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Human Sexual Orientation Has a Heritable Component

RICHARD C. PILLARD¹ AND J. MICHAEL BAILEY²

Abstract We present an overview of behavioral genetics research on homosexual and heterosexual orientation. Family, twin, and adoptee studies indicate that homosexuality and thus heterosexuality run in families. Sibling, twin, and adoptee concordance rates are compatible with the hypothesis that genes account for at least half of the variance in sexual orientation. We note observations of homosexual behavior in animal species, but the analogy to human sexual orientation is unclear. We discuss the reproductive disadvantage of a homosexual orientation and present possible mechanisms that could maintain a balanced polymorphism in human populations.

A powerful generalization about human sexual desire is that members of the two sexes are attracted to each other but attracted by different qualities. Traditionally, men seek youth and beauty in a woman (although the standard of beauty may vary with time and place), whereas women seek in a man good health, high status, and evidence of willingness to provide for children (Symons 1979). These generalizations are intuitively compatible with evolutionary theory. The healthy, the young (women), and the rich (men) are surely more likely to produce viable offspring and raise them to maturity than the sick, the old, and the poor. (One example of fecundity enhanced by wealth and status: the late King Sombhuza of Swaziland was reported to have sired over 600 children.)

For a given individual the selection of a mate may be an inexact marker of sexual attraction because in many societies the individual has limited mate choice and sometimes no choice at all. Community expectations and the social and political ambitions of the family often override individual desires. Also, atypical sexual desires result in censure and therefore may be effectively concealed. Nevertheless, heterosexual attraction, broadly speaking, must be the paradigmatic adaptation. Men and women attracted to one another suffi-

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ciently to copulate, pair bond, and raise children to self-sufficiency are a precondition for hominid evolution (Lovejoy 1981; Symons 1979).

The development and mechanisms of human sexual attraction have only recently become objects of study. Visual animals that we are, visual cues are doubtless important triggers of sexual response. Olfactory cues may also play a role in sexual attraction, although the nature of the cues and their relative strength remain in controversy (Kohl 1995). (It is interesting to note that blind persons report that they can be sexually attracted by a particular tone of voice.) Whatever cues attract men and women to each other, it is hard to escape the conclusion that they are more or less wired in, the product of an evolutionary history parallel to that of sexual reproduction itself.

Homosexuality, the sexual desire for a person of the same sex, is an interesting challenge to an evolutionary account of sexual attraction, one reason that psychosocial theories have been dominant. Homosexuality is not the only trait that poses the problem of the apparent selection of a reproductively disadvantageous trait. Schizophrenia is ubiquitous in humankind, too frequent (0.7–0.8%) to be the result of occasional mutations, and it is genetically influenced and results in decreased fecundity. What can one make of traits that seem so evidently to defeat the biological imperative of optimizing reproductive success?

Here, we present some background data about male and female sexual orientation and follow with some recent research that in our opinion suggests that sexual orientation has a genetic component. Finally, we comment on some possible explanations for the paradox presented by the persistence of a trait that appears inimical to reproductive success.

Phenotype

Sexual orientation refers to an individual's erotic desire for a member of his or her own sex (homosexuality), the opposite sex (heterosexuality), or both sexes (bisexuality). Recognition of one's orientation generally comes during adolescence, although some individuals are aware of sex-specific attractions in childhood. A homosexual orientation may be concealed for practical reasons, but by adulthood it is almost always a conscious and more or less permanent personality trait. Psychological constructs such as "unconscious" or "latent" homosexuality have use for some clinicians but have dropped out of the research literature.

The ascertainment of an individual's sexual orientation for research purposes is generally done by a questionnaire or a sexual history interview, ideally conducted by a clinician with experience in sex history interviewing. Alfred Kinsey and his colleagues pioneered sex history interviewing with volunteer subjects, and a detailed account of the technique and content of the interviews upon which their survey research was based has been published

(Kinsey et al. 1948, 1953). The information collected in a sexual history interview may include data about sexual feelings and behavior during the life epochs: childhood, adolescence, adulthood, and old age. Other information is obtained as the research protocol dictates, for example, the timing of developmental milestones (puberty, first sexual experience, marriage, menopause, etc.), the presence of sexual dysfunctions, safer sex practices, and sexual traumas.

As with any psychometric assessment, it is important to ensure the validity and reliability of the measures, and considerable work has been done on this issue (Abramson and Pinkerton 1996; Bogaert 1996; Catania et al. 1995). [Some researchers use physiological measures, such as contingent negative variation (Howard et al. 1994), penile plethysmography (Miner et al. 1995), or a vaginal probe, to evaluate sexual responsiveness to stimuli, usually presented by slides or videos. In this way responses to different erotic situations can be compared. These techniques, besides being somewhat invasive, require expensive instrumentation and their validity has not been fully established.] Questionnaire and interview responses can be valid and reliable indicators of sexual behavior; as one example, respondents' accounts of their sexual activity can predict the occurrence of sexually transmitted diseases. The studies cited in this article make use of interviews and questionnaires to ascertain the sexual orientation of research subjects. Despite sources of error, such as volunteer bias, pressure to give socially desirable responses, differences in interviewer technique and questionnaire items, these data give as clear and consistent a picture of the frequency and direction of sexual feelings and behavior as can be obtained from interview data on almost any other topic of interest to behavioral science.

Frequency of Homosexual Orientation

Some commentators in the early sexology literature believed that homosexuality was increasing because of the corrupting influences of city life (Kennedy 1988; von Krafft-Ebing 1901). What they probably observed was the urbanization of nineteenth-century Europe bringing to the cities gays and lesbians who recognized that the opportunities for discreet liaisons were maximized there. More recently, Laumann et al. (1994) found that the percentage of gay men in large US cities is much higher than that in rural areas. Some of this differential is the result of the migration of gays from country to city, but Laumann also found that gay men were disproportionately born in urban areas. This could result from environmental exposure, a reporting artifact (urban gays might be more candid about their orientation), or a genetic effect such that people with "gay genes" are more likely to be city dwellers.

Surveys of sexual orientation began with the Kinsey reports of 1948 and 1953 (Kinsey et al. 1948, 1953). Kinsey and his colleagues obtained

sexual histories from 12,000 men and 8,000 women, covering a wide variety of sexual practices. With respect to sexual orientation, the Kinsey team estimated the *relative* amounts of heterosexual and homosexual behavior, placing each subject on a 7-point scale from 0 (completely heterosexual) to 6 (completely homosexual) with intermediate points to describe mixtures of the two. Kinsey's data led to the much-cited estimate that 1 in 10 men are "more or less exclusively homosexual." Kinsey's colleague, Gebhard (1972), recognized the overrepresentation of subsamples with unusually high rates of homosexuality. By adjusting the sample weightings, Gebhard concluded that only 3–4% of men and 1–2% of women in the United States are exclusively homosexual or virtually so.

The Kinsey group also found that the frequency of more or less exclusive homosexuality was about the same in older subjects as in younger subjects. More recent surveys, although on a smaller scale, give estimates close to those from the Kinsey survey (as adjusted) a half-century ago (Rogers and Turner 1991; Diamond 1993; Seidman and Rieder 1994; Laumann et al. 1994). Thus, despite differences in definition, methodology, and time frame, these surveys taken together suggest that the frequency of gay and lesbian behavior in the United States has remained stable over several generations in spite of the revolutionary changes in the social status of homosexuality. Although comparable data from other countries would be useful, few are available (Diamond 1993; Sell et al. 1995). [Some recent surveys report a frequency of homosexual *behavior* in the 1–2% range. They are reviewed by Diamond (1993) and Sell et al. (1995).]

Bisexuality occupies a controversial place in the literature (Fox 1996; Klein et al. 1985). Kinsey was at pains to suggest that bisexuality was both common and normal. His graphic presentations using a cumulative frequency distribution make it difficult for the reader to recognize that he found more respondents toward the extreme homosexual end of the spectrum (5 and 6 on the Kinsey scale) than in the intermediate range. Diamond (1993) concluded from his own survey that "exclusive or predominantly exclusive homosexual activities are more common than bisexual activities" (p. 291). In our experience this bimodality is more evident among men, whereas bisexuality is relatively more common in women.

Bisexuality is also more frequently endorsed among the young. Adult subjects are usually unequivocally able to say which sex they prefer in a partner, that is, which sex most strongly engages their fantasies and desires. On the other hand, people engage in sexual relations with the nonpreferred sex for any number of reasons, and therefore frequency counts of behavior alone, particularly if sampled over a stretch of time, often result in a pattern that appears more bisexual than would be the case if desire alone prompted behavior. By the time they reach their mid-twenties, most men and most women give a clear and unambiguous answer when asked, Would you rather have sex with a woman or a man?

Gender Atypicality

Gay men and to a lesser extent lesbian women are often labeled as gender atypical. (The term “gender atypical” is chosen to avoid prejudging whether the behaviors at issue are typically those of the other sex or simply not typical of the assigned sex.) For men atypicality is evidenced in childhood by association with girl playmates, preference for girls’ toys and games, and avoidance of boyish rough-and-tumble play. In adulthood gay men often have preference for female-typical activities and vocations. Lesbian women recollect tomboy behavior in childhood and preference for boys’ games and companionship. As adults, lesbians tend to adopt male-typical social and vocational roles more often than do heterosexual women.

Gender atypicality as a forerunner of adult homosexuality has been noted in the sexology literature for more than 100 years (Ulrichs 1994). It is a robust phenomenon confirmed in both prospective and retrospective studies (Bailey, Miller et al. 1993; Bailey and Zucker 1995; Bailey, Nothnagel et al. 1995; Green 1987; Phillips and Over 1995). Whitam found that gender atypicality is a culturally invariable childhood trait for gay men (Whitam 1983) and women (Whitam and Mathy 1991) in such diverse cultures as Brazil, Peru, Guatemala, and the Philippines.

Of course there are many possible kinds of gender atypicality and many ways that a child or adult can feel and behave atypically. Nevertheless, comparing the gender behavior of gays and heterosexuals makes clear that this trait is not simply a matter of feeling lonely, isolated, different, or depressed. The feelings and behaviors are often strikingly and specifically those of the other sex (Pillard 1991).

Gender typical and atypical behaviors emerge in children at similar ages, around 2 to 4 years. Observers of gender-atypical children at play are struck by the pervasive and tenacious nature of this trait. Moreover, some gender-atypical children even *look* different. Zucker and his colleagues gave photographs of prepubertal gender-typical and gender-atypical boys (Zucker et al. 1993) and girls (Fridell et al. 1996) to raters blind to the child’s behavior status. The raters were simply asked to rate the children on the basis of how they looked in the photograph. Raters described gender-atypical boys as “cuter,” “prettier,” and “more attractive” than the gender-typical boys and described the converse for the atypical girls. Apparently, in addition to their behavior, something in the physiognomy of these children marks them already in childhood as gender atypical. What we know about the natural history of this trait suggests that a larger than expected percentage will become gay and lesbian adults. A theory of the development of sexual orientation must take account of the robust and frequently replicated data on the coincidence of atypical behavior in early childhood followed by same-sex attraction in adolescence and adulthood [for an alternative view, see Bem (1996)].

With the onset of adolescence same-sex or opposite-sex attractions become prominent in the gay or lesbian adult-to-be, but some measure of gender

atypicality usually remains. Standard personality tests often include so-called masculinity-femininity (M-F) scales purporting to reflect the degree to which an individual matches the "maleness" or "femaleness" typical of his or her sex. Items in M-F scales are chosen for their criterion validity; that is, they are items that show different endorsement rates between men and women. Most such items are transparent: "I think I would like the work of a nurse" or "I like to read *Popular Mechanics* magazine" obviously will have different endorsement rates for the two sexes. What is surprising is how large the differences are, how consistent they are across cultures, and how little they have changed over time despite the profound changes in available gender-appropriate activities and role models (Gough 1966; Gough et al. 1968). The endorsement of female-typical pursuits and interests by gay men found by Terman and Miles (1936) on their M-F scale can be replicated today, again despite profound changes in the roles and social status of women and of gays.

Are gays and lesbians also atypical in other domains in which the sexes differ, such as patterns of cognitive abilities, brain lateralization, or incidence of physical and mental illness? These questions have not been well studied, and results are uneven (Bogaert and Blanchard 1996; Hall and Kimura 1995; Reite et al. 1995). Furthermore, there are at least some traits on which gender atypicality seems to be minimal or absent; for example, gay men tend not to show a female-typical interest in child care (Stringer and Grygier 1976).

The research just cited naturally led investigators seeking neuroanatomical correlates of sexual orientation to look at the hypothalamus, because it subserves reproductive functions, and at nuclei within the hypothalamus known to be gender dimorphic. Two recent articles reported differences between gay and heterosexual men in the size of hypothalamic nuclei. LeVay (1991) found that gay men have a smaller anterior hypothalamic nucleus (INAH3), which is also smaller in women than in men. However, Swaab and Hoffman (1990) found that gay men have a larger suprachiasmatic nucleus, although it is *not* gender dimorphic. It thus appears that homosexual attraction and gender atypicality are more complex than simply a skewed mix of typically masculine and feminine qualities. [Transsexuals are individuals who feel that they are, psychologically, a member of the other sex, for example, a phenotypic man who feels that he innately is a woman despite his male body. Such persons are usually strongly gender atypical as children and might seem to lie at one end of the heterosexual-homosexual spectrum. This view is contradicted by the finding of transsexual men who are nevertheless heterosexual, that is, a phenotypic man who feels (non-delusionally) that he is a woman but is nevertheless attracted to women (Pillard and Weinrich 1987).]

Birth Order

Blanchard and Bogaert have recently reported that gay men tend to be born later in the sibship, and this trend is accounted for by the presence of

older brothers but not older sisters. A psychosocial explanation for this observation certainly seems plausible. Perhaps having an older brother stimulates homosexual attraction, perhaps the family's reaction to a younger brother is such as to bend him in a homosexual direction. There are also purely biological possibilities; for example, placental cells invade the uterine endometrium, and it is now known that protein fragments from these cells may remain in the maternal system for many years. Their effect (if any) is unknown, but their existence raises the possibility of an influence on later gestations (Blanchard and Bogaert 1996).

Observations in Animals

Homosexual behavior has been observed in many species, including primates both in the wild and in captivity (Chevalier-Skolnikoff 1976; Vasey 1995). Vasey (1995) noted that platyrrhine (New World) primates engage in homosexual behavior infrequently and that it appears to be directed toward nonsexual aims, such as play and dominance interaction. On the other hand, the more recently evolved catarrhine (Old World) primates show "an elaboration on the more basic platyrrhine pattern [including] frequent and more complex homosexual interactions involving consort bonding, reconciliation, tension regulation, and alliance formation. . . . Unambiguous homosexual mate choice, as well as intra- and intersexual competition for same-sex sexual partners are other features that distinguish this group" (Vasey 1995, p. 195).

Sex researchers remain skeptical about an analogy between animal and human homosexuality (Fausto-Sterling 1995). That preferential (although not exclusive) homosexuality can be observed in animal species does, however, open a research possibility: Such animals could be bred to see whether increased rates of homosexual behavior can be artificially selected.

Familial Aggregation of Male and Female Sexual Orientation

Characteristics of interest to the behavioral geneticist generally run in families; familial aggregation suggests but does not prove a genetic contribution to the trait. Sexologists a half-century ago observed that sexual orientation may be familial (Hirschfeld 1936), but systematic research on the issue is relatively recent. Pillard and Weinrich (1986) used newspaper and radio advertisements to recruit subjects for studies of "personality, sexual behavior, and mental abilities." Some ads were placed in papers with a mostly gay readership to enrich the participation of the minority orientation and were written to be candid yet to conceal the specific hypotheses of the study. Volunteers were interviewed and given psychological tests; then permission was

requested to recruit their sibs. A large number of sibs were enrolled and (to avoid bias) interviewed by a clinician who had not interviewed the proband.

Pillard and Weinrich's (1986) primary finding was that nonheterosexual male probands (2–6 on the Kinsey scale) had an excess of nonheterosexual brothers (22%), whereas heterosexual male probands (0 or 1 on the Kinsey scale) had only 4% nonheterosexual brothers, close to the population average. We use the term "nonheterosexual" to highlight another finding: The few probands who were bisexual (2–4 on the Kinsey scale) had as many gay brothers as did probands who were exclusively gay. Individuals who had "more than occasional" gay contacts, even if most of their contacts were heterosexual, shared the tendency toward familial aggregation as strongly as did the exclusive homosexuals. In other words, phenotypic extremity did not predict familiarity. An additional finding was that probands were able to accurately report their sibs' orientation so long as they made the assessment with a high degree of confidence.

Table 1 lists recent family studies of sexual orientation. The study by Bailey, Murphy et al. (1995) was unique in that gay and bisexual men were recruited from consecutive admissions to an HIV clinic. This method is more systematic than advertising for volunteers and may be less subject to self-selection biases.

To summarize the tabulated reports, we note that nonheterosexual male probands have from 2 to 5 times as many nonheterosexual brothers (most of whom were in the 5–6 range on the Kinsey scale) as do heterosexual probands. The heterosexual probands, in turn, have rates of nonheterosexuality among their brothers that are about equal to the population frequency, based on other large survey studies. Nonheterosexual women also appear to have more nonheterosexual sisters than do heterosexual women, although the familiarity estimates for women vary more widely.

Table 1 also shows information about the cofamiliarity of male and female homosexuality. There is a trend for nonheterosexual men to have more nonheterosexual sisters [however, this was not found by Pillard and Weinrich (1986)], whereas nonheterosexual women tend to have more nonheterosexual brothers. However, the estimates varied considerably, leaving open the important issue of cofamiliarity of male and female homosexuality.

Family trees with the systematically ascertained sexual orientation of parents, children, and other relatives of gay and lesbian probands are rarely published. Pillard et al. (1981, 1982) noted that, when male probands reported other gay or lesbian relatives, they usually came from the maternal (enate) side of the family, an observation also made by Hamer et al. (1993). This pattern suggests that some male homosexuality may be X-chromosome linked, an issue more fully discussed by Pattatucci (1998) (this issue).

Female and Male Twins and Adoptees

The traditional method used by behavioral geneticists to disentangle genetic and environmental components of trait variance is the comparison of

Table 1. Rates of Male and Female Homosexuality among Nontwin Siblings in Recent Studies

Study	Criterion for Sibling Homosexuality	Brothers		Sisters	
		Probands (%)	Controls (%)	Probands (%)	Controls (%)
Male proband					
Pillard and Weinrich (1986)	Sibling report, Kinsey score of 2-6	0.22 ^a	0.04	0.08	0.09
Bailey et al. (1991)	Subject's rating of sibling as homosexual or bisexual with certainty	0.10 ^a	0.00	0.02	0.00
Bailey and Pillard (1991)	Subject's rating of sibling as homosexual or bisexual with certainty	0.09	(b)	0.06	(b)
Bailey and Bell (1993)	Subject's estimation of sibling's Kinsey score as 2-6	0.09 ^a	0.04	0.03	0.01
Bailey, Murphy et al. (1995)	Subject's rating of sibling as homosexual or bisexual with certainty	0.09	(b)	0.04	(b)
Female probands					
Pillard (1990)	Sibling report, Kinsey score 2-6	0.13 ^a	0.00	0.25 ^a	0.11
Bailey and Benishay (1993)	Sibling report of homosexual or bisexual identification or, if unavailable, subject rating of sibling as homosexual or bisexual with certainty	0.07	0.01	0.12 ^a	0.02
Bailey, Pillard et al. (1993)	Subject's rating of sibling as homosexual or bisexual with certainty	0.05	(b)	0.14	(b)
Bailey and Bell (1993)	Subject's estimation of sibling's Kinsey score as 2-6	0.12 ^a	0.00	0.06	0.01
Pattatucci and Hamer (1995)	Subject's estimation of sibling's Kinsey score as 2-6	0.06	(b)	0.12	(b)

a. Rate for probands significantly exceeds that for controls.

b. Not assessed in this study.

Table 2. Concordance Rates for Twin Studies of Homosexuality

<i>Study</i>	<i>Monozygotic Concordance (%)^a</i>	<i>Dizygotic Concordance (%)^a</i>
Male studies		
Kallmann (1952)	100 (37/37)	15 (3/26)
Heston and Shields (1968)	60 (3/5)	14 (1/7)
Bailey and Pillard (1991)	52 (29/56)	22 (12/54)
Buhrich et al. (1991)	47 (8/17)	0 (0/3)
Female studies		
Bailey, Pillard et al. (1993)	48 (34/71)	16 (6/37)
Combined male and female		
King and McDonald (1992)	25 (5/20)	12 (3/25)
Whitam et al. (1993)	66 (25/38)	30 (7/23)

a. *N* concordant/total.

concordance between monozygotic (MZ) twins, dizygotic (DZ) twins, and adopted siblings (i.e., biologically unrelated individuals) reared together. If the influence of genes is paramount, MZ twins will be frequently concordant, whereas DZ twins will have the same concordance as nontwin siblings (in the absence of a congenital factor). Adopted siblings, sharing the family's environment but not their genes, will share the trait no more often than an average sample of the population.

Several twin studies of sexual orientation have been conducted recently, and they are listed in Table 2. Bailey and Pillard (1991) and Bailey, Pillard et al. (1993) recruited two kinds of gay probands: those with twins and those with adopted brothers or sisters. Probands were interviewed concerning the sexual orientation of their cotwin or adopted sib, who was contacted where possible. Probands were generally accurate in assessing their sibling's sexual orientation. In the male sample 56 MZ twins were ascertained, 52% of whom were concordant for a nonheterosexual orientation, 54 DZ twins were ascertained, 22% of whom were concordant [the same as for nontwin brothers according to Pillard and Weinrich (1986)], and 57 adopted male sibs were ascertained, 11% of whom were concordant with the gay male proband. Using the model-fitting program MX (Neale 1991), which fits multifactorial threshold models, we calculated heritabilities ranging from 0.31 to 0.74 under a variety of assumptions about volunteer bias and population trait frequency.

The female proband study yielded concordance rates of 48% for MZ twins, 16% for DZ twins, and 6% for adopted sisters. Heritability estimates for women were likewise substantial, mostly above 0.50. However, more recent data obtained by Bailey et al. (1996) on twins from an Australian twin registry showed little difference in concordance rates between female MZ and DZ twins and thus gave essentially zero heritability for females. This result may be due to the different manner in which the twins were recruited, as will be discussed in what follows.

It is worth noting that phenotypic extremity did not predict either sibling familiarity or twin concordance. That is, neither age of first recognition of gay or lesbian feelings, extreme Kinsey scale score, nor extent of childhood gender atypicality related to genetic liability for a homosexual orientation. However, both male and female *concordant* MZ twin pairs were also highly similar in their gender atypicality scores, suggesting a genetic basis for this trait.

Whitam et al. (1993) reported somewhat higher concordance rates for both MZ and DZ twins. They also reported three sets of triplets. One set consisted of an MZ male pair, concordant for homosexuality, and a heterosexual sister. A second set of three sisters consisted of an MZ pair, both lesbian, and a DZ heterosexual sister. The third set consisted of three MZ brothers, all gay.

The few available examples of MZ twins *raised apart* (Eckert et al. 1986; Whitam et al. 1993) show a degree of concordance, at least for males, similar to the cited observations of MZ twins raised together. Concordance, in several male MZ pairs reared apart extended to an interesting variety of personality traits as well.

The conclusion that sexual orientation has a heritable component depends on a set of assumptions, which we now examine. The primary assumption is that volunteer bias does not distort the outcome. Probands for the twin studies were obtained through advertisements in gay-oriented publications. It may be that persons who read these publications and who volunteer for a study are systematically different from the larger population of gay twins or siblings. This possibility can be tested by comparing volunteer data with those from a captive sample, such as from a clinic, or with subjects randomly drawn from a census tract or phone book.

There may also be a systematic concordant-dependent bias; that is, twins or sibs who share a trait may be more (or less) likely to volunteer than those who are discordant. The cited heritability analyses examined the effects of concordance-dependent bias and found that heritability estimates remained substantial over a wide range of assumptions about that kind of bias. Moreover, we found that the concordance rate of DZ twins was similar to the rate of nontwin siblings in other studies of men (Pillard and Weinrich 1986) and women (Bailey and Benishay 1993). We doubt that concordance estimates from the sibling studies were seriously biased because the hypothesis of those studies was concealed from subjects.

The possibility of *asymmetric* concordance-dependent bias could more seriously affect the heritability estimates. This could happen if, for example, concordant MZ twins were relatively more likely to volunteer than concordant DZ twins or adopted siblings. This possibility cannot be completely ruled out; however, the degree of volunteer asymmetry would have to be large to result in a true zero difference in concordance rates between MZ and DZ pairs.

Heritability calculations assume that MZ twins, DZ twins, and adopted siblings share environments that are not systematically different—in this case, not different on variables salient to sexual orientation. At first thought, it must seem that MZ twins are so alike that their family and friends could not help but treat them almost as one individual. Perhaps so, but studies suggest that a violation of the equal-environments assumption does not seem to have much effect. Twins whose parents make a deliberate effort to differentiate them (different clothing, names, schools, etc.) turn out to be as similar on a variety of personality traits as twins treated alike. Furthermore, MZ twins mistakenly thought by their family to be DZ twins are as similar as if they were correctly labeled (Plomin et al. 1990). However, it may be that we simply do not know the relevant environmental precursors of sexual orientation and so cannot judge the extent to which siblings share them.

Twin concordance estimates are affected by the way twins are selected. An estimate of true or pairwise concordance can be obtained only by diagnosing an entire cohort of twins unselected for the trait in question, for example, all the twins born in Boston in a given year or all the twins in an available twin registry. Hundreds of pairs may have to be screened to obtain a stable estimate of concordance for an infrequent trait. It is much easier just to advertise for twin probands expressing the trait of interest. This proband-wise concordance will always produce an overestimate of true (pairwise) concordance simply because there are more concordant individuals eligible to respond. Figure 1 provides a hypothetical illustration of this relationship.

Despite the overestimate, proband-wise concordance is preferable for two reasons. First, the degree to which one study's pairwise concordance approximates the true population pairwise rate is a function of the probability of ascertainment π . When π is low, concordant pairs will be nearly twice as likely to be ascertained as discordant pairs, and so the pairwise rate will be inflated. (If all pairs were ascertained, one could obviously get the true pairwise rate.) In contrast, proband-wise concordance is not dependent on π . Pairwise concordance is the probability that a pair with homosexuality will be concordant. Proband-wise concordance is the probability that a homosexual twin will have a homosexual cotwin. If two twins from a concordant pair are *independently* ascertained (i.e., not by ascertaining one and then contacting the other to get him into the study), then both are probands and the pair will figure twice in the proband-wise concordance. There is nothing illegitimate about this.

The second advantage of proband-wise concordance is that it, but not pairwise concordance, is directly comparable to recurrence rates obtained for other relative groups. So, for example, a family study computing the probability that a gay man will have a gay brother should be compared to proband-wise rates. It *is* in fact a proband-wise rate if it is in theory possible for two brothers to be independently ascertained and considered probands (Smith 1974).

P ₁	⊗	⊗	O
P ₂	⊗	⊗	O
P ₃	⊗	⊗	O
P ₄	⊗*	⊗	O
P ₅	⊗	⊗	O
P ₆	⊗*	⊗	O
P ₇	⊗	⊗	⊗*
P ₈	⊗	⊗	⊗*
P ₉	⊗	⊗	⊗
P ₁₀	⊗*	⊗	⊗
P ₁₁	⊗	⊗	⊗
P ₁₂	⊗*	⊗	⊗

Figure 1. Proband-wise recruitment overrepresents concordant twin pairs: hypothetical example. Each row, P₁, . . . , P₁₂, represents twin pairs. ⊗ = twin with trait; O = twin without trait. Pairwise concordance is 50%. ⊗* indicates subjects randomly recruited from the eligible subject pool. In this example a random one-third of the 18 eligible subjects volunteered. Pairs P₄ and P₆ are discordant; pairs P₇, P₈, P₁₀, and P₁₂ are concordant. The proband-wise concordance is 67%.

For clarity of exposition the discussion to this point has tacitly assumed a simple causal model for sexual orientation, an assumption that is almost certainly incorrect. It seems likely, for example, that the orientation of women and men may be differently determined. As already noted, women and men experience sexual attraction in different ways; women are more often bisexual than men, there seems to be less familiarity between than within the sexes, and the X-chromosome linkage site reported for men has not been replicated for women (Hu et al. 1995). Extrapolating from what is known about the genetics of other traits, one can see that there may be dozens or even hundreds of alleles relevant to sexual orientation. Some alleles may be quite rare, and some may interact with the environment in complex and unexpected ways. The physical and functional identification of genes for sexual orientation is still a distant goal.

Evolutionary Significance

Many human traits are thought to have a genetic component because they run in families and because twin and adoptee concordance rates are

compatible with the known principles of genetic transmission. Such traits include the shyness-extroversion axis, certain cognitive abilities, aggressiveness, manic-depressive illness, Tourette's syndrome, specific language disorders, self-esteem, some mental disorders, and some social attitudes [summarized by Plomin et al. (1994)]. A few of these traits (e.g., spatial ability) are thought to have animal analogs. However, for none of the named traits has a specific gene (or genes) been found. The pathway from gene to behavior is unknown. Environmental sources of variance, substantial in our studies, may include the biological environment, for example, prenatal hormone exposure, the psychosocial environment, or some combination of the two. The interplay between genetic predisposition and environmental releasers or suppressors of a trait is presumably complicated, and at present, nothing is known with respect to sexual orientation.

The special problems posed by the evolution of traits that reduce fecundity have interested biologists since Darwin. If an individual possesses a gene that reduces his or her reproductive ability even slightly, that trait will be negatively selected, although it may reappear in other kindreds by means of a new mutation. But, as noted 25 years ago by Moran (1972), the frequency of homosexual orientation is too great by orders of magnitude to make plausible that it is replenished by random mutations.

The selective disadvantage of homosexuality must be very large in modern society. Bell et al. (1981), in their San Francisco survey, found that homosexuals have only one-fifth as many children as heterosexuals. Lesbians and gay men without children are a common feature of the urban milieu and give rise to the further paradox that social tolerance toward gays is the very condition that should promote the negative selection of "gay genes" (Hamer and Copeland 1994). In societies remote from Western influence, lesbians and gay men may more often marry and have children, but some probably adopt nonreproductive roles as celibates, priests, and so forth. In these societies the reproductive loss would be diminished but still present. If a genetic predisposition for a homosexual orientation exists, what advantage could it confer to pay the cost of lost reproduction to the individual?

Three sorts of answers are usually given to this question. One proposes a reproductive advantage to the heterozygote. Fisher (1922) pointed out that if alleles persist for a condition that is reproductively deleterious in the homozygote, there must be a selective advantage for the heterozygote. This issue has been developed by Weinrich and others (Weinrich 1987; Kirsch and Weinrich 1991; MacIntyre and Estep 1993). The hypothetical advantage to the heterozygote need not have anything to do with sexual attraction. It could involve genes with other attributes: conferring resistance to an endemic disease, promoting a larger sibship (thereby offsetting the reproductive loss sustained by the phenotypically gay individual), or coding for personality traits or patterns of cognitive abilities that, for example, help their possessor to hunt the leopard or harvest the yams. It seems likely that the selecting environment

“sees” other associated traits, and sexual desire or behavior is carried along as an exaptation.

A second possibility to account for the persistence of “gay genes” is that they prompt their possessor to undertake acts of altruism toward kin such that kin survival more than offsets the reproductive loss (in genetic terms) to the altruist. (Altruism is defined as an act that benefits another at a cost to the altruist.) Examples of kin altruism are reported for animal species and clearly are evolved behaviors (Packer et al. 1991; Trivers 1971). There is some evidence, both anecdotal and systematic, that gay persons behave more altruistically (Salais and Fischer 1995), but whether this is the behavior that maintains the genotype is of course anyone’s guess.

A third possibility for persistence of homosexual-inducing alleles comes from the finding of a putative linkage site on the X chromosome (Hamer et al. 1993; Hu et al. 1995). A gene conferring reproductive advantage to females (e.g., by making them more beautiful, more desirable as mates) could persist, although it is detrimental to males. Women have two X chromosomes, whereas men have only one, so a fairly small genetic advantage to a female could offset the cost to the male. We reiterate that the three mechanisms are simply speculations, arguments on the general question of the persistence of a phenotype that reduces fecundity. There is no evidence that any one of these mechanisms operates to maintain “gay genes” in a balanced polymorphism in human populations.

A limitation of the family and twin studies is that they can give no clue about where the putative “gay genes” are or what they do. Specific gene-finding techniques are needed to address this issue. Should such genes be found, one question that begs for an answer is the transcultural nature of homosexuality. Herdt (1994) and others have described “third gender” members in various societies—shamans, priests, berdaches, hijras, celibates, etc. Some of these individuals are described as having cross-gender attributes and homosexual behaviors possibly analogous to gay and lesbian behavior in Western societies. One hypothesis is that there is a “gay genotype” of ancient origin, now widely dispersed in human societies, the phenotypic expression of which takes the many forms of third genderness described by social scientists.

Research on the presumed selective advantage of a gay genotype will be difficult to implement, first, because the environment that selected it, presumably over generations of prehistoric time, may be different from the one in which it now exists. Second, the selective advantage need be very small, only a percentage point or two, to balance the lost fertility of the individual gay or bisexual family member. These small effects are often buried in noise. Despite these formidable challenges to research on the genetics of sexual orientation, we believe that this topic has much to contribute to a more complete understanding of human nature.

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