



Socio-economic status and handedness in two large cohorts of French adults

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Left- and right-handers have coexisted since the Palaeolithic age. Hand preference is heritable. Moreover, there is extensive evidence of an association between left-handedness and several fitness costs. In this context, the persistence of the polymorphism is interesting. Here, we explore the associations between socio-economic status and handedness, analysing data from two large cohorts of adult men and women. Such associations are relevant to an evolutionary approach, as the socio-economic and the reproductive value are related. Our results partly support the hypothesis that left-handers have a socio-economic status advantage, countervailing the health issues. Although the models explain a small proportion of the variance observed, the frequency of left-handedness is significantly higher: (1) among women of higher educational level; (2) among categories of higher income; and (3) among individuals who have a higher position in the company. The importance of these findings for the evolution of the polymorphism of handedness is discussed.

Left- and right-handers have coexisted since the Palaeolithic age (Faurie & Raymond, 2004). Hand preference is heritable (see e.g. Francks *et al.*, 2002; McKeever, 2000; see e.g. McManus, 1991; Sicotte, Woods, & Mazziotta, 1999). Moreover, there is extensive evidence of an association between left-handedness and several health issues, for example lower birth weight, poorer health, and higher accident rates (e.g. Aggleton,

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Kentridge, & Neave, 1993; Coren & Halpern, 1991; Gangestad & Yeo, 1997; Mandal, Suar, & Bhattacharya, 2001; McManus & Bryden, 1991; O'Callaghan *et al.*, 1987). In this context, the persistence of left-handers is interesting. The frequency-dependent advantage of left-handers in physical fights is strongly suggested by both the study of interactive sports in industrialized societies (Brooks, Bussière, Jennions, & Hunt, 2003; Goldstein & Young, 1996; Grouios, Tsorbatzoudis, Alexandris, & Barkoukis, 2000; Raymond, Pontier, Dufour, & Møller, 1996) and a cross-cultural comparison of traditional societies (Faurie & Raymond, 2005). However, it is unclear how this advantage operates in Western societies. Moreover, left-handers may have other selective advantages.

Here, we propose to investigate the possibility of a socio-economic advantage of left-handers. A socio-economic advantage is necessarily frequency-dependent: the status of an individual is relative to the status of others in his/her social group. Socio-economic status is an important component of the reproductive value in most human societies (Bamshad *et al.*, 1998; Bereczkei & Dunbar, 1997; Betzig, 1986; Chagnon, 1979; Hill, 1984; Josephson, 1993; Mealey, 1985; Roskaft, Wara, & Viken, 1992; Taylor & Glenn, 1976; Turke & Betzig, 1985; Udry & Eckland, 1984; Volland & Chasiotis, 1998) and, despite the effects of demographic transition, it is true in Western societies as well (Buss, 1999; Elder, 1969; Kaplan & Hill, 1986; Pérusse, 1993).

In the literature, there are three main theories that account for the relationship between socio-economic status and hand preference. First, the genetic model advanced by McManus (1991) claims that left-handedness is caused by a recessive allele, which cancels out the pre-existing bias to the right. He believes that this recessive allele persists because it bestows left-handers with some cognitive advantages. Another model has been suggested by Annett (1985). She also believes that left-handedness is caused by a recessive allele. In this case, however, she believes that the allele persists because of a heterozygous advantage. Thus, individuals with a RS + ('right shift') and a RS- allele will have superior cognitive ability. Therefore, Annett's model would predict that left-handers have no special advantage. In fact, because they are homozygous for the RS- allele, they will be at a disadvantage. Finally, Crow, Crow, Done, and Leask (1998) suggest that people with weak lateralization will be at a disadvantage relative to those with strong lateralization (irrespective of the side). All three theories make very different predictions for the association between SES and hand preference.

An association between handedness and socio-economic status could be due to possible differences in cognitive abilities. Differences in brain organization have been observed between left- and right-handers (Annett, 1985; Christman & Propper, 2001; Galaburda, 1991; Galaburda, LeMay, Kemper, & Geschwind, 1978; Steinmetz, Volkman, Jäncke, & Freund, 1991; Witelson, 1992; Witelson & Kigar, 1988). Brain structures and functions are certainly linked to social and intellectual skills, on which socio-economic status depends.

There is indeed an abundance of literature on cognitive abilities and handedness. Left-handedness was found to be more frequent in specific populations with extremely high or extremely low scores on tests of cognitive abilities (Annett & Turner, 1974; Benbow, 1986, 1988; Hicks & Dusek, 1980; Levy, 1969; Miller, 1971; Netley & Rovet, 1984; Porac & Coren, 1980). However, negative findings have also been reported (Bishop, 1990; McManus, Shergill, & Bryden, 1993; Powls, Botting, Cooke, & Marlow, 1996; Saigal, Rosenbaum, Szatmari, & Houlst, 1992).

In the general population, several studies have investigated the relationship between laterality and various measures of intelligence, such as verbal, vocabulary and symbolic, non-verbal reasoning tests, IQ and memory tests, visual manipulation exercises, reading,

drawing or arithmetic abilities, and foreign language learning. Some studies found that left-handers have lower intellectual performance, while others found no differences between right and left-handers and an advantage for left-handers was observed in some studies. The results of these studies are summarized in Table 1.

A clear trend is difficult to observe in this published literature: no clear relationship emerges between intellectual ability and laterality. The different conclusions reached by these studies could follow from methodological differences, which makes it difficult to compare the results.

First, the various intellectual tests performed do not measure the same intellectual skills. Left- and right-handers may perform differently in the various intellectual tasks (Hicks & Beveridge, 1978). It is likely that left-handers differ in cognitive styles rather than cognitive abilities. Moreover, there seems to be considerable heterogeneity in cognitive abilities amongst non-right-handers, as suggested by the theory of a distinction between pathological and non-pathological left-handedness (Dellatolas *et al.*, 1993; McManus, 1983). Nettle (2003) found that extreme right-handers have minimal variance in IQ and left-handers have a large variance ($p < .001$). The increased variance in IQ among left-handers explains why a significant number of left-handers are observed at both the lower and higher ends of the distribution.

Second, gender-handedness interactions are common in the literature. For example, Faurie, Vianey-Liaud, and Raymond (2006) found a positive correlation between left-handedness and several measures of school performance and leadership skills for boys but a negative association for girls. Thus, gender effects can be another source of discrepancies between studies.

Finally, there are a large variety of handedness measures in these studies. Numerous discrepancies may result from the use of different measures of hand laterality, and in cases where several measures were used simultaneously, discrepancies may result from different decisions on how to deal with mixed-handedness (Nettle, 2003). Moreover, relative hand skill variables are not independent of the overall level of hand skill (left hand skill + right hand skill), which is correlated with IQ (correlation .18, $p < .001$, Nettle, 2003). Controlling for the confounding effects of overall hand skill, Nettle (2003) found that as laterality increases in either direction away from equal hand skill, the average IQ increases. Thus, the greatest cognitive abilities seem to be at the extremes of handedness.

It is possible that handedness and socio-economic status are related through occupational choice. Several studies have found left-handers to be more frequent in some professions and some educational fields, for example arts (Mebert & Michel, 1980; Peterson, 1979), music (Aggleton, Kentridge, & Good, 1994; Byrne, 1974; Hassler & Gupta, 1993; Quinan, 1922), mathematics (Annett & Manning, 1990; Casey, Pezaris, & Nuttall, 1992; Peters, 1991), and architecture (Peterson & Lansky, 1974). Several studies have found evidence that creativity and novelty seeking is higher among left-handers (e.g. Coren, 1995; Newland, 1981). However, the evidence is mixed and comprehensive scientific studies on a possible relationship between socio-professional categories and hand preference are scarce. Some studies found a higher prevalence of left-handedness in classes of higher social or educational status (Annett & Kilshaw, 1983; Noroozian, Lofti, Gassemzadeh, Emami, & Mehrabi, 2002), some found the opposite (Lamm & Epstein, 1999; Resch *et al.*, 1997), and some failed to find any relation at all (Brito, Brito, Paumgarten, & Lins, 1989). It is likely that there are a variety of types of left-handedness, which may explain the often inconsistent results in the literature on characteristics of that subpopulation.

Table 1. Empirical studies investigating the relationship between handedness and various measures of cognitive abilities. Studies were considered if the sampled population was random relative to the cognitive ability variable, and if the sample size was greater than 100. Due to the extensive literature on handedness, this list is certainly not exhaustive

Nature of the difference (LH compared to RH)	Direction and amplitude of the difference	Population	Sample size	Handedness assessment	References
Academic ability	Children close to equal hand skill (R = L) at increased risk of verbal and non-verbal deficits. Cognitive ability associated with hand skill difference	11 year-old children (National Child Development Study, UK)	12,782	Relative hand skill (box-ticking task): $(R - L)/(R + L) \times 100$	Crow, Crow, Done, and Leask (1998)
General ability (IQ)	No evidence for the deficit at the point of equal hand skill	5–8 year-old school boys (Austria)	530	Relative hand skill (peg-moving task): R – L	Mayringer and Wimmer (2002)
	LH = RH	Population of Oxfordshire villages (UK)	823	Seven-item preference questionnaire	Newcombe and Ratcliff (1973)
	R – L positively correlated with IQ, accounting for 1% of the variance, when controlling for (R + L), accounting for 3%	11 year-old children (National Child Development Study, UK)	8,525	Relative hand skill (box-ticking task): (R – L), adjusted for overall hand skill (R + L)	Nettle (2003)
LH = RH	General population of Oxfordshire (UK)	928	Seven-item preference questionnaire	Newcombe, Ratcliff, Carrivick, and Hiorns (1975)	
LH = RH		School students (UK)	224	Writing hand	Annett and Turner (1974)
LH < RH		General population, males 18–20 year-old (France)	24,433	General handedness (self-report)	Olivier (1978)
LH > RH		Primary school students (UK)	342	Writing hand	Annett and Manning (1989)
Non-verbal intelligence (Culture Fair Intelligence Test)	LH < intermediate = RH	16–30-year-old individuals (Germany)	545	Hand skill (line-drawing task)	Resch et al. (1997)

Table 1. (Continued)

Nature of the difference (LH compared to RH)	Direction and amplitude of the difference	Population	Sample size	Handedness assessment	References
Mathematics	LH < RH	Undergraduate students (USA)	523	Five-items preference questionnaire	Wittenborn (1946)
	LH = RH	School children grades one-six (California)	7,686	Writing hand	Hardyck, Petrino-vich, and Goldmann (1976)
	LH > RH	School children, 9-11-year-old (UK)	149	Writing hand	Annett and Manning (1990)
Verbal ability	Correlated with right hand skill (in both sexes)	College students aged 18-25 (University of Toledo, USA)	RH: 259	Hand skill (peg-moving task)	Cerone and McKeever (1999)
	No difference between classes of hand preference	College students aged 18-25 (University of Toledo, USA)	RH: 259	Hand preference items (Annett Handedness Inventory)	Cerone and McKeever (1999)
	RH > intermediate > LH	16-30-year-old individuals (Germany)	545	Hand skill (line-drawing task)	Resch et al. (1997)
Reading ability	Ambidextrous: lower scores than both LH and RH	Adults and 13-year-old or over children (Hawaii Family Study)	6,448	Self reported hand preference (general hand usage)	Ashton (1982)
	Verbal ability increases as a function of lateralization in either direction and associated with verbal ability	11 year-old children (National Child Development Study, UK)	12,782	Hand skill (box-ticking task)	Leask and Crow (2001)
	LH < RH	Shoppers in various London shops (UK)	506	Edinburgh handedness inventory (self-report)	Geschwind and Behan (1982)
LH = RH	11-13-year-old children (New Zealand)	203	Hand skill (peg-moving task)	Palmer and Corballis (1996)	
LH = RH	3-15-year-old students (UK)	219	Hand preference items (Annett Handedness Inventory)	Annett (1970)	

Table 1. (Continued)

Nature of the difference (LH compared to RH)	Direction and amplitude of the difference	Population	Sample size	Handedness assessment	References
Foreign languages	LH < RH	14-years-old students (Israel)	975	Hand writing	Lamm and Epstein (1999)
Memory	LH > RH	Undergraduate students with 3–4 years of musical training (USA)	129	Edinburgh handedness inventory (self-report)	Deutsch (1978)
	Episodic: RH (with LH in family) > RH (without), the opposite for semantic	US Air force recruits and RH undergraduate students (USA)	180 and 84	Edinburgh handedness inventory (self-report)	Christman and Propper (2001)
Visuospatial ability	Mixed-handers > (LH, RH)	14–15-year-old children (UK)	459	Hand preference items (Annett Handedness Inventory)	Annett (1992)
	Females: mixed-handers > (LH, RH) Males: LH > RH	College students (UK)	428	Hand skill (peg-moving task) Hand preference items (Annett Handedness Inventory)	Annett (1992)
	No difference between classes of hand preference	College students aged 18–25 (University of Toledo, USA)	259	Hand skill (peg-moving task) Hand preference items (Annett Handedness Inventory)	Cerone and McKeever (1999)
	Correlated with degree of asymmetry in men correlated with right hand skill in both sexes	College students aged 18–25 (University of Toledo, USA)	259	Hand skill (peg-moving task)	Cerone and McKeever (1999)

The objective of the present study is to explore the association between socio-economic status and handedness. We will seek to investigate the relationship in two large cohorts of adult men and women.

Methods

Study populations

Study 1: The SU.VI.MAX cohort

The objective of 'Supplémentation en Vitamines et Minéraux AntioXydants' (SU.VI.MAX) was to study the incidence of cancers and cardiovascular disease in a middle-aged general population (Herberg *et al.*, 1998, 2004). 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 were expected to return a signed informed consent and a completed self-administered questionnaire to screen for eligibility. This questionnaire comprised items on handedness and on socio-economic status. The protocol was approved by a medical ethics committee and the national committee for the protection of privacy and civil liberties. Among the 79,976 candidates, 14,406 eligible subjects were selected. In the present sample 13,017 French adults (7,876 females aged 35–60 and 5,141 males aged 45–60) were included.

Study 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). The study cohort was comprised of men aged 40–50 and women aged 35–50 at baseline. Since 1989, this cohort was followed 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.

Handedness and socio-economic status data

Study 1: SU.VI.MAX data

The data on handedness and socio-economic status were collected with a questionnaire. The question on handedness was formulated as follows: 'Do you consider yourself as (1) a right-hander; (2) a left-hander; and (3) a left-hander who was forced to switch to the right hand. The two latter groups were pooled into one single group of left-handers. This assessment of handedness will be subsequently referred as "general" handedness. The available information on socio-economic status included: (1) the educational level of the subject (seven categories) and (2) the occupational category of the subject (five categories, unordered).'

Study 2: GAZEL data

Questions on laterality were included in the self-administered questionnaire in 2003. It comprised six items, four of which were on hand preference: for writing, throwing,

manipulating a tool habitually used at work or in everyday life and turning a key in a keyhole. An additional questionnaire was sent in March 2004 to a subsample of the cohort (1,000 left-handers and 1,000 right-handers, based on the results of throwing handedness from the 2003 questionnaire). This new questionnaire included an item on hand preference for cutting with a knife (without holding a fork), for the focal individual, as well as for his genetic offspring. Data had also been collected in 2001 on 'general' handedness by Dr Emmanuel Lagarde, member of one of the GAZEL teams. As for the SU.VI.MAX study, we pooled the different categories of left-handers into a single group.

The information on socio-economic status available in the GAZEL cohort longitudinal database included data obtained through questionnaires since 1989 and data supplied by the EDF-GDF personnel department: (1) educational level of the individual in 1989 (five categories); (2) position of the individual in the company in 1989 (three categories); (3) occupational category of the individual in 1989 (five categories, unordered); (4) leadership level of the individual in the company (five-level scale) as enquired by the medical department in 1989; (5) monthly income of the household, based on a nine-level scale ranging from less than 5,000 Francs to more than 25,000 Francs in 1989 and on a 10-level scale ranging from less than 991 € to more than 6,098 € in 2002; (6) the number of persons in the household in 1989 and in 2002; and (7) the total value of the household's possessions owned by the individual in 2002 based on a nine-level scale ranging from less than 1,525 € to more than 457,347 € (1 Franc = 0.152 €).

Statistical methods

The nature and causality of the potential relationship between socio-economic status variables and handedness was unknown. The socio-economic status variable was *a priori* chosen as the response variable in the model, whenever possible that is when it was either a binary, continuous or count variable. The variable educational level was transformed into a binary variable (individual passed the final exam of high school or not). It was then analysed as the response variable. Otherwise, the response variable was hand preference (a binary variable, coded '0' for right-handers and '1' for left-handers). Generalized linear modelling was used with binary, Gaussian, or Poisson errors, depending on the type of dependent variable (respectively a categorical variable with only two levels, a continuous variable, or a numeric variable in the form of count data). In all cases, sex and date of birth were used as potential confounding variables and all possible two-way and three-way (when applicable) interaction terms were included in the initial model. The minimal model was obtained with the stepwise model simplification method, using either a Chi-square-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. For both cohorts, statistical analyses were performed with the S-Plus statistical software package (Crawley, 2002).

Results

Study populations

Study 1: SU.VI.MAX cohort

A total of 12,741 subjects contributed to analyses (Hercberg *et al.*, 2004). Among them, 846 had not answered the question on handedness. Consequently, the study sample

included 4,720 men born between 1930 and 1953 (mean age in 1994: 51.1 ± 4.7 years) and 7,175 women born between 1933 and 1960 (mean age in 1994: 46.3 ± 6.6 years).

Study 2: GAZEL cohort

In 2003, 14,732 subjects in the GAZEL cohort answered the self-administered questionnaire that is 74.8% of the 19,688 subjects were asked to complete the questionnaire. Of the respondents, 14,680 (99.6%) answered at least one item on hand preference. The present study is mainly based on the 14,649 subjects comprised of 10,890 men born between 1939 and 1948 (mean age in 2003: 59.0 ± 2.9 years) and 3,759 women born between 1939 and 1953 (mean age in 2003: 56.2 ± 4.2 years), who answered the question on throwing handedness (see explanations below). Among them, 2,000 were selected for the 2004 questionnaire. Of the 1,394 respondents (return rate of 69.7%), 1,379 answered the item on hand preference for knife use.

Handedness

Correlation coefficients between the various measures of hand preference in Study 2 are presented in Table 2.

Table 2. Correlation coefficients (Kendall's τ) between handedness measures in the GAZEL cohort. All are significant ($p < .0001$). As highlighted in grey, throwing handedness has the strongest correlation with hand preference for both knife use and tool use, which were previously used in cross-cultural studies (Faurie *et al.*, 2005)

	Writing	Throwing	Tool	Key	Knife
General	.13	.60	.62	.47	.62
Writing		.33	.34	.36	.27
Throwing			.79	.69	.77
Tool				.71	.71
Key					.68

The measures of hand preference chosen to explore the associations with socio-economic status in the GAZEL cohort were: (1) throwing handedness, because it was previously used in cross-cultural studies (Raymond & Pontier, 2004) and has the strongest correlation with hand preference for knife use and tool use, which were also previously used in cross-cultural studies (Faurie, Schiefenhövel, Le Bomin, Billiard, & Raymond, 2005), and because throwing was already an important adaptation for ancestral hominids that is subject to selection pressures (Watson, 2001) and (2) 'general' handedness, for comparison with the SU.VI.MAX study, for which it is the only measure of handedness available. The characteristics of the populations studied regarding these two measures are indicated Table 3.

Note that writing handedness is weakly correlated with all the other measures, including 'general' handedness. Writing handedness, for the generation of the individuals of the cohort (born between 1939 and 1953), was influenced by strong social pressures towards right hand use. The frequency of left-handed writers is only 1.6%, which is very low compared to throwing handedness (8.7%) and compared to what is found in youngest samples (13.56% in French schoolchildren: Faurie *et al.*, 2006).

Table 3. Hand preference characteristics of the populations studied. *N* refers to sample size

	'General' handedness % left-handers (<i>N</i>)	Throwing handedness % left-handers (<i>N</i>)
GAZEL cohort		
Men	10.55% (10,437)	9.00% (10,890)
Women	9.35% (3,517)	7.77% (3,759)
SU.VI.MAX cohort		
Men	10.38% (4,720)	–
Women	9.41% (7,175)	–

Study 1: SU.VI.MAX cohort

Educational level and handedness

A total of 360 individuals who reported that they have had no education were excluded from analyses. The other categories ranged according to the number of years of education: primary school (793 individuals); technical school, low level (1,356); secondary school (1,735); technical school, high level (1,334); high school (1,417); superior studies, low level (1,891); and superior studies, high level (2,938).

Response variable: 'General' handedness (binary). The minimal model obtained is constituted by all the single terms: educational level (seven categories), sex and age (11,464 individuals). The effect of educational level is significant ($\chi^2 = 16.83$, $df = 1$, $p = .02$). The trend is an increase in the frequency of left-handers in higher educational categories (0.87% of the variance explained).

Response variable: Success at the final exam of high school (binary). As the interaction between age and sex was found to have a significant effect ($\chi^2 = 17.57$, $df = 1$, $p = .00002$), the sexes were analysed separately. As shown on Figure 1a, in either men or women, the frequency of left-handers was higher among individuals who passed the exam, although this effect was significant only in women (men: $\chi^2 = 2.09$, $df = 1$, $p = .15$; women: $\chi^2 = 5.63$, $df = 1$, $p = .02$, 2.75% of the variance explained, odds ratio 1.11).

Occupational category and handedness

The five categories are: farmers, self-employed (760); managerial staff, professionals (3,208); intermediate (4,359); employees (2,605); and unemployed (484). As the unemployed category only contained five males, they were excluded from the analyses.

Response variable: 'General' handedness (binary). The minimal model obtained is comprised of the variables sex and age only (11,412 individuals). The effect of occupational category is not significant ($\chi^2 = 2.23$, $df = 4$, $p = .7$), even when the sexes were analysed separately ($\chi^2 = 2.55$, $df = 4$, $p = .6$ for men and $\chi^2 = 2.56$, $df = 4$, $p = .6$ for women).

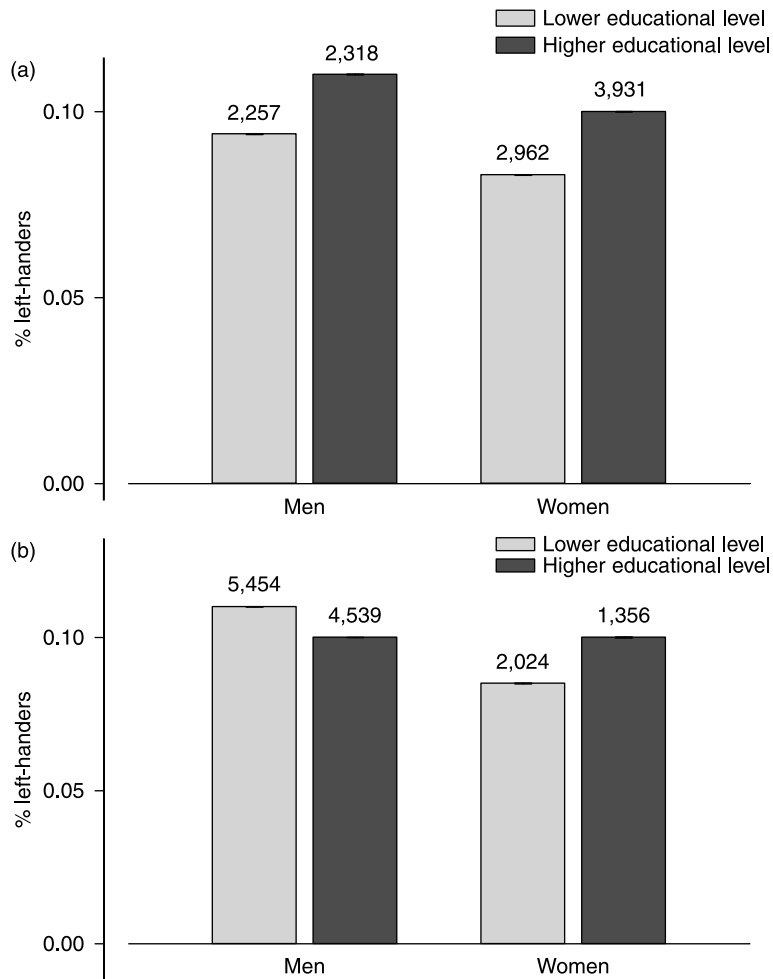


Figure 1. Frequency of left-handers according to educational level. (a) In the SU.VI.MAX cohort. Educational level categories were pooled into a binary variable, representing the success at the final exam of high school. In both men and women, the frequency of left-handers was higher among individuals who passed the exam. The effect of handedness in a logistic regression with educational level being the response variable is significant only for women (men: $p = .15$; women: $p = .02$). Sample sizes are indicated above the boxes. (b) In the GAZEL cohort. Educational level categories were pooled into a binary variable, representing success at the final exam of high school. The effect of 'general' handedness in a logistic regression with educational level being the response variable is not significant, although close to significant in women ($p = .1$). Sample sizes are indicated above the boxes.

Study 2: GAZEL cohort

Educational level and handedness

The categories correspond to the number of years of education: primary school (832 individuals); secondary school, first level (3,986); secondary school, second level (3,065); secondary school, third level (1,053); and superior studies (5,111).

Response variable: Handedness (binary). The minimal model obtained comprises the variables age and sex only (14,047 individuals). The effect of educational level is not significant (throwing handedness: $\chi^2 = 2.72$, $df = 4$, $p = .6$; 'general' handedness: $\chi^2 = 1.87$, $df = 4$, $p = .8$).

Response variable: Success at the final exam of high school (binary). As the interaction between age and sex was found to have a significant effect ($\chi^2 = 41.96$, $df = 1$, $p < .00001$), the sexes were analysed separately. For either men or women, the minimal model is comprised of the variable age only. Throwing handedness has no significant effect ($\chi^2 = 0.03$, $df = 1$, $p = .9$ for both men and women).

For comparison with the SU.VI.MAX study, similar analyses were also performed with 'general' handedness (Figure 1b). Because of interaction effects, sexes were again analysed separately. No effect of handedness was found in men ($\chi^2 = 0.81$, $df = 1$, $p = .4$). Among women, the effect of handedness was marginally significant: the frequency of left-handers was marginally higher among women who passed the exam (10 vs. 8.5%, $\chi^2 = 2.71$, $df = 1$, $p < .1$, 0.93% of the variance explained, odds ratio 1.10).

Occupational category and handedness

The five categories are: managerial staff, professionals (4,481); intermediate, administrative (4,092); intermediate, technical (6,155); intermediate, trade (864); and employees, workers (3,680).

Response variable: Handedness (binary). The minimal model obtained comprised all the single terms plus the interaction between age and occupational category, which was significant ($\chi^2 = 11.40$, $df = 4$, $p = .02$) and reflected changes over time. It explains 0.33% of the variance (13,742 individuals). When sexes are analysed separately, it appears that the effect of this interaction is present in men ($\chi^2 = 10.49$, $df = 4$, $p = .03$). For example, the frequency of left-handers in the highest category ('managerial staff, professionals') increases and becomes the greatest of all categories in the youngest generations (men born after 1946).

In comparison to the SU.VI.MAX cohort, the same analyses were also performed with 'general' handedness ($N = 13,096$) and similar results were obtained.

Income and handedness

Information on income was available for men and women of the GAZEL cohort. The nine categories in 1989 ranged from less than 5,000 Francs to more than 25,000 Francs and the 10 categories in 2002 ranged from less than 991 € to more than 6,098 €. Using average values, the variables were transformed into numerical variables. Then, we compiled the data from 1989 to 2002 to obtain the approximate average income in Francs.

Response variable: Throwing handedness. The maximal model included sex, age, income (averaged from data in 1989 and 2002) and the number of persons in the household (averaged from data in 1989 and 2002), plus two- and three-way interactions. The minimal model includes the variables age, sex, income, and the interaction between

age and income ($\chi^2 = 5.6$, $df = 1$, $p = .018$). The predicted values of the frequency of left-handers in the minimal model increase as a function of income, as represented on Figure 2.

Response variable: Average income for the years 1989 and 2002. In the minimal model, three significant interactions remained (12,433 individuals): between age and throwing handedness ($F = 4.35$, $df = 1$, $p = .037$); between age and sex ($F = 9.80$, $df = 1$, $p = .002$); and between sex and number of persons in the household ($F = 168.39$, $df = 1$, $p < .00001$).

When sexes were analysed separately, the minimal model for men contained age, handedness, number of persons in the household. The relationship between age and handedness was significant ($F = 5.18$, $df = 1$, $p = .02$). The model explained 1.75% of the variance. Figure 3 shows the predictions of the model: left-handers have a higher average income, when controlling for age and number of persons in the household.

For women, handedness has no significant effect ($F = 1.50$, $df = 1$, $p = .2$).

Ownership and handedness

The nine categories of ownership ranged from 1,525 € to 457,347 €. Using these values, the variable was transformed into a numerical variable.

Response variable: Total value of ownership in 2002. The minimal model contains the variables age, sex, number of persons in the household, the interaction between sex

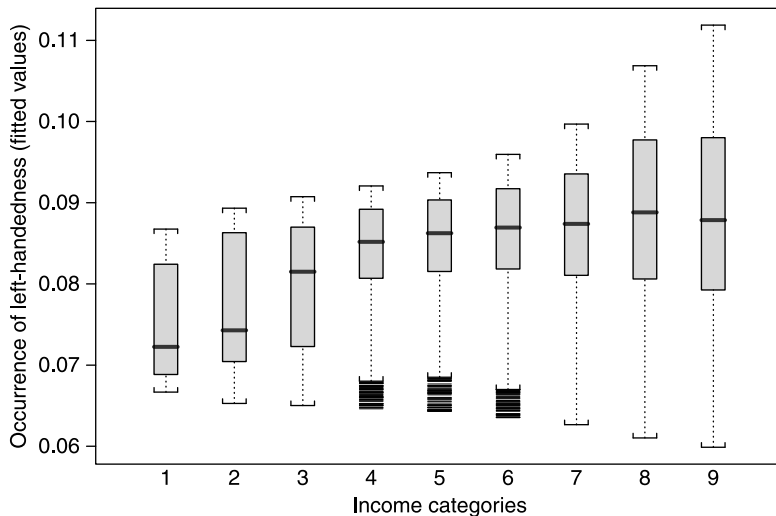


Figure 2. Predicted values of the frequency of left-handers in the GAZEL cohort, as a function of income in 1989, in the minimal model, which includes sex, age, income, number of persons in household, the interaction between income and age, and between income and number of persons in household (response variable: throwing handedness). The boxes show the limits of the middle half of the data, the lines inside the boxes represent the medians. The whiskers are drawn to the nearest value not beyond a standard span from the quartiles ($1.5 \times$ (inter-quartile range)); points beyond (outliers) are drawn individually.

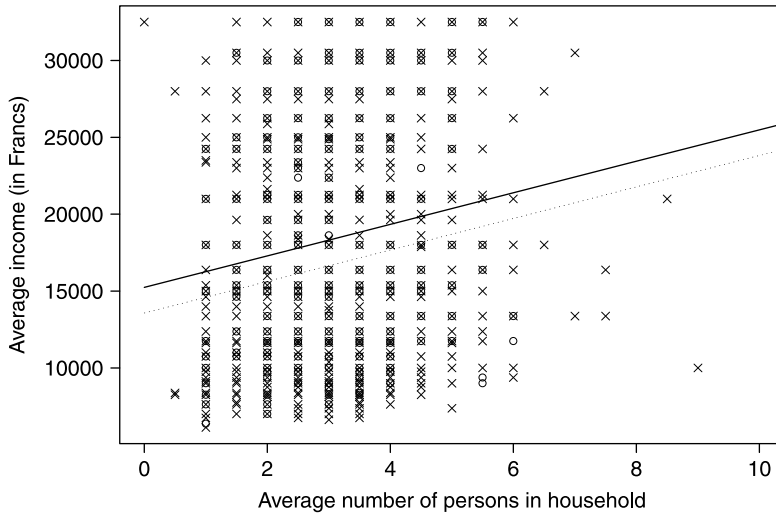


Figure 3. Average income (1989 and 2002) as a function of average number of persons in household, in men of the GAZEL cohort: observed data and predictions of the minimal model (response variable: income, controlling for age). Points: observed data for left-handers (open circles) and right-handers (crosses). Lines: fitted values for left-handers (continuous line) and right-handers (dotted line). One point (a right-handed man with 13.5 persons in household on average) is not represented.

and age and between sex and number of persons (11,895 individuals). Handedness did not have a significant effect ($p = .6$).

Position of the individual in the company and handedness

There are three different possible types of position in the EDF-GDF Company: 'workers' represents the lowest; 'control' is intermediate; and 'managerial staff' is the highest. They can be used as a simple measure of socio-economic status. In this sample, 14% of men and 26% of women belong to the 'execution' category, whereas 31% of men and 8% of women belonged to the 'managerial staff' category (total sample size: 10,592 men and 3,536 women).

The minimal model is constituted by the single terms age, sex and position (13,064 individuals). Left-handers are less frequent in low positions (7.4%) and high positions (8.2%), and more frequent in middle positions (9.3%) ($\chi^2 = 10.15$, $df = 2$, $p = .006$). The significance of the result is due to the difference in frequency of left-handers between the low and middle positions (pairwise comparisons). When the middle and high positions are pooled into a single category and the variable position in the company is used as the response variable in a logistic regression, the effect of handedness is significant ($\chi^2 = 5.36$, $df = 1$, $p = .02$; 2.78% of the variance explained, odds ratios: 1.08 for men, 1.18 for women). Left-handers are underrepresented in low positions and overrepresented in higher positions.

Leadership of the individual in the company and handedness

Response variable: Throwing handedness. The minimal model obtained contains only the terms age, sex and their interaction. Leadership has no significant effect ($p = .7$).

Response variable: Leadership (binary). The variable leadership was transformed into a binary variable: 'had at least sometimes a leadership position' or 'had never'. The minimal model contains only the terms age and sex. Handedness did not have a significant effect ($p = .5$).

Discussion

This report examined the hypothesis that handedness is associated with socio-economic status. Our main results are summarized in Table 4.

Educational level

In the present study, in both SU.VI.MAX and GAZEL cohorts, left-handedness was associated with a higher probability of passing the final exam of high school among women (see Figure 1 and Table 4).

There have been several previous attempts to relate handedness to educational level. Depending on the studies, left-handers seemed to have an advantage (Lansky, Feinstein, & Peterson, 1988; Noroozian, Lofti, Gassezadeh, Emami, & Mehrabi, 2002) or a disadvantage (Resch *et al.*, 1997). The discrepancy in these results could have various causes, for example the cross-cultural variability in educational systems, in social effects on handedness, or in gender effects on educational attainment.

Similar to the present study, several studies have revealed a gender effect on the relationship between handedness and school performance (Annett & Kilshaw, 1983; Faurie *et al.*, 2006; Sanders, Wilson, & Vanderberg, 1982).

Occupation and income

In the GAZEL cohort, a significant increase of the frequency of left-handers with increasing income is observed for both sexes, especially in men (see Figures 2 and 3, and Table 4). With respect to position in the company, left-handers are more frequent in high and middle positions, as compared to the low positions.

These aspects of socio-economic status were rarely considered in previous studies on handedness. (Lansky, Feinstein, & Peterson, 1988) found that among males, left-handers have a higher occupational status than expected by chance. Denny and O'Sullivan (2007) found a significant positive effect of left-handedness on male earnings and a negative effect on female earnings. (Ruebeck, Harrington, & Moffitt, 2007) also found an income advantage for left-handed men, but not for females.

Conclusions

We cannot conclude from our results that there is a causal relationship between handedness and educational level or income. However, the present study shows that associations, although rather weak, clearly exist.

Several limitations of this study are worth noting. The SU.VI.MAX cohort is constituted of volunteers of the general population, whereas in the GAZEL cohort, several professional categories were not represented, as all the subjects are workers in the EDF-GDF Company. The rate of response to the self-administered questionnaire

Table 4. Summary of the results

	Effect of handedness	Effect size	p-value	Variance explained	Odds ratio
Study 1					
Educational level	More LH in higher categories LH women have a higher probability of passing the final exam	$\chi^2 = 16.83, df = 1$ $\chi^2 = 5.63, df = 1$.02 .02	0.87% 2.75%	1.11
Occupational category	No significant effect				
Study 2					
Educational level	LH women have a higher probability of passing the final exam	$\chi^2 = 2.71, df = 1$	<.1	0.93%	1.10
Occupational category	Different frequencies of LH in different categories. Changes over time: increase in frequency of LH in highest categories for men	$\chi^2 = 11.40, df = 4$.02	0.33%	
Income	LH have a higher income (greater effect in men)	$\chi^2 = 5.6, df = 1$.02	1.75%	
Ownership	No significant effect				
Position in the company	More LH in higher positions	$\chi^2 = 10.15, df = 2$.006	2.78%	Men 1.08 Women 1.18
Leadership in the company	No significant effect				

in 2003 (74.8%) and in 2004 (69.7%) can be considered satisfactory. However, a selection bias cannot be totally excluded.

The strong points of this study should also be stressed. The study was based on two independent cohorts, which enables comparison. The sample sizes are very large, which enables us to tease out relatively small effects. In addition, the present study included both men and women, and as the sexes were analysed both together and separately, we were able to evaluate gender effects and explore sex-related differences regarding the relationship between handedness and socio-economic status. Our samples represent a fairly wide spectrum of the general population, and our analyses included several relevant confounding variables, thus reducing potential biases.

Globally, our findings reveal a complex association between handedness and socio-economic status. Although the effects are quite small, our results support the hypothesis that left-handers have a socio-economic status advantage, countervailing their costs. Left-handedness frequency is significantly higher: (1) among women of higher educational level; (2) among categories of higher income; and (3) among individuals who have a higher position in the company.

The observed relationship could be due to brain differences between left- and right-handers. Another possibility is that socio-economic status and hand preference may be related through cultural influences. It is likely that individuals with a high status were themselves raised in families of high socio-economic status. These families may have been more tolerant of individuality – such as left-handedness. They may also have sent their children to schools that were more tolerant of left-handedness. Thus, a higher incidence of left-handedness in individuals with higher socio-economic status may be the result of a more liberal developmental environment. Therefore, left-handers could be found in the higher status categories, not because of any special ability – but because they were brought up in a more tolerant environment. However, with the GAZEL cohort, we had the opportunity to collect information on hand preference for throwing, which is not likely to be influenced by familial and social pressures, like writing handedness.

The models explain a small proportion of the variance. However, the associations found are interesting from an evolutionary point of view, as reproductive value is not independent of socio-economic status. Is this advantage likely to act as a sufficient selective pressure to maintain the polymorphism of handedness in Western societies? The advantage of left-handers in fighting interactions, which has an important effect in traditional societies (Faurie & Raymond, 2005), is probably no longer significant in Western societies, where the type of violence has dramatically changed. In the present study, we show that left-handers have higher average incomes. This could constitute an important reproductive advantage (Buss, 1999; Elder, 1969; Kaplan & Hill, 1986; Pérusse, 1993). The incidence of left-handedness has been found to be very high in some social categories, as artists and musicians (Peterson, 1979; Quinan, 1922), mathematicians (Annett & Manning, 1990; Peters, 1991), and sport competitors (Raymond *et al.*, 1996). The extent to which the reproductive advantage of these categories (e.g. Faurie, Pontier, & Raymond, 2004) contributes to persistence of the polymorphism remains to be formally investigated.

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References

- Aggleton, J. P., Kentrige, R. W., & Good, J. M. M. (1994). Handedness and musical ability: A study of professional orchestral player, composers, and choir members. *Psychology of Music*, *22*, 148–156.
- Aggleton, J. P., Kentrige, 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.
- Annett, M. (1970). The growth of manual preference and speed. *British Journal of Psychology*, *61*, 545–558.
- Annett, M. (1985). *Left, right, hand and brain: The right shift theory*. London: LEA Publishers.
- Annett, M. (1992). Spatial ability in subgroups of left- and right-handers. *British Journal of Psychology*, *61*, 545–558.
- Annett, M., & Kilshaw, D. (1983). Right- and left-hand skill II: Estimating the parameters of the distribution of L-R differences in males and females. *British Journal of Psychology*, *74*, 269–283.
- Annett, M., & Manning, M. (1989). The disadvantages of dextrality for intelligence. *British Journal of Psychology*, *80*, 213–226.
- Annett, M., & Manning, M. (1990). Arithmetic and laterality. *Neuropsychologia*, *28*, 61–69.
- Annett, M., & Turner, A. (1974). Laterality and the growth of intellectual abilities. *British Journal of Educational Psychology*, *44*, 37–46.
- Ashton, G. C. (1982). Handedness: An alternative hypothesis. *Behavior Genetics*, *12*, 125–147.
- Bamshad, M. J., Watkins, W. S., Dixon, M. E., Jorde, L. B., Rao, B. B., Naidu, J. M., et al. (1998). Female gene flow stratifies Hindu castes. *Nature*, *395*, 651–652.
- Benbow, C. P. (1986). Physiological correlates of extreme intellectual precocity. *Neuropsychologia*, *24*(5), 719–725.
- Benbow, C. P. (1988). Sex differences in mathematical reasoning ability in intellectually talented preadolescents: Their nature, cause, effects, and possible causes. *Behavioral and Brain Sciences*, *11*, 169–232.
- Berczkei, T., & Dunbar, R. I. M. (1997). Female-biased reproductive strategies in a Hungarian gypsy population. *Proceedings of the Royal Society of London B*, *364*, 17–22.
- Betzig, L. L. (1986). *Despotism and differential reproduction. A Darwinian view of history*. New York: Aldine.
- Bishop, D. V. M. (1990). *Handedness and developmental disorder*. Hove: Erlbaum.
- Brito, G. N. O., Brito, L. S. O., Paumgarten, F. J. R., & Lins, M. C. F. (1989). Lateral preferences in Brazilian adults: An analysis with the Edinburgh inventory. *Cortex*, *25*, 403–415.
- 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*, *271*(Suppl. 3), S64–S66.
- Buss, D. M. (1999). *Evolutionary psychology, the new science of the mind*. Boston, MA: Allyn and Bacon.
- Byrne, B. (1974). Handedness and musical ability. *British Journal of Psychology*, *65*, 279–281.
- Casey, M. B., Pezaris, E., & Nuttall, R. L. (1992). Spatial ability as a predictor of math achievement: The importance of sex and handedness patterns. *Neuropsychologia*, *30*, 35–45.
- Cerone, L. J., & McKeever, W. F. (1999). Failure to support the right-shift theory's hypothesis of a 'heterozygote advantage' for cognitive abilities. *British Journal of Psychology*, *90*, 109–123.
- Chagnon, N. A. (1979). Is reproductive success equal in egalitarian societies? In N. A. Chagnon & W. Irons (Eds.), *Evolutionary biology and human social behavior: An anthropological perspective* (pp. 374–402). North Scituate, MA: Duxbury Press.

- Christman, S. D., & Propper, R. E. (2001). Superior episodic memory is associated with interhemispheric processing. *Neuropsychology*, *15*, 607–616.
- Coren, S. (1995). Differences in divergent thinking as a function of handedness and sex. *American Journal of Psychology*, *108*, 311–325.
- Coren, S., & Halpern, D. F. (1991). Left-handedness: A marker for decreased survival fitness. *Psychological Bulletin*, *109*, 90–106.
- Crawley, M. J. (2002). *Statistical computing. An introduction to data analysis using S-Plus*. West Sussex: Wiley.
- Crow, T. J., Crow, L. R., Done, D. J., & Leask, S. (1998). Relative hand skill predicts academic ability: Global deficits at the point of hemispheric indecision. *Neuropsychologia*, *36*, 1275–1282.
- Dellatolas, G., Luciani, S., Castresana, A., Rémy, C., Jallon, P., Laplane, D., *et al.* (1993). Pathological left-handedness. *Brain*, *116*, 1565–1574.
- Denny, K., & O'Sullivan, V. (2007). The economic consequences of being left-handed: Some sinister results. *Journal of Human Resources*, *42*, 353–374.
- Deutsch, D. (1978). Pitch memory: An advantage for the left-handed. *Science*, *199*, 559–560.
- Elder, G. H., Jr. (1969). Appearance and education in marriage mobility. *American Sociological Review*, *34*, 519–533.
- Faurie, C., Pontier, D., & Raymond, M. (2004). Student athletes claim to have more sexual partners than other students. *Evolution and Human Behavior*, *25*, 1–8.
- 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.
- Faurie, C., Vianey-Liaud, N., & Raymond, M. (2006). Do left-handed children have advantages regarding school performance and leadership skills? *Laterality*, *11*, 57–70.
- Francks, C., Fisher, S. E., MacPhie, I. L., Richardson, A. J., Marlow, A. J., Stein, J. F., *et al.* (2002). A genome-wide linkage screen for relative hand skill in sibling pairs. *American Journal of Human Genetics*, *70*, 800–805.
- Galaburda, A. M. (1991). *Asymmetries of cerebral neuroanatomy*. Paper presented at the Biological asymmetry and handedness, Ciba Foundation Symposium, London.
- Galaburda, A. M., LeMay, M., Kemper, T. L., & Geschwind, N. (1978). Right-left asymmetries in the brain. Structural differences between the hemispheres may underlie cerebral dominance. *Science*, *199*, 852–856.
- Gangestad, S. W., & Yeo, R. A. (1997). Behavioral genetic variation, adaptation and maladaptation: An evolutionary perspective. *Trends in Cognitive Sciences*, *1*, 103–108.
- Geschwind, N., & Behan, P. (1982). Left-handedness: Association with immune disease, migraine, and developmental learning disorder. *Proceedings of the National Academy of Sciences, USA*, *79*, 5097–5100.
- Goldberg, M., Chastang, J. F., Leclerc, A., Zins, M., Bonenfant, S., Bugel, I., *et al.* (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). 'Evolutionary' stable strategy of handedness in major league baseball. *Journal of Comparative Psychology*, *110*, 164–169.
- Grouios, G., Tsozbatzoudis, H., Alexandris, K., & Barkoukis, V. (2000). Do left-handed competitors have an innate superiority in sports? *Perceptual and Motor Skills*, *90*, 1273–1282.
- Hardyck, C., Petrinovich, L. F., & Goldmann, R. D. (1976). Left-handedness and cognitive deficit. *Cortex*, *12*, 266–279.
- Hassler, M., & Gupta, D. (1993). Functional brain organization, handedness, and immune vulnerability in musicians and non-musicians. *Neuropsychologia*, *31*, 655–660.

- Hercberg, S., Galan, P., Preziosi, P., Bertais, S., Mennen, L., Malvy, D., et al. (2004). The SU.VI.MAX Study: A randomized, 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., et al. (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. A., & Beveridge, R. (1978). Handedness and intelligence. *Cortex*, *14*, 304-307.
- Hicks, R. A., & Dusek, C. M. (1980). The handedness distributions of gifted and non-gifted children. *Cortex*, *16*, 479-481.
- Hill, J. (1984). Prestige and reproductive success in man. *Ethology and Sociobiology*, *5*, 77-95.
- Josephson, S. C. (1993). Status, reproductive success, and marrying polygynously. *Ethology and Sociobiology*, *14*, 391-396.
- Kaplan, H., & Hill, K. (1986). Sexual strategies and social class differences in fitness in modern industrial societies. *Behavioral and Brain Sciences*, *9*, 198-201.
- Lamm, O., & Epstein, R. (1999). Left-handedness and achievements in foreign language studies. *Brain and Language*, *70*, 504-517.
- Lansky, L. M., Feinstein, H., & Peterson, J. M. (1988). Demography of handedness in two samples of randomly selected adults ($N = 2,083$). *Neuropsychologia*, *26*, 465-477.
- Leask, S. J., & Crow, T. J. (2001). Word acquisition reflects lateralisation of hand skill. *Trends in Cognitive Sciences*, *5*, 513-516.
- Levy, J. (1969). Possible basis for the evolution of lateral specialisation of the human brain. *Nature*, *224*, 614-615.
- Mandal, M. K., Suar, D., & Bhattacharya, T. (2001). Side bias and accidents: Are they related? *International Journal of Neuroscience*, *109*, 139-146.
- Mayringer, H., & Wimmer, H. (2002). No deficits at the point of hemispheric indecision. *Neuropsychologia*, *40*, 701-704.
- 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. (1983). Pathological left-handedness: Does it exist? *Journal of Communication Disorders*, *16*, 315-344.
- McManus, I. C. (1991). The inheritance of left-handedness. In G. R. Bock & J. Marsh (Eds.), *Biological asymmetry and handedness* (Vol. 162, pp. 251-281). Chichester: 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., Shergill, S., & Bryden, M. P. (1993). Annett's theory that individuals heterozygous for the right shift gene are intellectually advantaged: Theoretical and empirical problems. *British Journal of Psychology*, *84*, 517-537.
- Mealey, L. (1985). The relationship between social status and biological success. *Ethology and Sociobiology*, *6*, 249-258.
- Mebert, C. J., & Michel, G. F. (1980). Handedness in artists. In J. Herron (Ed.), *Neuropsychology of left-handedness* (pp. 273-279). New York: Academic Press.
- Miller, E. (1971). Handedness and the pattern of human ability. *British Journal of Psychology*, *62*, 111-112.
- Netley, C., & Rovet, J. (1984). Hemispheric lateralization in 47, XXY Klinefelter's syndrome boys. *Brain and Cognition*, *3*, 10-18.
- Nettle, D. (2003). Hand laterality and cognitive ability: A multiple regression approach. *Brain and Cognition*, *52*, 390-398.
- Newcombe, P., & Ratcliff, G. (1973). Handedness, speech lateralization and ability. *Neuropsychologia*, *11*, 399-407.
- Newcombe, P., Ratcliff, G., Carrivick, P. J., & Hiorns, R. W. (1975). Hand preference and I.Q. in group of Oxfordshire villages. *Annals of Human Biology*, *2*, 235-242.

- Newland, G. A. (1981). Differences between left- and right-handers on a measure of creativity. *Perceptual and Motor Skills*, 53, 787-792.
- Noroozian, M., Lofti, J., Gassemzadeh, H., Emami, H., & Mehrabi, Y. (2002). Academic achievement and learning abilities in left-handers: Guilt or gift? *Cortex*, 38, 779-785.
- O'Callaghan, M. J., Tudehope, D. I., Dugdale, A. E., Mohay, H., Burns, Y., & Cook, F. (1987). Handedness in children with birthweights below 1,000 g. *Lancet*, 1, 1155.
- Olivier, G. (1978). Anthropometric data on left-handed. *Biométrie Humaine*, 13, 13-22.
- Palmer, R. E., & Corballis, M. C. (1996). Predicting reading ability from handedness measures. *British Journal of Psychology*, 87, 609-620.
- 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.
- Peters, M. (1991). Sex, handedness, mathematical ability, and biological causation. *Canadian Journal of Psychology*, 45, 415-419.
- Peterson, J. M. (1979). Left-handedness: Differences between student artists and scientists. *Perceptual and Motor Skills*, 48, 961-962.
- Peterson, J. M., & Lansky, L. M. (1974). Left-handedness among architects: Some facts and some speculations. *Perceptual and Motor Skills*, 38, 547-550.
- Porac, C., & Coren, S. (1980). Lateral preference in retardates: Relationships between hand, eye, foot, and ear preference. *Journal of Clinical Neuropsychology*, 2, 173-188.
- Powls, A., Botting, N., Cooke, R. W. I., & Marlow, N. (1996). Handedness in very-low birthweight (VLBW) children at 12 years of age: Relation to perinatal and outcome variables. *Developmental Medicine and Child Neurology*, 38, 594-602.
- Quinan, C. (1922). A study of sinistrality and muscle coordination in musicians, iron-workers and others. *Archives of Neurology and Psychiatry (Chicago)*, 7, 352-360.
- 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.
- Resch, F., Haffner, J., Parzer, P., Pfueller, U., Strehlow, U., & Zerahn-Hartung, C. (1997). Testing the hypothesis of the relationships between laterality and ability according to Annett's right shift theory: Findings in an epidemiological sample of young adults. *British Journal of Psychology*, 88, 621-635.
- Roskaft, E., Wara, A., & Viken, Å. (1992). Reproductive success in relation to resource-access and parental age in a small norwegian farming parish during the period 1,700-1,900. *Ethology and Sociobiology*, 13, 443-461.
- Ruebeck, C. S., Harrington, J. J. E., & Moffitt, R. (2007). Handedness and earnings. *Laterality*, 12, 101-120.
- Saigal, S., Rosenbaum, P., Szatmari, P., & Hoult, L. (1992). Non-right handedness among ELBW and term children at eight years in relation to cognitive function and school performance. *Developmental Medicine and Child Neurology*, 34, 425-433.
- Sanders, B., Wilson, J. R., & Vanderberg, S. C. (1982). Handedness and spatial ability. *Cortex*, 18, 79-80.
- Sicotte, N. L., Woods, R. P., & Mazziotta, J. P. (1999). Handedness in twins: A meta-analysis. *Laterality*, 4, 265-286.
- Steinmetz, H., Volkman, J., Jäncke, L., & Freund, H. J. (1991). Anatomical left-right asymmetry of language-related temporal cortex is different in left -and right- handers. *Annals of Neurology*, 29, 315-319.
- 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.
- Turke, P. W., & Betzig, L. L. (1985). Those who can do: Wealth, status, and reproductive success on Ifaluk. *Ethology and Sociobiology*, 6, 79-87.

- Udry, J. R., & Eckland, B. K. (1984). Benefits of being attractive: Differential payoffs for men and women. *Psychological Reports*, *54*, 47-56.
- Voland, E., & Chasiotis, A. (1998). How female reproductive decisions cause social inequality in male reproductive fitness: Evidence from 18th- and 19th- century Germany. In S. S. Strickland & P. S. Shetty (Eds.), *Human biology and social inequality* (pp. 220-238). Cambridge, MA: Cambridge University Press.
- Watson, N. V. (2001). Sex differences in throwing: Monkeys having a fling. *Trends in Cognitive Sciences*, *5*, 98-99.
- Witelson, S. F. (1992). Neuroanatomical bases of hemispheric functional specialization in the human brain: Developmental factors. In I. Kostovic, S. Knezevic, H. M. Wisniewski, & G. J. Spilich (Eds.), *Neurodevelopment, aging and cognition* (pp. 112-137). Berlin: Birkhauser.
- Witelson, S. F., & Kigar, D. L. (1988). Asymmetry in brain function follows asymmetry in anatomical form: Gross microscopic, postmortem and imaging studies. In J. G. Boller (Ed.), *Handbook of neuropsychology* (pp. 111-142). The Netherlands: Elsevier.
- Wittenborn, J. R. (1946). Correlates of handedness among college freshmen. *Journal of Educational Psychology*, *37*, 161-170.

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