Evolutionary Psychology

www.epjournal.net – 2011. 9(3): 354-370

Original Article

Left-handedness and Male-Male Competition: Insights from Fighting and Hormonal Data

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Abstract: Male-male competition can shape some behavioral or morphological traits of males. Here we investigate if this competition could play a role in the persistence of the polymorphism of handedness in human populations. A negative frequency-dependent selection mechanism has been hypothesized, based on the fact that left-handed men may benefit from a "surprise" advantage during fighting interactions because they are rare in human populations. This advantage may thereby enhance the probability of survival of left-handed men and/or their reproductive success through an increase in social status. In this study, we first explored the association between hand preference and lifetime fighting behavior in a population of 1,161 French men. No effect of hand preference on the probability of fighting was detected, suggesting that the innate propensity to fight does not differ between left- and right-handers. However, among men who had been involved in at least one fight during their lifetime, left-handers reported significantly more fights than right-handers. To explore the biological basis of this behavior, we also investigated the testosterone concentration in saliva samples from 64 French university students. Consistent

[1] Note: All authors contributed equally to this article.

with frequencies of fights, we found a significantly higher average testosterone concentration in left-handers than in right-handers. We suggest that these behavioral and hormonal differences may be acquired throughout life due to previous experiences in a social context and may favor the persistence of left-handers in humans.

Keywords: lateralization, hand preference, warfare, aggressiveness, humans, testosterone

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Introduction

Male-male competition is a key component of reproductive success and can include fighting behavior in many animal species, such as birds (e.g., black grouse; Hovi, Alatalo, and Siikamaki, 1995), mammals (e.g., mountain goat; Mainguy, Cote, Cardinal, and Houle, 2008) or insects (e.g., antler fly; Bonduriansky and Brooks, 1999). Male-male competition could therefore shape behavioral or morphological traits of males, as for instance the red color in agamid lizards (Healey, Uller, and Olsson, 2007) or the asymmetrical giant cheliped in fiddler crabs (Koga, Murai, and Yong, 1999). In fiddler crabs, the giant cheliped is on the right side of some individuals and on the left side of others, and the frequency of left- and right-handers is usually balanced, as shown for *Uca pugilator*, *Uca lactea* or *Uca burgersi* (Yamagushi, 1977). The proportion of left-handers was shown to be greater in human populations with higher homicide rates (Faurie and Raymond, 2005), suggesting that the evolution of hand preference frequencies could be influenced by the level of aggressive interactions involved in male-male competition.

In humans, hand preference is a heritable trait (Carter-Saltzman, 1980; Medland et al., 2009; Saudino and McManus, 1998; Sicotte, Woods, and Mazziotta, 1999) with heritability estimates ranging from 0.23 to 0.66 (Llaurens, Raymond, and Faurie, 2009b). Left-handers are likely to be an heterogeneous group and the determinism of hand preference is not fully characterized, but genetic (McManus, 1991), developmental (Yeo and Gangestad, 1993), and cultural (Hardyck, Goldman, and Petrinovich, 1975) factors have been identified to play a significant role.

Left-handers frequency has been observed to vary across human populations but to remain below 30% in all populations studied so far (Raymond and Pontier, 2004). This low frequency of left-handers is probably explained by the existence of survival costs, since left-handedness has been linked to a lower birth weight and a higher susceptibility to accidents and to some diseases (for a review see Llaurens et al., 2009b). Despite these costs, left-handers persist in human populations since at least the Paleolithic period (Faurie and Raymond, 2004). An evolutionary explanation has been suggested to explain the persistence of handedness polymorphism in humans. It has been suggested that left-handers benefit from their relative rarity due to a surprise effect in aggressive interactions, giving them a strategic advantage in fights (Raymond, Pontier, Dufour and Møller, 1996). Sport data are supportive of a frequency dependent advantage of left-handers in fights (Brooks, Bussière, Jennions, and Hunt, 2004; Goldstein and Young, 1996; Grouios, Tsorbatzoudis, Alexandris, and Barkoukis, 2000; Raymond et al., 1996). Because fights within and among human groups have probably been common throughout human evolution (Haas, 1990;

Keeley, 1996; Wrangham and Peterson, 1996), they might impose an important selective force shaping the evolution of handedness. However, the surprise effect of left-handers becomes weaker when they become less rare, thus their strategic advantage decreases when they increase in frequency, explaining the persistence of the polymorphism of handedness in human populations.

The idea of frequency-dependent selection is further supported by Faurie and Raymond (2005), who showed that the proportion of left-handers is greater in populations with higher homicide rates. This pattern may result not only from direct positive consequences of left-handers' fighting advantage for their survival but also from indirect consequences for their reproductive success via improved social status. For example, male involvement in athletic competition has been shown to be associated with a larger number of reported sexual partners (Faurie, Pontier, and Raymond, 2004) and a larger number of children (Llaurens, Raymond, and Faurie, 2009a). The prestige acquired through involvement in fights could thus provide an important sexual selection pressure. The present research aims to investigate whether left-handers exhibit behavioral and/or hormonal specificities that could improve their success in terms of male-male competition.

Although the fighting hypothesis does not imply any difference between right- and left-handers in their propensity to fight (because it is based on a simple frequency-dependent selection mechanism), the fact that left-handers are more numerous in populations in which homicides are more common raises the question of predisposition to violence. Indeed, the strategic advantage of left-handers might favor violent behavior. Because left-handers' chances of winning are greater due to the advantage of rarity (all else being equal), the self-confidence of these individuals might increase after fighting events, making them more likely to participate in future fighting interactions.

In this context, it is necessary to explore a possible biological basis for behavioral differences between right- and left-handers, in particular testosterone. Testosterone is indeed known to be correlated with aggressive behaviors in many species and to play a key role in competitive interactions and social dominance (Archer, 2006). Testosterone levels are plastic and respond to lifetime events (for a review see, e.g., Alvergne, Faurie, and Raymond, 2009), and in particular levels of testosterone have been observed to vary after fights in mice (Oyegbile and Marler, 2005) and humans (Booth, Shelley, Mazur, Tharp, and Kittok, 1989), or in a context of social competition in gulls (Ros, Dieleman, and Groothuis, 2002). Therefore, if differences between left- and right-handers exist in fighting behavior, these differences are expected to be reflected in testosterone levels. Furthermore, testosterone has long been suggested to be associated with handedness, based on the observation that there are more left-handed men than women (for review, see Papadatou-Pastou, Martin, Munafo, and Jones, 2008; Sommer, Aleman, Somers, Boks, and Kahn, 2008; Voyer, 1996). Theories about the organizational role of testosterone in brain development have led some authors to suggest an influence of testosterone *in utero* on adult hand preference (Geschwind and Galaburda, 1985; Grimshaw, Bryden, and Finegan, 1995; Lauter, 2007; Witelson and Nowakowski, 1991). Studies on the relative length of the second and fourth finger (2D-4D ratio), which appears to reflect prenatal testosterone exposure, have detected an association with handedness, indicating that, on average, left-handers were exposed to more testosterone *in utero* (Gillam, McDonald, Ebling, and

Mayhew, 2008; Manning and Peters, 2009). However, a meta-analysis of empirical studies failed to find support for this hypothesis concerning the influence of prenatal testosterone exposure (Pfannkuche, Bouma, and Groothuis, 2009). Few studies investigated testosterone concentration with respect to direction of hand preference in adult males. Higher testosterone levels were found in subjects pooled in a category of ‘anomalous dominance’: left-handers, mixed-handers, and right-handers with familial sinistrality (Tan, 1991). Using an index of handedness based on a combination of tasks, a significantly higher average testosterone level was found in right-handers (Moffat and Hampson, 1996), although this was not replicated by Moffat and Hampson (2000), in which no differences between groups were detected. A recent study (Beaton, Rudling, Kissling, Taurines, and Thome, 2010) did not find such differences either, using the peg-moving task to measure handedness. These studies used various indices and tasks to assess handedness and provided contrasted results. It was argued previously that the use of an index of hand preference combining several manual tasks is inappropriate for providing comparable handedness data, and that the tasks chosen to measure handedness should be logically related to the biological hypothesis tested (Faurie, Schiefenhövel, Le Bomin, Billiard, and Raymond, 2005). Thus, for example, if one wants to measure hand preference in the context of the hypothesis of a frequency-dependent advantage of left-handers in fights, the tasks chosen should be related to fighting actions. In the present study, we used reported hand preference for knife, because (1) cultural pressures are usually weaker for knife use than, for example, writing (see Llaurens et al., 2009b for a review); (2) knives are widely used throughout the world so that using this task allows multicultural comparisons (Faurie et al., 2005) and (3) since a knife can be used as a weapon, it seems relevant with respect to the frequency-dependent advantage of left-handers in fights.

In the first part of this study, we thus investigated the following questions: 1) Are left-handers intrinsically more inclined to fight (i.e., more likely to ever participate in a fight)? 2) Among men who had been involved in at least one fight, did left-handers fight more often than right-handers? For this purpose, we analyzed the self-reported lifetime number of fights in a sample of French adult males.

In the second part of this study, right- and left-handed men’s testosterone levels were measured in saliva samples from French university students.

Study 1: Self-Reported Lifetime Number of Fights

Materials and Methods

Study population

The study population was a subsample from the 2004 GAZEL cohort (employees in the national gas and electricity company), which included 19,688 subjects (men born between 1939 and 1948 and women born between 1939 and 1953). Since 1989, these subjects have been examined on a yearly basis using self-administered questionnaires and data collection by medical departments (Goldberg et al., 2001). The questionnaire sent in 2002 contained a question on self-perceived general health (8 categories) and a question on household monthly income (10 categories). In 2003, a section on laterality was included in the yearly questionnaire (Faurie, Goldberg, Hercberg, Zins, and Raymond, 2008).

Based on the results of general hand preference from the 2003 survey, the cohort was divided into left-handers and right-handers. A subset of 1,000 left-handers and 1,000 right-handers was randomly selected from the cohort. In 2004, an additional questionnaire was sent to this subset. The new questionnaire included an item on hand preference (hand used for cutting bread with a knife).

The questionnaire also contained the following questions: "How many times did you physically fight with a same-sex person since age 18?" and "For you, is it more difficult to win a physical fight against a right-hander, a left-hander or there is no difference?" (People were asked to choose 1 out the 3 possible answers). Date of birth, weight and height were available for all GAZEL cohort members. Only male participants were included in the present study.

This contribution to the GAZEL study was approved by the GAZEL Ethics Committee and by the French National Committee of Informatic and Liberties (CNIL) in 2002 (Declaration 903138).

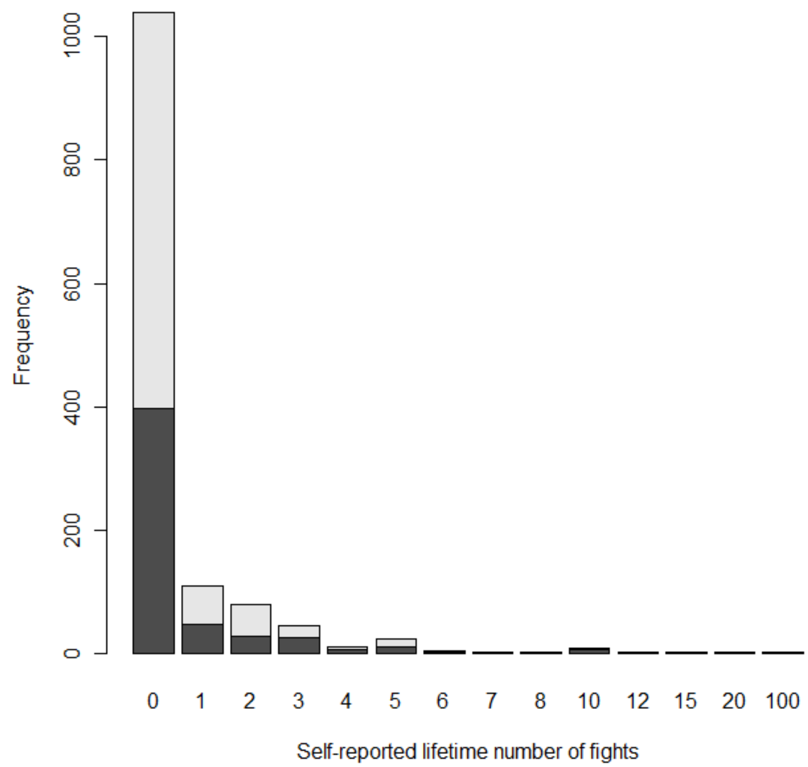
Analysis

The variable "self-reported lifetime number of fights" exhibits three characteristics that interfere with classical statistical analysis. First, the multimodal distributions of the raw data (see Figure 1) and residuals prevent the use of generalized linear models with Gaussian or Poisson distribution. Second, the large number of ties in the data (certain values, such as 5 and 10, are repeated many times due to psychological biases) leads to an incorrect estimate of the critical values from tables used in nonparametric tests. Third, the number of men that had never been involved in a fight was very large. Therefore, two GLMs were computed. First, the probability of ever having fought was treated as a binary variable by assigning a value of "0" to men who had never fought and a value of "1" to men who had been involved in at least one fight in their lifetime. Second, the rate of fighting ("rarely" versus "often") was treated as a binary variable by assigning a value of "0" to men who had been involved in one or two fights in their lifetime (rarely) and a value of "1" to men who had been involved in at least three fights (often). This categorization allowed us to partly circumvent a possible memory bias. The value of the threshold between "rarely" and "often" was selected by considering the mean (2.96) and the median (2.00) of the number of fights for men who had fought at least once.

The age of participants might have influenced the number of fights they had been involved in since the age of 18 because older men might have had more opportunities to fight than younger men. Physical condition (height and weight), socio-economic status, and health level might also have had an influence on the number of fights. Consequently, complete models were first built using hand preference, age, height, weight, socio-economic status and health level as explanatory variables, and interactions between hand preference and all other variables. Variables or interactions exhibiting no significant effect were then removed, to build a simplified model. For all models, the percentage of deviance explained, and/or odd-ratios and 95% confidence intervals, were reported for hand preference effect, when significant, to provide an estimation of effect sizes. All statistical analyses were performed using the software R 2.5.1 (R Core Development Team, 2005).

The perception of the left-hander's advantage in physical fights was analyzed as follows: Among the people perceiving an uneven wining chance between right and left-handers, a binomial variable was computed with value '0', when right-handers were perceived as advantaged, and '1' when left-handers were perceived as advantaged. This binomial variable was analyzed with a GLM.

Figure 1. Self-reported lifetime number of fights in the study population (*n* = 1,161 men): Distribution of raw data.



Note: Dark grey represent the proportion of left-handers; light grey represents the proportion of right-handers

Results

Description of the sample

Among the 2,000 persons who received the questionnaire, 70% responded. After eliminating incomplete questionnaires and considering only male participants, our sample size was 1,156 individuals. This sample was composed of 462 left-handers and 699 right-handers for knife use. The average age in this sample was 59.9 (± 2.9) when the study was conducted in 2004. On average, left- and right-handers exhibited no difference in height (Wilcoxon test; $W = 45325$, $p = 0.55$), weight (Wilcoxon test; $W = 45868$, $p = 0.39$), health status (Wilcoxon test; $W = 159349$; $p = 0.19$) and socio-economic status (Wilcoxon test; $W = 146551$; $p = 0.50$) but they slightly differed in age (Wilcoxon test; $W = 148723.5$, $p = 0.046$), with left-handers being younger ($M = 59.7 \pm 2.8$) than right-handers

($M = 60.1 \pm 2.9$). The average lifetime number of fights was 0.7 ± 3.4 and the median was 0. Among men who had been involved in at least one fight during their lifetime, the average lifetime number of fights was 2.96 ± 6.34, and the median 2. Among them, 122 were left-handers and 153 were right-handers (i.e., 26% of left-handers had been involved in at least one fight during their lifetime, compared to 22% of right-handers).

Concerning the perception of left-handers advantage in fights, only 24% thought there is an uneven winning chance between right- and left-handers. Among those people, 79.8% thought left-handers were more likely to win a fight. The hand preference had a significant effect on the knowledge of this advantage: Among people who perceive an uneven winning chance between right- and left-handers, left-handers were more likely to perceive left-handers as advantaged as compared to right-handers ($\chi^2 = 4.55$, $p = 0.03$), controlling for age, height and weight.

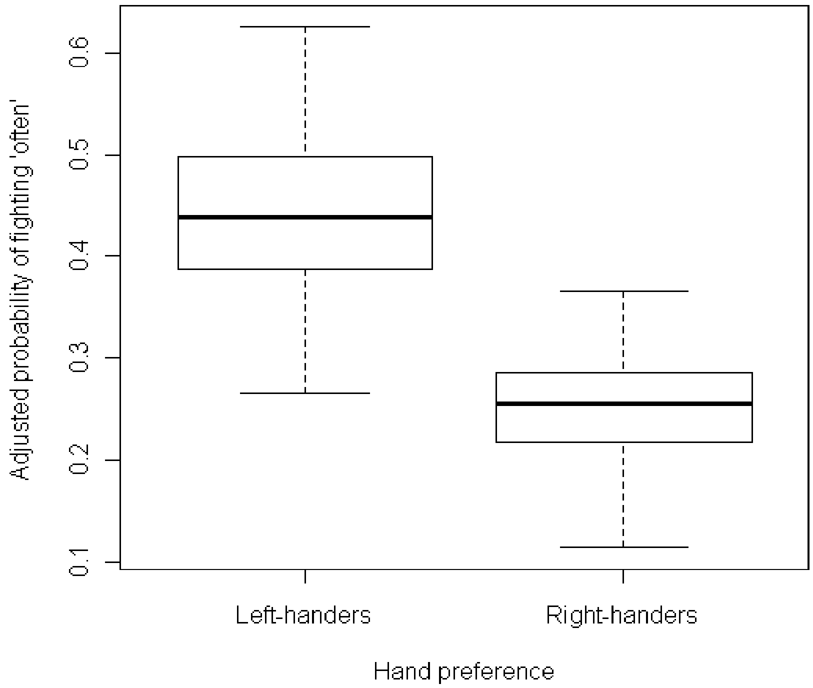
Probability of ever fighting

Socio-economic status, height and weight had a significant effect on the probability of ever having fought: Both socio-economic status and height had a negative effect ($\chi^2_1 = 7.35$; $p = 0.007$, and $\chi^2_1 = 4.90$; $p = 0.03$, respectively), whereas weight had a positive effect ($\chi^2_1 = 7.80$; $p = 0.005$). After controlling for socio-economic status, height and weight, hand preference had no significant effect on the probability of ever fighting ($\chi^2_1 = 0.17$; $p = 0.68$; 0.003 % of deviance explained; *Odd-ratio* = 0.92 [0.61- 1.39] with left-handers as a reference). Neither age ($\chi^2_1 = 0.003$; $p = 0.95$) nor health ($\chi^2_1 = 1.3723$; $p = 0.24$) had a significant effect on the probability of ever fighting, and there was no significant effect of interactions between hand preference and all control variables. Replacing the variables height and weight by the variable BMI (Body Mass Index) did not qualitatively change the association between hand preference and probability of ever fighting ($\chi^2_1 = 0.17$; $p = 0.68$, controlling for BMI and socio-economic status).

Frequency of fights

When considering only men who had fought at least once during their lifetime ($n = 275$), the proportion of men who had often been involved in fighting interactions was greater among left-handers (41.8%) than among right-handers (29.4%). Height had a marginally significant negative effect on the frequency of fights ($\chi^2_1 = 3.50$; $p = 0.06$), whereas weight had a significant positive effect ($\chi^2_1 = 3.93$; $p = 0.048$). Controlling for height and weight, hand preference had a significant effect on the frequency of fights ($\chi^2_1 = 5.21$; $p = 0.02$: 2.96 % of deviance explained; *Odd-ratio* = 0.43 [0.20 - 0.89] with left-handers as a reference). Left-handers were more likely to fight "often" as compared to right-handers (see Figure 2). Neither age ($\chi^2_1 = 0.06$; $p = 0.81$), nor socio-economic status ($\chi^2_1 = 0.08$; $p = 0.77$), nor health level ($\chi^2_1 = 0.38$; $p = 0.54$) had a significant effect on the frequency of fights, and there was no significant effect of interactions between hand preference and all control variables. Replacing the variables height and weight by the variable BMI (Body Mass Index) did not qualitatively change the association between hand preference and frequency of fights ($\chi^2_1 = 4.97$; $p = 0.02$, controlling for BMI).

Figure 2. Men's lifetime adjusted probability of fighting "often" versus "rarely" (binomial model) as a function of hand preference, adjusted for height and weight.



Study 2: Testosterone Concentration in Saliva Samples

Materials and Methods

Samples

Saliva samples were collected from 64 voluntary undergraduate male students aged 21.32 ± 2.78 years old (27 left-handers and 37 right-handers). Because testosterone release displays a circadian rhythm, with the highest concentrations in the morning and the lowest in the evening (Dabbs, 1990), we collected both morning and afternoon saliva samples. Other data were collected using a questionnaire. Students were asked to report what hand they preferred to use to cut a piece of bread with a knife (without fork) to be consistent with the handedness measurement used in Study 1. Volunteers also reported their age, body weight and height. They signed an informed-consent form as specified in the protocol approved by the French National Committee of Information and Liberty (CNIL authorization 1321739).

Measure of free testosterone concentration in saliva

Testosterone is a steroid of the androgen family that circulates in human blood, mainly linked to plasma proteins. Only a small proportion of testosterone (1-2%) is free and biologically active. In this study, testosterone concentrations were measured in saliva samples. This non-invasive technique has been previously validated and yields testosterone levels that are highly correlated with levels of free testosterone in the serum (Ellison, 1988;

Read, 1993).

Salicaps kits (IBL-Hamburg) were used to collect saliva samples. Each man was given labeled tubes and straws, and saliva was sampled twice a day: morning (9–11 AM) and afternoon (5–8 PM). For 50% of participants, morning and afternoon samples were collected on two consecutive days. For the others participants, two samples were collected the same morning and two samples were collected the same afternoon (with 30 minutes delay between the two samples collections of the morning and of the afternoon, respectively). Participants were asked to rinse their mouths with fresh water and to wait five minutes before providing saliva. Subjects were instructed not to eat or brush their teeth during the 30 minutes prior to collection and to immediately refrigerate each sample after collection. Saliva samples were brought back to the lab and immediately stored at –20°C. Each kit was returned with the self-questionnaire described above.

Testosterone levels in saliva samples were determined using Luminescence Immunoassay (LIA) kits (IBL, Hamburg) (Westermann, Demir, and Herbst, 2004). Saliva tubes were defrosted and centrifuged at 2400 rpm for 10 minutes. Standards, controls and samples were transferred in duplicate into wells of a microtiter plate. Freshly prepared enzyme conjugate and testosterone antiserum were then added into each well. The plate was incubated for four hours. The incubation solution was then discarded and the plate was washed four times with diluted wash buffer. After the excess solution was removed, the AP chemiluminescence reagent was introduced into each well, and relative luminescence units (RLU) were measured with a luminometer 10 minutes later. The measured RLU values of six standards (0 to 760 pg/mL) were plotted against their concentrations, allowing sample concentrations to be calculated directly from the standard curve (Microwin software). The sensitivity of this technique is 2.5 pg/ml at 30-110 pg/ml.

The saliva samples were set on 96 wells plates containing two controlled samples with low and high testosterone concentration, respectively (T1 and T2), which were already known. The inter-assay CV, i.e., the mean difference between measured and expected values of the control samples (T1 and T2) from the different plates, were 0.22 for low-concentration controls (T1) and 0.08 for high-concentration control (T2). The four saliva samples were also run in duplicate, and the intra-assay CV, i.e., the variation between the two measures from the same sample, was low (0.04 on average), giving us a confident measure of testosterone concentration. The pairs of samples collected in the morning exhibited a significant correlation for testosterone concentration ($r = 0.36$; $p < 0.04$), as well as the pairs of samples collected in the afternoon ($r = 0.51$; $p < 0.001$). The average of the two morning samples and the average of the two afternoon samples were thus used in the statistical analyses. The average of these two measures was used as average testosterone concentration of an individual.

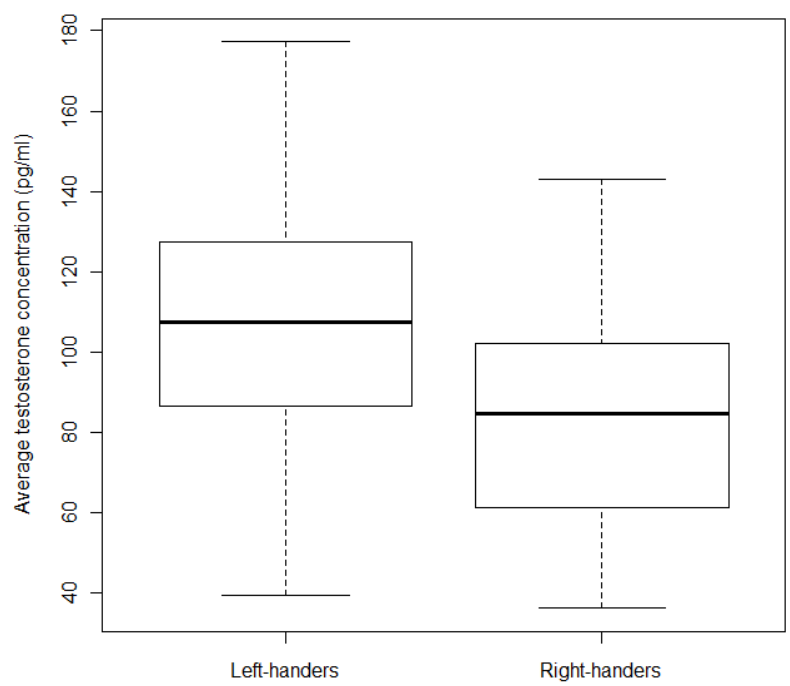
Statistical analyses

All statistical analyses were performed using the software R 2.5.1 (R Core Development Team, 2005). Using GLM, we tested the effect of hand preference on the average testosterone concentration (mean of morning and afternoon testosterone) as the response variable, while controlling for age, weight and height, which are all known to be linked to testosterone levels (Harman, Metter, Tobin, Pearson, and Blackman, 2001). The residuals of the model were assumed to follow a Gaussian distribution, which was verified by a Shapiro test.

Results

Figure 3 shows that average testosterone concentration was higher in left-handed men (M = 104.60 ± 35.26 pg/ml) than in right-handed men (M = 84.31 ± 29.99 pg/ml). This difference was significant, $F_{(1, 59)} = 4.00$; $p = 0.05$ (6.31% of deviance explained controlling for age, height and weight). The residuals of this model did not depart from the Gaussian distribution (Shapiro test: $W = 0.99$; $p = 0.93$). However, neither age ($F_{(1, 59)} = 0.12$; $p = 0.7$), nor weight ($F_{(1, 59)} = 0.47$; $p = 0.5$), nor height ($F_{(1, 59)} = 0.023$; $p = 0.9$) were significantly associated with average testosterone concentration. Replacing the variables height and weight by the variable BMI did not qualitatively change the association between hand preference and testosterone level ($\chi^2_1 = 4.32$; $p = 0.04$; controlling for age and BMI).

Figure 3. Average salivary testosterone concentrations among left- and right-handers (n = 64 men)



When removing the non-significant control variables, the positive relation between left-handedness and average testosterone concentration was still significant ($F_{(1, 63)} = 6.16$; $p = 0.02$; 9.03% of deviance explained).

The testosterone concentrations of morning and afternoon samples were significantly correlated ($r = 0.35$, $p = 0.006$). However, the difference between right- and left-handers in average testosterone concentration was due to the difference in the testosterone concentration in morning samples: Left-handers had a higher morning testosterone level compared to right-handers ($F_{(1, 58)} = 8.39$; $p = 0.005$), whereas the effect of hand preference on afternoon testosterone was not significant ($F_{(1, 60)} = 0.59$; $p = 0.45$). The residuals of these models did not depart from the Gaussian distribution (Shapiro test: $W = 0.98$; $p = 0.61$ and $W = 0.97$; $p = 0.14$, respectively).

Discussion

Involvement in fights

Since the proportion of left-handers is greater in populations with higher homicide rates (Faurie and Raymond, 2005), it has been questioned whether left-handers could have a more aggressive behavior. However, in the present data, no significant effect of handedness was found on the probability of ever having fought, which supports the hypothesis of no innate difference between right- and left-handers. These results thus support the hypothesis that previous successful experiences lead to an increase in fighting behavior, since a greater involvement of left-handers in fighting interactions was found among men who had fought at least once during their lifetime. The causal relations involved in the association between handedness and fighting behavior are not yet known. We hypothesize that left-handers tend to fight more often because of the psychological consequences of their increased chances to win a fight, due to their frequency-dependent advantage in fighting. Such a strategic advantage in previous fighting experiences could indeed improve their self-confidence. Only about a third of our sample noticed that handedness could influence the probability of winning a fight, but among them, a large proportion considered left-handers as advantaged, and this proportion was even higher among left-handers. Moreover, success in past experiences may increase left-handers' self-confidence, even without being conscious of their advantage being due to left-handedness. Hence the self-confidence of left-handers may increase throughout their lifetime and make them prone to fight more often. If winning a fight increases the probability to engage in future fights, then one can expect that more left-handers than right-handers will engage in more than one fight, due to the well described fighting advantage of lefties. Concerning the first fight in life, statistical analyses don't reveal any difference between left- and right-handers. This could either be due to a lack of power, an insufficient sample size, or to the fact that there really *is* no difference. An absence of difference is, however, not incompatible with the fighting hypothesis. It may not be possible to adopt a fighting strategy in order to take advantage of fighting superiority before being aware (consciously or not) of this superiority.

The information on who started the fight and who won would allow better testing of this hypothesis. Obviously, if left-handers take part in more fights but lose the majority of their fights, then this would not be in support of the fighting hypothesis. Such measures need to be incorporated in further research. Whatever the psychological and biological basis of such behavioral differences, the greater involvement of left-handers in fights may improve their success in male-male competition.

Health status and age exhibit no significant association with the probability of ever fighting and with the frequency of fights, whereas the socio-economic status does. Weight (and height, to a lesser extent) was associated in this sample with the probability of ever fighting and with the frequency of fights. Heavier men seemed more prone to fighting. Weight could indeed confer a greater probability of winning, and successful past experiences might have similarly improved the heavier men's self-confidence and increased their desire to fight.

Note that participants might have interpreted the term "physical fight" differently: some might include pushing or grabbing, whereas others might only consider punching, beating or kicking as real physical fighting. Such variability would, however, not challenge our results, provided that the definition of fights is not systematically biased according to hand preference. The estimation of the number of fights by self-reports might be distorted by memory bias or deceptive response. However, fighting events are probably less subject to oblivion than more common or daily events, although this has not been formally measured. In addition, data have been categorized, thus reducing the effects of a possible memory bias. Direct behavioral observations of both fighting behavior and hand preference would allow further testing of our hypothesis.

Another bias is possible, due to a response bias: Although our questionnaire was sent to 50% of right- and 50% of left-handers, our final sample comprises only 40% of left-handers. If non-respondents have fought significantly less than respondents, there is potentially a bias.

Hormonal differences between right- and left-handers

Study 2 was designed to examine whether handedness is associated with one of the hormonal factors that influence aggressive behaviors: testosterone. Left-handers were shown to have on average a testosterone concentration about 20% higher than right-handers (see Figure 2). We found a greater effect of hand preference in morning samples as compared to afternoon samples. The biological significance of such daily variations is yet unknown and further research is required to be able to interpret them.

Previous studies have shown that elevated testosterone levels have a negative impact on men's health (Booth, Johnson, and Granger, 1999) due to their immunosuppressive effect. Our findings may thus partially explain the greater susceptibility of left-handers to various diseases (see Llaurens et al., 2009b for a review).

Testosterone, aggressive behavior and mating strategies

Higher testosterone concentrations in left-handers could be linked to their greater involvement in male-male competition through physical fighting observed in Study 1. Testosterone concentration is known to be correlated with social competition in men (Archer, 2006). For instance, the testosterone levels of male tennis players increase before the beginning of the game (Booth et al., 1989). Similar results have been found for players of videogames (Gladue, Boechler, and McCaul, 1989) and chess (Mazur, Booth, and Dabbs, 1992). In these papers, they also demonstrated that after athletic competition, testosterone concentrations continue to increase in winners but decrease in losers. Due to this plasticity of testosterone concentrations, we are not able to infer the direction of the possible causal relationship between left-handers' higher testosterone concentrations and their greater involvement in fighting interactions. Hormonal differences between right- and left-handers could be either innate or acquired during past social interactions. A longitudinal study of testosterone levels at various ages would be necessary to understand the origin of hormonal differences between right- and left-handers. There are other possible explanations of the association between hand preference and testosterone. For example, birth stress, which is linked to handedness in some cases (McManus, 1981), could also be responsible for a higher testosterone level (possibly indirectly, via stress hormones).

Levels of testosterone have been shown to be associated with mating strategies. In humans, male reproductive success is influenced by the trade-off between mating effort and parenting investment (Waynforth, 1999). This trade-off has been shown to be mediated by testosterone concentration. For instance, testosterone concentration has been observed to be higher in men with multiple sexual partners than in men engaged in a monogamous relationship (Van Anders, Hamilton, and Watson, 2007), and higher in men with several wives in polygynous societies (Alvergne et al., 2009). High testosterone levels thus seem to be associated with competitive mating behavior in men (Archer, 2006). The higher level of testosterone detected in left-handers may lead to increased competitiveness in mating effort. Thus, testosterone levels may be linked to differences in both aggressive behavior and mating strategies. Therefore, this hormonal difference between left- and right-handed men is likely to have an important impact on fitness components and could shape the evolution of left-handedness frequency in humans.

This study focused on handedness in men only, but it would be interesting to investigate these questions with women too. It has been shown that left-handedness could be maintained in women because of an indirect fitness benefit through left-handed sons (Billiard, Faurie, and Raymond, 2005): If left-handed males have greater reproductive success, this might bring an indirect fitness benefit to their mothers. Comparing men and women concerning the link between handedness, fighting behavior, and testosterone concentration might allow evaluating the relative importance of direct and indirect benefits of left-handedness in both sexes.

Conclusions

The differences between right- and left-handed men in fighting behavior and in testosterone concentrations suggest an increased competitiveness of left-handers. This study thus highlights that male-male competition could play an important role in the persistence of the polymorphism of handedness during human evolution.

However, our study of fighting behavior does not imply any general conclusion on left-handers' aggressive behavior; it only opens trails for further research, as for instance the three following: (1) our study on lifetime number of fights focuses on a single population and the trend found here needs to be investigated in other populations; (2) this study is based on reported number of fights, and actual number of fights could perhaps be estimated more accurately; (3) the differences in testosterone concentration between right- and left-handers is not directly transposable into behavior: Indeed, the density and receptivity of testosterone receptors should also been characterized.

Acknowledgements: The authors would like to thank the Medical Committee of EDF–GDF and all the volunteers who participated in the GAZEL study and the saliva-sample collection. The authors would also like to thank A. Courtiol for useful comments on statistical analyses, V. Durand for bibliographic help and two anonymous reviewers for useful comments on the manuscript. This is contribution ISEM 2011-103 of the Institute of Evolutionary Science of Montpellier.

Received 17 January 2011; Revision submitted 23 June 2011; Accepted 28 July 2011

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