LATERALITY, 2004, *9* (1), 35–51

Is there geographical variation in human handedness?

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Right- and left-handed individuals are present in all cultures. However, while it is known that handedness is a heritable trait, little is known about how handedness varies between populations—and without this knowledge, the significance of the left/right polymorphism is hard to interpret. We reviewed the literature to assess the extent of geographical variation of throwing or hammering handedness. These two tasks were chosen because they are present in all known cultures (unlike, for example, writing), and make sense within the context of several adaptive theories on the origin of laterality, or maintenance of handedness polymorphism, which state that tool or weapon manipulation are pivotal. A total of 81 samples were found with primary data on throwing or hammering handedness, spanning 14 countries and concerning more than 1,214,000 individuals studied between 1922 and 1998. A global logistic regression was performed to assess the significance of the country of the study, controlling for several potentially confounding variables (date of the study, sex and age of individuals). Country always had a significant effect, consistent with substantial geographical variation of throwing and hammering handedness. Curiously, left-handedness frequency estimates for a given country were not always consistent across datasets, perhaps due to missing variables, such as educational level or socio-economic status. Results are discussed in the context of the evolution of handedness and the significance of the current polymorphism.

Handedness is a specialisation of one hand or arm for a particular function. Is there a geographical variation of human handedness? While it is known handedness is a heritable trait (Annett, 1973; Levy & Nagylaki, 1972; McManus,

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We thank M. Corballis, A. Cournil, C. Faurie, J.-M. Gaillard, E. Gazave, O. Judson, I.B. Perelle, F. Rousset, and one anonymous reviewer for their helpful comments on the manuscript, and I.B. Perelle for sending the raw data on his international study. Contribution 02.088 of the Institut des Sciences de l'Evolution de Montpellier (UMR CNRS 5554).

http://www.tandf.co.uk/journals/pp/1357650X.html DOI:10.1080/13576500244000274

1991), little is known about how handedness varies between populations—and without this knowledge, the significance of the left/right polymorphism is hard to interpret. One way to investigate variation in human handedness is to compare handedness populations. Yet the question of geographical variation of handedness remains surprisingly without a clear answer in the literature. The obscurity of the present situation is probably the result of confusion about two points. First, a wide variety of distinct handedness parameters have been used (for a review see e.g., Harris, 1992), which precludes a direct comparison between most studies. Handedness parameters fall into two categories: measures of a functional task (e.g., writing, throwing, tooth brushing, etc.) or measures of an arbitrary task (e.g., the peg-moving task: the time taken by each hand to move all items from one slot to another). In addition, several measures on the same individuals are often combined to obtain a quantitative index, with the idea of measuring a ''general handedness''. Again, the list of tasks considered varies across studies, as does the manner of computing the index.

The second point of confusion is an absence of consensus of how to collect handedness data. Three broad categories of methods exist—performance data, preference data (answer to questionnaires or interviews), and handedness depicted in artwork—and a cross-validation between them is not always available. In addition, the category ''lefthander'' for a particular task could represent several classes of individuals—for example ''pathological lefthanders'' (Dellatolas et al., 1993, but see McManus, 1983) who have been subject to a prenatal insult of their left hemisphere, which controls the right side of their body—and these classes are difficult to identify. However, this situation does not prevent the study of a ''lefthander'' category, it just suggests caution in the interpretation of the results.

Handedness polymorphism is often viewed as a mere consequence of indirect selection. For example, the ''right-shift theory'' states that handedness is a by-product of a factor that induces lateralised speech representation in the brain, and that there is overdominance at this major genetic factor, RS+/− individuals having an overall cognitive advantage over either RS+/+ or RS−/−, due to interference of RS+ and RS− with distinct cognitive functions (Annett, 1985). Other propositions have been made on gene action of putative genetic factors, all of them assuming an indirect selection on handedness (e.g., Corballis, 1997; Corballis & Morgan, 1978; McManus, 1991), see also the Geschwind and Galaburda theory of prenatal testosterone (Geschwind & Galaburda, 1985a, 1985b, 1985c; McManus, 1991). So far, only one hypothesis has been proposed for a direct selective cause of this polymorphism, i.e., through frequency dependence during aggressive interactions (Raymond, Pontier, Dufour, & Møller, 1996). The idea is that lefthanders have an advantage when fighting against a right-hander—this advantage is frequency-dependent, being greatest when the frequency of left-handers is smallest—because left-handed individuals usually interact with right-handers, who are more numerous and are therefore more accustomed to encountering other right-handers. This frequency-dependence hypothesis has received some support. Left-handedness gives a substantial advantage in interactive sports (e.g., sports related to face-to-face combat, such as fencing, boxing, table tennis, etc.) but not in noninteractive ones (such as athleticism, darts, swimming, etc.), as expected (Grouios, Tsorbatzoudis, Alexandris, & Barkoulis, 2000; Raymond et al., 1996). Thus, within the context of the frequency-dependence hypothesis, handedness should be measured using tasks or gestures related to fighting or aggressive interactions.

The present study addresses a simple question: is there any evidence of geographical variation of handedness related to aggressive interactions? As levels of male:male aggression vary cross-culturally (Betzig, 1986; Daly & Wilson, 1989; Daly, Wilson, & Weghorst, 1982), we expect to observe a similar cross-cultural variation of handedness related to aggressive interactions. However, to our knowledge, handedness of traits directly related to fighting (e.g., the preferred hand with which to stab someone, to fight with one's fist, etc.) is almost absent from the literature. For example, handedness for holding a machete, a now common tool/weapon in many horticulturalist or hunter-gatherer societies, seems to be reported only from one sample of a southern Cameroon society (Carrière & Raymond, 2000). Therefore, we used a less direct measure of handedness, throwing, which still belongs to the gesture repertoire associated with aggressive interactions. Throwing handedness is pivotal in some interactive sports, and interactive sports could be seen as a particular class of fights, where the rules are clear and strict. For example, in the pitcher–batter interaction in baseball, throwing handedness seems to evolve through frequency-dependent selection towards an evolutionary stable frequency (Goldstein & Young, 1996). Thus throwing handedness could be used to address various points related to the frequency-dependence hypothesis. In addition, throwing is central within the context of the theory of handedness suggesting that tool or weapon manipulation was a driving force for the occurrence of functional handedness (Calvin, 1982, 1993; Frost, 1980). Moreover, throwing corresponds to activities present in all existing or extinct cultures of our species, and it also exists in other extinct hominids and in other apes (Goodall, 1964; Hopkins, 1996; Jordan, 1982; McGrew & Marchant, 1996; Plooij, 1978; Thieme, 1997; Watson, 2001). There are no reported social or familial pressures for throwing handedness, unlike, for example, for writing or eating (De Agostini, Hassan Khamis, Ahui, & Dellatolas, 1997; Granet, 1973; Teng, Lee, Yang, & Chang, 1976). In addition, throwing handedness has been studied by various authors in various countries, allowing a global analysis of a large dataset. For comparison purposes, hammering handedness was also analysed.

METHOD AND MATERIALS

Primary data

To find primary data on handedness, we proceeded in two ways. First, to find recent publications, we performed literature searches on accessible databases. Second, to find older data, we scanned cited literature. In addition, inspection of 10 review articles or books from 1976 to 1998 (Annett, 1985; Hardyck & Pertinovitch, 1977; Hardyck, Petrinivich, & Goldmann, 1976; Harris, 1992; Hécaen, 1984; Marchant & McGrew, 1998; McGrew & Marchant, 1994; Porac & Coren, 1977; Salmaso & Longoni, 1985; Searleman, Porac, & Coren, 1989) ensured that no major old papers were overlooked. All papers that displayed raw data (or from which raw data could be unambiguously reconstructed) on throwing or hammering handedness were considered. Data on sporting individuals were excluded (left-handedness is an advantage in some sports, Grouios et al., 2000; Holtzen, 2000; Raymond et al., 1996), as well as data concerning mentally defective individuals (left-handedness has a higher reported prevalence in this category, Hardyck et al., 1976) or twins (it is unclear from the literature whether or not left-handed twins are more frequent than single-born individuals, Annett, 1985; Hécaen, 1984; Wilson & Jones, 1932). The raw data of the international study of Perelle and Ehrman (1994) were obtained from I.B. Perelle upon request. Data were excluded when the sample size was lower than 100 or when the mean age was lower than 8 years old, as ''handedness'' is usually considered to be established around 3–5 years (De Agostini, Paré, Goudot, & Dellatolas, 1992; Hécaen, 1984; McManus, Sik, Cole, Mellon, Wong, & Kloss, 1998). Two samples from Italy (Perelle & Ehrman, 1994; Salmaso & Longoni, 1985) were excluded, because they report a very unusual high frequency of left-handedness (30.8% and 42.0%, respectively). This may well represent a true geographical variation; however for a conservative test of a possible geographical variation, these samples were omitted. Some papers containing raw data will certainly have remained unnoticed, due to the difficulty of locating them among an extensive literature devoted primarily to medical or psychological aspects of handedness in humans.

Recorded variables

For each dataset on throwing or hammering handedness, the focal qualitative variable (the country of data collection, or CNTR), and several potentially confounding variables were recorded. The confounding variables were (quantitative variables are in italics) *YEAR*, the year of data collection, or by default the year of publication or submission of the publication; SEX and *AGE*, for the sex and mean age of individuals in the dataset. When mixed sex samples were present, the sex ratio (*SR* = proportion of males) of the sample was used instead of SEX. When the mean age was not indicated, it was either estimated by the mean of the extreme age values if available, or assigned arbitrarily if additional information was present (e.g., 20 years for a university student sample; 40 years for a working professional sample, and 70 years for a sample of retired individuals). All these nonfocal variables have been shown to explain some variation of left-handedness frequency, at least for some handedness measurements (e.g., Brackenridge, 1981; Fleminger, Dalton, & Standage, 1977; Gilbert & Wysocki, 1992).

The problem of data based on questionnaires

Questionnaires (e.g. ''Which hand do you use to throw a ball?'') used to collect handedness data have a variable number of possible answers across studies: two (right or left), three (right, left, or both) or five (always right, usually right, both, usually left, always left). The last case is especially problematic, as there is a significant tendency for individuals to be inconsistent. This is illustrated by the data available in Bryden (1977), where two distinct questionnaires, both containing the same question on throwing handedness, were administered to the same group of individuals: answers were significantly (Fisher exact test, 2×5 contingency table, $p < 10^{-5}$) different between questionnaires, for both males ($N = 620$) and females ($N = 486$). This suggests that the difference among the successive five handedness categories does not reflect true handedness variation. The difference between questionnaires vanishes (Fisher exact test, 2×2 contingency table, $p > .1$ for each sex) when categories 1–2 ($\approx$ right-thrower) and 3–5 ($\approx$ left-thrower or ambidextrous) are pooled, suggesting that differences between these two categories reflect true handedness variation. Following these results, all data based on five-answer questionnaires were pooled into two categories as above. For three-answer questionnaires on throwing or hammering handedness, test–retest gave 100% concordance ($N = 27$, Coren & Porac, 1978; $N = 27$, Raczkowski, Kalat, & Nebes, 1974). However, for comparisons with other questionnaires, left-handed and ambidextrous were pooled in a single category.

Statistics

The variation in handedness frequencies according to the recorded variables was tested using a logistic regression, which takes into account the sample size of each study. The measure of discrepancy to assess the goodness of fit of the model to the data is the deviance (a logarithm of the ratio of two likelihoods, for details see Crawley, 1993). Model selection was performed using the Akaike Information Criterion (AIC), a heuristic measure that can be compared between unrelated models fitted on the same data (AIC = deviance + $2 \times$ df) (Akaike, 1973). Whenever present, overdispersion was corrected and the selected model was then simplified according to Crawley (1993): higher-order terms were first tested, and the least and nonsignificant ($p > .05$) ones were removed. Factor levels of qualitative variables that were not different from one another in their parameter estimates were lumped together, following the procedure described in Crawley (1993): levels of the least significant pair difference were first pooled, then the significance level of each remaining pair differences was re-computed. This process was continued until all remaining pair differences were significantly different from zero. This procedure gives the minimal adequate model. All computations were performed with GLIM version 4 (Baker, 1987).

Independence of rows and columns in a R $\times$ C contingency table was tested using Fisher's exact test (Fisher, 1935), and an unbiased estimate of the *p*-value of this test was performed using the STRUC program (Raymond & Rousset, 1995).

RESULTS

A total of 81 samples were found with primary data on throwing or hammering handedness, spanning 14 countries and concerning more than 1,214,000 individuals studied between 1922 and 1998. While the vast majority of studies (99.7%) are based on questionnaires or interviews, a low percentage (0.3%) corresponds to data collected from observation of performance.

Data based on performance

A total of 11 samples on throwing handedness based on performance were found (Table 1), corresponding to 3036 individuals belonging to three countries—Papua New Guinea (or PNG), UK, and USA. All possible models taking into account the sex ratio of the sample (*SR*), the year of study (YEAR), the mean age of individuals (*AGE*), and the country (CNTR) were considered. According to the AIC criteria (Table 2), the best model is *SR* + CNTR (AIC_{min} = 13.45), which explains 84.5% of the total deviance. This model was simplified according to Crawley (1993), i.e., the least significant terms were first removed until all remaining terms were significant ($p < .05$). This provides the model with one variable, CNTR. Factor levels (i.e., countries) of CNTR that were not different from one another in their parameter estimates were lumped together, according to the procedure of Crawley (1993). The resulting minimal adequate model explains 76.1% of the total deviance, and displays no overdispersion (scaled deviance/residual df = 1.04). The estimated proportion of left-throwers is 7.1% in the USA, 12.4% in the UK, and 19.6% in PNG (Table 4).

Four samples on hammering handedness were found (Table 1), corresponding to three countries (PNG, UK, and USA). Although there is a substantial and significant variation (Fisher exact test on 3 $\times$ 2 contingency table, $p = .023$) of the frequency of left-hammerer individuals across countries (PNG: 15.0%; UK: 8.9%; USA: 7.0%), there are not enough degrees of freedom (i.e., samples) to control for possible confounding variables (e.g., *AGE* and *SR*).

TABLE 1
Available data on throwing or hammering handedness in humans, based on performance

Study	*Country*	*Locality; category*	*Year*	*SR*	*Age*	*L+RL*	*N*	*%*	*Reference*
Throwing									
1	PNG	Western Highland province; middle Jimi valley	1990	0.64	16.5[a]	21	107	19.6	(Connolly & Bishop, 1992)
2	UK	Hull; school children	*1970*	0.46	10.5[a]	36	278	12.9	(Annett, 1970)
3	UK	Manchester; primary school children	*1992*	0.59	9.5[a]	14	125	11.2	(Connolly & Bishop, 1992)
4	USA	San Francisco; journeymen mechanics	*1922*	1	40[b]	4	100	4.0	(Quinan, 1922, 1930)
5	USA	San Francisco; professional musicians	*1922*	1	40[b]	8	100	8.0	(Quinan, 1922, 1930)
6	USA	San Francisco; relief-home inmates	*1922*	1	70[b]	5	100	5.0	(Quinan, 1922)
7	USA	California; undergraduate students	*1929*	1	18.5	77	1000	7.7	(Quinan, 1930)
8	USA	California; junior & senior high school students	*1932*	1	15.2	21	277[c]	7.6	(Wilson & Jones, 1932)
9	USA	California; junior & senior high school students	*1932*	0	15.2	16	244[c]	6.6	(Wilson & Jones, 1932)
10	USA	Baltimore; participants of a long. study of ageing	*1984*	1	57.5	38	461	8.2	(Plato et al., 1984)
11	USA	Baltimore; participants of a long. study of ageing	*1984*	0	52.8	10	244	4.1	(Plato et al., 1984)
Hammering									
1	PNG	Western Highland province; middle Jimi valley	1990	0.64	10.5[a]	16	107	15.0	(Connolly & Bishop, 1992)
2	UK	Manchester; primary school students	*1992*	0.59	9.5[a]	11	125	8.9	(Connolly & Bishop, 1992)
3	USA	Baltimore; participants of a long. study of ageing	*1984*	1	57.5	36	461	7.8	(Plato et al., 1984)
4	USA	Baltimore; participants of a long. study of ageing	*1984*	0	52.8	13	244	5.3	(Plato et al., 1984)

The number of left-handed and ambidextrous individuals (L + LR), the corresponding percentage (%), and the sample size (N) are indicated. ''Year'' refers to the year of study or, when in italics, to the year of publication of the study. The sex ratio (or SR, proportion of males) in the sample is indicated (''0'' and ''1'' for pure male or female samples, respectively), as well as the mean age of the sample.

[a] Not indicated in the original paper. Mean of lowest and highest age in the sample.

[b] Not indicated in the original paper. Estimated at 20 for students, 40 for workers, and 70 for retired individuals.

[c] Partially based on performance.

TABLE 2
Model selection for the frequency of left-hand throwers from performance data

Model	*% TD*	*Residual deviance*	*Residual df*	*Dispersion of residuals*	*AIC*
NULL	–	34.7	1	3.47	36.75
YEAR	17.2	28.8	9	3.20	32.76
SR	0.1	34.7	9	3.86	38.70
CNTR	76.1	8.3	8	1.04	14.32
AGE	20.9	27.5	9	3.05	31.47
YEAR + CNTR	76.4	8.2	7	1.17	16.21
SR + CNTR	84.3	5.4	7	0.78	13.45
SR + CNTR + *SR*.CNTR	85.6	5.0	6	0.84	15.04
AGE + CNTR	77.9	7.7	7	1.09	15.66
SR + *YEAR* + CNTR	84.3	5.4	6	0.91	15.44
AGE + *YEAR* + CNTR	78.3	7.5	6	1.26	17.54
AGE + *SR* + CNTR	85.8	4.9	6	0.82	14.93
YEAR + SR + *AGE* + CNTR	87.9	4.2	5	0.84	16.20
YEAR + *SR* + *AGE* + CNTR + (*YEAR* + *SR* + *AGE*).CNTR	90.0	3.2	4	0.79	17.15

Some models with the four variables (*YEAR*, *SR*, *AGE*, and CNTR) are indicated (all other possible models not depicted have an AIC > 16.5). ‘‘.’’ indicates an interaction between a quantitative and a qualitative variable. %TD refers to the part of the total deviance explained, and ‘‘AIC’’ to the Akaike Information Criterion. The lowest AIC value is underlined.

Data based on questionnaires

A total of 33 samples on throwing handedness based on questionnaire or interview were found, corresponding to 1,208,606 individuals belonging to 13 countries (Table 3). Of these samples 17 are from only one study. All meaningful models taking into account the sex ratio of the sample (*SR*), the year of study (*YEAR*), the mean age of individuals (*AGE*), and the country (CNTR) were considered. Samples were also classified according to whether or not they belonged to the large study by Perelle and Ehrman, which contributed 12 of the 20 samples. This variable was labelled DAT.

According to the AIC criteria, the best model is *SR* + CNTR + DAT + *SR*.CNTR + *SR*.DAT + CNTR.DAT, with all terms being significant ($p < .05$). As the origin of the sample matters even in the interaction terms, the dataset was split in two: all the data from Perelle and Ehrman's study (PER dataset; 17 samples), and all the other data from other studies (OT dataset; 16 samples). For the PER dataset, the best model is SEX + CNTR (details not shown). Factor levels of CNTR that were not different from one another in their parameter estimates were lumped together (i.e., some countries were pooled). The resulting minimal adequate model explains 80.8% of the total deviance, and displays no overdispersion ($\approx$ 0.99). For the OT dataset, the best model is *SR* + CNTR +

TABLE 3

Available data on throwing or hammering handedness in humans, based on questionnaires

Study	*Country*	*Locality; category*	*Year*	*SR*	*Age*	*L+LR*	*N*	*%*	*Type*	*Reference*
1	Algeria	Constantine; medical faculty students	*1989*	1	23.6	30	330	9.1	3	(Nedjar et al., 1989)
2	Algeria	Constantine; medical faculty students	*1989*	0	22.7	47	360	13.1	3	(Nedjar et al., 1989)
3	Côte d'Ivoire	Abidjan; students of various high schools	1992	0.49	16.4	74	378	19.6	3	(De Agostini et al., 1997)
4	Nigeria	Unspecified; black	*1994*	0	20.4	21	119	17.6	3	(Perelle & Ehrman, 1994)
5	Nigeria	Unspecified; black	*1994*	1	26.4	19	131	14.5	3	(Perelle & Ehrman, 1994)
6	Sudan	Khartoum; undergraduate students	1993	0.53	22.4	66	753	8.8	5	(De Agostini et al., 1997)
7	Australia	Unspecified; white	*1994*	0	23.7	52	303	17.2	3	(Perelle & Ehrman, 1994)
8	Australia	Unspecified; white	*1994*	1	26.8	47	283	16.6	3	(Perelle & Ehrman, 1994)
9	France	Unspecified; staff & students of hospitals & research labs	*1988*	0.44	33.6	143	880	16.3	3	(Dellatolas et al., 1988)
10	France	Unspecified; white	*1994*	0	25.7	76	276	27.5	3	(Perelle & Ehrman, 1994)
11	France	Unspecified; white	*1994*	1	30.0	42	162	25.9	3	(Perelle & Ehrman, 1994)
12	Spain	Unspecified; white	*1994*	0	20.1	162	661	24.5	3	(Perelle & Ehrman, 1994)
13	Spain	Unspecified; white	*1994*	1	21.8	89	509	17.5	3	(Perelle & Ehrman, 1994)
14	UK	Hull; undergraduate students & new recruits servicemen	1970	0.73	18.0	249	2321	10.7	3	(Annett, 1970)
15	Canada	Univ. Waterloo; undergraduate students	*1977*	1	21.5	79	538	14.7	5	(Bryden, 1977)
16	Canada	Univ. Waterloo; undergraduate students	*1977*	0	21.5	96	620	15.5	5	(Bryden, 1977)
17	Canada	Unspecified; white	*1994*	0	21.1	45	255	17.6	3	(Perelle & Ehrman, 1994)
18	Canada	Unspecified; white	*1994*	1	23.4	21	166	12.7	3	(Perelle & Ehrman, 1994)
19	Mexico	Unspecified; white	*1994*	0	26.9	24	109	22.0	3	(Perelle & Ehrman, 1994)
20	Mexico	Unspecified; white	*1994*	1	30.1	20	138	14.5	3	(Perelle & Ehrman, 1994)
21	USA	Univ. of Yale; undergraduate students	*1946*	1	18.0	47	407	11.5	2	(Wittenborn, 1946)
22	USA	Throughout USA; readers of the National Geographic	1986	1	43.6	48119	513304	9.4	2	(Gilbert & Wysocki, 1992)
23	USA	Throughout USA; readers of the National Geographic	1986	0	43.0	47264	664203	7.1	2	(Gilbert & Wysocki, 1992)
24	USA	Unspecified; black	*1994*	0	24.6	31	201	15.4	3	(Perelle & Ehrman, 1994)
25	USA	Unspecified; native American	*1994*	0	26.9	99	600	16.5	3	(Perelle & Ehrman, 1994)
26	USA	Unspecified; native American	*1994*	1	26.6	58	429	13.5	3	(Perelle & Ehrman, 1994)
27	USA	Unspecified; white	*1994*	0	27.3	270	1796	15.0	3	(Perelle & Ehrman, 1994)
28	USA	Unspecified; white	*1994*	1	27.2	221	1397	15.8	3	(Perelle & Ehrman, 1994)
29	USA	Florida; univ. stud. during normal eye exams	*1998*	1	20.0	9	100	9.0	3	(Portal & Romano, 1998)
30	Brazil	Niteroi; univ. students, faculty & staff	*1989*	1	36.0	43	471	9.1	3	(Brito et al., 1989)
31	Brazil	Niteroi; univ. students, faculty & staff	*1989*	0	36.0	36	488	7.4	3	(Brito et al., 1989)
32	Japan	Kyoto; primary school students	*1934*	1	10.2	654	8418	7.8	2	(Komai & Fukuoka, 1934)
33	Japan	Kyoto; primary school students	*1934*	0	9.9	375	7500	5.0	2	(Komai & Fukuoka, 1934)

The number of left-handed and ambidextrous individuals (L + LR), the corresponding percentage (%), and the sample size (N) are indicated. The country of the sample and additional information, whenever available, are indicated. ''Year'' refers to the year of study or, when in italics, to the year of publication. The sex ratio (or SR, proportion of males) in the sample is indicated (''0'' and ''1'' for pure male or female samples, respectively), as well as the mean age of the sample. ''Type'' refers to the number of answers proposed in the questionnaire.

SR.CNTR (details not shown), and after lumping together factor levels of CNTR that were not different from one another in their parameter estimates, this model explained 99.8% of the total deviance, and displayed a slight underdispersion ($\approx$ 0.48). Left-handed throwers varied from must a few percent (e.g., Japan), up to 22% (women from Côte d'Ivoire) of the population (Table 4). Estimates for the countries that are present in both datasets (USA, France, and Canada) are not particularly consistent, with the exception of Canada (14.7% and 15.1% for males in PER and OT, respectively). The effect of sex was either constant across countries (in the PER dataset, with a higher prevalence of left-handedness in females), or variable (in the OT dataset, left-handedness present in higher percentage in males or females depending on country).

A total of 23 samples on hammering handedness based on questionnaire or interview were found, corresponding to 12,566 individuals belonging to 11

TABLE 4
Percentage estimates of left-handed throwers or hammerers according to the best model for each dataset

Data source	*Model*	*Male (%)*	*Female (%)*
THROWING			
Performance data	CNTR		
PNG		19.6	
UK		12.4	
USA		7.1	
Questionnaire data (PER)	CNTR + SEX		
Australia, Canada, Mexico, Nigeria, USA		14.7	16.4
Spain		20.2	22.4
France		25.3	27.9
Questionnaire data (OT)	CNTR + SR + CNTR.SR		
Algeria, UK		9.7	13.3
Côte d'Ivoire		17.9	21.4
France, Canada		15.1	16.0
Brazil, USA		9.4	7.1
Sudan		7.5	10.4
Japan		4.4	5.0
HAMMERING			
Questionnaire data (PER)	CNTR + SEX		
France, USA, Canada		20.7	15.7
Nigeria		9.7	7.1
Australia		17.9	13.5
Mexico, Spain		15.0	11.2
Questionnaire data (OT)	CNTR		
Algeria, Côte d'Ivoire, Sudan, UK		11.4	
France		15.2	

Only significant differences between countries are shown. See text for explanations.

countries (details not shown). Of these samples 17 are from only one study. As previously, the dataset was split in two: all the data from Perelle and Ehrman's study (PER dataset; 17 samples), and all the other data from other studies (OT dataset; 6 samples). For the PER dataset, the best model is SEX + CNTR (details not shown). Factor levels of CNTR that were not different from one another in their parameter estimates were lumped together. The resulting minimal adequate model explains 70.5% of the total deviance, and showed some underdispersion ($\approx$ 0.69). For the OT dataset, the best model is CNTR (details not shown), and after lumping together factor levels of CNTR that were not different from one another in their parameter estimates, this model explained 82.4% of the total deviance, and displayed some underdispersion ($\approx$ 0.51). Left-handed hammerers varied from 11.4% (four countries), up to 15.2% (France) of the population (Table 4). Estimates for the country that is present in both datasets (France) are not particularly consistent. The effect of sex was either constant across countries (in the PER dataset, with a higher prevalence of left-handedness in males), or absent (in the OT dataset).

DISCUSSION

The variation of frequency of left-handed (for throwing or hammering) individuals in a sample is explained by the country of origin. However, in some datasets, sex ratio and mean age also have a significant effect. This result is valid independently of the mode of data collection (performance or questionnaire, see Tables 2 and 4), suggesting that it represents compelling evidence for significant variation of handedness frequency across countries.

However, there is one point to consider: the various estimates across datasets are not consistent. For example, the percentage of left-handed male throwers in the US samples is estimated at 7.1%, 20.2%, or 9.4% depending on the dataset; again, the percentage of left-handed hammerers is 20.7% in one French sample and 15.2% in another (Table 4). This indicates that additional factors, not necessarily related to laterality, have interfered somehow in some datasets. It is obvious that a questionnaire cannot be filled in independently of some psychological factors, as shown above by the re-analysis of the data in Bryden (1977). The discrepancy of estimates across questionnaire studies thus reflects either a bias related to environmental or psychological conditions, or a true difference described by variables not taken into account in the present review. One important variable that may be important is educational or socio-economic status. However, not all studies consider this variable, and those that do generate conflicting results. For example, some studies failed to find any relationships between social class and hand preference (Brito, Brito, Paumgartten, & Lins, 1989), although others do find a higher prevalence of left-handedness (at least for males) in classes of higher educational or socio-economic status (Annett & Kilshaw, 1983; Leiber & Axelrod, 1981; Perelle & Ehrman, 1994). In addition, a significant difference in frequency of left-handed throwers exists between racial groups in the USA (Gilbert & Wysocki, 1992). Problems of comparison are further compounded because a variety of handedness measures are used. Therefore, how throwing or hammering handedness (or any handedness measures related to weapon or tool manipulation) is distributed across socio-economic classes in any culture is currently unknown. Perelle and Ehrman (1994) have presented results on writing handedness, although further analyses of their data (provided upon request by I.B. Perelle) suggest a significant effect (Fisher exact test on 7×2 contingency table, $p < .008$) of throwing handedness across educational levels for females. Clearly, educational or socio-economic status must be considered as possible confounding variables explaining apparent discrepancies between studies on one country.

Performance data are not exempt from possible bias—for example when performances are solicited and recorded publicly in small communities, in sessions especially organised for such a purpose, subjects may behave differently from usual (see page 23 of Connolly & Bishop, 1992). However, within a single study (OT data), there are significant left-handedness variations across literate countries belonging to the same global cultural group (UK and France, Table 4) i.e., in a situation probably homogeneous for some psychological factors associated with questionnaire studies. This suggests that despite the possible biases, a true geographical variation exists for throwing or hammering handedness. In addition, there is also the particularly high prevalence of left-handed throwers or hammerers in Italy, found in two independent studies (which have not been included in the global analysis, for a conservative test of the null hypothesis).

The sex effect is puzzling. A higher prevalence of left-throwers was detected in females in the PER dataset, and a complex effect in the OT dataset (left-handedness was more prevalent either in males or in females, depending on the country). Whether or not this complex effect reflects a biological reality remains to be established. No sex effect was apparent in the performance data. A higher prevalence of male left-handedness is generally reported in the literature in cases when the writing hand or various other indices are used as handedness measures (see, e.g., Table 4.4 of Annett, 1985; Gilbert & Wysocki, 1992; Perelle & Ehrman, 1994; but see Silverberg, Obler, & Gordin, 1979). At this point, the data are not conclusive as to whether the incidence of left-handedness for throwing or hammering is higher overall for males than for females.

Despite the huge literature devoted to this topic, the origin of human handedness remains problematic, and the polymorphism of laterality observed worldwide is not explained. It is worthy of note that there are suggestions that prenatal testosterone (which is a possible proximal cause of left handedness, see McManus, 1991) varies geographically (Manning et al., 2000). Thus the substantial geographical variation of left-handedness frequency is consistent with this theory.

The present study shows the existence of geographical variation of the frequency of left-handedness related to two functional tasks (throwing and hammering). As far as we can tell, right- and left-handed individuals (for some functional tasks) have long coexisted. The oldest undisputed and published evidence of hand laterality polymorphism in hominids is from the middle and early upper Pleistocene (Bermùdez de Castro, Bromage, & Fernàndez Jalvo, 1988; Lalueza & Frayer, 1997), where incisive marking indicates the existence of right- and left-handed *Homo neanderthalensis* for sharp tool manipulation, to slice meat held between the front teeth and the other hand (for a contemporary description of this technique for the Inuits, see Boucot, 1990, p. 663). Possibly some evidence also exists from osteological data for older taxon (Bridges, 1996). In the *H. sapiens* taxa, the oldest evidence is—to our knowledge—probably from the upper Palaeolithic, when right and left tube holders for paint blowing were both present, as indicated by the record of negative hand painting in caves (Groenen, 1988, 1997a). Interestingly, a close look at the published raw data (N = 343 negatives hand with an unambiguous laterality, Groenen, 1997b) suggests a significant geographical variation (Fisher exact test, $p < .02$) of the frequency of left-handers across southern Europe. Considering that the handedness polymorphism is probably ancient, many cultures should display frequencies of left-handers above 50% if this trait is neutral (i.e., for a given polymorphic population, higher or lower handedness frequencies are equally likely for the next generation). This is clearly not the case, as no left-handedness frequency above 50% is reported for any unifunctional task (for bimanual tasks, the definition of right- and left-handedness is arbitrary). This pattern in itself is not sufficient to formally reject neutrality, although it suggests that some sort of balancing selection is acting to maintain this polymorphism.

The current geographical variation of handedness is an opportunity to identify the selective forces involved, through for example correlation analyses or experimental studies. Both beneficial and deleterious effects associated with left-handers have already been proposed (e.g., Annett, 1985; Coren, 1989a, 1989b; Gorynia & Egenter, 2000; Raymond et al., 1996; Yeo & Gangestad, 1993), and both are required to maintain a polymorphism. However, these beneficial or deleterious effects are not always defined for the same tasks in the literature, and are associated with different measures of handedness, so that the current picture is unclear. Correlation analyses could not be performed in the present study due to the absence of most datasets of the putative confounding variables describing educational or socio-economic status.

Studies on human handedness must be performed within a clear theoretical background. In particular, the type of measure of handedness must be consistent with the question addressed. The pre-eminence of the writing hand as a measure of handedness in most studies is especially problematic in this respect. Writing is often considered as the most important task to take into account, although this activity was probably not common in most human populations until few centuries ago. In addition, cultural pressures towards conformity for right-hand writing is an annoying confounding factor, which varies in space and time. Functional handedness for other tasks was apparent before writing was invented, suggesting that writing handedness is not necessarily to be given a high priority if an explanation for the origin of handedness is being sought. Also, computation of scores or indices from several laterality tasks assume the existence of a ''general handedness'' at the individual level, which has neither a clear definition nor independent empirical support. The ways of measuring handedness must be carefully considered, as questionnaire data on handedness are particularly problematic. Further work will hopefully provide useful information on how the polymorphism of functional handedness is maintained in *H. sapiens*.

Manuscript received 28 February 2002
Revised manuscript received 3 October 2002

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