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Right handedness of *Homo heidelbergensis* from Sima de los Huesos (Atapuerca, Spain) 500,000 years ago☆

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Abstract

Handedness is a product of brain specialization, which in turn seems to be responsible for the higher cognitive capabilities of humans, such as language and technology. Handedness in living humans is well established and shows the highest degree of manual specialization. Studies on hand laterality in nonhuman primates, particularly in chimpanzees, remain a matter of controversy as results tend to vary depending on factors such as the tasks performed and the environment in which the individuals live. Studies in several disciplines have attempted to determine where in the course of human evolution handedness established itself, with evidence collected from sources such as paleoneurological analyses, stone tool flaking, zooarchaeological studies and dental wear analyses, the last one of which have proven the most reliable source of information. Here we report an experimental and paleoanthropological study on hand laterality of a sample of 28 hominids from Sima de los Huesos (Atapuerca, Spain), dated at about 500,000 years ago, and compare our results with dental microwear analysis in other fossil samples such as that from Krapina (Croatia), as well as modern traditional societies. Our results indicate that European Middle Pleistocene *Homo heidelbergensis* was already as right-handed as modern populations.

Keywords: Hand laterality; Dental microwear; Middle pleistocene; *Homo heidelbergensis*; Preneanderthals; Human evolution

1. Introduction

Handedness is a product of brain laterality and, thus, a product of evolution. Handedness in living humans shows the highest degree of manual specialization — about 95%. The best method for identifying the existence of hand laterality is to observe individuals handling tools in spontaneous tasks (Faurie, Schiefenhövel, Bomin, Billiard, & Raymond, 2005). The ratio of right- to left-handers varies notably from community to community. The ratio of right-handers to left-handers is higher in Western societies than in traditional societies (Faurie et al., 2005), leading researchers to suggest an influence of social relations and culture.

Many studies have been conducted on hand laterality in our closest living relative, the chimpanzee. These works have focused on observations in both wild and captive conditions, with differing results. However, most authors agree that chimpanzees do not display any hand preference at a population level when performing spontaneous and simple tasks (Harrison & Nystrom, 2008; McGrew & Marchant, 2001; Mosquera et al., 2007).

So, when did hand laterality finally install itself in human evolution? Was it a gradual and progressive trait adopted by more and more individuals, or did it occur quickly? Once installed, were the ratios between right- and left-handers already similar to those today? Obviously, the answers to these questions cannot be found in the

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observation of individuals manipulating objects. Alternatives to this approach have come from four disciplines: paleoneurology, zooarchaeology, lithic technology and dental microwear analyses.

Paleoneurological studies on the earliest hominins analyze the features of fossil endocranea in search of anatomical brain asymmetries. These asymmetries are related to functional specializations such as hand laterality, language, etc. However, traces found in the very few sufficiently complete specimens may point to different interpretations. For example, the approximately 1.9-myr-old endocranium of KNM-ER 1470 (*Homo rudolfensis*) shows a modern position of the third lower frontal circumvolution (Holloway, 1996; Tobias, 1987). This specimen and some others, such as *Homo ergaster* (1.8 myr), and even *Australopithecus africanus* (Taung specimen, 3 myr), show hemispheric torque (Holloway, 1983; Holloway & Lacoste-Lareymonde, 1982). The position of the third lower frontal circumvolution seems to be related to several capabilities, such as language, hand lateralization and tool-using behavior. Hemispheric torque is related in modern humans to individual hand laterality, which might be useful in many contexts, for example, throwing. Thus, it is not easy to conclude exactly when and for what original purpose brain laterality evolved.

The topic has also been approached from a lithic technology perspective. Tool production sequences reconstructed in some early African sites have led researchers to conclude that *Homo habilis/rudolfensis* were right-handed hominins (Toth, 1985). Also, use-wear analyses on the edges of tools used by the hominins of Galería (Atapuerca, Spain) (400 to 200 ky) point to a dominance of right-handers (Ollé, 2003).

Finally, zooarchaeology has approached hominin handedness through the study of cutmarks left by tools on bone surfaces when defleshing prey (Bromage & Boyde, 1984; Bromage, Bermúdez de Castro, & Fernández-Jalvo, 1991; Shipman & Rose, 1983). However, this methodology has also recently been brought into question (Pickering & Hensley-Marschand, 2008).

2. Dental microwear

A fourth approach to establishing the existence of hand laterality in fossil hominins is dental wear. Since the earliest stages of human evolution, hominins have used their teeth to process food and to handle other materials. The simultaneous use of hands and teeth allows a wide variety of tasks to be performed and involves contact between the anterior teeth and other materials. This process produces marks and traces on dental surfaces, which are known as dental wear of cultural origin (Larsen, Teaford, & Sandford, 1998; Leigh, 1925; Merbs, 1968, 1983; Molnar, 1972; Ryan & Johanson, 1989; Turner & Cadien, 1971).

These marks are diagonally oriented scratches, as first noted by Martin (1923) on a Neanderthal incisor from La Quina (France). However, De Lumley (1973) was the first researcher to suggest that these types of scratches may have a cultural origin. Similar traces have also been documented in *Homo heidelbergensis,* Neanderthals and modern humans from different sites (Bermúdez de Castro, Bromage, & Fernández-Jalvo, 1988; Lalueza-Fox, 1992; Lalueza-Fox & Pérez-Pérez, 1994; Puech, 1979; Puech, 1982; Trinkaus, 1983), including the Neanderthals of Krapina (Croatia) (Lalueza-Fox & Frayer, 1997). Dental grooves have also been documented in living populations of Eskimos, Aleutians, Tasmans, Fuegians and Australian Aborigines (Lalueza-Fox, 1992; Merbs, 1968).

Furthermore, dental wear of this type has been identified on the anterior teeth of some individuals from Sima de los Huesos (SH), the site of the world's richest collection of *Homo heidelbergensis* remains, convincing researchers of the cultural origin of these grooves caused by using the teeth as a third hand (Bermúdez de Castro et al., 1988; Lozano, Bermúdez de Castro, Martinón-Torres, & Sarmiento, 2004). However, these studies were preliminary, as only a small sample of teeth was analyzed and only one experiment performed.

This work analyzes the entire sample of anterior teeth from the SH collection and crosses the results with data derived from an experimental study in order to confirm a generalized behavior of the European *Homo heidelbergensis* population over 500,000 years ago and to conclusively establish their hand laterality. Furthermore, we compare evidence from paleontology and living populations to determine whether the strength of hand laterality in Middle Pleistocene populations was as high as it is today and also whether the ratio between right- and left-handers is consistent with any living community.

3. The Sima de los Huesos site

The SH site is located in the Atapuerca karst system in Burgos, Spain (Fig. 1). Systematic excavations at SH have yielded the most complete collection of European Middle Pleistocene human population remains (Arsuaga, Martínez, Gracia, & Lorenzo, 1997). Several dating methods have been applied to this deposit (Bischoff et al., 1997, 2003; Cuenca-Bescos, Conesa, Canudo, & Arsuaga, 1997; Parés, Pérez-González, Weil, & Arsuaga, 2000), but new high-precision dating techniques have ascertained a minimum age of 530 kyr (Bischoff et al., 2007).

All of the human fossils come from the same unit and were apparently deposited during the same sedimentation period (Bischoff et al., 1997). Only human and carnivore remains have been found at the site (García, Arsuaga, & Torres, 1997; Torres, 1987), with a single lithic tool, a quartzite handaxe, also recovered (Carbonell et al., 2003). Currently, the SH hominin sample comprises more than 4500

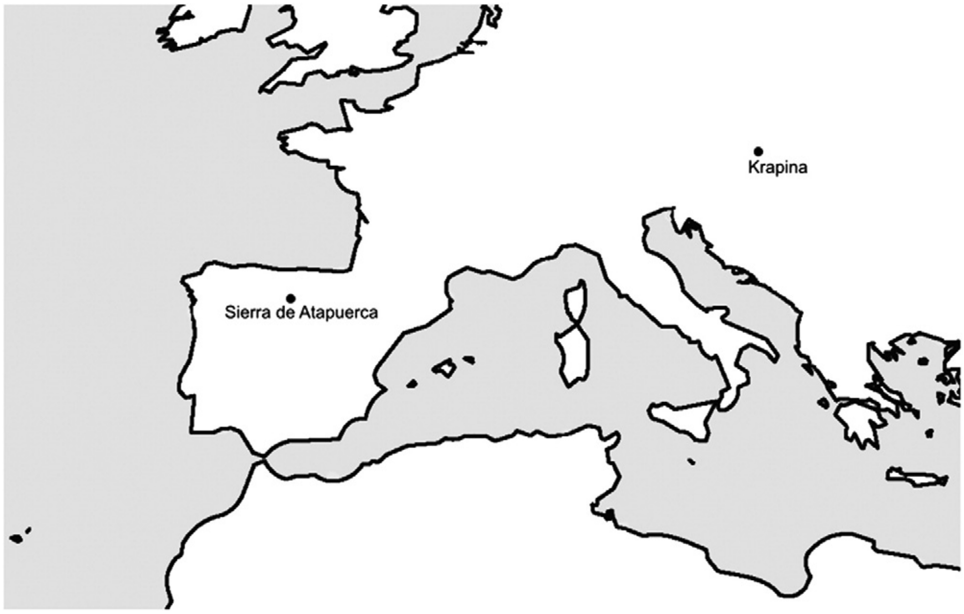

Fig. 1. Geographic setting of the *Homo heidelbergensis* sites of Sierra de Atapuerca (Spain) and Krapina (Croatia).

fossil remains, including all the skeletal elements of the same biological population of *Homo heidelbergensis.*

4. Material and methods

The minimum number of individuals was determined through the analysis of the maxillae, mandibles and isolated teeth. Examination of these elements suggests that a minimum of 28 individuals are represented in the SH record (Bermúdez de Castro, Martinón-Torres, Lozano, Sarmiento, & Muela, 2004). Sex and age at death of these individuals have been estimated by paleodemographic analyses (Bermúdez de Castro et al., 2004; Rosas, 1997) (Table 1).

Previous studies have demonstrated the efficacy of dental microwear in making dietary and dental wear pattern inferences about archaeological samples of early hominids and modern humans (Bullington, 1991; Fine & Craig, 1981; Grine, 1987; Pérez-Pérez, Espurz, Bermúdez de Castro, de Lumley, & Turbón, 2003; Puech, 1979; Teaford, 1991; Ungar & Spencer, 1999). Specimens were prepared in accordance with standard dental microwear procedures, and high-resolution replicas were made (Lozano, Bermúdez de Castro, Carbonell, & Arsuaga, 2008; Pérez-Pérez, Bermúdez de Castro, & Arsuaga, 1999; Rose 1983). A detailed analysis of the labial surface was performed with a Jeol JSM 6400 scanning electron microscope (SEM). The replicas were first examined at magnifications of ×43 and ×100 to locate and identify wear features. The level of magnification was then gradually increased, up to ×800, to obtain a more detailed view of the wear features. Digitized SEM images of the chosen surfaces were later taken at different levels of magnification.

Micrographs were analyzed using Microware 4.0 semi-automated software for image analysis (Ungar, 1995). The following data were analyzed per tooth and per individual: (1) feature density, (2) mean feature length, (3) mean feature width and (4) feature long axis orientation. However, the angles and lengths of labial striations were measured from digitized photographs (at a magnification of ×20) taken with an Olympus SZ11 stereomicroscope using MicroImage 3.0 software. Striations were classified into four orientation categories, ranging from 0° to 180°: horizontal (H) (0–22.5°/

Table 1
Number of striations for each orientation at the SH hominids sample

SH Individuals	Age/sex	V	H	RO	LO
I	16–17/female	13	16	*36*	7
II	12.5–14.5/–	16	12	*52*	5
III	15–17/female	11	2	*23*	3
V	+35/–	1	0	*5*	2
VII	24–30/male	2	2	*12*	4
IX	3–4/–	0	0	*2*	0
X	15–17/female	1	0	1	1
XI	13–15/female	0	0	*3*	0
XII	17–19/male	*2*	0	1	1
XV	17–18/female	*4*	0	1	2
XVI	12.5–14.5/–	12	0	*22*	0
XVIII	9.5–11.5/male	8	8	*29*	2
XX	12.5–14.5/male	9	1	*30*	0
XXI	+35/male	*4*	1	3	2
XXII	20–26/male	6	0	*13*	2
XXIII	14–16/female	*14*	1	0	3
XXIV	12.5–14.5/–	5	2	*7*	0
XXV	11–13/female	8	1	*9*	0
XXVII	20–26/male	2	0	*3*	2
XXXI	24–30/female	6	0	*15*	2

Values in italics represent individuals with a preferential orientation for their labial striations.

Table 2
Average of the labial striations' width for each raw material flakes

	Experimental work	
	Right handed (μm)	Left handed (μm)
Quartz	46.34	36.16
Quartzite	35.02	33.21
Sandstone	39.1	35.47
Flint	39.1	53.96
Total	39.7	41.1

157.5–180°); vertical (V) (67.5–112.5°); left oblique (LO) (22.5–67.5°); and right oblique (RO) (112.5–157.5°) (based on Lalueza-Fox & Frayer, 1997).

All previous research into these striations has hypothesized that SH hominins cut pieces of different materials with stone tools while holding the material between the maxillary and the mandibular incisors and canines, scratching dental enamel in the process (Bermúdez de Castro et al., 1988; Lozano, 2001; Lozano et al., 2004). Therefore, labial striations on teeth have the same morphology as cutmarks on bone. In order to test the similarity between cutmarks and labial striations on human teeth, an experimental reproduction was conducted using teeth (n=23) obtained from surgical extractions with no preexisting evidence of dental microwear of any kind at the magnifications we used in this study (Lozano, 2005; Lozano et al., 2004, 2008).

Experimental cutmarks were made with flakes of different raw materials, using the most abundant types in the Atapuerca archaeological records (Table 2). Research has shown that flakes were commonly used as cutting tools, particularly for meat processing (Márquez, Ollé, Sala & Vergès, 2001). The teeth were divided into sets and each of them glued into a mouthguard (similar to those used by sportspeople) in the appropriate positions to simulate the prognathism and dental arcade of *Homo heidelbergensis*. We were helped by two assistants, one right-handed and one left-handed. Each assistant inserted a mouthguard with one set of teeth into his mouth. They made cuts directly on the labial surface by simulating cutting activities. The same procedure was repeated with different sets of teeth and flakes of different lithic raw materials.

5. Results

In the fossil sample studied, 157 (94.48%) of the 163 SH teeth show striations on the labial surface (Table 3). All 20 SH individuals examined show this type of wear on all or almost all teeth. The edges of labial striations are linear, well defined and parallel to each other along most of their length. The bottom of the striations usually displays a V-shaped transverse section and is ploughed by several parallel microscratches. The morphological traits, particularly the width and shape of labial striations, are exactly the same as those displayed by cutmarks on bone made by lithic cutting tools (Shipman & Rose, 1984).

Table 3
Data of studied samples with labial striations

	Sima de los Huesos	Krapina	Experimental work	
			Right handed	Left handed
No. of teeth	163	82	17	6
No. of teeth with labial striations	157 (94.48%)	66 (81%)	17	6
No. of individuals	20	13	1	1
No. of individuals with preferred orientation	19; 15 (RO) 4 (V)	7; 6 (RO) 1 (LO)	1 (RO)	1 (LO)
Width of labial striations (μm)	29.76–65	25.5–67.7	19.1–80.5	19.7–59.6

The margins of the labial striations are generally smoothed by the action of the saliva and tongue and normal masticatory use of teeth, so none of the striations displayed sharp or fresh edges (Teaford & Oyen, 1989). Also, many striations were superimposed, suggesting that they were formed at different times. Therefore, we conclude that the striations were produced during the lifetime of the SH hominins. Most labial striations are on incisors, particularly on the central upper incisors (Fig. 2). The older the individual, the greater the number of superimposed labial striations and the further across the labial surface they extended. Starting from the central point represented by the upper central incisors, we observed that the total number of labial striations decreases towards the distal part of the anterior teeth (i.e., towards the cheek teeth). Several

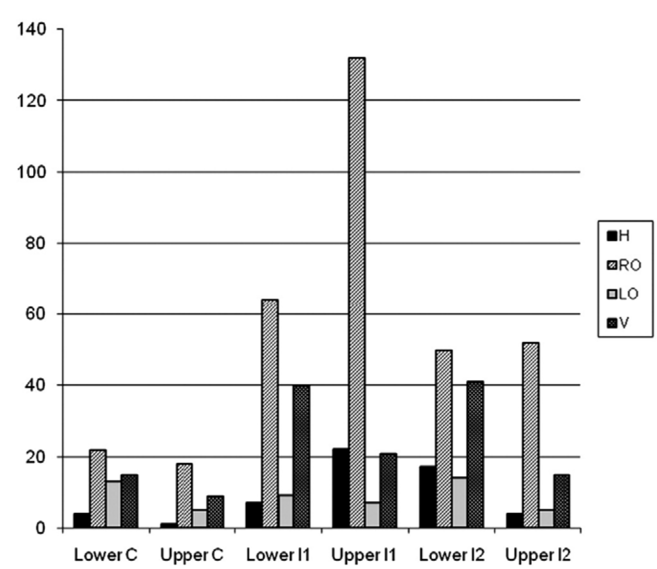

Fig. 2. Orientation of labial striations in each dental category at the SH sample. Vertical axis: number of striations. Horizontal axis: dental categories (lower C: lower canines; upper C: upper canines; lower I1: lower first incisives; upper I1: upper first incisives; lower I2: lower second incisives; upper I2: upper second incisives).

Table 4
Results of Student's t test to check the homogeneity of the width of labial striations (i.e., the null hypothesis according to which the groups do not differ)

Labial striations — width		
	Sima de los Huesos	Experimental
Sima de los Huesos	–	0.11 (t=0.6196; df=516)
Experimental	0.11 (t=0.6196; df=516)	–

The sample is completely homogeneous for width because no p values below the .01 significance level were found. Numbers outside the parentheses are the probability values.

quantitative variables were measured, such as width and angle of orientation. Striation width in SH samples ranges from 29.76 to 65 μm (Table 3). We recorded the orientation of 592 striations from all SH individuals and from teeth not assigned to any individual. The most common category is RO with 342 striations, followed by V with 141. Lesser represented categories are H (n=55) and LO (n=54). Of 20 individuals in the SH sample, 19 had a preferential orientation for their labial striations (Table 1): 15 had a preferential orientation RO and four had a preferential V orientation. None of the individuals show H or LO preferential orientation.

Experimental work was performed to check the hypothesis supporting the utility of labial striations in determining handedness in fossil hominins. The morphology and metric values of the experimental striations matched well with the striations documented in the SH teeth. All the experimental cutmarks have a similar width, regardless of material and hand used (Table 2 for width). The average width of both the experimental and the SH fossil striations was statistically homogeneous (Table 4). The experimental work shows that the right-handed individual made a total of 46 striations, 41 (89.1%) of which were RO. The rest (n=5) are V. The left-handed individual made a total of 51 striations, 40 (78.4%) of which showed LO orientation. The rest (n=11, 21.6%) were V. Horizontal striations were not documented in any case.

6. Discussion

Striations on the labial face of incisors and canines were produced when different materials clenched between the anterior teeth were cut with a lithic tool. Occasionally, the flake may have come into contact with the enamel and produced labial striations. Brace (Brace, 1967; Brace, Rosenberg, & Hunt, 1987) referred to this behavior as *stuff and cut*. This hypothesis has now been confirmed through the experimental reproduction of labial striations presented in this work. Labial striations were produced by hominins when they used one of their hands, so we can obtain information about handedness from fossil hominins.

From the 20 individuals in the SH sample, the labial striations in 19 (95%) showed a preferential orientation (Table 1). Of these 19 individuals, 15 had a preferential RO orientation and four had a preferential V orientation. None of the individuals had preferential H or LO orientations. Our experimental work establishes that a right-handed individual produces striations with a preferential RO orientation, while a left-handed individual produces LO striations. Vertical orientation was found to be a minor product of both categories of handedness. The experimental results allow us to infer that the dominance of RO striations denotes the preferential use of the right hand. Therefore, the SH *Homo heidelbergensis* population was preferentially right-handed. A previous preliminary study reached similar conclusions (Bermúdez de Castro et al., 1988), although it focused on a sample of only 19 teeth from SH. Furthermore, the experiment was conducted with (1) few porcelain, not real teeth; (2) only one experimenter (right-handed); and (3) only one type of raw material tool. In addition, the authors did not measure the width of the striations to confirm their etiology. All these issues have been addressed in this experiment.

These types of striations have been documented not only in SH teeth, but in other Middle and Upper Pleistocene hominins as well. However, only the striations on the teeth found at Krapina have been studied in depth. The Neanderthal remains from Krapina (Croatia) are 130,000 years old (Lalueza-Fox & Frayer, 1997). Research results (Table 3) showed that 66 (81%) of 82 anterior teeth displayed labial striations similar to both the SH and the experimental striations presented here. Unfortunately, the authors did not count the number of marks on each tooth, which in our view more objectively determines the prevailing orientation of each individual. In contrast to SH, where almost all (95%) of the individuals show preferential orientation (RO in 15 cases), just 13 individuals (54%) from Krapina show an orientation pattern, RO in six cases and LO in one case. Interestingly, none of the SH individuals showed this LO pattern.

Incisor labial striations have also been noticed in some modern preindustrial populations. Bax and Ungar (1999) studied labial striations of four Amerindian groups representing diverse patterns of subsistence. The authors concluded that these types of striations do not provide information about laterality because V orientation prevailed in all four groups. They therefore reject the possibility that labial striations on fossil hominins may reflect handedness. However, the labial striations examined by these authors did not have the morphology of cutmarks, so they did not result from the interaction of a lithic tool and the dental enamel. That is, none of the four studied groups show evidence of *stuff-and-cut* behavior. As the authors do not present data about the width and length of the striations, it is not possible to compare their measurements with our experimental and fossil samples. Indeed, it seems that the striations examined by Bax and Ungar (1999) would have simply been caused when biting food with the anterior teeth. Striations like these have also been found on SH teeth

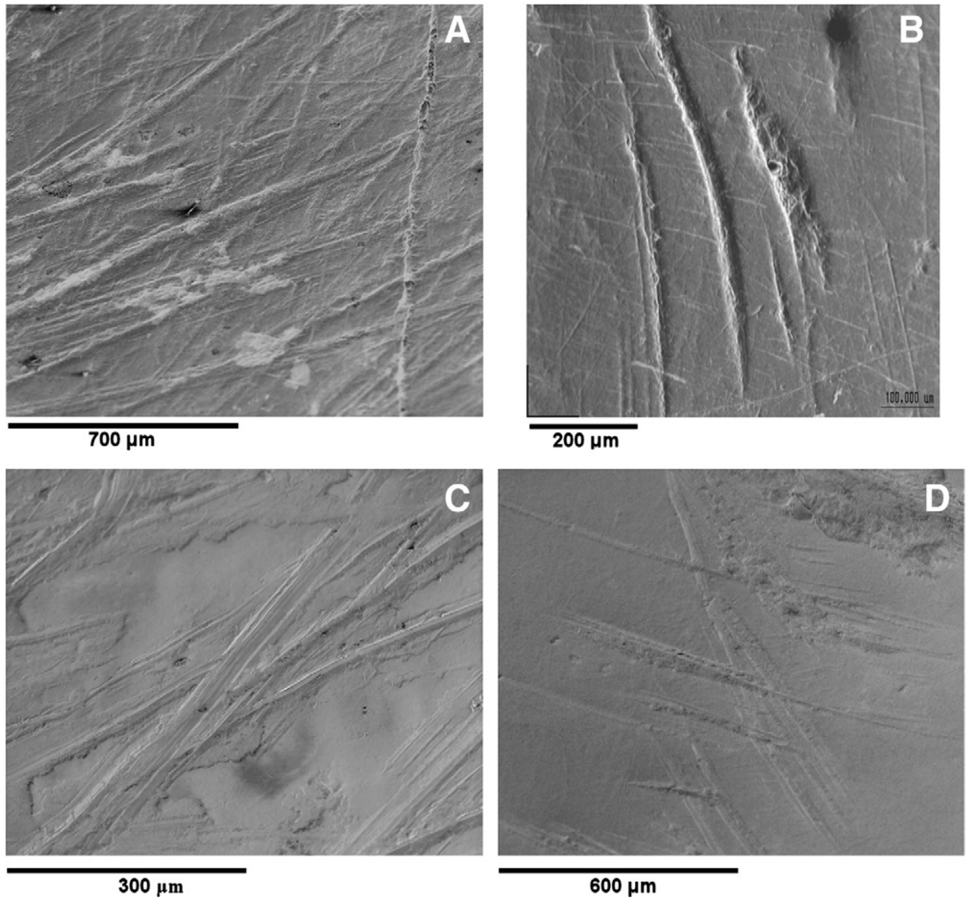

Fig. 3. (A) Right oblique labial striations on labial surface of the upper left central incisor (AT-198, not associated with an individual) (×75). (B) Vertically oriented labial striations on labial surface of the lower lateral incisor (AT-1123, individual XX) There are other thinner and shorter striations caused by biting food. (×90). (C) Experimental striations made by a right-handed person. Note their RO orientation. (D) Experimental striations made by a left-handed person. Note their LO orientation. All SEM images were taken in secondary electron emission mode with an accelerating voltage of 15 kV. Replicas were coated with a 25-nm gold layer in high vacuum sputter coater unit (BAL-TEC SCD004).

(Fig. 3B): they are V and differ in size from labial striations. They do not have the same etiology as fossil cutmarks, so their conclusions cannot be equally applied to them.

7. Conclusions

Labial striations on the teeth of the SH Middle Pleistocene *Homo heidelbergensis* population were caused by the interaction between a lithic tool, one hand and the anterior teeth. These striations occurred when a material was held tightly with the anterior teeth and one hand, using the other hand for cutting the material with a stone tool. During this process, the edges of the stone flake can cut the enamel of the teeth, leaving characteristic cutmarks with specific shapes and orientations.

The morphology, width, length and orientation of the labial striations found in the SH specimens were analyzed and preferential orientations were found to be right oriented. An experiment conducted with one right-handed and one left-handed individual shows that the former mostly caused right-oriented striations, while the latter resulted in the opposite, left-oriented pattern. Therefore, comparing the striations of the fossil population and the experimental sample allows us to conclude that labial striations are useful for inferring handedness. It is plausible to deduce that hand laterality was already installed in human evolution at the time of *Homo heidelbergensis*, about 500,000 years ago. Furthermore, this species was already as preferentially right-handed as modern populations. Interestingly, none of the SH individuals studied (n=20) seems to have been left-handed, which can probably be attributed to coincidence. In any case, the high proportion of individuals at SH with oriented striations points to a strong handedness index, similar to that observed in postindustrial societies, where the task of writing, the most complex and lateralized task, is generalized (Faurie et al., 2005). Furthermore, our results emphasize that activities depending on the use of the teeth as a third hand represent a common behavior among Middle Pleistocene hominin populations, since striations are present on the teeth of all the SH individuals, including those of a 3- to 4-year-old.

Similar studies with earlier species may help to answer whether human hand laterality developed through a progressive process or through fast evolutionary adoption in human evolution. They may also provide information about other hemispheric specializations, such as language and technology, which are the highest milestones of our complex behavior. In fact, recent results in nonhuman primates performing complex tasks (Fletcher & Weghorst, 2005; Llorente, Mosquera, & Fabré, 2009; Lonsdorf & Hopkins, 2005), and dental wear studies on hominin samples (Bermúdez de Castro et al., 1988; de Lumley, 1973; Lalueza-Fox & Frayer, 1997; Lozano et al., 2004; Trinkaus, 1983), have given rise to the suggestion that technology may have played a major role in the acquisition of human handedness.

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