

Handedness frequency over more than ten thousand years

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Although there are quite important geographical variations in the frequency of left-handers around the world, nothing is known about its temporal evolution. During the upper Palaeolithic (ca. 35 000–10 000 YBP), in Western Europe, humans painted 'negative hands' in caves by blowing pigments onto their own hand applied on the rock, through a tube held in the other hand. The frequency of left-handers prevailing during this period could thus be assessed. For comparison, the handedness of French university students has been observed for the same task. No difference was detected between the two proportions of left-handers, separated by more than 10 000 years. Implications for the evolution of the polymorphism of handedness are discussed.

Keywords: *Homo*; polymorphism; stabilizing selection; asymmetry; laterality; Palaeolithic

1. INTRODUCTION

Several studies indicate that the coexistence of both right- and left-handed individuals has been maintained for a long time in hominids. The oldest undisputed evidence is from the middle (ca. 425 000–180 000 YBP) and early upper Pleistocene (upper Pleistocene was 180 000–10 000 YBP), where marking on incisors indicates the existence of *Homo neanderthalensis* individuals who were right- or left-handed for sharp tool manipulation, while slicing meat held between the front teeth and the other hand (Bermúdez de Castro *et al.* 1988; Lalueza & Frayer 1997). In the *Homo sapiens* taxon, indications of handedness polymorphism come from studies of stone artefacts, hole-making rotation movements in wood and wear marks on spoons (e.g. Palaeolithic: Keeley (1977); Cornford (1986) and Westergaard & Suomi (1996); Neolithic: Bocquet (1978)). The oldest known evidence is from the upper Palaeolithic, with the negative hand paintings in caves in France and Spain (Groënen 1997).

There is still today a polymorphism of handedness in humans, in all populations so far investigated (e.g. Connolly & Bishop 1992; Carrière & Raymond 2000). The evolutionary significance of this polymorphism is unclear. However, the heritability of this trait is clearly established (e.g. Sicotte *et al.* 1999; McKeever 2000; Francks *et al.* 2002). It is known that the frequency of left-handers is variable across geographical areas (Raymond & Pontier 2004), but nothing is known about its temporal

evolution. We propose to compare the proportion of left-handers among the people who painted the negative hands in the Palaeolithic with the current proportion.

Detailed studies suggest that negative hands were probably made by blowing paint onto the back of one hand applied on the rock surface, the other hand holding a blowing tube (Groënen 1988). Thus a right negative hand corresponds to a left-hander for the task of holding a tube for paint blowing. These negative hands have different sizes and are located at different heights, suggesting the existence of different painters. Moreover, the caves are often far apart in space, and the paintings were done over a long period of time (30 000 to 10 000 YBP; Valladas *et al.* 2001). They can thus be used to estimate the proportion of left-handers in this period. Although we cannot rule out the possibility that some individuals painted their own hand more than once, the ratios should remain similar (all things being equal). In the following work, we use experimentation to compare this proportion with the current proportion.

2. METHODS

(a) Palaeolithic record

There are 507 known negative hands from the upper Palaeolithic of France and Spain (10 000 to 30 000 YBP). Laterality can be unambiguously determined for 343 of them (Groënen 1997). There are 79 right negative hands; this provides an estimate of 23% of left-handers.

(b) Experiment

We placed our experimental subjects in hand-painting conditions that were similar to the original situations. For comparison, we also observed handedness for more usual tasks: throwing and writing handedness were measured on the basis of performance.

(i) Subjects

The subjects were university students, attending the first and second year in the University of Montpellier, France. They were recruited on a voluntary basis, and were not told the purpose of the study. They came one by one to the experimental room, so that they did not have any opportunity to influence each other. The tests were anonymous.

(ii) Throwing handedness

The subject was asked to pick up a ball placed on the middle of a table in front of him and to throw it as close as possible to the centre of a target 3.5 m distant. This way, the choice of the throwing hand is not influenced by the configuration of the experiment. The presence of the target increases the precision of the tasks, which ameliorates the determination of the handedness of the individual (Hopkins 1997).

(iii) Negative hand painting

The subjects were given a special pen that projects ink at one extremity when they blow at the other (see www.blopens.com for details). Each subject was instructed to paint a negative hand on a blank paper. The technique is thus very similar to the pigment tube-blowing technique attributed to the Palaeolithic artists.

(iv) Questionnaire

Subjects were asked to give the following information: age, sex and writing hand.

(c) Data analysis

Three handedness variables were thus recorded: throwing handedness, hand painted while holding the tube with the other hand, and writing handedness. These qualitative variables have two possible values: left or right.

The frequency of left and right negative hands obtained in our experiment and as recorded in the caves were compared using a Fisher's exact test. We tested with the same method the independence between the three handedness variables. Non-parametric statistics (Kendall's τ) were used to measure the correlations between variables. These analyses were performed with the SAS software, v. V8.

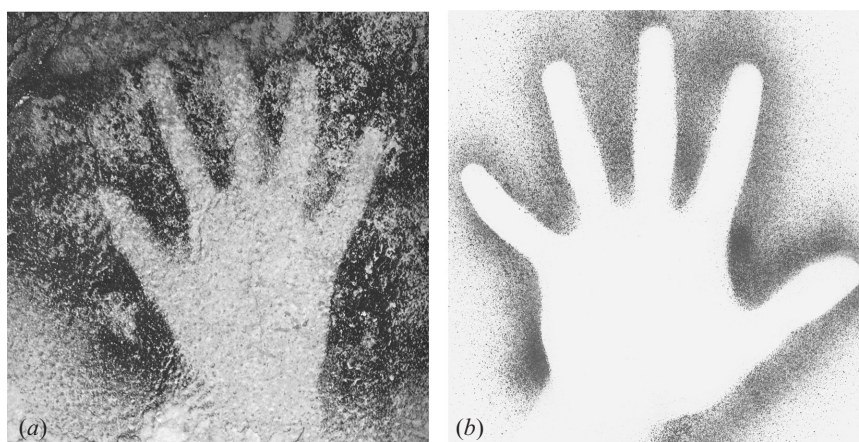


Figure 1. (a) Right negative hand from the cave of Le Pech-Merle (Lot, France; photograph by J. Vertut). (b) Left negative hand made by a subject in our experiment.

Table 1. Number of right and left negative hands recorded in the caves and from university students.

	negative hands	
	left	right
Palaeolithic ^a	264 (77.0%)	79 (23.0%)
Present	138 (77.1%)	41 (22.9%)

^a Data from Groënen (1997).

3. RESULTS

One hundred and seventy-nine students participated in the study (58 males and 121 females, aged 19.8 ± 1.1 years). Figure 1 shows a Palaeolithic negative hand, and one made by one of the students. The percentage of them that made a right negative hand was 22.9%. No effect of sex was observed (Fisher's exact test, $p = 0.85$). The results of the experiment are compared with the Palaeolithic record in table 1. There is no significant difference between the frequency of right negative hands in our sample and in the Palaeolithic sample (Fisher's exact test, $p = 0.99$).

Left-handed writers and throwers were 8.9% and 7.8%, respectively. The three measures of handedness are highly dependent (Fisher's exact test, $p < 0.0001$). No effect of sex was observed (Fisher's exact test, $p = 0.78$ and $p = 0.77$ respectively). The handedness for holding the tube while making the negative hand is positively correlated with writing (Kendall's $\tau = 0.48$, $p < 0.0001$) and throwing ($\tau = 0.49$, $p < 0.0001$) handedness. Among subjects who made a left negative hand, almost all (99.3%) are right-handers for throwing. Among subjects who made a right negative hand, however, only 31.7% are left-handed for throwing.

4. DISCUSSION

The proportion of right and left negative hands in our latterday experiment is not different from the proportion recorded by Groënen in the European caves. The absence of significant variation in the frequency of left-handers (for the task of holding a tube to paint the other hand) over more than 10 000 years is surprising. It suggests that

handedness is a trait under some functional constraint that has not substantially changed since the upper Palaeolithic.

This is the first information, to our knowledge, on the temporal variations of the frequency of left-handers for one particular task. The only exception concerns the twentieth century increase of left-handers in western societies, probably explained by the relaxing of social pressures (Porac *et al.* 1980). Studies based on human subjects depicted in artworks sampled over 50 centuries (Coren & Porac 1977) are irrelevant, because the conventional—and often religious—representation of a lateralized human has no necessary link, in this respect, with a real individual (Needham 1973).

To our knowledge, handedness for painting negative hands has never before been measured in a contemporary population. In the present sample, it is significantly correlated with writing and throwing handedness. Surprisingly, the correlation found is not as strong as the correlation linking writing and throwing handedness: a substantial proportion (17%) of right-handed throwers hold the tube with the left hand. Inference on the frequency of left-handed throwers during the upper Palaeolithic requires the assumption that the level of the observed positive correlation was already present at that time, which is difficult to establish.

Negative hands are described in several locations (Australia, South America, Indonesia). They all date from Neolithic to contemporary times. The negative hands of Western Europe are the most ancient (upper Palaeolithic; Leroi-Gourhan *et al.* 1995).

The significance of the negative hands painted in caves or shelters has long been a mystery. In some cultures (e.g. in South Africa), traditional rock painting is still practised (or was still practised very recently). The hand prints are made by shamans and have a sacred meaning (Lewis-Williams 1983). A comparative analysis indicated that the negative hands from the upper Palaeolithic probably have the same interpretation (Lewis-Williams & Dowson 1988; Clottes & Lewis-Williams 1998). A more adequate sample to estimate the present handedness would then be the shamans themselves. A comparison of the frequency of right and left negative hands from these locations would be useful to know if the stability of the proportion of left-handers over more than 10 000 years in Western Europe is also found elsewhere.

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