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Handedness and reproductive success in two large cohorts of French adults

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Abstract

Left- and right-handers in humans coexist at least since the Paleolithic, and this variation in hand preference has a heritable basis. Because there is extensive evidence of an association between left-handedness and several fitness costs, the persistence of the polymorphism requires an explanation. It is not known whether the frequency of left-handedness in Western societies is stable or not. If the polymorphism is at equilibrium and maintained by frequency dependence, it implies that the fitness of left-handers equals that of right-handers. On the contrary, if left- and right-handers have a different fitness, the polymorphism will evolve. Using two large cohorts of French adults (men and women), we investigated the relations between handedness and several estimators of the reproductive value: marital status, number of sexual partners (of the opposite sex), number of children, and number of grandchildren. Left-handers seem to have disadvantages for some life-history traits, such as marital status (for women) and number of children. For other traits, we observed sex-dependent interactions with socioeconomic status: for high-income categories, left-handed women report less sex partners and left-handed men have more grandchildren. These kinds

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of interactions are to be expected under the hypothesis that the polymorphism of handedness is stable.

Keywords: *Homo*; Polymorphism; Handedness; Life-history traits; Reproductive success

1. Introduction

Left- and right-handers in humans coexist at least since the Paleolithic (Faurie & Raymond, 2004), and this variation in hand preference has a heritable basis (see, e.g., Francks et al., 2002; McKeever, 2000; McManus, 1991; Sicotte, Woods, & Mazziotta, 1999). Because there is evidence of an association between left-handedness and several fitness costs, the persistence of left-handers requires an explanation. These costs include a lower life expectancy, an elevated accident risk, a lower birth weight, a lower height in adulthood, and an association with various neurological and immune disorders (e.g., Aggleton, Kentridge, Neave; Coren & Halpern, 1991; Gangestad & Yeo, 1997; McManus & Bryden, 1991). The importance of these costs is confirmed by the observation that no human population shows a frequency of left-handers higher than 50% (Faurie & Raymond 2005; Faurie, Schiefenhövel, Le Bomin, Billiard, & Raymond, 2005; Raymond & Pontier, 2004). One possible explanation for the maintenance of left-handedness is the frequency-dependent advantage of left-handers in physical fights. There is strong support for this theory both from the study of interactive sports in Western societies (Brooks, Bussière, Jennions, & Hunt, 2003; Goldstein & Young, 1996; Grouios, Tsorbatzoudis, Alexandris, & Barkoukis, 2004; Raymond, Pontier, Dufour, & Moller, 1996) and from a cross-cultural comparison in traditional societies (Faurie & Raymond, 2005). It is however unclear how this advantage operates in Western societies. Moreover, left-handers may have other selective advantages, including frequency-dependent ones such as socioeconomic advantages (Faurie, Goldberg, Hercberg, Zins, & Raymond, submitted for publication).

Information about the temporal evolution of left-handedness is scarce in the literature. The 20th century increase in the frequency of left-handed writers is most probably explained by the relaxing of social pressures toward right-hand use (Berdel Martin & Barbosa Freitas, 2003; Dellatolas et al., 1988; Salmaso & Longoni, 1985; Teng, Lee, Yang, & Chang, 1976). Studies based on human subjects depicted in artworks sampled over 50 centuries (Coren & Porac, 1977) are irrelevant because the conventional and often religious artistic representation has no necessary link, in this respect, with a real individual (Needham, 1973).

Consequently, it is not known whether the frequency of left-handedness in Western societies is stable or not. Since a polymorphism is present, if the population is at equilibrium for this trait and if the polymorphism is maintained by frequency dependence, it implies that the fitness of left-handers would be predicted to equal that of right-handers. On the contrary, if left- and right-handers have a different fitness level, the polymorphism with evolve.

The fitness of an individual is his or her contribution to the gene pool of future generations. It cannot be directly measured, but several estimators can be used. There are three common estimators of it: the number of children, the number of grandchildren, and the number of sexual partners (of the opposite sex).

The relation between handedness and number of children has previously been investigated, and left-handers were found to have fewer offspring (Gangestad & Yeo, 1994; McManus & Bryden 1992). However, there are several problems with using the number of children as a measure of fitness:

1. The number of children cannot be known with certainty for men (Ashton, 1980; Peñaloza et al., 1986; Pérusse, 1994). This problem could be bypassed by studying only women, but the variance in the number of children is much lower in women, which makes differences between categories of individuals (e.g., left- and right-handers) more difficult to detect. Moreover, some differences may be sex specific.
2. Even if the number of children could be exactly known, it would not be a truthful fitness estimator because one can have many children who may not have children of their own. In environmental conditions where the risk of not reproducing at all is high, as in societies where the demographic transition took place, the main problem in terms of fitness is to avoid contributing nothing at all to the gene pool. The mere number of children does not capture the overall fitness output generated by one's children: their survival and fertility could dramatically differ, and these traits are not independent from the characteristics of the father.

The number of grandchildren is probably closer in contributing to the future gene pool, and it is therefore a better way to estimate fitness, although the problem of uncertainty regarding paternity remains. The number of sexual partners is a different way to assess reproductive value. It is correlated to attractiveness (Pérusse, 1993) and, thus, to the possibility to access high-quality mates for reproduction (Buss, 1999; Cartwright, 2000; Taylor & Glenn, 1976). However, it cannot be reliably assessed, as overestimation (for men) and underestimation (for women) are common (Morris, 1993; but see also Brewer et al., 2000). For women, an increase in number of sex partners has not been proven to increase the number of children. Therefore, the evolutionary significance, in the interest of women, of polyandry, sequential polyandry, or female infidelity is still unclear. Hence, each of these estimators has disadvantages and advantages and has to be interpreted with caution.

The objective of the present study was to investigate the relations between handedness and all these fitness estimators. Using marital status, the number of sexual partners (of the opposite sex), the number of children, and the number of grandchildren, we compared left- and right-handers, in two large cohorts of French adults (men and women). To our knowledge, this is the first study to investigate the link between handedness and number of sex partners as well as the link between handedness and number of grandchildren.

2. Methods

2.1. Study populations

To investigate the link between handedness and fitness, we partly used not only data already available from two studies, which have been initially designed for other purposes, but also data that we ourselves have collected later on, on the same individuals.

2.1.1. The SU.VI.MAX cohort

The objective of the "Supplémentation en Vitamines et Minéraux Antioxydants" (SU.VI.MAX) study was to test in a randomized, placebo-controlled trial if an intake of antioxidant nutrients reduces the incidence of cancers and cardiovascular diseases in a middle-age general population (Hercberg et al., 2004; Hercberg et al., 1998). In March–July 1994, information on the outline of the study was presented in various public media, along with a call for volunteers (women, aged 35–60, or men, aged 45–60, living in France). Candidates responded via phone or mail. They were expected to return a signed informed consent and a completed self-administered questionnaire to screen for eligibility. Eligibility criteria were lack of disease likely to hinder active participation or threaten 5-year survival, acceptance of the idea of a placebo and of the implications of participation, lack of regular supplementation with any of the vitamins or minerals in the supplement, and absence of extreme beliefs or behavior regarding diet. The protocol was approved by a medical ethics committee and the national committee for the protection of privacy and civil liberties. The questionnaire comprised items on handedness and socioeconomic status. Among the 79,976 candidates after the media campaign, 14,406 eligible subjects were selected, of which 13,017 attended the enrollment visit (7876 females aged 35–60 and 5141 males aged 45–60), but 276 subjects withdraw consent. A total of 12,741 French adults were included in the SU.VI.MAX study (Hercberg et al., 2004).

Our study sample included 11,895 individuals: 4720 men, born between 1930 and 1953 (mean age in 1994: 51.1±4.7 years), and 7175 women, born between 1933 and 1960 (mean age in 1994: 46.3±6.6 years). Data were available on both handedness and marital status for 11,732 individuals and on both handedness and number of children for 11,676 individuals.

2.1.2. The GAZEL cohort

The GAZEL study is an ongoing longitudinal study, and its primary aim was to investigate the occupational risk factors of impaired physical and mental health (Goldberg et al., 2001). The GAZEL cohort was established in 1989 and originally included 20,624 subjects working at French Electricity and Gas Company (EDF–GDF), comprising men aged 40–50 and women aged 35–50 at baseline. Since 1989, this cohort has been followed up by means of yearly self-administered questionnaires and by data collection from the company's personnel and medical departments. The present contribution to the GAZEL study was approved by a medical ethics committee and the national committee for the protection of privacy and civil liberties in 2002.

In 2003, 14,732 subjects in the GAZEL cohort answered the self-administered questionnaire, that is, 74.8% of the 19,688 subjects asked to complete it (937 of the 20,625 subjects in the initial 1989 cohort were not sent a questionnaire in 2003, 750 of whom had died and the others had been lost to follow-up). The present study is mainly based on the 14,649 subjects who answered the question on throwing handedness, comprising 10,890 men born between 1939 and 1948 (mean age in 2003: 59.0±2.9 years) and 3759 women born between 1939 and 1953 (mean age in 2003: 56.2±4.2 years). Among them, 2000 were selected for the 2004 questionnaire (1000 left-handers and 1000 right-handers). Of the 1394 respondents (return rate of 69.7%), 1292 answered the question on number of sex partners during the last 3 years, 1244 answered the question on lifetime number of sex partners, 1384 answered the question on number of children, and 1381 answered the question on number of grandchildren.

2.2. Handedness and reproductive success variables

2.2.1. SU.VI.MAX data

The data on handedness and reproductive success were collected by means of a questionnaire. The question on handedness was formulated by the researchers of the SU.VI.MAX study as follows: Do you consider yourself as (a) a right-hander, (b) a left-hander, or (c) a left-hander who was forced to switch to the right hand. The last two groups were pooled into one single group of left-handers. This assessment of handedness will be subsequently referred as "general" handedness. General handedness was the only measure of handedness provided by the SU.VI.MAX database.

The variables available to estimate reproductive success included the following: (a) marital status (seven categories: single, married, widowed, separated or divorced, widowed and remarried, divorced and remarried, living-in couple) and (b) the number of children (born alive).

The variable concerning marital status was simplified to create two categories: living alone (n=1849) or as a couple (n=9669). The widowers were excluded.

2.2.2. GAZEL data

General handedness does not provide an accurate measure of handedness. Indeed, hand preference can vary across tasks. Consequently, as we had the opportunity to improve this measurement for the GAZEL cohort, we included a question on hand preference for throwing in the self-administered questionnaire of the cohort for the year 2003. Recording writing hand is not an appropriate method of assessment of handedness. First, although it used to be a conventional method in the literature on handedness, which essentially concerned Western societies, it does not allow any cross-cultural perspective, with preliterate and preindustrial societies (see Faurie et al., 2005). Second, writing handedness was (and is still sometimes) submitted to strong social pressures against the use of the left hand. In the GAZEL cohort, many left-handers are likely to have been forced to write with their right hand. Finally, the task used to measure handedness has to be complex enough for hand preference to be fully and consistently expressed. Therefore, hand preference is best assessed for a task such as throwing. Data on general handedness had also been collected in 2001 by Emmanuel Lagarde, a researcher of the GAZEL team, which were useful in comparing the two cohorts. For this measure, as for the SU.VI.MAX study, we pooled the different categories of left-handers into a single group.

The information on reproductive success available in the GAZEL longitudinal database included data obtained through yearly questionnaires since 1989 and data supplied by the EDF–GDF personnel department: (a) the marital status of the individual, as inquired for each year since 1989 (six categories: single, married, living-in couple, separated, divorced, widowed) and (b) whether the individual had a partner or not in 1994 and in 2000. Using the marital status inquired each year since 1989, we compiled a summary variable as representing the proportion of time living as a couple (whether married or not) since 1989. The widowers were excluded. This variable has a value between 0 and 1. The total number of years for which the data are available and, thus, the accuracy of the variable vary between individuals. The data concerning partnership/couple life from the 1994 and 2000 questionnaires were combined into a single variable that has three categories: alone in both questionnaires (n=1230), alone in one questionnaire and with a partner in the other (n=4742), and with a partner in both questionnaires (n=9931).

An additional questionnaire was sent in March 2004 to a subsample of the cohort, composed of 1000 left-handers and 1000 right-handers, based on the results on throwing handedness of the 2003 questionnaire. This new questionnaire provided data on (a) the number of sexual partners of the opposite sex during the past 3 years, (b) the number of sexual partners of the opposite sex during the total lifetime of the subject, (c) the number of biological children, and (d) the number of biological grandchildren.

2.3. Statistical methods

To explore the associations between handedness and reproductive success, we used generalized linear modeling with binary, Gaussian, or Poisson errors, depending on the type of the dependent variable (a categorical variable with only two levels, a continuous variable, or a numeric variable in the form of count data, respectively). With the nature and the causality of the potential relations between reproductive success variables and handedness being unknown, the reproductive success variable was *a priori* chosen as the response variable in the model, when it was possible. Otherwise, the response variable was hand preference (a binary variable, coded "0" for right-handers and "1" for left-handers).

In all models, sex and age were included to control for potential confounding effects, and all possible two- and three-way (when applicable) interaction terms were included in the initial model. When this information was available, we additionally controlled for income (as inquired in 1989) and its interactions with other terms.

The minimal model was obtained with the stepwise model simplification method, using either a χ^2 test (for binary or Poisson error) or an F test (for Gaussian error) to compare models differing by only one term. When the minimal model contained interaction terms involving the variable sex, men and women were studied separately to explore gender-specific associations. Overdispersion (scaled deviance/residual degrees of freedom) was evaluated for Poisson errors. Nonparametric tests (Kendall's rank partial correlation tests) were used for the lifetime number of sex partners because of a skewed distribution.

For both cohorts, statistical analyses were performed with the S-Plus statistical software package (Crawley, 2002).

3. Results

3.1. Handedness

The handedness-related characteristics of the populations studied are indicated in Table 1. In both cohorts, the frequency of left-handers is lower in females than in males. Fisher's Exact Tests on sex differences give significant results for the GAZEL cohort (general handedness: p=.047; throwing handedness: p=.014) but not for the SU.VI.MAX cohort (p=.07).

3.2. Marital status and handedness

3.2.1. SU.VI.MAX cohort

Left-handers had a 4% reduced likelihood of living as a couple compared with right-handers (n=11,518).

With couple status being the response variable, the minimal model was composed of the single terms sex and handedness. The effect of handedness was significant (χ^2=12.55, df=1, p=.0004). The model showed that left-handers were more often living alone than right-handers. When sexes were analyzed separately, we observed that the effect of handedness was mainly due to an effect among women: it was not significant for men (χ^2=1.56, df=1, p=.2), although it was significant for women (χ^2=11.49, df=1, p=.0007).

3.2.2. GAZEL cohort

3.2.2.1. Couple status since 1989: proportion of time living as a couple. Left- and right-handers spent, on average, 90.0% and 89.7% of their time as a couple, respectively (n=14,649).

Table 1
Handedness-related characteristics of the populations studied

	General handedness, % left-handers (n)	Throwing handedness, % left-handers (n)
GAZEL cohort		
Men	10.55 (10,437)	9.00 (10,890)
Women	9.35 (3517)	7.77 (3759)
SU.VI.MAX cohort		
Men	10.38 (4720)	–
Women	9.41 (7175)	–

n refers to sample size.

With proportion of time living as a couple since 1989 being the response variable, the minimal model was composed of the single main term sex. The effect of throwing handedness was not significant (F=0.008, df=1, p=.9). Very similar results were obtained when using general handedness.

3.2.2.2. Couple status in 1994 and 2000. Left- and right-handers had the same likelihood of living as a couple (69% reported living with a partner in both the 1994 and the 2000 questionnaires, 24% only in one of them, and 7% in none; n=13,543).

With throwing handedness being the response variable, the minimal model was composed of the main terms age and sex. The effect of couple status was not significant (χ^2=0.1414997, df=2, p=.93). Very similar results were obtained when using general handedness.

3.3. Number of sexual partners during the past 3 years and handedness (GAZEL cohort)

During the past 3 years, men reported, on average, as having 1.09 sex partners [±1.75 (S.D.); range, 0–30] and women, 0.96 (±2.46; range, 0–36). Note that for statistical reasons, one male individual who reported 180 sexual partners was excluded from the sample.

Left-handed men reported, on average, less partners than right-handed men (1.02 vs. 1.16; n=1074). On the opposite, left-handed women reported, on average, more partners than right-handed women (1.14 vs. 0.78; n=217).

With the number of partners in the past 3 years being the response variable, the three-way interaction between age, sex, and handedness was significant (χ^2=4.17, df=1, p=.04), as well as the interaction between sex and income (χ^2=7.003408, df=1, p=.008). The model was not overdispersed (overdispersion=1.1).

Sexes were therefore analyzed separately. For men, the minimal model was composed of the terms age (χ^2=10.33, df=1, p=.001) and handedness (χ^2=4.91, df=1, p=.027). The fitted values showed that left-handed men had fewer partners than right-handed men. However, the model explained only 1.3% of the deviance. The interactions involving income were not significant (the closest to significance was handedness by income: χ^2=2.09, df=1, p=.15), as well as the effect of the main term income, after the interaction terms were removed (χ^2=0.02, df=1, p=.9).

For women, the minimal model was composed of the terms age, handedness, income, and interaction between income and handedness (χ^2=8.64, df=1, p=.003). The predictions of the model are represented in Fig. 1. Left-handed women had more partners than right-handed women, except for high-income categories. The model explained 14.6% of the deviance.

3.4. Lifetime number of sexual partners and handedness (GAZEL cohort)

Men reported, on average, as having 6.96 sex partners (±15.01; range, 0–300) and women, 4.21 (±6.07; range, 0–50). Note that for statistical reasons, one male individual who reported 2000 sexual partners was excluded from the sample.

Left-handed men reported, on average, less lifetime partners than right-handed men (6.23±9.83; range, 0–100 vs. 7.71±18.82; range, 0–300; n=1025). Similarly, left-handed

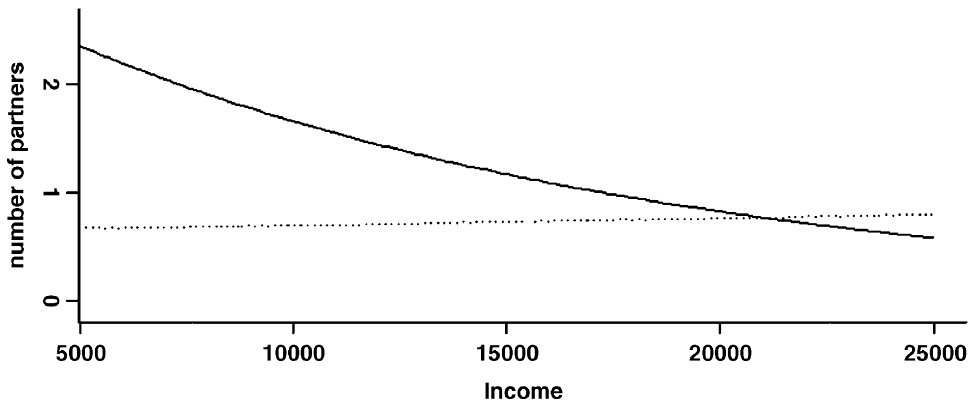

Fig. 1. Number of partners during the past 3 years, as a function of income (in francs), in the GAZEL cohort: fitted values of the minimal model (response variable: number of partners, controlling for age) for left-handed (continuous line) and right-handed women (dotted line). The interaction between income and handedness was significant (χ^2=8.64, *df*=1, *p*=.003).

women reported, on average, less lifetime partners than right-handed women (5.60±8.62; range, 0–50 vs. 7.67±10.82; range, 0–60, *n*=218).

The number of partners was first analyzed as the response variable in a generalized linear model with Poisson errors, controlling for age, sex, and throwing handedness, plus all possible two- and three-way interaction terms. Overdispersion was high (10.6), indicating that this model was inappropriate. Several other models were used: sexes were analyzed separately, an additional variable was introduced (income), but overdispersion remained high (details not shown).

Consequently, nonparametric Kendall's partial correlation tests were performed. For men, the correlation between handedness and number of partners was not significant when controlling for age (Txy.z=−0.009, *p*=.09) or when controlling for income (Txy.z=−0.007, *p*=.21). For women, the correlation between handedness and number of partners was not significant when controlling for age (Txy.z=0.01, *p*=.16), but it was significant when controlling for income (Txy.z=0.02, *p*=.016): again, left-handed women had more partners than right-handed women.

3.5. Number of children and handedness

3.5.1. SU.VI.MAX cohort

Men reported, on average, as having 2.19 children (±1.13; range, 0–8) and women, 1.99 (±1.18; range, 0–9).

Among men, the average number of children was the same for left- and right-handers (2.19±1.13; range, 0–6 and 2.19±1.13; range, 0–8; *n*=4624). Left-handed women reported, on average, less children than right-handed women (1.85±1.17; range, 0–6 vs. 2.01±1.18; range, 0–9; *n*=7052).

With the number of children being the response variable, the minimal model was composed of the variables sex and age. Left-handers tended to have fewer children than right-handers, but the effect of handedness was not significant (χ^2=3.20, *df*=1, *p*=.07), and the analyses by sex showed that it was mainly due to an effect in women.

3.5.2. GAZEL cohort

Men reported, on average, 2.00 children (±0.96; range, 0–7) and women, 1.59 (±0.96; range, 0–4). In both sexes, left-handers reported fewer children. Left-handed men reported, on average, 1.94 children (±0.94; range, 0–7) and right-handed men, 2.07 (±0.98; range, 0–5; *n*=1157). Left-handed women reported, on average, 1.50 children (±0.90; range, 0–4) and right-handed women, 1.69 (±1.00; range, 0–4; *n*=227).

With the number of children being the response variable, the maximal model included age, sex, income (as inquired in 1989), and throwing handedness, plus all possible two- and three-way interaction terms. The minimal model was composed of the variables sex and age. The model was slightly underdispersed (0.6). Left-handers tended to have fewer children than right-handers, but the effect of throwing handedness was not significant (χ^2=3.09, *df*=1, *p*=.08). Very similar results were obtained when using general handedness.

3.6. Number of grandchildren and handedness (GAZEL cohort)

Men reported, on average, 1.67 grandchildren (±1.91; range, 0–17) and women, 1.59 (±1.98; range, 0–11). In both sexes, left-handers reported fewer grandchildren. Left-handed men reported, on average, 1.57 grandchildren (±1.71; range, 0–9) and right-handed men, 1.76 (±2.08; range, 0–17; *n*=1154). Left-handed women reported, on average, 1.58 children (±2.04; range, 0–11) and right-handed women, 1.60 (±1.94; range, 0–10; *n*=227).

With the number of grandchildren being the response variable, the interactions between sex and age (χ^2=18.78, *df*=1, *p*=.00001), between age and handedness (χ^2=3.70, *df*=1, *p*=.05), and between income and handedness (χ^2=5.45, *df*=1, *p*=.02) were significant. Therefore, the sexes were analyzed separately.

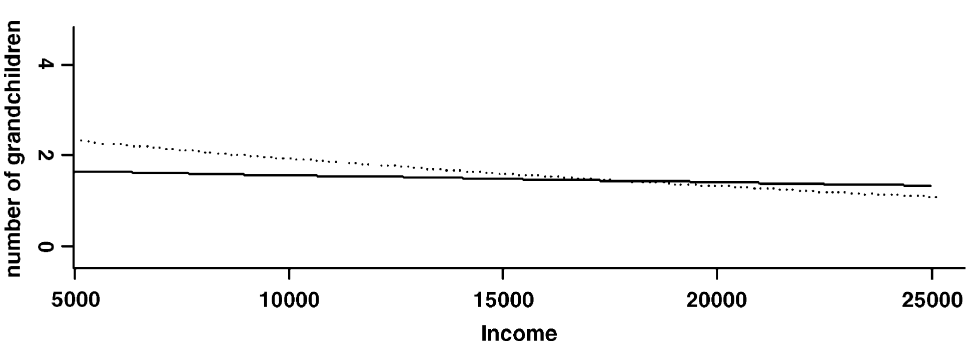

Fig. 2. Number of grandchildren, as a function of income (in francs), in the GAZEL cohort: fitted values of the minimal model (response variable: number of partners, controlling for age) for left-handed (continuous line) and right-handed men (dotted line). The interaction between income and handedness was significant (χ^2=8.63, *df*=1, *p*=.003).

For men, the minimal model includes the variables age, handedness, income, and the interaction between income and handedness (χ^2=8.63, *df*=1, *p*=.003). The fitted values of the model are represented in Fig. 2. Left-handers have fewer grandchildren in low-income categories and more grandchildren in high-income categories. The model explains 12.9% of the deviance.

For women, after correction for overdispersion (2.29), the minimal model contains only the term age. Left-handed women tended to have more grandchildren, but the effect of handedness is not significant (χ^2=.02, *df*=1, *p*=.9).

4. Discussion

The persistence of the handedness polymorphism requires a mechanism such as frequency dependence. If the frequency of left-handedness is at equilibrium in Western Europe under a frequency-dependent selection mechanism, we do not expect to find overall fitness differences between the two phenotypes (right- and left-handers). However, we do expect right- and left-handers to display differences for some life-history traits, with the sign of the difference being variable depending on the trait. This report represents an attempt to investigate whether they are fitness differences related to handedness.

We used marital status, the number of sex partners, and the number of children and grandchildren as life-history traits related to reproductive success, and several putative confounding variables were also considered: sex, age, and income. The results of this study are summarized in Tables 2a and 2b.

Table 2a
Summary of the effects of handedness on fitness-related traits in the two cohorts, after controlling (when significant) for the effects of sex, age, and income when available, plus all possible two- and three-way interactions

Cohort	Couple status (alone vs. couple)	Proportion of time living as a couple since 1989	Number of children
SU.VI.MAX	(*n*=11,518) Men: NS		(*n*=11,676) Left-handers have fewer children (NS: χ^2=3.20, *df*=1, *p*=.07)
	Women: left-handers are more often alone than right-handers (χ^2=11.49, *df*=1, *p*=.0007)		
GAZEL	(*n*=13,543) NS	(*n*=14,569) NS	(*n*=1384) Left-handers have fewer children (NS: χ^2=3.09, *df*=1, *p*=.08)

NS, nonsignificant.

Table 2b
Summary of the effects of handedness on additional fitness-related traits available only for the GAZEL cohort, after controlling (when significant) for the effects of sex, age, income, plus all possible two- and three-way interactions

Number of sex partners during the past 3 years (n=1291)	Lifetime number of sex partners (n=1243)	Number of grandchildren (n=1381)
Men: left-handers have fewer partners (χ^2=4.91, df=1, p=.03)	Men: NS	Men: left-handers have fewer grandchildren in low-income categories and more grandchildren in high-income categories (interaction: χ^2=8.63, df=1, p=.003)
Women: left-handers have more partners in low-income categories and fewer partners in high-income categories (interaction: χ^2=8.64, df=1, p=.003)	Women: left-handers have more partners, controlling for income (Txy.z=0.02, p=.016).	Women: NS

In the case of lifetime number of sex partners, only nonparametric statistics have been used because of overdispersion problems in parametric models. NS, nonsignificant.

4.1. Marital status

Marital status was related to handedness in the SU.VI.MAX cohort (left-handers living more often alone than right-handers, especially for women). Hicks and Kinsbourne (1976) have reported that divorce and remarriage are more frequent in left-handers. Similarly, McManus (1979) has found that left-handers are more likely to divorce. Additionally, he found evidence that left-handers have relatively younger mothers. Lansky, Feinstein, and Peterson (1988) also found a significant relation between handedness and marital status: they observed that left-handers are more often in the category “never married” and that mixed-handers are more often in the category “separated” than right-handers.

4.2. Number of sex partners

In the literature, we did not find any report on number of sex partners and handedness. However, handedness, developmental instability, and number of sex partners seem to be related. Yeo and Gangestad (1993) found an increased incidence of minor physical anomalies and fluctuating asymmetries (FAs) in left-handers. Males who are lower in developmental instability (as indexed by low FA) tend to have more sex partners (Thornhill & Gangestad, 1994; Waynforth, 1998), have more sex partners outside of a relationship, and are more often chosen as a sex partner outside of a mate’s relationship (Gangestad & Thornhill, 1997).

Concerning the number of partners during the past 3 years in the GAZEL cohort, left-handed men were found to have fewer partners than right-handed men. Left-handed women were found to have more partners than right-handed women in low-income categories and fewer partners in high-income categories.

Concerning the lifetime number of partners in the GAZEL cohort, only nonparametric tests could be performed. Left-handed women appeared to have more partners than right-handed women, when controlling for income.

Why women (and females in general) have several sex partners and (possibly) extramarital relationships is not well understood in terms of evolutionary psychology, as these behaviors are not obviously and directly related to their number of children. There is considerable debate in the literature on this aspect of female polyandry (for a review, see Hrdy, 2000; Judson, 2002). Female polyandry is probably more beneficial than previously thought. A larger number of sex partners may open the possibilities to choose a more suitable male and have better-quality children. Polyandrous mating may also have evolved as a protection against male infanticide (Hrdy, 2000). Finally, having multiple partners can be a way to increase the amount of resources provided to the offspring and therefore their survival, as shown, for example, by Beckerman et al. (1998). An alternative hypothesis is to consider that having several sex partners results from a lack of success in forming a long-term relationship. More studies are required to understand the significance of the number of sex partners in females. This trait is likely to be linked somehow to the female fitness. Indeed, female infidelity, for example, is widely observed in humans and many other animals.

4.3. Number of children and grandchildren

From the literature, it seems that left-handers have fewer children than right-handers, although the opposite result has also been reported. According to Rife (1940), left-handers tend to have fewer children than right-handers. Gangestad (1994) has compared the average number of children as a function of parents' handedness, controlling for age. Their data lead to predict 2.03 children at the age of 45 for a right-handed parent and 1.62 for a left-handed parent (n=661). Combining 16 studies, McManus and Bryden (1992) have revealed a tendency for R×R matings to produce more offspring than R×L matings, who have more offspring than L×L matings (2.84, 2.72, and 2.56, respectively; n=15,303 couples). However, in the National Child Development Study (UK), left-handed children tend to come from larger households (n=11,029; McManus, 1979; McManus & Bryden, 1992). The data reported by Hicks and Kinsbourne (1976) and by McManus (1979), showing that divorce and remarriage are more frequent in left-handers, could suggest a higher number of children (Nettle, 2002). In the present study, in both cohorts, left-handers tend to have fewer children than right-handers. This result still holds when age, sex, and income are controlled for.

The number of grandchildren has apparently not been considered in the published literature on handedness. In the GAZEL cohort, left-handed men were found to have fewer grandchildren in low-income categories and more grandchildren in high-income categories; no significant effect of handedness was found for women. One limitation is that the children of the GAZEL cohort's members may not have "completed" their reproductive life and that, therefore, the current number of grandchildren does not absolutely reflect overall lifetime reproductive success.

4.4. Conclusion

Left-handers show lower performances than right-handers for some life-history traits, such as number of children. For other traits, such as number of sex partners or number of grandchildren, left-handers have an advantage only for some values of another trait (income) and a disadvantage for the other values. This sort of trade-off seems to be sex limited: for high-income categories, female left-handers had fewer sex partners (than right-handed women) and left-handed men had more grandchildren (than right-handed men). These interactions with income are interesting and need to be further investigated. Such interactions are to be expected under the hypothesis that the polymorphism of handedness is stable.

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References

Aggleton, J. P., Kentridge, R. W., & Neave, N. J. (1993). Evidence for longevity differences between left handed and right handed men: An archival study of cricketers. *Journal of Epidemiology and Community Health*, *47*, 206–209.

Ashton, G. C. (1980). Mismatches in genetic markers in a large family study. *American Journal of Human Genetics*, *32*, 601–613.

Beckerman, S., Lizarralde, R., Ballew, C., Schroeder, S., Fingelton, C., Garison, A., & Smith, H. (1998). The Bari partible paternity project: Preliminary results. *Current Anthropology*, *39*, 164–167.

Berdel Martin, W. L., & Barbosa Freitas, M. (2003). Mean mortality among Brazilian left- and right-handers: Modification or selective elimination? *Laterality*, *7*, 31–44.

Brewer, D. D., Potterat, J. J., Garrett, S. B., Muth, S. Q., Roberts, J. M., Kasprzyk, D., Montano, D. E., & Darrow, W. W. (2000). Prostitution and the sex discrepancy in reported number of sexual partners. *Proceedings of the National Academy of Sciences United States of America*, *97*, 12385–12388.

Brooks, R., Bussière, L. F., Jennions, M. D., & Hunt, J. (2003). Sinister strategies succeed at the cricket World Cup. *Proceedings of the Royal Society of London B, (Suppl. 3)*.

Buss, D. M. (1999). *Evolutionary psychology, the new science of the mind*. London: Allyn and Bacon.

Cartwright, J. (2000). Evolution and human behavior: Darwinian perspectives on human nature. Cambridge, MA: The MIT Press.

Coren, S., & Halpern, D. F. (1991). Left-handedness: A marker for decreased survival fitness. *Psychological Bulletin*, *109*, 90–106.

Coren, S., & Porac, C. (1977). Fifty centuries of right-handedness: The historical record. *Science*, *198*, 631–632.

Crawley, M. J. (2002). *Statistical computing. An introduction to data analysis using S-Plus*. West Sussex: John Wiley & Sons Ltd.

Dellatolas, G., De Agostini, M., Jallon, P., Poncet, M., Rey, M., & Lellouch, J. (1988). Mesure de la préférence manuelle par autoquestionnaire dans la population française adulte. *Revue de Psychologie Appliquée*, *38*, 117–136.

Faurie, C., Bonenfant, S., Goldberg, M., Hercberg, S., Zins, M., & Raymond, M. (submitted for publication). Socio-economic status and handedness in two large cohorts of French adults. *British Journal of Psychology*.

Faurie, C., & Raymond, M. (2004). Handedness frequency over more than 10,000 years. *Proceedings of the Royal Society of London B*, *271*, S43–S45.

Faurie, C., & Raymond, M. (2005). Handedness, homicide and negative frequency-dependent selection. *Proceedings of the Royal Society of London B*, *272*, 25–28.

Faurie, C., Schiefenhövel, W., Le Bomin, S., Billiard, S., & Raymond, M. (2005). Variation in the frequency of left-handedness in traditional societies. *Current Anthropology*, *46*, 142–147.

Francks, C., Fisher, S. E., MacPhie, I. L., Richardson, A. J., Marlow, A. J., Stein, J. F., & Monaco, A. P. (2002). A genomewide linkage screen for relative hand skill in sibling pairs. *American Journal of Human Genetics*, *70*, 800–805.

Gangestad, S. W., & Thornhill, R. (1997). The evolutionary psychology of extrapair sex: The role of fluctuating asymmetry. *Evolution and Human Behavior*, *18*, 69–88.

Gangestad, S. W., & Yeo, R. A. (1994). Parental handedness and relative hand skill: A test of the developmental instability hypothesis. *Neuropsychology*, *8*, 572–578.

Gangestad, S. W., & Yeo, R. A. (1997). Behavioral genetic variation, adaptation and maladaptation: An evolutionary perspective. *Trends in Cognitive Sciences*, *1*, 103–108.

Goldberg, M., Chastang, J. F., Leclerc, A., Zins, M., Bonenfant, S., Bugel, I., Kaniewski, N., Schmaus, A., Niedhammer, I., Piciotti, M., Chevalier, A., Godard, C., & Imbernon, E. (2001). Socioeconomic, demographic, occupational, and health factors associated with participation in a long-term epidemiologic survey: A prospective study of the French GAZEL cohort and its target population. *American Journal of Epidemiology*, *154*, 373–384.

Goldstein, S. R., & Young, C. A. (1996). "Evolutionnary" stable strategy of handedness in Major League Baseball. *Journal of Comparative Psychology*, *110*, 164–169.

Grouios, G., Tsorbatzoudis, H., Alexandris, K., & Barkoukis, V. (2000). Do left-handed competitors have an innate superiority in sports? *Perceptual and motor skills*, *90*, 1273–1282.

Hercberg, S., Galan, P., Preziosi, P., Bertais, S., Mennen, L., Malvy, D., Roussel, A. -M., Favier, A., & Briançon, S. (2004). The SU.VI.MAX study, a randomised, placebo-controlled trial of the health effects of antioxidant vitamins and minerals. *Archives of Internal Medicine*, *164*, 2335–2342.

Hercberg, S., Preziosi, P., Briançon, S., Galan, P., Triol, I., Malvy, D., Roussel, A. -M., & Favier, A. (1998). A primary prevention trial using nutritional doses of antioxidant vitamins and minerals in cardiovascular diseases and cancers in a general population: The SU.VI.MAX study—Design, methods, and participant characteristics. *Controlled Clinical Trials*, *19*, 336–351.

Hicks, R. E., & Kinsbourne, M. (1976). Human handedness: A partial cross-fostering study. *Science*, *192*, 908–910.

Hrdy, S. B. (2000). The optimal number of fathers. Evolution, demography, and history in the shaping of female mate preferences. *Annals of the New York Academy of Sciences*, *907*, 75–96.

Judson, O. (2002). *Dr Tatiana's sex advice to all creation. The definitive guide to the evolutionary biology of sex*. London: Chatto & Windus.

Lansky, L. M., Feinstein, H., & Peterson, J. M. (1988). Demography of handedness in two samples of randomly selected adults (N=2083). *Neuropsychologia*, *26*, 465–477.

McKeever, W. F. (2000). A new family handedness sample with findings consistent with X-linked transmission. *British Journal of Psychology*, *91*, 21–39.

McManus, I. C. (1991). The inheritance of left-handedness. In G. R. Bock, & J. Marsh (Eds.), *Biological asymmetry and handedness, Ciba Foundation Symposium* (pp. 251–281). London: Wiley.

McManus, I. C., & Bryden, M. P. (1991). Geschwind's theory of cerebral lateralization: Developing a formal, causal model. *Psychological Bulletin*, *110*, 237–253.

McManus, I. C., & Bryden, M. P. (1992). The genetics of handedness, cerebral dominance and lateralization. In I. Rapin, & S. J. Segalowitz (Eds.), *Handbook of Neuropsychology* (pp. 115–144). Amsterdam: Elsevier.

Morris, M. (1993). Telling tails explain the discrepancy in sexual partner reports. *Nature*, *365*, 437–440.

Needham, R. (1973). Essay on dual symbolic classification. Right and left. Chicago: The University of Chicago Press.

Nettle, D. (2002). Height and reproductive success in a cohort of British men. *Human Nature*, *13*, 473–491.

Peñaloza, R., Nuñez, C., Alatorre, S., Lagunes, R., Garcia Escobar, B., Salamanca, F., & Zavala, C. (1986). Frecuencia de paternidad extraconygal en una muestra de la poblacion Mexicana. *Revista de Investigaciòn Clinica*, *38*, 287–291.

Pérusse, D. (1993). Cultural and reproductive success in industrial societies: Testing the relationship at the proximate and ultimate levels. *Behavioral and Brain Sciences*, *16*, 267–322.

Pérusse, D. (1994). Mate choice in modern societies: Testing evolutionary hypotheses with behavioral data. *Human Nature*, *5*, 255–278.

Raymond, M., & Pontier, D. (2004). Is there geographical variation in human handedness? *Laterality*, *9*, 35–52.

Raymond, M., Pontier, D., Dufour, A. -B., & Moller, A. P. (1996). Frequency-dependent maintenance of left handedness in humans. *Proceedings of the Royal Society of London B*, *263*, 1627–1633.

Rife, D. C. (1940). Handedness with special reference to twins. *Genetics*, *25*, 178–186.

Salmaso, D., & Longoni, A. M. (1985). Problems in the assessment of hand preference. *Cortex*, *22*, 533–549.

Sicotte, N. L., Woods, R. P., & Mazziotta, J. P. (1999). Handedness in twins: A meta-analysis. *Laterality*, *4*, 265–286.

Taylor, P. A., & Glenn, N. D. (1976). The utility of education and attractiveness for females status attainment through marriage. *American Sociological Review*, *41*, 484–498.

Teng, E. L., Lee, P. -H., Yang, K. -S., & Chang, P. C. (1976). Handedness in a Chinese population: Biological, social, and pathological factors. *Science*, *193*, 1148–1150.

Thornhill, R., & Gangestad, S. W. (1994). Human fluctuating asymmetry and sexual behavior. *Psychological Science*, *5*, 297–302.

Waynforth, D. (1998). Fluctuating asymmetry and human male life-history traits in rural Belize. *Proceedings of the Royal Society of London B*, *265*, 1497–1501.

Yeo, R. A., & Gangestad, S. W. (1993). Developmental origins of variation in human preference. *Genetica*, *89*, 281–296.