Frequency-dependent maintenance of left handedness in humans

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SUMMARY

The percentage (10–13 %) of left handedness in humans has apparently not changed since the Neolithic. Left handedness is heritable and appears to be repeatedly associated with some reduced fitness components; the persistence of left handedness implies that left handers have a fitness advantage in some situations. We propose that left handers have a frequency-dependent advantage in fights and for that reason a fitness advantage. To test this hypothesis, left handedness frequencies in the general population and in sporting individuals (both students and the sporting elite) have been compared, as sporting performance is likely to be a good indicator of fighting abilities. The higher proportion of left-handed individuals in interactive sports (reflecting some fighting elements), reaching 50 % in some sports categories, but not in noninteractive sports, is consistent with the fighting hypothesis. The greater frequency of left handedness in males than in females is also consistent with this hypothesis, as male-male fights are universally more frequent than other combinations. The frequency-dependent advantage in fights of left handers might explain the stability of left handedness.

1. INTRODUCTION

The great majority of humans (*Homo sapiens*) are right handed for object manipulation, but around 10–13 % are left-handed, with some cultural variations (Connolly & Bishop 1992; Gilbert & Wysocki 1992; Marchant *et al.* 1995 and references therein). This percentage has apparently not changed during historical times, and probably not greatly during the Neolithic or at least during the upper Palaeolithic period (Coren & Porac 1977). A right-hand bias in tool making or tool use is still apparent in several Hominine taxa, up to 1.9 million years ago (Toth 1985). This contrasts with their closest living relatives (*Pan sp.*), which do not seem to present population level hand bias asymmetry comparable with that of humans (Finch 1941; Boesch 1991; Hopkins & Morris 1993; Ward & Hopkins 1993).

Left handedness is heritable (e.g. Levy 1972; Annett 1985; McManus 1991), although the relative importance of genetical (including the corresponding number of genes involved) and cultural inheritance is still unsettled (Yeo & Gangestad 1993; Laland *et al.* 1995). Two aspects of handedness are surprising. First, there is a significant sex effect, the proportion of left-handed men exceeding left-handed women. For example, among 5500 English aged 31–40 years, 10 % of men and 8 % of women use their left hand for writing (Davis & Annett 1994). In the United States, in a sample of more than one million individuals aged 10–50 years, 10.1 % of men and 7.6 % of women use their left hand to throw a ball (Gilbert & Wysocki 1992). Second, left handedness is repeatedly associated with various developmental disorders and reduced fitness components (see reviews in Coren 1992; Yeo 1993). For example left handers are generally shorter, lighter, older at puberty and have a lower life expectancy (Olivier 1978; Coren 1989; Coren & Halpern 1991; Coren 1992; Aggleton *et al.* 1993; Yeo & Gangestad 1993; Fudin *et al.* 1994). Although much controversy surrounds the latter point (see e.g. Wood 1988; Rothman 1991; Harris 1993), recent extensive data from another laboratory seems to confirm the lower life expectancy of left handers (Aggleton *et al.* 1993).

The persistence of left handedness in humans has always been puzzling (e.g. Toth 1985; Connolly & Bishop 1992; Yeo & Gangestad 1993), as left handedness is heritable and appears to be associated with reduced fitness; this persistence requires that left handers have a fitness advantage in some situations. This advantage should have prevailed in prehistoric and historical times, and in all cultures, in order to explain the archaeological and current records of left handedness.

Left handers have a frequency advantage when they engage in combat. This is because left-handed individuals usually interact with right handers who are more numerous, and are therefore more accustomed to encountering other right handers. Thus, when a right-left (R-L) conflict occurs, the right-handed person is in a relatively unfamiliar situation. Winning a fight could have varied fitness-related consequences. The most proximate consequence is that the combatant survives the fight itself, but more subtlely the winner may gain a higher dominance rank or a better social status. He may also directly increase his fecundity, for example, in warfare directed to kidnap females, as commonly found for example, in the Yamomamo Indians (Gibbons 1993).

The hypothesis of a higher advantage of left handers during fights or aggressive interactions may be indirectly tested by considering handedness of individuals involved in various sports. Sporting performance is likely to be a good indicator of fighting abilities. For example, fencing is related to fighting with a weapon, and boxing, karate, judo and martial arts are related to some aspects of hand-to-hand combat. Other sports are more indirectly related to fighting, but interactions between two or more opponents are still apparent, as in tennis, table tennis, badminton and team games like rugby and handball. Other kinds of sports such as gymnastics, swimming, athletics, and ten-pin bowling are noninteractive.

To test the fighting hypothesis, data on handedness in students devoted to sports and in the sporting elite have been collected, and compared to handedness in the general population. The null hypothesis is that no difference in the percentage of left handedness should exist between the general population and sporting individuals. The alternative hypothesis is that the proportion of left handers is higher in interactive sports (reflecting some fighting abilities), but not in non-interactive sports. Both sporting students and the elite have been analysed, to detect at which level any left-hand advantage was apparent.

2. MATERIALS AND METHODS

A questionnaire was given to 350 sporting students registered for 'sport sciences' in Lyon I University, France. Sports were sorted within two categories: 'interactive sports', when two or more opponents are involved (martial arts, tennis, table tennis, badminton, rugby, soccer, volleyball, basketball and ice hockey) and 'noninteractive sports', when no direct opponent could be clearly identified (swimming, gymnastics, athletics, skiing, climbing, rowing, archery, sailing, cycling, ice dancing and kayaking.). Participants provided information on their age, sex, body mass, and height. They also reported which hand (left or right) they used for writing and which eye and foot they considered dominant. Specific instructions were given for the last two parameters. Data on eye and foot dominance will be reported elsewhere.

Table 1. *Percentage of young male and female left-handers in large samples as reported in the literature*

(Data concerning 18–40 years individuals are selected from a recent English survey (Davis & Annett 1994) and from the 1986 smell survey of National Geographic readers (Gilbert & Wysocki 1992). Left handedness is recorded for either handwriting or ball throwing. Underlined values correspond to the maximum values for each sex and both types of handedness and are used as conservative values when the alternative hypothesis is an increase in left handedness. Italic values equate to the corresponding minimum values, used when the alternative hypothesis is no increase in left handedness.)

	N	male	female
handwriting			
English 1980–1986:			
18–30 years	8935	12.5	9.9
31–40 years	5530	*10.0*	*8.0*
smell survey 1986:			
18–30 years	197187	<u>13.0</u>	<u>10.7</u>
31–40 years	328263	13.0	10.2
throwing			
smell survey 1986:			
18–30 years	197187	*10.0*	*7.5*
31–40 years	328263	<u>10.3</u>	<u>7.7</u>

Handedness of the elite in major leagues of various sports was collected from official records or published data. Functional handedness was determined from the hand that holds the racquet, the bat, the ball, the bowl, the cue or the dart (for tennis, table tennis, badminton, cricket, baseball, ten-pin bowling, snooker and darts), the sword, sabre, or foil (for fencing) or the javelin, discus or shot (for athletics). Handedness (for hand writing or throwing) in the general population was estimated from published sources considering recent large samples in which sex and age effects were controlled.

The difference between the percentage of left handers in the general population and the sample analysed was tested using a one-sided Fisher exact test on 2×2 contingency tables (Fisher 1970). The counts of right and left handers in large samples were used as estimates of the true proportion in the general population. For each test, the P value corresponded to the probability of finding a higher or equal number of left handers than observed. Global tests were performed by combining individual P values using Fisher's method (Fisher 1970).

We tested for an overall effect of sex (qualitative variable SEX) and type of sport (interactive vs noninteractive, qualitative variable TYPE) on the incidence of left handedness in champions across studies. The homogeneity of the proportion of left handers across studies was first evaluated, taking into account SEX and TYPE as well as their interaction, using a logistic regression. Homogeneity was not accepted (residual variance = 396.72, df = 56, $P < 10^{-5}$), thus the regression model was not adequate. An analysis of variance on the proportions of left handers was used to test for the effect of SEX and TYPE, as well as for their interaction, where each proportion is weighted by its binomial variance. In this analysis, the residual variance is a measure of heterogeneity between studies. Models were fitted using GLIM software (Baker 1987).

Two large surveys have been performed recently to estimate handedness in males and females of known age. The first concerns 33401 English individuals (Davis & Annett 1994), the second comprised 1177507 readers of National Geographic participating in a smell survey (Gilbert & Wysocki 1992). Depending on the study, people who used their left hand to write represented 10.0 or 13.0% of young males, and 8.0 or 10.7% of young females (table 1). For the same age classes, people using their left hand for throwing represented a maximum of 10.3% for males and 7.7% for females (table 1). When the alternative hypothesis is an increase of left handedness (as for interactive sports), the maximum of those values for each sex are used as estimate of the true population parameters (table 1). When the alternative hypothesis is no increase of left handedness (as for noninteractive sports), the minimum of those values for each sex are used as estimates of the true population parameters (table 1). This ensures that all tests presented are conservative.

3. RESULTS

(*a*) *Handedness among sporting students*

Left handedness has a greater frequency in male or female sporting students than in the general population, although these increases are not significant ($P = 0.094$ and $P = 0.079$, respectively). A global test across sexes (Fisher's method) is however significant at the 0.05 significance level (table 2). When only noninteractive sports are considered, no significant ($P > 0.20$) increase of left-handed students are apparent. However, when only interactive sports are analysed, left handers are at a significantly greater frequency (table 2).

(*b*) *Handedness among the sporting elite*

Data on functional handedness have been collected for elite or champions in various sports. To detect an increase of functional left handedness, a comparison with the percentage of left-throwers in the general population has been performed. The percentage of left throwers could represent a direct measure of functional handedness, at least for some sports like baseball. In addition, handedness for throwing (ball, dart, etc.) or holding a racquet are almost identical (Peters & Murphy 1992). However, as there are fewer left throwers than left writers (Gilbert & Wysocki 1992), conservative tests using the percentage of left writers in the general population have also been performed for comparison.

In general, the percentage of functional left-handed sporting elite is higher than in the general male or female population (using either left throwers or left writers as a reference), reaching around 15% for tennis, 18.5% for cricketers, 23% for badminton, 32% for table tennis, 41% for first-base men in baseball and 50% for fencing (table 3). These values are significantly higher than the general population value, except in a few cases where the sample size is low (between 17 and 33). Moreover, this increase is generally greater for males than for females. As expected for noninteractive sports, the percentage of left handers was not different from that of the general population (table 3). Globally, the average weighted proportion of left handers was 0.32 in interactive sport and 0.11 in noninteractive sports, the difference (0.21 ± 0.14) being highly significant ($P = 0.004$). The effect of sex ($P = 0.13$) as well as the interaction between sex and type of sport ($P = 0.77$) were not significant.

Table 2. *Handedness for writing among sporting students from Lyon, France*

(N: sample size; %L: percentage of left-handers. The P-value refers to the unilateral 2×2 Fisher exact test, when the population percentage of left-handed writers is conservatively estimated as 13.0% for males and 10.7% for females (see table 1) when the alternative hypothesis is an increase of left-handedness (as for sporting students and interactive sports), and 10.0% for males and 8.0% for females when the alternative hypothesis is no increase of left-handedness (as for noninteractive sports). Bold characters indicate significant ($P < 0.05$) values. 'All' refers to a global test using using Fisher's method. See text for details.)

	N	% Left handers	P-value
All sports			
male	208	16.4	0.097
female	142	14.8	0.080
all			**0.046**
noninteractive sports			
male	57	14.0	0.21
female	69	10.1	0.32
all			0.25
interactive sports			
male	151	17.2	0.084
female	73	19.2	**0.022**
all			**0.013**

Three exceptions were noticeable for the general increase of functional left handedness in interactive sports. First, baseball elites playing as infielders or catchers were all right handed. Second, no increase in left handedness was significant for elite female tennis players. Third, the increase in the percentage of left-handed fencers using sabre was moderate compared with fencers using a sword or a foil (table 3).

4. DISCUSSION

Several evolutionary hypotheses have been proposed to explain right handedness in humans. The ultimate cause for the emergence of right handedness is assumed to be the development of language in the left hemisphere (e.g. Annett 1985; Levy, 1972), a rapid motor sequence in the left hemisphere for throwing ability during hunting (Calvin 1982), a postural asymmetry during feeding as observed in prosimians (MacNeilage *et al.* 1987; MacNeilage 1993), a preferred left side for infant cradling, freeing the right hand for other purposes (Hopkins *et al.* 1993), a specialization of hands in tool behaviour, and a competition for neural space (Frost 1980). None of these makes *a priori* predictions of the existence of a stable fraction of left handers.

The fighting hypothesis leads to a stable polymorphism of left- and right-handed individuals. Without the reduction in some fitness components observed

Table 3. *Functional handedness for elite or champions of various sports*

(N: sample size; $\%L$: percentage of left-handers. The P-value refers to the unilateral 2×2 Fisher exact test, when the population percentage of left throwers is conservatively estimated as 10.3% for males and 7.7% for females (see table 1) when the alternative hypothesis is an increase of left handedness (for interactive sports), and 10.0% males or 7.5% females when the alternative hypothesis is no increase of left handedness (as for noninteractive sports). Bold characters indicate significant ($P < 0.05$) values. Underlined characters indicate significant ($P < 0.05$) values, when the population percentage of left writers is conservatively estimated as 13.0% males or 10.7% females (for interactive sports), and 12.5% males or 9.9% females (for noninteractive sports). Handedness of young elite gymnasts and goalkeepers refers to hand writing.)

	male			female			
	N	% left handers	P	N	% left handers	P	references
interactive sports							
tennis							
Wimbledon 1978	128	15.6	**0.040**	96	9.4	0.320	(Annett 1985)
champions 1947–1978	33	15.2	0.251	33	6.1	0.733	(Annett 1985)
world ranking							
Top 200, 1980	200	17.0	**0.003**	—	—	—	(Azémar *et al.* 1983)
Top 100, 1981	85	16.5	0.053	90	11.1	0.154	(Wood & Aggleton 1989)
Top 100, 1982	100	16.0	0.051	—	—	—	(Annett 1985)
Top 100, 1986	100	14.0	0.149	98	11.2	0.133	(Wood & Aggleton 1989)
Top 100, 1987	100	13.0	0.232	—	—	—	(Annett 1985)
Top 100, 1994	100	16.0	0.051	100	5.0	0.891	this study
table tennis							
Danish elite:							
boys/girls	22	31.8	**0.005**	16	6.3	0.722	this study
junior	15	30.0	**0.015**	16	25.0	**0.030**	this study
senior	20	20.0	0.145	16	25.0	**0.030**	this study
world ranking							
top 146, 1994	146	17.8	**0.004**	146	16.4	**$< 10^{-4}$**	this study
badminton							
Danish elite	22	22.7	0.070	17	11.8	0.381	this study
fencing							
French Natl. Team 1965	20	55.0	$< 10^{-5}$	—	—	—	(Azémar *et al.* 1983)
champions 1979–1993							
sabre:							
registered	550	13.6	**0.009**	—	—	—	(Azémar & Stein 1994)
last 8	56	12.5	0.357	—	—	—	(Azémar & Stein 1994)
sword:							
registered	879	23.9	$< 10^{-5}$	145	21.4	$< 10^{-5}$	(Azémar & Stein 1994)
last 8	56	37.5	$< 10^{-5}$	8	37.5	**0.019**	(Azémar & Stein 1994)
foil:							
registered	807	33.3	$< 10^{-5}$	659	27.0	$< 10^{-5}$	(Azémar & Stein 1994)
last 8	56	50.0	$< 10^{-5}$	56	33.9	$< 10^{-5}$	(Azémar & Stein 1994)
world ranking							
Top 25, 1980	25	48.0	$< 10^{-5}$	—	—	—	(Coren 1992)
boxing							
Danish amateurs	95	6.3	0.936	—	—	—	this study
Danish champions	26	23.1	**0.046**	—	—	—	this study
baseball							
Up to 1975:							
pitchers	3707	26.0	$< 10^{-5}$	—	—	—	(Coren 1992)
1994:							
pitchers	233	21.0	$< 10^{-5}$	—	—	—	this study
Top 30	30	20.0	0.083	—	—	—	this study
batters	445	24.0	$< 10^{-5}$	—	—	—	this study
Top 30	30	36.6	$< 10^{-4}$	—	—	—	this study
first base	32	40.6	$< 10^{-5}$	—	—	—	this study
outfielders	100	29.0	$< 10^{-5}$	—	—	—	this study
infielders and catchers	128	0.0	1.00	—	—	—	this study
cricket							
1868–1988	3165	18.5	$< 10^{-4}$	—	—	—	(Aggleton *et al.* 1993)
batsmen 1968–1988	371	15.6	**0.001**	—	—	—	(Wood & Aggleton 1989)
bowlers:							
1937	150	15.3	**0.036**	—	—	—	(Wood & Aggleton 1989)
1949	137	21.2	$< 10^{-3}$	—	—	—	(Wood & Aggleton 1989)

Table 3. (*cont.*)

	male			female			
	N	% left handers	*P*	*N*	% left handers	*P*	references
1961	141	17.7	**0.005**	—	—	—	(Wood & Aggleton 1989)
1973	150	26.1	**$<10^{-4}$**	—	—	—	(Wood & Aggleton 1989)
1985	139	17.3	**0.008**	—	—	—	(Wood & Aggleton 1989)
Noninteractive sports:							
young elite gymnasts	—	—		36	11.0	0.484	(Feigley 1985)
goal keepers	167	9.6	0.663	—	—	—	(Wood & Aggleton 1989)
discus, javelin & shott put champions, 1995	28	10.7	0.539	22	4.5	0.820	this study
darts							
best English players	100	3.0	0.998	—	—	—	(Aggelton & Wood 1990)
official dart diary	55	5.5	0.922	—	—	—	(Aggelton & Wood 1990)
ten-pin bowling							
Top 1987 season	131	9.9	0.551	213	6.6	0.733	(Aggelton & Wood 1990)
snooker							
1987 world list	125	8.8	0.713	—	—	—	(Aggelton & Wood 1990)

in left handers, the stable equilibrium would have been a 1:1 ratio in the population. The current value, around 10% of left throwers in the male population, reflects the equilibrium between the deleterious effects associated with left handedness (review in Yeo & Gangestad 1993) and the proposed fighting advantages. These fighting advantages are frequency dependent, being zero when left and right handers are equally numerous, and increasing when the frequency of left-handed fighters decreases. The fighting hypothesis offers an ultimate explanation for the existence and the persistence of left handers, and is not in disagreement with other suggestions offering only a proximal cause for this polymorphism, such as Annett's right-shift model (Annett 1964, 1985).

The generally higher proportion of left-handed individuals in interactive sports, but not in non-interactive sports, is consistent with the fighting hypothesis (tables 2–4). The case of javelin or discus throwers, dart, ten-pin or snooker players, and of shot putters is particularly interesting, as these non-interactive sports requires a high degree of lateralization. This indicates that lateralization *per se* is not responsible for the frequency increase of left handers in interactive sports. This higher proportion of left handers is apparent in sport students, indicating that left handedness is already advantageous within the first steps of selection towards international sporting levels.

Handedness among sporting individuals sometimes has surprising distributions (table 3). In baseball, left handedness seems advantageous in some positions (pitchers, batters, first base, and outfielders) but not in others (second and third base, short stops and catchers). Left-handed fencers have an advantage, if they use a sword or a foil, but it is less if they use a sabre. These differences are probably explained by the specific setting and rules for each kind of sport. For example, the fielding of the baseball game is asymmetric, and to cover the passage of balls from infield to outfield all but the first basemen should be right-handed (R. Trivers, personal communication). For fencing, there are numerous different rules and tactics depending on whether a sabre, a sword or a foil is used. For example, sabre fighters are at a greater distance from each other than sword or foil fighters, despite the shorter conventional length of the sabre because, by convention, the hand and the arm are potential targets only for sabre fighters (Revenu & Thomas 1992). Either of these specific rules probably explains why left-handed fencers do not experience the same advantage for sabre, foil and sword. Such differences, due to arbitrary conventions, indicate the limits of using sports performance as a model of direct aggressive ability in humans. The higher proportion of left handers in some sports has previously been reported (e. g. Annett 1985; Coren 1992), and a supposed neurological advantage has been ruled out (Wood & Aggleton 1989). A frequency-dependent advantage has been proposed to explain this higher frequency (Wood & Aggleton 1989), but its significance to explain the maintenance of left handedness has apparently been overlooked.

The fighting hypothesis is consistent with the greater frequency of left-handed males than females. Aggressive interactions manifest a large, cross-culturally universal sex difference: male/male fights are far more frequent than other combinations (e.g. Daly & Wilson 1990). Two non-mutually exclusive mechanisms can operate: either through sex-specific expression of left handedness genes or by a less frequent expression of the fighting advantage in females. The difference between male/male and female/female competition is also apparent in sports, as there are generally more sporting men than women. This probably explains the smaller increase of left handers among sporting women compared to sporting men (table 3), although this effect was globally non significant.

These results have implications for the measurement of handedness. They support the view that handedness of weapon manipulations, throwing ability and other aggressive behaviours should be recorded in addition to other classical parameters. These functional measurements are rarely considered in humans and other primates, but they are probably pivotal in the understanding of the evolution of handedness in primates and in hominids. For example, the chimpanzee (*Pan troglodytes*) is able to use various objects as a weapon and eventually throw them at conspecifics, predators or prey (Goodall 1964; van Lawick-Goodall 1970; Menzel 1972), but information on handedness for those behaviours is scarce (Plooij 1978; Hopkins *et al*. 1993). Recent reviews of handedness in wild or captive chimpanzees do not mention throwing handedness (Boesch 1991; Hopkins & Morris 1993), or acknowledge a lack of such data (Marchant & McGrew 1991).

Evidence of intra-specific fights within the hominids is almost as old as the fossil record, with no evidence of a decreasing trend since the Neolithic. As an illustration, more than two deaths per 10000 individuals due to aggressive interactions were recorded in 1972 in an American town (Daly & Wilson 1990), which is probably a large underestimate of the annual rate of fighting frequencies. Among the 188 existing countries, and only for the year 1992, around 19% have experienced either a war, a civil war, or a major political or economic crisis requiring an armed intervention (Anonymous 1993). The fighting advantage of left handers during these contexts is probably high.

Our results support the hypothesis that the stability of left handedness probably results from an equilibrium between the deleterious effects associated with left handedness, and the various advantages they provide during an aggressive interaction, but this does not formally exclude other alternative hypotheses.

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