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Why are there more same-sex than opposite-sex dizygotic twins?

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STUDY QUESTION: Are there more same-sex (SS) than opposite-sex (OS) pairs among dizygotic twins?

SUMMARY ANSWER: In violation of Weinberg's Differential Rule, there are significantly more SS than OS pairs among dizygotic twins in nationally representative samples both in the UK and the USA.

WHAT IS KNOWN ALREADY: Since at least 1874, twin researchers have assumed that dizygotic twins were equally likely to be SS or OS (later formalized as Weinberg's Differential Rule). However, recent research on the sex-specific nature of breastmilk suggests that OS twins might be at a developmental disadvantage relative to SS twins. There may therefore be evolutionary selection for the tendency to have SS twins and against the tendency to have OS twins.

STUDY DESIGN, SIZE, DURATION: We analyze two population samples (not subject to Lykken's rule of two-thirds): the National Child Development Study in the UK ($n = 17\,419$) from 1958 to present, and the National Longitudinal Study of Adolescent Health in the USA ($n = 20\,745$) from 1994 to present.

PARTICIPANTS/MATERIALS, SETTING, METHODS: We performed a one-sample *t*-test of the proportion of SS dizygotic twins against the theoretical null value of 0.5022.

MAIN RESULTS AND THE ROLE OF CHANCE: The proportion of SS pairs among dizygotic twins was 0.6043 ($t(325) = 3.838$, $P = 0.00015$) in the UK and 0.5739 ($t(520) = 3.398$, $P = 0.00073$) in the USA.

LIMITATIONS, REASONS FOR CAUTION: Twin type (monozygotic versus dizygotic) was classified by the mother, not by DNA typing, although supplementary data suggest that misclassification was negligible and supplementary analysis shows that potential misclassifications do not change our main conclusions.

WIDER IMPLICATIONS OF THE FINDINGS: Weinberg's Differential Rule may be incorrect in its assumption of independence of sexes within dizygotic pairs, and there may be evolutionary selection for SS, and against OS, dizygotic pairs.

STUDY FUNDING/COMPETING INTERESTS: None.

Key words: sex-biased breastmilk / secondary sex ratio / Trivers–Willard hypothesis / inclusive fitness / genetic evolution

Introduction

Before modern genetic knowledge and technology, it was impossible to determine the zygosity of same-sex (SS) twins with certainty, and it was therefore difficult to estimate accurately the population incidence of monozygotic (MZ) and dizygotic (DZ) twins. It was in this context that the French statistician Jacques Bertillon (1874) first speculated that the number of DZ twins would equal twice the number of opposite-sex (OS) twins and that the remaining twins would be MZ. Weinberg (1901) later formalized Bertillon's idea and proposed what is now known as Weinberg's Differential Rule (WDR).

WDR is premised on two assumptions (Fellman, 2013): (i) the probability of conception of male and female fetuses is identical (= 0.5); and (ii) the sexes of DZ twins are determined independently; therefore, DZ twins would be equally likely to be SS as OS. Despite the fact that we now know that the secondary sex ratio (the ratio of boys to girls at birth) deviates slightly from 1.00 (it is instead 1.05, 105 boys for every 100 girls), and that some have questioned its validity

(James, 1979), WDR has been largely supported. For example, Fellman and Eriksson (2006) analyzed twin data from Sweden and Finland, and concluded that 'WDR is robust and, despite its simplicity, gives reliable results when large national birth registers are considered' (p. 254).

A couple of theoretical reasons cast doubt on the second assumption—the independent determination of sexes in DZ twins—and thus the validity of WDR itself. First, the Trivers–Willard hypothesis proposes that parental condition influences the secondary sex ratios, such that parents in good environmental and physiological condition are more likely to have sons while parents in poor environmental and physiological condition are more likely to have daughters (Trivers and Willard, 1973). Because twins share their parents and parental condition, they are more likely to be SS—either both male if the parental condition is good or both female if the parental condition is poor.

Second, recent research in developmental psychology and biology also questions the independent determination of sexes in DZ twin pairs. Several studies have shown that human and other mammalian breastmilk may be tailored for the sex of the offspring, such that mothers may produce breastmilk of different chemical composition for male and female newborns. For example, among humans, mothers both in Massachusetts, USA (Powe *et al.*, 2010) and in Singapore (Thakkar *et al.*, 2013) produced milk with greater energy, lipids, polyunsaturated fatty acids, phospholipids and gangliosides for sons than for daughters. In contrast, a study of Filipino mothers did not find a significant difference in fat, protein, sugars and energy between breastmilk for sons and daughters (Quinn, 2013). Consistent with the Trivers–Willard hypothesis (Trivers and Willard, 1973), economically sufficient mothers in northern Kenya produced milk with higher fat concentration for sons than for daughters, whereas relatively poor mothers produced milk with higher fat concentration for daughters than for sons (Fujita *et al.*, 2012).

If human mothers tailor the contents of their breastmilk for the offspring of each sex to facilitate their health and growth most efficiently, then it suggests that breastmilk might not be as closely tailored for OS twins as it is for SS twins. Whether they are male or female, SS twins can benefit from the sex-tailored breastmilk just as singletons can. In contrast, the breastmilk of the mothers of OS twins cannot specifically and simultaneously be tailored for both sexes; it must be either tailored for neither sex specifically or tailored for the wrong sex for half of the OS twins. OS twins may therefore be at a developmental disadvantage relative to SS twins. Consistent with this logic, Kanazawa and Segal (2017) found that, net of sex, age, birthweight and zygosity, breastfed SS twins were on average about 1 inch taller and 12 pounds heavier than breastfed OS twins throughout adolescence and early adulthood. In contrast, never-breastfed SS twins were no taller or heavier than never-breastfed OS twins, and they even tended to be slightly shorter and lighter.

If OS twins have been at a developmental disadvantage relative to SS twins over the course of human evolutionary history, then evolutionary logic suggests that there may have been selective forces for the tendency to produce SS twins and against the tendency to produce OS twins. If so, then, in violation of the second assumption of WDR, determination of the sexes in DZ twins may not be independent, and there may be more SS DZ twins than OS DZ twins.

As early as nearly half a century ago, James (1971) noticed, in a secondary analysis of eight published studies, that there were more SS DZ twins than OS DZ twins. James's original discovery, however, suffers from both theoretical and empirical difficulties. Theoretically, James's (1986) explanation for the excess of SS pairs among DZ twins was entirely proximate. He argued that the sex of the fetus was largely determined by the timing of conception during the menstrual cycle and the hormonal environment of the uterus at the time of conception. Since twins are (with presumably rare exceptions in the event of superfecundation or superfetation; see Segal, 2017) conceived at the same time, they share the timing of conception and the hormonal environment of the uterus, and are therefore more likely to be SS. If correct, this may answer the how question of proximate mechanisms in terms of endocrinology, but it does not answer the why question of ultimate evolutionary function.

Empirically, all of the studies reviewed by James (1971) to demonstrate the excess of SS DZ twins rely on volunteer samples of twins, who are specifically recruited to participate in the study because they are twins. Volunteer samples in twin research suffer from Lykken's 'rule of two-thirds' (Lykken *et al.*, 1978, 1987). Typically, about two-thirds of respondents in such volunteer twin samples are female, and about two-thirds are MZ. These twins are therefore unlikely to be representative of the entire population of twins, and estimates of the relative frequencies of SS and OS pairs among DZ twins are at the very least inefficient and possibly biased.

Fellman and Eriksson (2006) found support for WDR in their analysis of twin data from Sweden and Finland. The twin registry in Finland, which includes virtually all twins born in the country (Kaprio *et al.*, 2002), showed no excess of SS DZ twins; in the most recent data, the proportion of SS pairs among DZ twins in Finland was 0.4698 (Kaprio, personal communication). Due to the availability of comprehensive twin registries in Scandinavian and Nordic countries, a large proportion of twin studies are conducted there. To our knowledge, no test of WDR has been conducted outside of northern Europe since James' (1971) meta-analysis nearly half a century ago.

In this paper, we use two large population samples not subject to Lykken's rule of two-thirds—the National Child Development Study (NCDS) in the UK and the National Longitudinal Study of Adolescent Health (Add Health) in the USA—to estimate the relative frequencies of SS and OS pairs among DZ twins and to test the hypothesis that there are significantly more SS DZ twins than OS DZ twins. It is important to note that the twins in both studies were conceived naturally, prior to the introduction of IVF, which occurred in the UK in 1978 and in the USA in the early 1980s (Segal, 2017). IVF might have allowed parents to choose SS or OS twins for various reasons. It is also largely responsible for the recent rise in DZ twinning in western nations (Pison *et al.*, 2015).

Materials and Methods

National Child Development Study (UK)

Data and sampling

NCDS is a large ongoing prospectively longitudinal study that has followed a population of British respondents since birth for over half a century. The study included all babies ($n = 17\,419$) born in Great Britain (England, Wales and Scotland) during 1 week (03–09 March 1958). The respondents were subsequently reinterviewed in 1965 (Sweep 1 at age 7; $n = 15\,496$), 1969 (Sweep 2 at age 11; $n = 18\,285$), 1974 (Sweep 3 at age 16; $n = 14\,469$), 1981 (Sweep 4 at age 23; $n = 12\,537$), 1991 (Sweep 5 at age 33; $n = 11\,469$), 1999–2000 (Sweep 6 at age 41–42; $n = 11\,419$), 2004–2005 (Sweep 7 at age 46–47; $n = 9534$), 2008–2009 (Sweep 8 at age 50–51; $n = 9790$) and 2013 (Sweep 9 at age 55; $n = 9137$). All ages in this study are in calendar years. There were more respondents in Sweep 2 than in the original sample (Sweep 0) because Sweep 2 sample included eligible children who were in the country in 1969 but not in 1958. In each sweep, personal interviews and questionnaires were administered to the respondents, to their mothers, teachers and doctors during childhood, and to their partners and children in adulthood. Virtually all (97.8%) of the NCDS respondents were Caucasian.

MZ/DZ and SS/OS status

During Sweep 1, the mother of the respondent was asked whether the respondent was a twin, and, if so, whether he/she was MZ or DZ, and, if DZ, whether he/she was SS or OS. There were 326 individual DZ twins (158 female, 168 male), of whom 129 were OS (65 female, 64 male) and 197 were SS (93 female, 104 male). Note that, unlike most studies in twin research (Segal, 2012; Frazier *et al.*, 2014), our samples in both studies contained only one of the twins, not both.

In 2008, NCDS conducted a twin sub-study with 244 twin respondents and attempted to ascertain their zygosity by using the six 'peas in a pod' questions. Sample items were: 'In childhood, which of the following would best describe you and your twin? As alike as peas in a pod/of ordinary sibling likeness,' and 'At school, did teachers have trouble telling you apart?' The same questions were used by researchers in the well-known St. Thomas's Twin Research Unit Register. Past studies show that these questions can accurately classify the zygosity of twins with nearly 100% accuracy (Cederlöf *et al.*, 1961; Torgersen, 1979). NCDS classified 18.8% of twin respondents in the 2008 sub-study as MZ by these 'peas in a pod' questions, whereas 20.5% of the respondents self-reported as MZ. Thus, the extent of potential misclassification of twin zygosity by self-report appeared very small (1.7%).

Critical (null) value

WDR assumes that the probability of male conception is 0.5000, which implies the critical value—the proportion of SS pairs among DZ twins—of 0.5000: $P(BB) = 0.5000 \times 0.5000 = 0.2500$; $P(BG) = 0.5000 \times 0.5000 = 0.2500$; $P(GB) = 0.5000 \times 0.5000 = 0.2500$; $P(GG) = 0.5000 \times 0.5000 = 0.2500$; $P(\text{SS DZ}) = P(BB) + P(GG) = 0.2500 + 0.2500 = 0.5000$, where, B = boy, G = girl. However, we now know that the probability of male conception is 0.5122, which implies the critical value of 0.5002: $P(BB) = 0.5122 \times 0.5122 = 0.2623$; $P(BG) = 0.5122 \times 0.4878 = 0.2499$; $P(GB) = 0.4878 \times 0.5122 = 0.2499$; $P(GG) = 0.4878 \times 0.4878 = 0.2379$; $P(\text{SS DZ}) = P(BB) + P(GG) = 0.2623 + 0.2379 = 0.5002$. Using Swedish data, Fellman and Eriksson (2010) estimate the probability of male conception among all twins to be slightly lower at 0.5079. The critical value using their estimate, however, turns out to be exactly the same: $P(BB) = 0.5079 \times 0.5079 = 0.2580$; $P(BG) = 0.5079 \times 0.4921 = 0.2499$; $P(GB) = 0.4921 \times 0.5079 = 0.2499$; $P(GG) = 0.4921 \times 0.4921 = 0.2422$; $P(\text{SS DZ}) = P(BB) + P(GG) = 0.2580 + 0.2422 = 0.5002$. We therefore used the critical value of 0.5002 in our one-sample *t*-tests with both samples.

Add Health (USA)

Data and sampling

Add Health is a large on-going, nationally representative, and prospectively longitudinal study of young Americans. A sample of 20 745 adolescents was personally interviewed in their homes in 1994–1995 (Wave I; mean age = 15.6 years). They were again interviewed in 1996 (Wave II; $n = 14\,738$; mean age = 16.2 years), 2001–2002 (Wave III; $n = 15\,197$; mean age = 22.0 years) and 2007–2008 (Wave IV; $n = 15\,701$; mean age = 29.1 years). Additional details of sampling and study design are provided at http://www.cpc.unc.edu/projects/addhealth/design.

MZ/DZ and SS/OS status

Add Health assessed the zygosity of each twin during Wave I by asking the mother, 'In your opinion, are _____ and _____ identical twins or fraternal twins?' The mother could respond as follows: 1 = definitely identical, 2 = probably identical, 3 = probably fraternal or 4 = definitely fraternal. We collapsed 'definitely' and 'probably' and created a binary measure of zygosity. There were 521 individual DZ twins (270 female, 251 male), of whom 222 were OS (112 female, 110 male) and 299 were SS (158 female, 141 male). Add Health conducted DNA analysis at Wave III and discovered that only 9% ($n = 34$) of the twins' zygosity was misclassified by mothers' self-report at Wave I (Harris *et al.*, 2006, p. 992).

Statistical analysis

We performed one-sample *t*-tests, with the critical value of 0.5002, with both samples, using SPSS 23 (IBM, NY, USA). We adopted the conventional level of statistical significance ($\alpha = 0.05$).

Results

National Child Development Study (UK)

The proportion of SS pairs among DZ twins in the UK was 0.6043, which was significantly higher than the critical value of 0.5002 ($t(325) = 3.838$, $P = 0.00015$). Fellman (2013) and Fellman and Eriksson (2006) suggest that the variances of MZ and DZ twinning rates might be larger than previously assumed, at least by a factor of 2, and thus that it might be necessary to multiply the standard deviation of MZ and DZ twinning rates by at least $\sqrt{2}$. Applying the 'Fellman correction' yields $t(325) = 2.714$, $P = 0.00701$.

Add Health (USA)

The proportion of SS pairs among DZ twins in the USA was 0.5739, which was significantly higher than the critical value of 0.5002 ($t(520) = 3.398$, $P = 0.00073$). Applying the Fellman correction yields $t(520) = 2.403$, $P = 0.01660$.

Discussion

The proportion of SS pairs among DZ twins was significantly higher than expected by chance in both NCDS in the UK and Add Health in the USA. These findings are consistent with our prediction that there are more SS than OS twins because OS twins are at a developmental disadvantage relative to SS twins, and there may be selection for the tendency to produce SS twins and against the tendency to produce OS twins. We hasten to add, however, that, while our empirical results are consistent with our evolutionary hypotheses, they do not provide direct evidence of the evolutionary selection that we posit. There may potentially be other mechanisms that produce a preponderance of SS pairs among DZ twins.

Further consistent with the evolutionary selection mechanism based on the Trivers–Willard hypothesis (Trivers and Willard, 1973), the analysis of the Add Health data showed that, in a sample of SS twins ($n = 511$), controlling for zygosity, mother's education (as an indicator of social class) significantly predicted the sex of the twin ($b = 0.110$, $P = 0.011$). Mothers with more education were significantly more likely to have male SS twins and mothers with less education were significantly more likely to have female SS twins. The same pattern was not evident in the NCDS data, however. The greater social welfare system in the UK compared to in the USA might account for the national difference and why social class has a smaller impact on the offspring sex in the UK. There is a greater degree of income transfer from the wealthy to the poor, and thus the class differences by education are less pronounced, in the UK than in the USA.

A potential limitation of our data is that zygosity was assessed by the respondent's mother, which is not always accurate (Segal, 2011). If many MZ twins, who are always SS, are misclassified as DZ, then it would artificially inflate the proportion of SS pairs among DZ twins, as the proportion of OS pairs is always accurate because they cannot be misclassified as MZ. However, both the DNA analysis and questionnaire data showed a very small departure from mothers' reports, increasing our confidence in the findings. Further, our calculations (Supplementary Data) show that our conclusion that there are more SS than OS pairs among DZ twins is extremely robust under a wide range of possible misclassifications of twins by zygosity.

Our results are inconsistent with earlier studies by Fellman and Eriksson (2006) and Kaprio *et al.* (2002). It is not immediately obvious what accounts for the divergent empirical findings. As noted above, their data come from Scandinavian and Nordic nations whereas ours come from Anglo-Saxon nations. Genetic and/or environmental differences between these nations might potentially account for the divergent findings. More research is necessary to explore and replicate the relative frequencies of SS and OS pairs among DZ twins with different samples.

The Trivers–Willard hypothesis has been supported in numerous species, such as the Venezuelan opossum (Austad and Sunquist, 1986), red deer (Clutton-Brock *et al.*, 1986) and spider monkey (Symington, 1987), and mothers' breastmilk appears to be tailored for the sex of the offspring in other species, such as macaques (Hinde, 2007, 2009; Hinde *et al.*, 2013), cows (Hinde *et al.*, 2014), Iberian red deer (Landete-Castillejos *et al.*, 2005), bank voles (Koskela *et al.*, 2009) and tammar wallabies (Robert and Braun, 2012). We would therefore predict that there are higher-than-expected proportions of SS versus OS twins and multiple births in nonhuman species as well. At the same time, more human data are clearly necessary to establish whether there is indeed an excess of SS pairs among DZ twins.

Supplementary data

Supplementary data are available at *Human Reproduction* online.

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Authors' role

S.K. conducted the data analyses and wrote the first draft. S.K. and N.L.S. contributed to revisions. D.d.M. proposed the original idea and performed the calculations presented in the Supplementary Data.

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Conflict of interest

None.

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