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New Evidence of Genetic Factors Influencing Sexual Orientation in Men: Female Fecundity Increase in the Maternal Line

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Abstract There is a long-standing debate on the role of genetic factors influencing homosexuality because the presence of these factors contradicts the Darwinian prediction according to which natural selection should progressively eliminate the factors that reduce individual fecundity and fitness. Recently, however, Camperio Ciani, Corna, and Capiluppi (Proceedings of the Royal Society of London, Series B: Biological Sciences, 271, 2217–2221, 2004), comparing the family trees of homosexuals with heterosexuals, reported a significant increase in fecundity in the females related to the homosexual probands from the maternal line but not in those related from the paternal one. This suggested that genetic factors that are partly linked to the X-chromosome and that influence homosexual orientation in males are not selected against because they increase fecundity in female carriers, thus offering a solution to the Darwinian paradox and an explanation of why natural selection does not progressively eliminate homosexuals. Since then, new data have emerged suggesting not only an increase in maternal fecundity but also larger paternal family sizes for homosexuals. These results are partly conflicting and indicate the need for a replication on a wider sample with a larger geographic distribution. This study examined the family trees of 250 male probands, of which 152 were homosexuals. The results confirmed the study of Camperio Ciani et al. (2004). We observed a significant fecundity increase even in primiparous mothers, which was not evident in the previous study. No evidence of increased paternal fecundity was found; thus, our data confirmed a sexually antagonistic inheritance partly linked to the X-chromosome that promotes fecundity in females and a homosexual sexual orientation in males.

Keywords Male homosexuality · Fecundity · Evolution · Sexually antagonistic genetic model · Birth order

Introduction

At present, various research avenues suggest the presence of genetic factors as partly associated with male homosexuality. One line of evidence comes from the familiality of homosexuality. Family studies of biological brothers, adoptive brothers, and monozygotic twins have found that homosexuality is more common in brothers of homosexual probands (Bailey & Pillard, 1991). Hamer, Hu, Magnuson, Hu, and Pattatucci (1993) studying homosexual brothers with DNA linkage analysis found an increased rate of homosexuality in the maternal line. Hamer et al. (1993) hypothesized a putative genetic factor located on the long arm of the X-chromosome in the q28 region (Hu et al., 1995). This finding has been difficult to replicate, but new genetic findings have been suggested (Bailey et al., 1999; DuPree, Mustanski, Bocklandt, Nievergelt, & Hamer, 2004; Rice, Anderson, Risch, & Ebers, 1999).

A second independent avenue of research, not incompatible with genetic hypotheses, comes from studies that suggest a role of maternal immune reactions when the fetus is male. This hypothesis suggests that the immune system of the mother could activate an immune reaction against the H-Y antigen produced by the male fetus at an early stage during pregnancies, acting against a male differentiation of the brain. This response would increase in the mother with every subsequent pregnancy with a male fetus. Thus, the immunological conflict between mother and male offspring increases the probability of developing a homosexual orientation in later-born boys with older brothers (Blanchard & Klassen, 1997). This happens only in biological brothers, confirming prenatal causes rather than postnatal ones (Bogaert, 2006).

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In the evolutionary literature, there is a long debate on the role of genetic factors influencing homosexuality, because the presence of these factors contradicts the Darwinian prediction that natural selection should progressively eliminate the factors that reduce individual fecundity and fitness, and there is unanimous agreement that homosexuals reproduce significantly less than heterosexuals (Bell & Weinberg, 1978; Moran, 1972). This Darwinian paradox has been the central theme of several studies. An intriguing hypothesis suggests that male-male bonds might help survival in social-living non-human primates (Vasey, 1995), but this has never been shown in humans.

Wilson (1975), in an effort to solve the Darwinian paradox, suggested a hypothesis based on kin selection. He suggested that homosexuals would have an adaptive role as helpers in their families, through affectionate or economic means or both, promoting the fitness in their close kin, and thus balancing their own direct fitness loss. Recently, however, various researchers have failed to confirm the kin selection hypothesis. In fact, they found that homosexuals do not contribute in presence or in economic and affective terms more than heterosexuals (Bobrow & Bailey, 2001; Muscarella, 2000; Rahman & Hull, 2005; Vasey, Pocock, & VanderLaan, 2007).

Lastly, in a recent study, Camperio Ciani, Corna, and Capiluppi (2004) found that ascending females in the maternal line of homosexual probands were significantly more fecund (they produced approximately 33% more offspring) than females in the maternal line of heterosexuals. (The term "ascending females" is used here to denote females born in generations before the subject's generation). Camperio Ciani et al. (2004) could not find significant differences, however, when comparing ascending females from the paternal line. This effect applied both to homosexuals and bisexuals in the same way (Camperio Ciani, Iemmola, & Blecher, 2008). The results of this research strongly confirm the existence of biological factors previously suggested to partly explain male homosexuality. These results, if confirmed, would provide the final solution to the Darwinian paradox by showing that there are reproductive advantages that balance the fitness loss of male homosexuals. The idea is a sexually antagonistic genetic model that promotes fecundity in females and homosexual orientation in males.

The first indirect confirmations are coming. An interesting study confirmed that homosexual families are significantly larger, compared with those of heterosexuals, but this applies only in white families and not black families (Q. Rahman, personal communication, 2006; Rahman et al., 2008). King et al. (2005) showed that homosexuals have larger families compared with heterosexuals irrespective of the paternal line and maternal line. The fecundity increase of homosexual's mothers is further confirmed in a non-Western society (Vasey & VanderLaan 2007). Furthermore, a number of studies have found that homosexuals have more older brothers than heterosexuals (Blanchard, 2004; Blanchard & Klassen, 1997).

As suggested by the results of Blanchard and Lippa (2007), the study by Camperio Ciani et al. (2004) needs replication on a wider sample with a larger geographic distribution to find if the higher fecundity in homosexual's female relatives really exists and if it is unique to the maternal line, or is found in both lines, as hypothesized by King et al. (2005).

Method

Participants

We recruited 250 probands, according to the following inclusion criteria: male sex, age over 18 years, and not adopted. In this study, we used the same sampling method and the same questionnaires and data analysis as in the previous study by Camperio Ciani et al. (2004). There were 98 heterosexual probands and 152 homosexual probands.

Participants were recruited in the following locations: of the 152 homosexual probands, 40 were recruited at beaches and seaside resorts, 25 among working hotel employees and vacationers, 39 in bars and night clubs, 28 in gay clubs, 15 at university institutes, and 5 in gyms; of the 98 heterosexual participants, 20 were recruited in beaches and seaside resorts, 15 among working hotel employees and vacationers, 11 in bars and night clubs, 25 in football clubs, 25 at university institutes, and 2 in gyms. Since many participants were recruited in holiday locations, the participants came from all over Italy, although with a majority from Northern Italy.

All social and demographic variables in the two groups had very similar values: the minimum age was 18 and maximum age was 63 years old for both groups. The 98 heterosexual probands had an average age of 32.51 years (SD = 8.85), and the 152 homosexual probands had an average age of 32.34 years (SD = 9.56).

Homosexuals were more frequently not married (90%) compared with heterosexuals (58%). Most participants from both groups came from central north Italy: Veneto (44%), Toscana (13%), Lombardia (10%), and Liguria (9%). The most common academic degree was high school (heterosexuals, 62%; homosexuals, 56%), followed by college (heterosexuals, 23%; homosexuals, 32%). Most participants in both groups were either students or employed workers.

Procedure

Considering the locations of recruitment and in order to reduce the probability of refusal, in beaches and seaside resorts, in bars and night clubs, university, and gyms, the approach was generally made towards participants caught in moments of temporary inactivity and relaxation.

Once the availability of the participant was confirmed, the questionnaire and a pen were personally handed over with the instruction to complete every part of it within approximately ten minutes (time estimated to be sufficient for its completion), at the end of which the questionnaire was collected. The same procedure was used for participants contacted in clubs or recruited at work (employees, etc.). Responses from probands were considered reliable for the following reasons. Questions were identical to the previous study by Camperio Ciani et al. (2004), which was validated through a pre-test. All questions were simple, only regarding close relatives (parents, grandparents, number of brothers, sisters, uncles, aunts, and cousins) and questions were again tested for their intelligibility through a pre-test in the present study. To further increase comprehension, researchers explained personally all the details of the questionnaire and were always present nearby ready to clarify any doubt.

Measure

The investigation tool used was the self-administrated questionnaire. This included a cover letter with general information on the purposes of the research and a brief presentation of the following sections of the questionnaire. There were three sections:

1. Biographical information (seven questions): age, region of birth, region of actual domicile, highest academic degree, profession, marital status, and birth order.
2. The Kinsey scale (Kinsey, Pomeroy, & Martin, 1948), to record the self-identification of the proband on a 7-point scale (0 = exclusively heterosexual to 6 = exclusively homosexual), and all four other classic sexual orientation questions on a 7-point scale, included in the Kinsey questionnaire (Table 1).
3. In the last section, we investigated fecundity as number of live-born offspring ever produced. There were five questions that investigated quantitatively the number and fecundity of the maternal and paternal relatives of the proband as parents, grandparents, uncles, aunts, brothers, sisters, and cousins. Half of the probands were asked information first about the maternal line and the other half were asked first about paternal lineage, in order to avoid sequential systematic errors.

Classification of Probands

Each proband answered each of four questionnaire items about their sexual orientation by endorsing one of seven ordered response options (maximally heterosexual to maximally homosexual) modelled on the Kinsey scale (Kinsey et al., 1948). Each proband was rated according to the score obtained by averaging his responses to these four items. Sexual orientation is a continuum; however, for our research purposes we had to classify probands into two classes, homosexuals and heterosexuals. We defined as heterosexuals all those probands with average Kinsey scores between 0 and 1. We defined as homosexuals all those probands with average Kinsey scores between 2 and 6 (in this study, we did not differentiate between possible bisexuals and exclusive homosexual). These two classes were then subject to statistical analysis. After determining that the two groups did not differ on any social or demographic variable, we then calculated the average fecundity of all classes of relatives included in three ascending generations for each proband.

Table 1 Kinsey scale definitions and related key questions

0 Completely heterosexual							
1 Predominantly heterosexual but occasionally (rarely) attracted to other men							
2 Heterosexual but also attracted by men more than occasionally							
3 Completely bisexual, interested both in men and women							
4 Homosexual but also attracted by women more than occasionally							
5 Predominantly homosexual but occasionally (rarely) attracted to women							
6 Completely homosexual							
(1) How would you define yourself according to the Kinsey scale, shown above	0	1	2	3	4	5	6
Answer the following questions by choosing a score between 0 and 6 where 0 is "always and only women" and 6 is "always and only men"							
(2) If, at a party, you were to desire a sexual relationship, which sex of partner would you choose?	0	1	2	3	4	5	6
(3) When you fantasize sexual intercourse, what is the sex of your partner?	0	1	2	3	4	5	6
(4) In the last year, what was the sex of your sexual partners?	0	1	2	3	4	5	6
(5) In the last five years of your life, what was the sex of your sexual partners?	0	1	2	3	4	5	6

Results

Fecundity

When we compared fecundity between the heterosexual and homosexual probands, a significant difference appeared. The heterosexuals had an average of 0.58 children (SD = 0.91) and the homosexuals had an average of 0.12 children (SD = 0.49), $p < .01$, Mann–Whitney test.

Table 2 presents the results of this study. It shows that the increase of fecundity in the maternal line of the homosexual males was confirmed. The p-values reported in this table were computed with the Mann–Whitney test, in order to make the present results directly comparable to those of Camperio Ciani et al. (2004). Our data showed that the fecundity of mothers, including firstborn mothers, maternal aunts, and also the cumulated fecundity (of mothers, aunts and uncles in the maternal line) was significantly greater than that found for the corresponding maternal heterosexual classes. The fecundity of the father was excluded from the paternal line because it overlaps with that of the mother. This protocol replicates the previous one where Camperio Ciani et al. (2004) were searching for possible fecundity effects of the X-chromosome. In sons, this chromosome is transmitted by the mother and not by the father. The difference in fecundity in maternal grandparents in this study was marginally significant ($p = .09$). Most importantly, the significant fecundity increase was found again only in the maternal line. All paternal line differences between homosexuals and heterosexuals were not significant, except for the fecundity of uncles, which was opposite in direction to the general trend, being lower in homosexuals than in heterosexuals, $p < .05$.

Birth Order

In this study, we once again confirmed an excess of older brothers compared with older sisters in the sibships of homosexual men [observed: 97 older brothers, 69 older sisters; expected (based on the known human sex ratio of 106 males for every 100 females born): 85.4 older brothers and 80.6 older sisters, $p < .04$, one-tailed binomial test].

Furthermore, the homosexuals had a significant greater number of older brothers (M = 0.64, SD = 0.85) compared with the heterosexuals (M = 0.27, SD = 0.55), $t(248) = 3.82$, $p < .001$, two-tailed. Mean numbers of older sisters, younger brothers, and younger sisters did not differ between the homosexuals and the heterosexuals.

Discussion

This study used a new, larger, and more representative sample. The probands had a nationwide distribution, and not a regional one like the previous study by Camperio Ciani et al. (2004). Furthermore, the probands were recruited in more diverse locations and situations, allowing a much larger variety of homosexuals to be recruited.

The results reconfirmed the thesis of genetic factors that, in terms of inclusive fitness, would produce a balance between the low direct fitness of male homosexuals and the increase of fitness in their maternal female relatives, as expected in a partially sexually antagonistic genetic model of inheritance.

Our data showed that the homosexuals had sired, at this stage of their reproductive lives, about one fifth of the offspring produced by the heterosexuals, thus confirming a strongly reduced fitness as previous described by Moran (1972) and Bell and Weinberg (1978). It should be noted this result was particularly significant because our heterosexual sample was especially low in fertility. One reason is that the heterosexuals were still young (although the homosexuals had the same average age). The second and most important reason is the constraint imposed by our sampling strategy. We needed to recruit the heterosexual controls in exactly the same manner as the homosexual probands; we never recruited homosexuals in family environments; therefore, we never recruited heterosexuals in family environments either. Thus, we oversampled not yet married heterosexuals.

Table 2 Maternal line and paternal line fecundity comparison between the two sexual orientation groups

Class of relatives	Likelihood of sharing X-chromosome	Homosexuals			Heterosexuals			p
		N	Average fecundity	SD	N	Average fecundity	SD	
Mothers	1	152	2.73	1.46	98	2.07	1.08	.001
Mothers of first borns	1	55	1.78	0.69	56	1.54	0.81	.02
Maternal aunts	0.75	121	1.96	1.06	62	1.43	0.98	.001
Maternal uncles	0.25	88	1.90	0.98	66	1.77	0.78	n.s.
Maternal grandparents	0.5	149	3.62	1.57	97	3.28	1.65	.09
Sons and daughters of maternal grandparents[a]	0.25–1	361	2.19	0.91	226	1.72	0.69	.001
Paternal aunts	0	96	1.86	0.93	59	1.74	1.06	n.s
Paternal uncles	0	85	1.75	1.20	49	2.00	0.93	.05
Paternal grandparents	0	146	3.16	1.52	95	2.85	1.25	n.s.
Sons and daughters of paternal grandparents (excluding father)[b]	0	181	1.78	0.85	108	1.84	0.84	n.s.

[a] Cumulated fecundity of mothers, maternal aunts, and maternal uncles

[b] Cumulated fecundity of paternal aunts and paternal uncles

In this study, a clear difference emerged in the average fecundity of the female relatives in the maternal line of homosexuals, a difference that was even more marked and significant than in the previous one. In particular, we found not only differences in mothers and maternal aunts, but also in the cumulated fecundity of maternal females and in the mothers of firstborns. These findings in Camperio Ciani et al. (2004) were not so clear.

These results confirm once again that fecundity was significantly higher only in the maternal line. This is somehow in conflict with the study of King et al. (2005), who found larger family size in homosexuals, irrespective of the paternal or maternal line. This requires some comment. The results of King et al. (2005) were based on a rather large sample; however, sampling procedures are particularly delicate and need special attention. We have discussed elsewhere the possibility that homosexuals might appear more frequently in large families, as a sampling artefact (Camperio Ciani et al., 2004). That is because the families included in sexual orientation studies derive from selected probands, in this case with the homosexual trait, and homosexuality is a relatively rare trait compared to heterosexuality. This might favor the overrepresentation of large families for the rarest trait population (homosexuals). This phenomenon is referred to as “small population sampling bias.” This bias is avoided by comparing groups who face equal obstacles in entering the study (Camperio Ciani et al., 2004; Spreen & Marius, 1992; Watters & Biernacki, 1989). However, this bias does not account for why the high fecundity was limited to the maternal line and not in the paternal one, as in our case.

In our study, the paternal relatives of homosexuals and heterosexuals showed no differences in fecundity with only one exception (the lower fecundity in the paternal uncles of the homosexual group), and that result was contrary to the findings of King et al. (2005). A possible reason why the pattern of results obtained by King et al. (2005) differs from that obtained by the present writers relates to how paternal and maternal family size was calculated in King et al. (2005). Furthermore, in our work we followed the protocol of tracking fecundity effects linked to the X-chromosome by limiting comparisons to classes of relatives who were homogeneous in their probability of sharing the X-chromosome with the proband. In contrast, King et al. (2005) compared classes of relatives of mixed sexes without distinguishing the X-chromosome provenance. As an example, King et al. (2005) included brothers and sisters both in paternal and maternal family sizes. These classes however, received the X-chromosome only from the maternal line and not from the paternal one. Hence, these classes should not be included in the paternal line, otherwise they might overestimate paternal contribution. Excluding family size, King et al. (2005) reported just a marginally higher number of paternal cousins of homosexuals compared with heterosexuals (M = 6.0, SD = 6.3 vs. M = 5.1, SD = 6.0) and a significantly higher number of paternal uncles and aunts of homosexuals (M = 3.0, SD = 2.3 vs. M = 2.6, SD = 2.3).

Neither of these results, which would falsify our hypothesis, was confirmed in our completed studies (Camperio Ciani et al., 2004; the present study) or in forthcoming studies (Camperio Ciani, Cermelli, & Zanzotto, 2008; Camperio Ciani, Iemmola, & Lombardi, 2008). Further studies will definitively clarify this crucial point, because our data support a sexually antagonistic hypothesis partly connected to the X-chromosome, whereas the data of King et al. (2005) suggest an over-dominance hypothesis, whereby autosomal factors that promote fecundity might result in promoting homosexuality if overrepresented (Gavrilets & Rice, 2006). Only testing the prediction of the two different genetic models against the empirical data collected to date will definitively resolve who gave the correct interpretation.

A higher fecundity in homosexuals’ mothers is also indirectly suggested by the immunological hypothesis of Blanchard, which predicts a higher number of older brothers in the sibships of homosexuals. Indirectly, because Blanchard never suggested it, but in an extremely low fecundity population such as the Italian one the fact of having at least an older brother is already an indication of having a larger family than average (Blanchard, 1997, 2004; Blanchard & Lippa, 2007). Blanchard’s predictions were also confirmed in our study: we found that the homosexuals had an excess of older brothers compared with their own number of older sisters and compared with the heterosexuals’ number of older brothers. The homosexual and heterosexual groups did not differ with regard to the other three classes of siblings.

Our study found something more, however, because Blanchard’s hypothesis predicts neither an increase of fecundity in maternal aunts of homosexual probands (who, by the way, only occasionally have homosexual sons; Camperio Ciani et al., 2004) nor an increased fecundity in mothers who have a homosexual son as their firstborn child (and who, by definition, can produce only younger brothers and younger sisters of the homosexual son). These facts can be explained only by the hypothesis of genetic factors transmitted in the maternal line (at least partly through the X-chromosome). These factors show different effects in their carriers: when present in a female, they would promote fecundity; when present in a male, they would influence sexual orientation toward homosexuality. However, homosexuality is not only influenced by these, yet unidentified, factors that promote fecundity in mothers and maternal aunts, but it is also definitely facilitated by the birth of older brothers, as found by Blanchard (1997, 2004).

Gavrilets and Rice (2006) analyzed a number of genetic models to understand the location of candidate genes promoting homosexuality. They compared single locus models based on sexually antagonistic selection, over-dominance, maternal effect, and genomic imprinting with a series of empirical researches (Blanchard, 2004; Camperio Ciani et al., 2004; King et al., 2005; Mustansky et al., 2005). The results showed that under the random mating assumption a few single locus models are virtually possible, but highly unstable. This means that with small variation of female or male fecundity, the genetic factors promoting male homosexuality can rapidly disappear or reach complete fixation in the population. Such results were reviewed by Savolainen and Lehmann (2007) and widely quoted in the press, which suggested that in the near future male bisexuality might rapidly grow in the population. We believe, on the contrary, that these single locus models are inadequate, and the instability they show is the consequence of this fact. Homosexuality has always been present in practically all human populations, under extremely variable fecundity and social conditions, always at relative low frequency. We do not see why it should just now explode or disappear. We hence believe that a multilocus model might be much more adequate to explain the transmission of male homosexuality, and our laboratory is working on this (Camperio Ciani et al., 2008).

In conclusion, if these results can be replicated elsewhere, perhaps in a non-Italian sample, this will suggest the existence of genetic factors transmitted through the maternal line that both increase the probability of becoming homosexual in males and promote fecundity in females (sexually antagonistic selection).

The genetic one is not, however, the only explanation for sexual orientation variety; other physiological and environmental effects contribute. As in most aspects of human nature, the behavioral phenotype of homosexual orientation should be the result of the interactions of innate factors and experience before and during the lifetime (Churchill, 1967; Enquist, Ghirlanda, Wachtmeister, & Lundqvist, 2002).

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