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Handedness, homicide and negative frequency-dependent selection

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Humans exhibit hand preference for most manual activities in which they are specialized. Right- and left-handers have coexisted at least since the Upper Palaeolithic, and left-handers are in the minority in all human populations. The persistence of the polymorphism of handedness is a puzzle because this trait is substantially heritable and several fitness costs are associated with left-handedness. Some countervailing benefit is required to maintain the polymorphism. Left-handers may have a frequency-dependent advantage in fights—the advantage being greater when their frequency is lower. Sports data from Western societies are consistent with this prediction. Here, we show that the frequency of left-handers is strongly and positively correlated with the rate of homicides across traditional societies. It ranges from 3% in the most pacifistic societies, to 27% in the most violent and warlike. This finding is consistent with a frequency-dependent selection mechanism maintaining left-handedness in these societies.

Keywords: evolution; violence; fighting; frequency-dependent selection; handedness; *Homo*

1. INTRODUCTION

Right- and left-handers have coexisted at least since the Upper Palaeolithic (Faurie & Raymond 2004), and left-handers are in the minority in all human populations (Raymond & Pontier 2004). The persistence of the polymorphism of handedness requires an explanation because this trait is substantially heritable (McManus 1991; Sicotte *et al.* 1999; McKeever 2000; Francks *et al.* 2002), and several fitness costs are associated with left-handedness (Coren & Halpern 1991; McManus & Bryden 1991; Aggleton *et al.* 1993; Gangestad & Yeo 1997). Some countervailing benefit necessarily exists, maintaining the polymorphism.

Left-handers have an advantage in sports involving dual confrontations, such as fencing, tennis and baseball (pitchers/batters), but not in non-interactive sports, such as gymnastics (Raymond *et al.* 1996; Grouios *et al.* 2000). This advantage is frequency-dependent: left-handers have an advantage when they are uncommon, as both left- and right-handers are less familiar with this category of competitor. Detailed analyses of cricket and baseball have, indeed, concluded that the frequency of left-handers in these sports is best explained by a negative frequency-dependent selection mechanism (Goldstein & Young 1996; Brooks *et al.* 2004).

From an ethnological perspective, interactive sports in Western societies are special cases of fights, with strict rules, including in particular the prohibition of killing or intentionally wounding the opponent. The frequency-dependent advantage of left-handers in sports might, thus, have a wider interpretation in the general context of aggressive interactions and wars in humans. If this is true, then the advantage of being left-handed should be greater in a more violent context, which should result in a higher

frequency of left-handers. Without any other selection pressure, the resulting equilibrium should be a 1 : 1 ratio of right-/left-handers. This has never been observed in any population, owing to costs associated with left-handedness (Coren & Halpern 1991; Aggleton *et al.* 1993; Gangestad & Yeo 1997). The existence of these costs is well established, although their origin, probably related to a distinct organisation of the brain, remains unclear (McManus & Bryden 1991). In any given society, the observed prevalence of left-handedness should, therefore, be a balance between its cost and its advantage in fights. As levels of male–male aggression vary cross-culturally (Daly & Wilson 1988), we expect to find a positive correlation between the frequency of left-handers and the level of violence across populations (if the cost of left-handedness is constant). The case of Western and westernized cultures needs to be considered cautiously: the level of violence has dramatically changed, as well as the type of violence (predominant use of long-range and powerful weapons, which probably do not offer a particular advantage to left-handers). Hence, the above prediction should preferably be tested in traditional societies.

To our knowledge, data on both violence and handedness are available in the literature only for three traditional societies. We extended this data set to five other cultures by field studies and a literature search for homicide rates. Despite the problems inherent in the comparative method (e.g. overlooking potentially important group variation), it is a powerful way of searching for patterns in the data. The results presented here should not be systematically biased, as the potential sources of ambiguity in our estimates are most probably unrelated to the frequency of left-handers.

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2. METHODS

(a) *Frequency of left-handers*

(i) *Evaluation during field studies*

In 2003, the frequency of left-handers was assessed, for machete-use, in the Kreyol people of Dominica. All the inhabitants of the village of Bwa Mawego were interviewed in their native language and indicated whether they preferred to use their left or right hand when using a machete. Information was crosschecked, by observation of spontaneous use, for 15.3% of the subjects. Children under 5 years were excluded from the sample, as handedness is often not stable before this age.

(ii) *Literature data*

The frequency of left-handers has been assessed for the Ntumu people of Cameroon in 1998 (Carrière & Raymond 2000), for the Dioula-speaking people of Burkina Faso in 2000 and the Baka people of Gabon in 2002 (Faurie *et al.* 2004). The method was exactly the same for these three field studies as in Dominica, i.e. hand preference was assessed for machete-use, and the entire population of the area (group of villages) was assessed.

The frequency of left-handers was assessed for the Inuit people, and for the Eipo people (Irian Jaya, New Guinea), through the observation of spontaneous manual activities from photographs taken during anthropological field studies. For the Inuit people, we used hand preference for the knife. The photographs were taken in Greenland, Alaska and Canada, by several anthropologists, between 1892 and 1971 (for details, see Faurie *et al.* 2004). For the Eipo people, the photographs were taken by the anthropologist Wulf Schiefenhövel between 1974 and 1980. The method considered adult men's hand preference for bow shooting (for details, see Faurie *et al.* 2004). Therefore, we studied the relationship between hand preference for bow shooting and hand preference for knife use in a sample of 66 French adult men, to perform a correction on the estimated frequency of left-handers. In this sample, 35.3% of left-handers for bow shooting prefer to use the knife with their right hand, and 4.1% of right-handers for bow shooting prefer to use the knife with their left hand. Consequently, assuming that the relationship between these two measures of handedness is similar for Eipo and French men, the resulting estimation of the frequency of left-handers for knife use among Eipo men was compiled in the cross-cultural comparison.

The frequencies of 'non-right-handers' for hammer-use in the middle Jimi valley in the Western Highlands of Papua New Guinea, and for general unimanual tool-use in the Yanomamö people of Venezuela, were obtained from the studies of Connolly & Bishop (1992) and Marchant *et al.* (1995), respectively.

(b) *Homicide rate*

(i) *Evaluation during field studies*

Homicide rates (number of adult homicides per 1000 individuals per year) were evaluated for the Dioula-speaking people in Burkina Faso (mainly Sambla, Bobo and Mossi villages), the Baka people in Gabon and the Kreyol people in Dominica during field studies in 2000, 2002 and 2003, respectively. Initially, information on all homicides that occurred in the area during the past 50 years was recorded by interviewing older individuals and key informants. Every account was cross-checked with different informants. Secondly, official police statistics were consulted, when available (Baka and Kreyol people); in this case, we averaged the values estimated from recall data and from police records. The population sizes were obtained from complete census data from

our fieldwork, or provided by collaborators (Kreyol people; Flinn & England 1997).

(c) *Literature data*

For the four other populations, homicide rates were calculated on the basis of the following information available in the literature. We restricted our sources to those providing estimates over at least 40 years and for a population of at least 500 inhabitants.

For the Ntumu people, two homicides were reported over 50 years (before 1998) (Carrière & Raymond 2000). The population size was obtained from a complete census (Bley *et al.* 1999). In 12 Yanomamö villages, 282 homicides have occurred over 50 years (before 1987) (Chagnon 1988; also providing the population size). For the Inuit people, the only suitable quantitative evaluation available was seven homicides reported over 84 years (before 1968) (Robert-Lamblin 1997; also providing the population size). As no quantitative information was available for the Jimi valley (Western Highlands, Papua New Guinea), although they are described as warlike (Gratton 1991), we averaged the homicide rates for five geographically and culturally similar groups in the same area when evaluated over more than 40 years (Gebusi: Knauff 1987; Gailala: Knauff 1987; Nalumin: Bercovitch 1989; Kunimaipa: McArthur 1961; Etoro: Kelly 1993).

3. RESULTS AND DISCUSSION

The results are summarized in table 1. The frequency of left-handers and homicide rate are significantly and positively correlated (Spearman's correlation coefficient $\rho = 0.83$, $p = 0.01$, two-sided; figure 1). Thus, this result strongly supports the fighting hypothesis. More generally, it points to the importance of violence in understanding the evolution of handedness in humans.

Nevertheless, alternative hypotheses should be considered. Firstly, the cost associated with left-handedness was measured in Western societies, and could vary across cultures. If this variation is independent of the level of violence, it represents a nuisance variable and not a confounding one. The observed pattern could have a different interpretation only if the cost is inversely proportional to violence. Although this possibility cannot be formally excluded, there is no theoretical basis, and no empirical evidence, to assume or support such a relation. Secondly, owing to the higher prevalence of left-handedness in males (Annett 1985), and to the correlation between severity of conflicts and excess of males in the population (Mesquida & Wiener 1999), there could be an indirect relation between left-handedness and violence. This effect would, however, be proportional to the sex difference in left-handedness, which is generally less than 5% (Annett 1985), and, therefore, could not account for the large variation of left-handedness frequencies observed in our dataset (almost 24%). Finally, homicide rates are probably underestimated, owing to the dubiousness of recall data (e.g. some homicides may be concealed as accidents). As the underestimation might be culture-dependent, it represents another nuisance variable. Our test is, thus, conservative, and the finding of a significant positive correlation between homicide rates and left-handedness frequencies, despite several nuisance parameters, suggests an even stronger relation.

Fights may have important consequences for social status and reproductive value, even when not leading to death (Hill 1984; Chagnon 1988; Archer *et al.* 1995).

Table 1. Homicide rate and frequency of left-handers for eight traditional/sub-traditional societies.

population	country or geographic area	handedness frequency			homicide rate		
		left-handers (%)	sample size	reference	homicides per 1000 inhabitants per year	sample size	reference
Dioula	Burkina Faso	3.4	346	Faurie <i>et al.</i> 2004	0.013	3000	this study
Ntumu	Southern Cameroon	8.1	246	Carrière & Raymond 2000	0.017	2375	Carrière & Raymond 2000
Kreyol	Dominica	6.6	333	this study	0.03	750	this study
Inuit	Greenland, Canada, Alaska	6.3	64	Faurie <i>et al.</i> 2004	0.17	500	Robert-Lamblin 1997
Baka	Gabon	10.7	403	Faurie <i>et al.</i> 2004	0.5	535	this study
Eipo	Irian Jaya	26.9/20.4 ^a	1295	Faurie <i>et al.</i> 2004 and this study	3	2000	Schiefenhövel 1980
Yanomamö	Venezuela	22.6	37	Marchant <i>et al.</i> 1995	4	1400	Chagnon 1988
Jimi valley	Papua New Guinea	13	185	Connolly & Bishop 1992	5.4	—	see § 2

^a 20.4% is the frequency of left-handers obtained for the Eipo, applying a correction to the frequency of left-handers for bow-shooting (26.9%), according to the correlation between hand preference for bow shooting and for knife use (measured for French men).

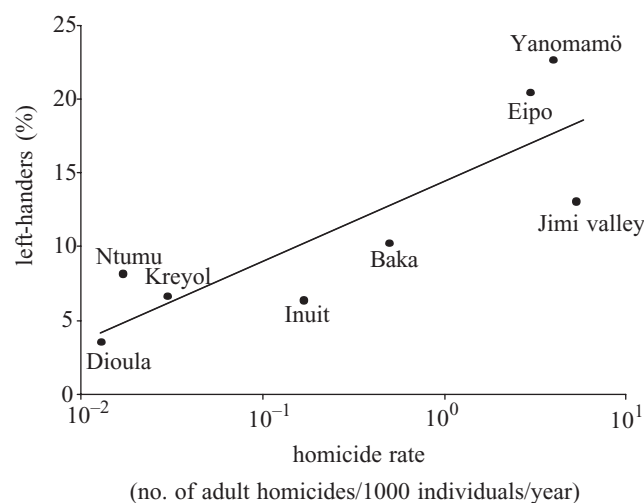


Figure 1. Percentage of left-handers and homicide rate in traditional/sub-traditional cultures. Handedness refers to hand preference for machete use (Kreyol, Ntumu, Dioula, Baka), knife use (Inuit, Eipo) and tool use (Yanomamö, Jimi Valley). Homicide rate was computed as the number of homicides per 1000 individuals per year.

Thus, homicide rate, which includes cases of capital punishment, executions and multi-male raids, is probably not the best estimator of the prevalence of one-to-one fights (Knauff 1987; Kelly 1993), where left-handers have a frequency-dependent advantage. A truthful estimation of the strength of the selection pressure, related to fighting, would be worthwhile in understanding the polymorphism of handedness.

In Western societies, no adequate information is available on possible recent variations in the frequency of left-handers. Firstly, for our purposes, information on the particular case of writing handedness is not relevant: the increase in left-handed writers during the twentieth

century is probably explained by the decrease in the practice of forcing a child to switch writing hand from the left to the right (Porac *et al.* 1980). The frequency of left-handedness for other tasks may not have changed. Secondly, retrospective studies, based on works of art (Coren & Porac 1977), are irrelevant because the conventional—and often religious—artistic representation of a lateralized human has no necessary link, in this respect, with a real individual (Needham 1973). Owing to the recent historical changes in types of violence, the frequency of left-handers in Western societies may not yet have reached equilibrium. In addition, the importance of fighting in these societies is not clearly established.

It is possible that other advantages are associated with left-handedness. Therefore, the costs and benefits need to be quantified to predict future trends in the evolution of the polymorphism of handedness in human populations.

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