

PREVALENCE AND DISTRIBUTION OF SEXUAL ORIENTATION

Three recent large surveys of sexual behavior from Great Britain (1994), France (1992), and the United States (Laumann et al. 1994) have provided estimates of adult homosexual behavior. These estimates vary with the stringency of the respective definitions. For men, the least stringent definition examined in the studies—any homosexual experience ever—yielded an estimate of 4.1, 6.1, and 7.1 percent for the three samples, respectively. A much more stringent criterion—same-sex activity during the year preceding the survey—yielded rates of 1.1, 1.1, and 2.7 percent for the three samples, respectively. The criterion closest to that of self-identification as "gay" or "bisexual" was employed only in the American study, and applied to 2.4 percent of men. In general, the rates for female homosexuality appear to be about half that for males. For example, same-sex activity during the year preceding the survey yielded a rate of 1.3 percent in the American survey. In addition, male and female sexual orientation appear to be distributed differently in the general population. For men, sexual orientation appears to be bimodally distributed (heterosexual or homosexual, and rarely bisexual), whereas for women, it tapers gradually from exclusively heterosexual to exclusively homosexual (Bailey et al. 2000). Defining sexual orientation psychologically, rather than just behaviorally as some older studies with higher prevalence figures did, is what most current researchers do. Psychological sexual orientation (e.g., attraction and fantasy) is less likely to be constrained by societal pressures compared to behavioral sexual orientation, and in this sense it is a more stable and

fundamental trait and is the method used in most of the studies demonstrating familiarity and heritability.

GENDER ROLE BEHAVIOR

Gender identity refers to an individual's sense of being male or female, which is typically consolidated by age three or four years. *Gender role behavior* refers to aspects of an individual's behavior that are consistent with cultural definitions of masculinity or femininity. Sexual orientation is empirically closely linked to some aspects of gender roles, including childhood play behavior and gender identity, and aspects of adult sex-typed behavior as well, particularly occupational and recreational interests. Bailey and Zucker (1995) conducted a meta-analysis of 48 retrospective studies comparing childhood sex-typed behavior in homosexual and heterosexual men and women. Homosexuals recalled substantially more childhood cross-gender behavior than did heterosexuals. Though significantly larger for males, the effect sizes reported for both sexes are among the largest ever reported in the realm of sex-dimorphic behaviors. Prospective studies have supported the above findings for men; analogous studies for women remain to be done.

BEHAVIOR GENETIC STUDIES

As currently practiced, behavior genetics research proceeds in three main stages: *family studies* are initially conducted to determine whether a trait or characteristic (often called a phenotype) runs in families by comparing rates in families of probands (i.e., individuals possessing the trait) versus families of controls (that typically represent the base rate in the general population). If there is a heritable genetic contribution to a trait, one expects to find familial aggregation; however, the mere demonstration of clustering of a trait in families does not prove a genetic influence because some traits run in families for environmental reasons.

In order to separate genetic from familial environmental effects, *twin studies* may be conducted, which compare the similarity of monozygotic (MZ, also called identical) and same sex dizygotic (DZ, also called fraternal) twins who have been reared together. MZ twins are 100 percent genetically identical, whereas DZ twins are like all full siblings in that an average of only 50 percent of their genes are inherited from the same parent, or identical by descent. Since both twins share the same pregnancy, it is assumed that they experience essentially the same prenatal environment. Because both twins have also been reared together, postnatal environmental similarity is assumed to be approximately equal. Thus, if MZ twins are more similar (i.e., concordant) on a trait than DZ twins, this is thought to reflect their greater genetic similarity and is evidence that genetic factors influence the phenotype. Twin studies allow one to estimate heritability, defined as the proportion of the variance in expression of the trait due to all genetic influence(s) combined. Results from twin studies support a significant environmental contribution to most behavioral traits, since MZ twins are not 100 percent concordant. Finally, *adoption studies* are a further method used to separate the effects of genes from the environment. Adoption produces family members who share family environment but are not genetically related, and vice versa. Thus, this method allows one to estimate

the contribution of family environment to family resemblance. Studies exist from all three stages of research regarding both male and female sexual orientation.

FAMILY STUDIES

Both male and female homosexuality appears to run in families. Table 1 contains the results of recent family studies. The rate of homosexuality among brothers of homosexual males has been around 9 percent. These results have exceeded those for heterosexual controls, as well as the prevalence estimates from recent large-scale epidemiological surveys, suggesting that male homosexuality is familial. Homosexual women also appear to have more homosexual sisters than do heterosexual controls, though the familiarity estimates have varied more widely for women. There is also a trend (Table 1) for gay male probands (in this case, the first person identified as gay in a family) to have more gay brothers than lesbian sisters and for the opposite pattern to obtain for lesbian probands, suggesting that at least some of the familial factors influencing male homosexuality differ from those influencing female homosexuality. However, the degree of cofamiliarity (reflecting common familial influences) of male and female homosexuality remains inconclusive.

TWIN STUDIES

Several twin studies have been conducted in recent years, and their results are given in Table 2. These studies have been generally consistent in detecting moderate to large heritabilities for both male and female sexual orientation. However,

Table 1. Rates of Homosexuality for Nontwin Siblings in Recent Studies

Study	Criterion	Brothers		Sisters	
		Probands	Controls	Probands	Controls
Male Probands					
1986	Kinsey 2-6	0.22	0.04	0.08	0.09
1991	Subject's rating	0.10	0.00	0.02	0.00
1991	Subject's rating	0.09	NA	0.06	NA
1993	Subject's rating	0.09	0.04	0.03	0.01
1999	Subject's rating	0.09	NA	0.04	NA
Female Probands					
1990	Kinsey 2-6	0.13	0.00	0.25	0.11
1993	Subject's rating	0.07	0.01	0.12	0.02
1993	Subject's rating	0.05	NA	0.14	NA
1993	Subject's rating	0.12	0.00	0.06	0.01

Table entries are proportions. Probands are homosexual, and controls are not. NA entries indicate that studies did not assess the respective rate. See Dawood and Bailey (2000) for individual references.

genetics and the development of human sexual orientation

Table 2. Concordance Rates for Twin Studies of Homosexuality

Study	MZ Concordance	DZ Concordance
Male Studies		
1952	1.00	0.15
1968	0.60	0.14
1991	0.52	0.22
1991	0.47	0.00
2001	0.20	0.00
Female Studies		
1993	0.48	0.16
2001	0.24	0.15
Combined Male and Female		
1992	0.25	0.12
1993	0.66	0.30
2002	0.32	0.13

Table entries are proportions. See Dawood and Bailey (2000) for individual references prior to 2000; also see Bailey et al. (2000) and Kendler et al. (2000).

there have been methodological limitations; in particular, most of the large twin studies of sexual orientation recruited probands via advertisements in gay or lesbian publications. Such sampling is likely to result in volunteer bias that affects twin concordances and heritability analyses, though in most scenarios this would be more likely to lead to a false negative study. The largest twin study of sexual orientation to date (Bailey et al. 2000) recruited twins systematically from a twin registry and reported lower twin concordances for homosexuality than in prior studies, although their findings were also consistent with moderate to large heritabilities for male and female sexual orientation.

ADOPTION STUDIES

A few of the family and twin studies listed in Tables 1 and 2 have included adoptive siblings who were reared in the same household as the homosexual probands in their samples. Hence, rates of homosexuality have been estimated for genetically unrelated adoptive siblings. Consistent with a genetic hypothesis, for both sexes the proportion of homosexuals (and bisexuals) was significantly greater for MZ cotwins than for either DZ same-sex cotwins or adoptive siblings.

MOLECULAR GENETIC STUDIES

Once a solid foundation of support for significant genetic influence on a trait has been built by means of behavior genetics (family, twin, and adoption studies),

as has occurred especially for male sexual orientation, molecular genetic studies are a next logical step. The two primary varieties of these studies are *linkage* and *association*. *Linkage* analysis exploits the process of meiotic recombination during sperm and egg formation. During meiosis, crossing over occurs, in which homologous maternally and paternally derived chromosomes lie in close proximity and exchange genetic material. Genes and other genetic markers (DNA sequence variations known as polymorphisms) that are close together are less likely to be separated by this process than are those that are farther apart. Therefore, they are usually inherited together by the progeny cells and are said to be genetically linked. Due largely to the complexity of the genetic contributions to male sexual orientation and uncertainty regarding key parameters (mode of inheritance, number of relevant genes, etc.), the type of linkage analyses preferred are nonparametric allele-sharing methods, and more specifically, the affected sibling pair (ASP) method. With ASP designs, the frequency with which a genetic marker allele (or variant) is identical by descent (IBD) in a pair of siblings both manifesting the trait is measured. Presence of a trait-influencing gene is revealed when the IBD allele sharing between affected siblings exceeds the expected 50 percent.

Association studies are based on linkage disequilibrium (LD). This means that a gene variant influencing a trait was initially associated with specific alleles of nearby polymorphic loci. Association studies explore the relation between genetic variation at a specific locus and phenotypic variation. Across generations, the trait-influencing gene and marker allele may remain statistically associated partly because their proximity reduces the number of crossovers between them. An advantage of association tests is that the chromosomal region examined is usually much smaller than the region examined by testing for linkage in families. Association studies require a very specific hypothesis, in contrast to linkage studies, which may search the entire genome and examine genetic markers rather than genes. Association is often more powerful than linkage in that a valid association may be detected in a sample when linkage is not detectable, even when the gene is playing only a modest role. Most association studies in the past were of the population-based type, in which the allele frequencies of a group of unrelated cases were compared against those of a group of unrelated controls, and this is the only type of association study done with male sexual orientation. A potential pitfall of population-based case-control studies is that some populations, although they appear homogeneous to superficial examination, are in reality composed of different ancestral human groups, each one potentially with a different allele distribution at the studied loci. If one or more such groups is represented in a largely different proportion in one of the samples of an association dataset (i.e., either in the controls or in the cases), false negative or false positive association findings may easily arise due to methodological artifacts.

LINKAGE

The observations from behavior genetic studies predict that the genetics of male homosexuality will not be simple, and this prediction is consistent with the results of linkage research thus far. Several linkage analyses of male homosexuality

genetics and the development of human sexual orientation

to the X chromosome have previously been reported (see Hamer 1999 for individual references). These studies have been largely based on the assumption that oligogenic (a "few" genes contribute) transmission was most likely and therefore relied on the ASP method of linkage analysis. See Table 3 for a comparison and contrast of the samples examined. While the Xq28 chromosomal region in one group's 1993 study showed a significant linkage signal, with supporting data in a second dataset from the same group in 1995, it is still indeterminate (as in many complex traits) whether this finding represents a true positive. A second group found inconclusive evidence of linkage to Xq28 in 1998, and a third group found no support for linkage to Xq28 in 1999. Combining all four linkage studies, with respective affected sibling pair (ASP) sample sizes of 40 (1993), 33 (1995), 54 (1998), and 52 (1999), yields a "Multiple Scan Probability" (MSP) of 0.00003, which is a suggestive p-value when considering all of the chromosomes, that is, the entire genome. The replication MSP (excluding the original positive report from 1993) of 0.07 is at the level of a "trend" and thus not quite significant. This pattern of results is one that has been predicted for complex traits with oligogenic inheritance on the basis of simulation studies: stochastic variation in the degree of co-segregation of any one locus with a trait, which produces variation in the magnitude of linkage findings across samples. Of course, the sample size of

Table 3. Sample Characteristics of Linkage Male Homosexuality Samples

Study	Subject sources	ASPs	DNA	Tools	Inclusion	Exclusion
1993	local clinics, local homophile organizations, homophile publications	40	proband, homosexual brothers, parents, other siblings	interview, Kinsey Scale, family history	2 (exactly) homosexual brothers	maximum of one lesbian per family, no male to male transmission
1995	local clinics, local homophile organizations, homophile publications	33	proband, homosexual brothers, parents, other siblings	interview, Kinsey Scale, family history	2 (exactly) homosexual brothers	maximum of two lesbians per family, no male to male transmission, no bisexuals
1998	homophile organizations, homophile media	54	proband, homosexual brothers, parents	Kinsey Scale, family history	2 (or more) homosexual brothers	no known evidence of male to male transmission
1999	homophile media	52	probands, homosexual brothers	interview, family history	2 (or more) homosexual brothers	none stated

Number of ASPs are calculated by the $n-1$ method for independent ASPs where n is the number of homosexual brothers per sibship. DNA refers to the family members from whom blood was sought for genetic analyses. Tools refers to the clinical methods used to assess the trait of sexual orientation. Major inclusion and exclusion criteria for families are listed. See Hamer (1999) for individual references.

the individual linkage studies should be considered a major factor. Because of the conflicting replication results, the status of the Xq28 linkage finding is unresolved. When studies are small, replications count more than failures to replicate. Nevertheless, larger studies will be needed to determine whether male sexual orientation is influenced by a gene in Xq28.

ASSOCIATION

To date, two association studies have been performed for male homosexuality. The first one used population-based case-control association methods on a sample of 197 homosexual males and about 213 unselected (with respect to sexual orientation) male controls with variants of the androgen receptor located on the X chromosome (but not at Xq28), and it found no evidence for association (Macke et al. 1993). This gene was selected for examination partly due to its location on the X chromosome, since there is some evidence for excess maternal transmission of male homosexuality, which would be consistent with X-linked transmission. It was for similar reasons that the X chromosome was the first chromosome to be examined by linkage methods also. It should also be noted that linkage analysis using pairs of homosexual brothers was conducted with variants of this gene in the same study, but no evidence for linkage was found (Macke et al. 1993). Sibling pairs concordant for homosexuality were no more likely than chance to share the same androgen receptor allele. Another reason the androgen receptor was chosen for examination was not due to its position, but rather due to its function, which is to transduce messages from androgens ("male" hormones) to the nucleus of the cell, thus affecting other genes responsive to androgens. Thus, it was reasoned that some variants of the androgen receptor gene may well affect sexual differentiation of the brain. However, the study reported no significant differences in the distributions of mutations in homosexual and heterosexual men. More recently, DuPree et al. (2004) reported results from a candidate gene study of aromatase cytochrome P450 (CYP19), which is necessary for the conversion of androgens to estrogens and plays an important role in the sexual differentiation of the brain. Both linkage and association analysis was performed on the CYP19 locus from a large sample of 144 families with two or more gay brothers. Results from multipoint linkage analysis showed no relationship between the inheritance of the CYP19 locus and sexual orientation. Furthermore, no association was reported for any of the alleles, suggesting that this gene is unlikely to play a significant role in the development of sexual orientation in human males.

ANATOMIC AND NEUROPHYSIOLOGICAL STUDIES

Any genetic (or environmental) contributor to behavior must eventually act through the brain. Consequently, several investigators have searched for neural and behavioral differences among individuals with different sexual orientations. Relevant findings in the literature (see McFadden and Pasanen 1998 and Puts et al. 2006 for individual references) include a larger suprachiasmatic nucleus of hypothalamus in homosexual males (1990), a smaller third interstitial

nucleus of the anterior hypothalamus in homosexual males (1991), a larger anterior commissure in homosexual males (1992), diminished otoacoustic emissions (1988) and increased eyeblink response to acoustic stimuli (2003) in homosexual women, and elevated non-right-handedness in homosexual men and women (2000). It should be noted that, except for those on handedness, these findings await replication by independent groups, though there have been attempts to do so for the second and third ones. Because the first three of these findings rely on brains arriving to autopsy, care must be taken to ensure that potential confounding factors such as infection with HIV are controlled for, and, of course, ability to directly assess sexual orientation is generally limited to examination of the medical record. The fourth through sixth findings examine neurophysiological and behavioral rather than anatomic measures and hence are conducted with living subjects.

Because sexual differentiation in the mammalian nervous system is mediated primarily by sex-specific hormonal regimes, most researchers of sexual orientation suspect a role of sex hormones in sexual orientation. Rates of homosexuality are higher in females exposed to elevated prenatal androgens due to congenital adrenal hyperplasia, and several possible anatomical markers of androgen exposure, including finger- and arm-length ratios, suggest elevated exposure to androgens in homosexual females. The data on male sexual orientation are less clear. Male sexual orientation is influenced by the number of biological older brothers through the mother. Each older brother increases a male's probability of homosexuality by about 30 percent of the population base rate of 2–3 percent. A number of observations suggest that this "fraternal birth order effect" is prenatal, and it has been hypothesized that older brothers affect sexual orientation in younger brothers by provoking a maternal immune response to male-specific antigens that affects the neural development of subsequent male fetuses, perhaps by modulating androgen signaling. Although plausible, such explanations for the fraternal birth order effect remain speculative.

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Mildred [MilDréd] Gerestant (1971–)

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Khytam Daswood and David Puts

Mildred [MilDréd] Gerestant (1971–)

An American drag king of Haitian descent, Mildred Gerestant was born in Brooklyn. A self-described "lesbian since I was born," Gerestant found herself drawn to drag, explaining, "I've been butch and femme, top and bottom, and so drag feels natural to me." In 1995, Gerestant began publicly performing as Dréd, and she soon became a regular at Club Casanova, the first drag king club in New York City, founded by Mo B. Dick and Mistress Formika in 1996. As Dréd, Gerestant explores female masculinity and challenges preconceived notions of gender. She was named winner of the 1996 Drag King of the Year contest.

As a performer and singer, Dréd parodies popular black male icons, including P. Diddy, Sly Stone, Superfly, and Shaft. Her shows are unique combinations of dance, vocals, theatrical performance, poetry, and comedy. She has appeared on numerous television shows, including *Ricki Lake*, *Sex in the City*, and *Maury Povich*, and performs regularly on stage. Gerestant took her one-woman show, "D.R.E.D.: Daring Reality Every Day—Exposures of A Multi-Spirited, Haitian-American, Gender-Illuminating WoMan!—And Then Some!" on a world tour that coincided with the premier of *Venus Boyz*, the documentary on drag kings directed by Gabriel Baur, in which she is one of the featured performers. In 2004, she created a new show, "DRED! The GoD/Dess in Me—Scary Beautiful and Drunk on Self-Love." That same year, she was also featured in the Steven Spielberg film, *The Terminal*, in which she sings a Haitian Creole hymn she wrote. More recently, she was in the film *Knives in My Throat: The Year I Survived While My Mind Tried to Kill Me* (Dir. Abiola Abrams, 2005). Today, Gerestant lectures and performs but has found new strength in her Haitian spirituality. She defines both her sex and gender identity as fluid.