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Genetic factors predisposing to homosexuality may increase mating success in heterosexuals☆

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Abstract

There is considerable evidence that human sexual orientation is genetically influenced, so it is not known how homosexuality, which tends to lower reproductive success, is maintained in the population at a relatively high frequency. One hypothesis proposes that while genes predisposing to homosexuality reduce homosexuals' reproductive success, they may confer some advantage in heterosexuals who carry them. However, it is not clear what such an advantage may be. To investigate this, we examine a data set where a large community-based twin sample (N=4904) anonymously completed a detailed questionnaire examining sexual behaviors and attitudes. We show that psychologically masculine females and feminine men are (a) more likely to be nonheterosexual but (b), when heterosexual, have more opposite-sex sexual partners. With statistical modelling of the twin data, we show that both these relationships are partly due to pleiotropic genetic influences common to each trait. We also find a trend for heterosexuals with a nonheterosexual twin to have more opposite-sex partners than do heterosexual twin pairs. Taken together, these results suggest that genes predisposing to homosexuality may confer a mating advantage in heterosexuals, which could help explain the evolution and maintenance of homosexuality in the population.

Keywords: Homosexuality; Sexual orientation; Genetic; Environmental; Mating success; Evolution; Antagonistic pleiotropy; Darwinian paradox; Heritability; Gender identity; Masculinity; Femininity

1. Introduction

Estimates of the prevalence of homosexuality in modern Western populations vary greatly depending on how it is defined and measured and on how the samples are ascertained, but are generally in the approximate range of 1–10% and are usually lower for females than for males (Grulich, de Visser, Smith, Rissel, & Richters, 2003; Johnson, Wadsworth, Wellings, Bradshaw, & Field, 1992; Michael, Gagnon, Laumann, & Kolata, 1995). Research suggests that sexual orientation is influenced, in part, by genetic factors. Homosexuality tends to run in families (Bailey & Bell, 1993; Pattatucci & Hamer, 1995); in particular, identical [monozygotic (MZ)] twins, who share all of their genes, are more likely to be concordant in their sexuality than are nonidentical [dizygotic (DZ)] twins, who only share, on average, half of their genes (Kendler, Thornton, Gilman, & Kessler, 2000; Kirk, Bailey, Dunne, & Martin, 2000).

In contemporary Western societies, homosexual individuals tend to have fewer children than heterosexual individuals (Bell & Weinberg, 1978; Bell, Weinberg, & Hammersmith, 1981; Pattatucci & Hamer, 1995; Van de Ven, Rodden, Crawford, & Kippax, 1997), and lowered reproductive fitness in homosexuals may have been the case in ancestral times as well (Pillard & Bailey, 1998). How, then, has homosexuality evolved, and how is it maintained in the population at a relatively high frequency? Numerous

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theoretical explanations have been proposed for this "Darwinian paradox," many of which are critically reviewed in Rahman and Wilson (2003). Most of these theories are based on the idea that relatives of homosexuals are somehow at a reproductive advantage and thereby pass on their genes and balance the fitness cost of the homosexual phenotype. Indeed, recent evidence suggests that homosexual men, compared to heterosexual men, tend to come from larger families (Camperio-Ciani, Corna, & Capiluppi, 2004; King et al., 2005), which has been interpreted as greater fecundity in relatives of homosexual men. However, it could also be a corollary of the frequently observed "birth-order effect," where males with a greater number of *older* brothers (Camperio-Ciani et al., 2004; Cantor, Blanchard, Paterson, & Bogaert, 2002) and sisters (Bogaert, 1998; King et al., 2005) are more likely to be homosexual; if homosexual men tend to be higher in birth order, it follows that they will tend to come from larger sibships and—if fecundity runs in families—from larger extended families as well.

If relatives of homosexuals *are* at a reproductive advantage, why might this be? The most frequently cited explanation is the kin selection or kin altruism model, where it is proposed that homosexuals provided resources and child care to family members. In doing this, homosexuals could have increased the reproductive fitness of their family members and hence increased their inclusive fitness, even while not having their own children. Although theoretically possible, this theory is generally not supported by empirical evidence (Bobrow & Bailey, 2001; Rahman & Hull, 2005).

A less discussed hypothesis is that genes predisposing to homosexuality are advantageous in heterosexuals who carry them. In this hypothesis, the genes should have the same effect on heterosexuals and homosexuals, and there should be a corresponding trait that is associated with homosexuality but confers some selective advantage in heterosexuals. The traits most reliably associated with homosexuality relate to masculinity–femininity; homosexual men tend to be more feminine than heterosexual men, and homosexual women tend to more masculine than heterosexual women. Could this sex atypicality be advantageous when expressed in heterosexuals? Although perhaps counterintuitive, there is evidence that females are more attracted to males with certain feminine behavioral traits such as tenderness, considerateness, and kindness (Buss & Barnes, 1986; Howard, Blumstein, & Schwartz, 1987). They also prefer men with feminized faces (Boothroyd, Jones, Burt, & Perret, 2007; Penton-Voak et al., 1999; Perrett et al., 1998; Rhodes, Hickford, & Jeffery, 2000), although the preferred degree of feminization differs across the menstrual cycle and between short-term and long-term mating goals (Penton-Voak et al., 1999). There has been less research on what masculine traits in females may be attractive to men, but it should be noted that masculine traits such as competitiveness (Deaner, 2006) and unrestricted sociosexuality (Ostovich & Sabini, 2004) (willingness to engage in uncommitted sexual relations; Simpson & Gangestad, 1991) could contribute to a mating advantage. Indeed, psychologically more masculine women have a greater number of opposite-sex sexual partners in their lifetime (Mikach & Bailey, 1999).

Our hypothesis is that a number of pleiotropic (more than one effect) genes predispose to homosexuality but also contribute to reproductive fitness in heterosexuals. In the case of males, there are a number of alleles that promote femininity; if only a few of these alleles are inherited, reproductive success is enhanced via increased levels of attractive but typically feminine traits such as kindness, sensitivity, empathy, and tenderness. However, if a large number of alleles are inherited, even the feminine characteristic of attraction to males is produced. In females, the converse explanation could be used—a low gene dose could lead to advantageous typically masculine characteristics such as sexual assertiveness or competitiveness, and a large dose could further lead to attraction to females. This hypothesis was proposed in detail by Miller (2000), but it has not been tested. Here we empirically test the hypothesis using questionnaire responses from a large (N=4904) community-based twin sample. Before doing so, though, we need to clarify how we conceptualize the major variables involved: sexual orientation, gender identity, and mating success.

1.1. Sexual orientation

Previous taxometric analyses of our data suggest that a dichotomous factor underlies the full range of sexual orientations in men and women, and that a much higher percentage (up to 15% for men and 10% for women) belong to the taxa associated with homosexuality than actually consider themselves homosexual (Gangestad, Bailey, & Martin, 2000). For the purposes of the following analyses, we operationally define those with any degree of sexual attraction to the same sex (using the 7-point Kinsey attraction scale) as nonheterosexuals, and the associated trait as nonheterosexuality. This gives us a rate of 11% for men and 13% for women, comparable with the taxa percentages given above. Note that we use sexual attraction as the indicator, rather than sexual behavior or sexual identity, because we believe that it is less affected by mate availability and social/cultural constraints and is, in this sense, more fundamental (Sell, Wells, & Wypij, 1995).

1.2. (Continuous) gender identity

We use the term "gender identity" to refer to masculine–feminine self-concept. Our conceptualization and scale imply that this trait is continuous (from no identification with the other sex to strong identification with it), whereas others often treat it as a dichotomous trait. Gender identity is not well understood (Bailey, 2003). Early approaches to identifying basic dimensions of personality were based on factor analyses of pools of personality adjectives, from which descriptors that differed between sexes were excluded (Schmitt & Buss, 2000). Presumably as a result, aspects of gender, including gender identity, have been relatively ignored in the personality literature. The most common