

ARTICLE

Right-handed fossil humans

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Abstract

Fossil hominids often processed material held between their upper and lower teeth. Pulling with one hand and cutting with the other, they occasionally left impact cut marks on the lip (labial) surface of their incisors and canines. From these actions, it possible to determine the dominant hand used. The frequency of these oblique striations in an array of fossil hominins documents the typically modern pattern of 9 right- to 1 left-hander. This ratio among living *Homo sapiens* differs from that among chimpanzees and bonobos and more distant primate relatives. Together, all studies of living people affirm that dominant right-handedness is a uniquely modern human trait. The same pattern extends deep into our past. Thus far, the majority of inferred right-handed fossils come from Europe, but a single maxilla from a *Homo habilis*, OH-65, shows a predominance of right oblique scratches, thus extending right-handedness into the early Pleistocene of Africa. Other studies show right-handedness in more recent African, Chinese, and Levantine fossils, but the sample compiled for non-European fossil specimens remains small. Fossil specimens from Sima del los Huesos and a variety of European Neandertal sites are predominately right-handed. We argue the 9:1 handedness ratio in Neandertals and the earlier inhabitants of Europe constitutes evidence for a modern pattern of handedness well before the appearance of modern *Homo sapiens*.

KEYWORDS

laterality, labial tooth striations, archaic *Homo*, Neandertals

1 | INTRODUCTION

Today, the primary function of the incisors and canines is to preprocess food, before shifting it to the posterior teeth for additional crushing. Prehistoric humans used their anterior teeth to a much greater extent to manipulate and process nondietary items such as fiber^{1–3} or other items.^{4,5} These behaviors produced a characteristic differential occlusal

wear pattern between the front and back teeth,⁶ with the incisors and canines being more worn than the premolars and molars. This is especially true for hunter-gatherers as compared to agricultural groups.^{7,8} In Neandertals, this type of wear is accentuated, with the incisors and canines typically much more worn than the premolars and molars.⁹ Estalrich and Rosas¹⁰ have shown a sex difference in the degree of differential wear among the El Sidrón Neandertals, implying a sexual

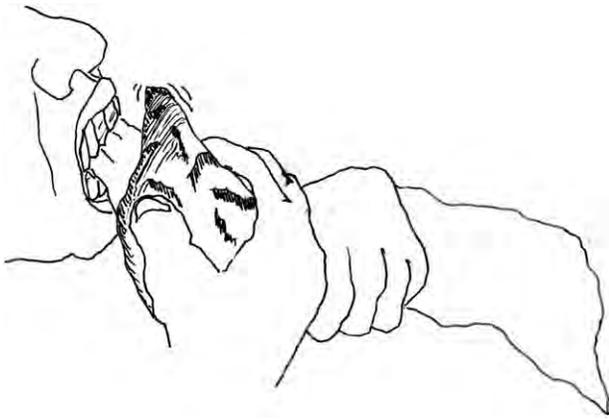


FIGURE 1 Demonstration of how marks were likely made on the incisors and canines. A right-hander pulls down with a stone tool, cutting through the object held between the anterior teeth. Occasionally, when the tool accidentally strikes the tooth's surface, it leaves a permanent striation on the labial tooth face. Repetitive marking of the labial face allows for the assessment of which hand was used in this bimanual task

division of labor, at least in this group, when using their jaws and teeth in these kinds of nonmasticatory activities. Other early *Homo* fossils typically show differential wear, indicating a shift in tooth function away from *Australopithecus*.⁹

Fossil human teeth often show an array of scratches on their labial face. These scratches run in different directions, angled from horizontal to perpendicular to the bite plane. Sometimes the striations intersect or cross over each other; some have sharp edges and many have smoothing of the cut-mark margins. Clearly, these cut marks were not made with a single action, but represent a complicated record of how items were processed; that is, when something was clenched between the upper and lower front teeth, a tool was dragged over the object to process it. These nonocclusal marks are made when the stone tool accidentally contacts the labial surface of the tooth.¹¹ They appear only on the labial faces of the incisors and canines, not on premolars or molars and never on the lingual surface of any teeth.

Such scratches, first reported by Martin¹² on a La Quina Neandertal upper incisor, have been noted by many workers, especially in Neandertals.^{13–20} Not all researchers have quantified the striations,^{21–26} but they are commonly found on Neandertal incisors and canines. Multiple, differently angled scratches are preserved on the labial faces of incisors and canines, but diagonal striations, which point to the handedness of the tooth's "owner," are especially important. Because of their larger size, these striations tend to be concentrated on the upper incisors, but they appear on upper canines and lower teeth as well (Figure 1).

Some experimental work has been done to replicate the labial striations. Bermúdez de Castro, Bromage, and Fernández-Jalvo¹¹ fitted the latter with a mouth guard, who used a stone tool to cut through meat held between the anterior teeth. This replication showed that oblique marks were typically produced by a right-handed action; a left-hander made oppositely angled marks. Lozano et al.²⁷ used flint, sandstone, quartz, and quartzite flakes to produce similar striations on

extracted human incisors mounted in mouth guards. Both of these studies demonstrated that the labial striations were a byproduct of clenching an object between the jaws and processing it with a stone tool. More importantly, based on the frequency of oblique striations, it was possible to distinguish which hand was used in the primary action from the obliquity of the marks. These experimental results closely matched the patterns seen on fossil Europeans.

Humans are not unique in their handedness. Bimanual tasks are documented in captive and wild apes. In observational studies, there is a dominant hand, which directs the primary movement, while the other hand holds or positions the object. However, African apes, whether in the wild or captivity, do not hold objects in their mouth and cut or process them with a stone tool. They also never reach the 9:1 ratio seen in humans. Thus, while there are some parallels, the dominant ratio of right-handers in humans is unique (Box 1).

2 | THE SAMPLES

We have studied many different samples of humans, from the single case of a fossil in the early Pleistocene site of Olduvai Gorge (OH-65) to the anterior dentitions of some recent people. The greatest number of scratches appears in fossil samples. Although modern *Homo sapiens* groups have not been systematically studied, they show few labial striations. Here we review the diachronic history of labial scratches from ~1.8 million years ago to Neandertals, ending with a limited sample of modern humans. Our total sample comprises five different types of humans (*Homo habilis*, *Homo antecessor*, the Sima de los Huesos fossils, European Neandertals, and modern *Homo sapiens*). All were analyzed using similar methods, as outlined in Box 2.

The teeth from the adult OH-65 are the oldest, but so far only a single example from this species has been studied.^{47,48} Next in age come the remains from the Gran Dolina TD6 at the Sierra de Atapuerca in Spain, dated at 860–936 kya.^{49,50} These consist of 165 human fossil remains assigned to *Homo antecessor*. They represent a minimum of eleven individuals, ranging from immatures to adults. Eight individuals preserve anterior teeth.^{51–53}

A later sample comes from the Sima de los Huesos (SH) site in a different locality at the Sierra de Atapuerca. The most recent age, by uranium-series dating of limestone cemented to a hominin cranium, gives a minimum age of 430 kyr.⁵⁴ More than 6,500 remains derive from the same stratigraphic unit and belong to the same biological population.^{52,55,56} Formerly assigned to *Homo heidelbergensis*, the species was once considered to be ancestral to Neandertals.^{57,58} Subsequent mtDNA analysis removed the Sima de los Huesos individuals from *Homo heidelbergensis* and likely ancestry to Neandertals.⁵² More recently, nuclear DNA results once again linked the Sima de los Huesos fossils to Neandertals; for now, they should be considered their likely ancestors.⁵⁹ At Sima de los Huesos, 20 of the 28 individuals have anterior teeth, but only 15 preserve enough scratches for analysis. These individuals ranged in age from 4.5 years to more than 35 years; eight individuals have been designated as females, seven as males, and five are of unknown sex.^{27,58,60,61}

Box 1. Handedness across the animal world and the high frequency of right-handedness in humans

Humans are considered to be uniquely right-handed, with a species-wide ratio of right-handedness to left-handedness of $\sim 9:1$. Yet research has shown that many other animals also show limb preference and laterality. Ströckens, Güntürkün, and Ocklenburg²⁸ reviewed 119 species, from fish to nonhuman primates, and found that many animals show fin/limb preferences, but that the “strong and consistent rightward population-level asymmetry observed for human handedness is not [common].” Among some Australian marsupials Giljov et al.²⁹ found that bipedal kangaroos show population-level, forelimb left preference. In the genus *Pan*, our closest primate relatives, differences in the ratios for handedness exist between not only wild and captive animals, but also chimpanzees and bonobos. In the wild, some studies have shown no consistent handedness at the species level among chimpanzees^{30–32}; others have documented a sex difference in bimanual tasks, with males more likely to be left-handed and females typically right-handed in the wild.³³ A captive study³⁴ yielded similar results. In the most comprehensive study of captive apes compiled so far, Hopkins et al.³⁵ reported data for tube tests of 777 great ape adults and juveniles. In these tests, one hand holds a tube and the other fishes out food with a finger. Hand dominance is determined by which hand is used to pull food from the tube. For a large sample of chimpanzee adults and juveniles, right-handedness was more common than left-handedness (266/421:63.2%) when only the right or left hand was tabulated. Bonobos exhibited no hand preference (51/101:50.5%). This result was consistent with another study of sanctuary bonobos ($n = 48$) in which, though were individually lateralized, there was no difference in which hand was dominant in the tube test.³⁶ It is possible that the presence of humans influenced these captive chimpanzees, but another complicating factor is the high frequency recorded in ambiguous or ambipreferent hand preference.

Ambiguous is defined in laboratory or zoo settings when it is unclear from the experimental situation which hand was dominant in the action; ambipreferent is when a specific ape does not have a preferred hand in performing a specific task. It is unclear whether ambiguous and ambipreferent directly correlate with human ambidexterity, in which either hand can perform a task equally well, but it is clear that these chimpanzee frequencies differ from studies of humans in which one hand is consistently preferred. Chimpanzees especially have a high frequency of individuals that use either hand to complete a bimanual task. When “ambiguous” is included in the tallies, the percentages for captive adult and juvenile chimpanzees are 49% right, 22% ambiguous 29% left. In a smaller sample of captive chimpanzees, Regaioli, Spiezio, and Hopkins³⁷ measured hand preference in foraging, manipulation and locomotion. They found a low incidence of left handedness, but a high frequency of ambipreference — 41.1%, 58.9%, and 82.4% — respectively, in all three actions.

In comparison, humans show a consistent right-handed bias, with a low frequency of left-handedness and ambiguous hand preference.^{38,39} Michal et al.⁴⁰ argue that “most members of a group of [human] ‘ambilaterals’ manifest poor manual skill with either hand,” which may explain why humans are so strongly right-handed in tool use. Support for this comes from an ethnographic study in which Marchant, McGrew, and Eibl-Eibesfeldt⁴¹ documented handedness in three human groups of different subsistence classes from videos. For the G/wi San (hunter-gatherers; $n = 41$), Himba (pastoralists; $n = 37$), and Yanomamo (horticulturalists; $n = 31$) “mixed handedness” was common, except during tool use, in which they were distinctly right-handed. In these three groups, right-handed frequencies varied from 79–91%. Studies cited here point to an evolutionary basis for handedness in our nearest, primate relatives and demonstrate that humans are consistently different, having a high frequency of right-handedness for tool use.

The European Neandertal sample is composed of anterior teeth from eight separate sites. The oldest Neandertal teeth come from Krapina, in Croatia, and are dated to 130,000 years ago.⁶² These are followed by Regourdou 1, in France, at 75,500 BP,⁶³ then by Valdegoba, Spain, at 73,000 BP.⁶⁴ The large sample of human remains from El Sidrón, Spain, is dated at 49,000 BP.⁶⁵ Thirteen individuals have been identified; eleven have associated anterior teeth.⁶⁵ Unlike other samples, these teeth are of known sex, based on preserved X and Y chromosomes.⁶⁶ They represent four adult females, three adult males, two adolescent males, one adolescent female, and one juvenile male.^{60,66–68} Teeth from Cova Negra in Spain, Hortus I France, and La Quina in France are likely between these in age.¹⁴ Specimens from the G1 level at Vindija, in Croatia, are now dated to $\sim 44,000$ BP,⁶⁹ but there has been considerable movement, at least of broken tools and flakes, from various levels at the site.⁷⁰ Questions remain about whether or not these dates actually derive from G1. The latest specimen in the sample

is the single tooth from Vergisson, dated at $\sim 40,000$ BP.⁷¹ In the entire sample, striations are primarily found on permanent teeth; the only exceptions are an upper and three lower deciduous anterior teeth from El Sidrón and a lower deciduous incisor from Krapina.

Scratches like those found on many Middle Paleolithic and earlier specimens have rarely been documented on the anterior teeth of European Upper Paleolithic or Mesolithic specimens, or at least the ones we have studied, which have come, for example, from Mladeč in the Czech Republic and Ofnet in Germany. No systematic survey of the entire European Upper Paleolithic or Mesolithic has yet been done. The only exceptions are two individuals from Dolní Věstonice where Willman⁷² has documented a single right-hander (DV 15) in a right I². A second individual (DV13) shows a significantly higher number of right oblique scratches on a left I¹ when only left and right oblique scratches are compared.⁷² However, in the individuals he studied the most common labial marks were vertical striations, not the oblique ones we find in the

Box 2. Methods for determining handedness from teeth

In Paleolithic teeth, labial striations are visible to the naked eye. The labial faces of incisors and canines can be heavily scored with striations, while the lingual faces are free of scratches. In this way, natural origins, such as trampling or sediment damage, which would have left their marks on all sides, can be eliminated as causes of the striations. To tabulate the scratches and for more detailed microscopic views, we obtained high-resolution epoxy and polyurethane replicas of the original specimens held in museums or research institutions. Replicas were made by standard techniques.^{17,18,20}

Two types of scratches appear on labial surfaces. Fine dietary striations are present on most teeth, but are distinctly different from manipulative scratches; that is, dietary scratches are shallow, small and very narrow.^{18,42,43} They tend to be visible only at magnifications higher than 80x. We traced only the more distinct longer and deeper scratches to quantify striation pattern, ignoring the fainter dietary scratches. We applied the same techniques to a variety of modern *Homo sapiens* samples from the Spanish Chalcolithic and Bronze Age,^{44,45} as well as samples of Australian Aborigines and Greenland Inuits.^{17,18}

For all teeth, we quantified reflected light and scanning electron-microscopic (SEM) images to document the scratches. Most of samples were scored using a binocular microscope at 20-40x magnification.^{20,27} In the Neandertal count, we added a few specimens from the literature since these investigators used similar techniques.¹⁴ Although conservative in its categorizations, we followed the angle breakdowns first proposed by Bermúdez de Castro et al.,¹¹ since these produced the largest samples.

Thus, striations were separated into four orientation categories: horizontal (H: 0°–22.5°, 157.5°–180°), vertical (V: 67.5°–112.5°), right oblique (RO: >22.5°–<67.5°), and left oblique (LO: >112.5°–<157.5°). This underestimates the number of right or left handers; for example, an oblique mark of 21° would be classified as horizontal, so if the intervals were expanded²⁰ the tooth being examined would have come from a right-hander. However, since most studies have not published the raw data and have used the Bermúdez de Castro et al.¹¹ intervals, we also used them.

Many of the teeth are isolated, especially in the Krapina sample. For this site we used Wolpoff's reassembled tooth sets, each of which he labeled as a Krapina Dental Person (KDP).⁴⁶ His tooth associations were based on similar morphology, occlusal wear, and interlocking interproximal facets, not on the presence of labial scratches. It is unlikely that any of the KDPs in our sample can be grouped together into a smaller number of individuals.

European Middle Paleolithic. Clearly, more work needs to be done in the European Upper Paleolithic and Mesolithic. For now, the general absence of these marks in populations following Neandertals represents a discontinuity between the Middle and Upper Paleolithic. We suspect this is related to differences in technological efficiency in these latter groups,²⁰ but more work is necessary here as well.

We studied a sample of twenty-seven Holocene individuals from the El Mirador site in Sierra de Atapuerca. Twenty-three of these individuals are from Chalcolithic levels dated at 4,760-4,200 BP. The other four individuals are from Early Bronze Age levels at the same site, dated to 4,400-4,100 BP.⁴⁵ The sample includes representatives of two modern hunter-gatherer groups from late nineteenth to early twentieth centuries. Both groups are housed in the Duckworth Collection in the Leverhulme Centre of Cambridge University in the UK and include thirty-one Australian Aborigines sampled across Australia and seven Inuits from Vancouver Island, Greenland, and the Labrador Peninsula.⁴⁴

The beauty of analyzing the oblique scratches on teeth is that large samples can be generated for determining handedness, even when the material is fragmentary. From a single isolated tooth, providing enough scratches are preserved, the handedness of the "owner" can be estimated. Other techniques, like comparing the different dimensions of the right and left humerus, require a much more complete collection of bones (Box 3) Using common procedures in our studies of labial incisor

and canine striations, we have been able to compile an extensive sample of fossil humans showing hand preference over time.

3 | PATTERNS OF THE OBLIQUE SCRATCHES THROUGH TIME

The earliest patterns of labial scratches appear on OH-65, which shows a complex array of scratches on the anterior teeth, especially the two central incisors, the right lateral incisor, and right canine (Figure 2). Of a total of 559 scratches on all six anterior teeth, 46.5% are right oblique and only 11.3% are left oblique⁴⁸ — the remainder are either horizontal (18.8%) or vertical (23.4%). The right oblique pattern is the most common. Statistically, this pattern is significantly different from the number of left-handed marks.

For the European sample, labial scratches on the left I₂ of the 18-year-old hominid 4 from Gran Dolina-TD6 site in Spain represent the oldest scratches so far documented at Sierra de Atapuerca. These are the only labial scratches for the Gran Dolina sample and possibly are related to the young age of all other individuals. However, there are an insufficient number of striations (Figure 3a) to identify TD6 as a right- or left-hander.⁴⁵

For Sima de los Huesos, the majority of individuals show numerous labial scratches. Wear of the crowns and the class of tooth heavily influence the presence of scratches, most of which are on the upper

Box 3. Other ways of determining handedness

Because of the unique worldwide dominance of right-handedness in modern humans, numerous ways have been devised to determine how far back into the past this can be traced. The most direct approach is to measure right and left arms to see if there are size and robusticity differences indicating which arm was habitually used. Yet this is of limited value, since preservation of both sides or equivalent parts of the skeleton is uncommon before intentional burials. An exception is Lucy (AL 288-1), who has portions of both arms, but for comparable segments there are only minor differences.

It is not until an early African *Homo erectus*, WT-15000, that comparable right and left segments show side differences, and here it is dimensions of the clavicles and ulnas. From these differences, Walker⁷³ argued that WT-15000 was right-handed. After this, there is a huge time gap until matching arm parts are preserved. These occur in the Neandertals, but excluding pathological specimens like Feldhofer 1, with its severely arthritic elbow, there are still only four European Neandertals, (La Chapelle-aux-Saints, La Ferrassie 1, Regourdou 1 and Spy 2), along with two from the Levant (Kebara 2 and Tabun 1), in which equivalent parts are preserved. For these, all were right-handed.⁶³ But even this is equivocal since Komar and Buikstra⁷⁴ argue that “there exists no well-accepted forensic method [in modern populations] for assigning handedness” from skeletal remains. Others maintain that, based on a more rugged life style, differences between right and left arm dimensions should be better expressed in the past.⁷⁵ But in any case, the sample is small and will likely remain so, given the rarity of finding intact upper limb skeletons from the Paleolithic.

Using brain endocasts, Holloway and de la Coste-Lareymondie⁷⁶ suggested that brain impressions signaled hemispheric laterality, even as they argued that there is no “obligatory relationship between handedness and cerebral lateralization.” In any case, this sample is small, being limited to crania with full endocasts.⁷⁷ Toth attempted to infer handedness from stone-tool flaking patterns,⁷⁸ but this has been met with doubt⁷⁹ and appears to be unreliable.⁸⁰ Most recently, Bargalló, Mosquere and Lozano⁸¹ have analyzed various aspects of flake structure as indicators of the dominant hand used in tool manufacture. Among 200 flakes from the Spanish sites of Grana Dolina and Abric Romaní, they identified five that they attributed to right-handers. However, there is no way to determine how many right-handed people made the flakes from this type of analysis. Analysis of hand stencils on cave walls has also been used to estimate the frequency of right- and left-handers. Based on a series of European sites with hand stencils in caves, Faurie and Raymond⁸² found a right:left ratio of 77:23 for negative prints. This assumes that the palm side of the hand was held against the wall while a tube loaded with pigment held in the opposite hand was used to spray the impression. Steele and Uomini⁸³ summarized research for world-wide samples and found that the majority of hand stencils were made by right-handers. While these data are interesting, the stencils are all associated with modern *Homo sapiens* and thus are not informative about earlier periods. In short, striations on teeth generate the largest sample size for Paleolithic specimens and do not require anything more than an incisor or a canine.

central permanent incisors. In contrast, deciduous teeth and newly erupted teeth of younger individuals preserve few or no scratches.

In general, the heavier the occlusal wear, the greater number of scratches.¹⁸ Older individuals have superimposed scratches, as in later Neandertals, suggesting that the scratches appeared at different intervals during varied times during the life of an individual (Figure 3b). In these individuals, as the crown wore down, the scratches approached the junction between the crown and the root, documenting a long history of manipulations performed between the anterior teeth.¹⁸ Some younger individuals have a few striations, indicating that they engaged in the same oral manipulations as those that created the scratches in adults. Most often, the scratches occur on upper permanent incisors and canines, but a few are found in lower incisors and canines.

All fifteen individuals from Sima de los Huesos consistently preserve right-handed obliquity of the marks, indicating that these individuals clenched objects in their mouths, pulled with the left hand, and processed materials primarily with a tool held in their right hand.^{11,17,18,27,84} In the Sima de los Huesos sample, individual XVIII, at 9-11 years of age, was the youngest in the sample to have a clear right-handed pattern.

Many Neandertals have labial scratches on their anterior teeth in a pattern similar to the Sima de los Huesos teeth. Not all Neandertal incisors and canines preserve labial scratches. However, whenever the scratches are found in sufficient numbers, the orientation pattern of the Neandertal samples is primarily right-handed; for example the right I₂ from El Sidrón (Figure 3c). At Krapina, nine of the eleven Neandertals were right-handed, while two (KDP 4, KDP 35) show a left-handed scratch pattern (Figures 3d, e). Compared to an earlier study¹⁵ our recent work has documented a deciduous lower incisor with a right-handed scratch pattern.²⁰ This is the only deciduous tooth at Krapina with a discernible handedness preference. Together with the three deciduous teeth (di₁-dc₁) at El Sidrón, which have the same pattern,¹⁰ these represent the youngest age in the ontogenetic establishment of inferred manual laterality in any fossil human sample.

Following Wolpoff's Krapina ages for permanent teeth,⁴⁶ it clear that striation patterns began early in a Neandertal's life, with the youngest pattern on a permanent tooth from a ten-year-old individual. We found an average age of 18 (range = 10-23) years at death for the eleven sampled specimens from Krapina. Overmarking on many of the

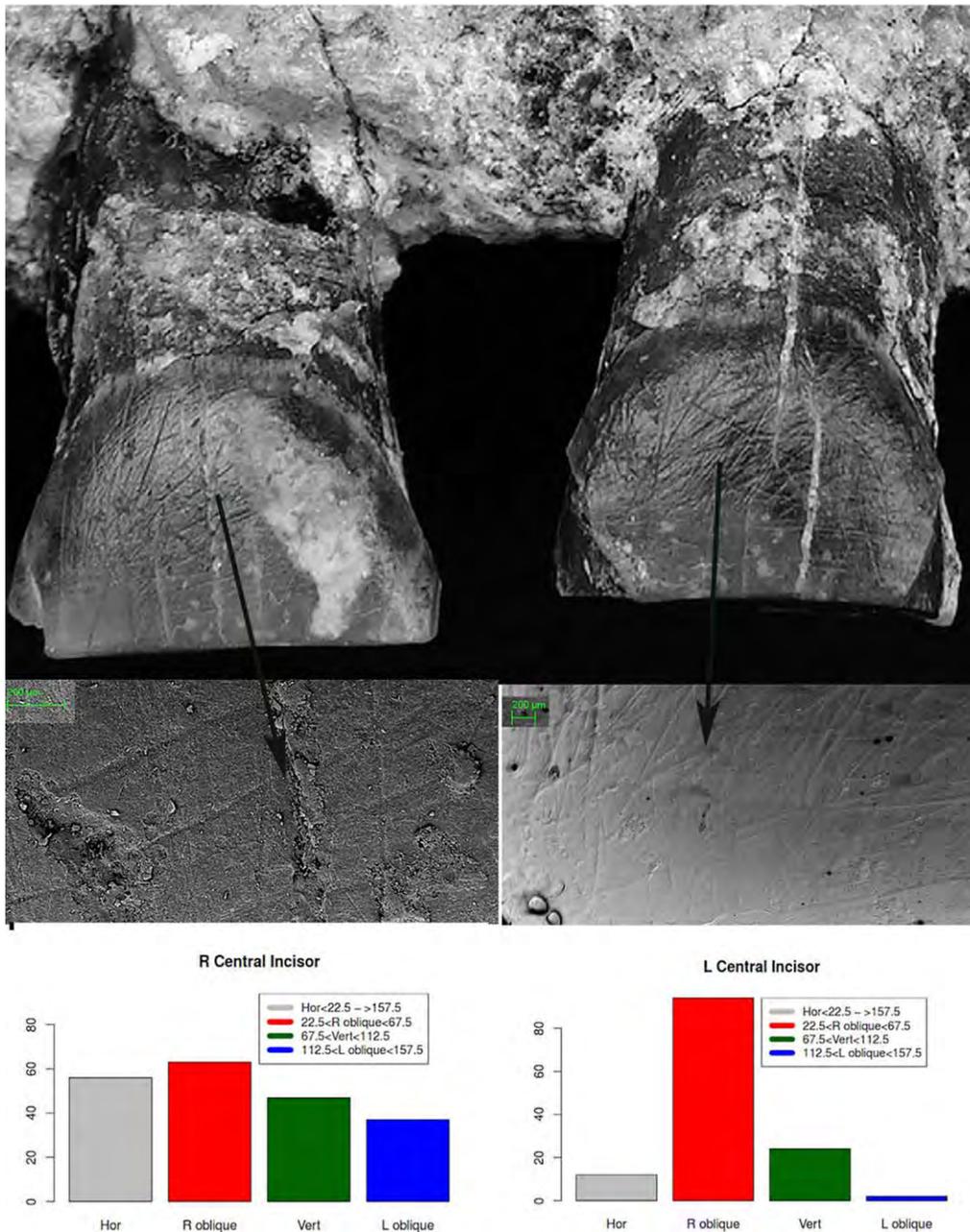


FIGURE 2 OH-65 shows a concentration of striations on the labial faces of the anterior teeth. These are visible to the naked eye. Microscopically, they conform to the striations found in much later hominids. The striations are mainly confined to the left and right I¹s, the right I², and right C¹. Right oblique scratches predominate, leading to the identification of OH-65 as a right-hander. (n = number of striations per category) [Color figure can be viewed at wileyonlinelibrary.com]

teeth shows that this activity continued throughout the lifetime of these individuals (Figure 4). There is even a male from El Sidrón who appears to have changed hands, with left-handed marks overstriking an earlier right-handed pattern, presumably as a result of oral pathology on his left side.¹⁰

Following Krapina, teeth at the earliest to latest dated sites, Regourdou, Spy, Valdegoba, Cova Negra, La Quina 5, El Sidrón, and Vindija, based on the prevalence of right-oblique oriented scratches, were all from right-handed individuals. Only at Hortus does a third left-hander show up, but four other specimens from the same site were

right-handers. We have added a fourth left-hander based on the single upper incisor from Vergisson.¹⁷

In all, we have data for 36 European Neandertals, with a frequency of 88.9% right-handed Neandertals. If we add the pre-Neandertal data from Sierra de Atapuerca, the frequency of right-handed Pleistocene Europeans rises to 92.2%. This completely contrasts with evidence of incisor and canine scratches on Chalcolithic, Bronze Age, Australian Aborigine, and Inuit teeth. Given their modernity, there is no reason to question a right-hand dominance, but we find no significant evidence of labial scratches of any kind. Whatever actions produced the

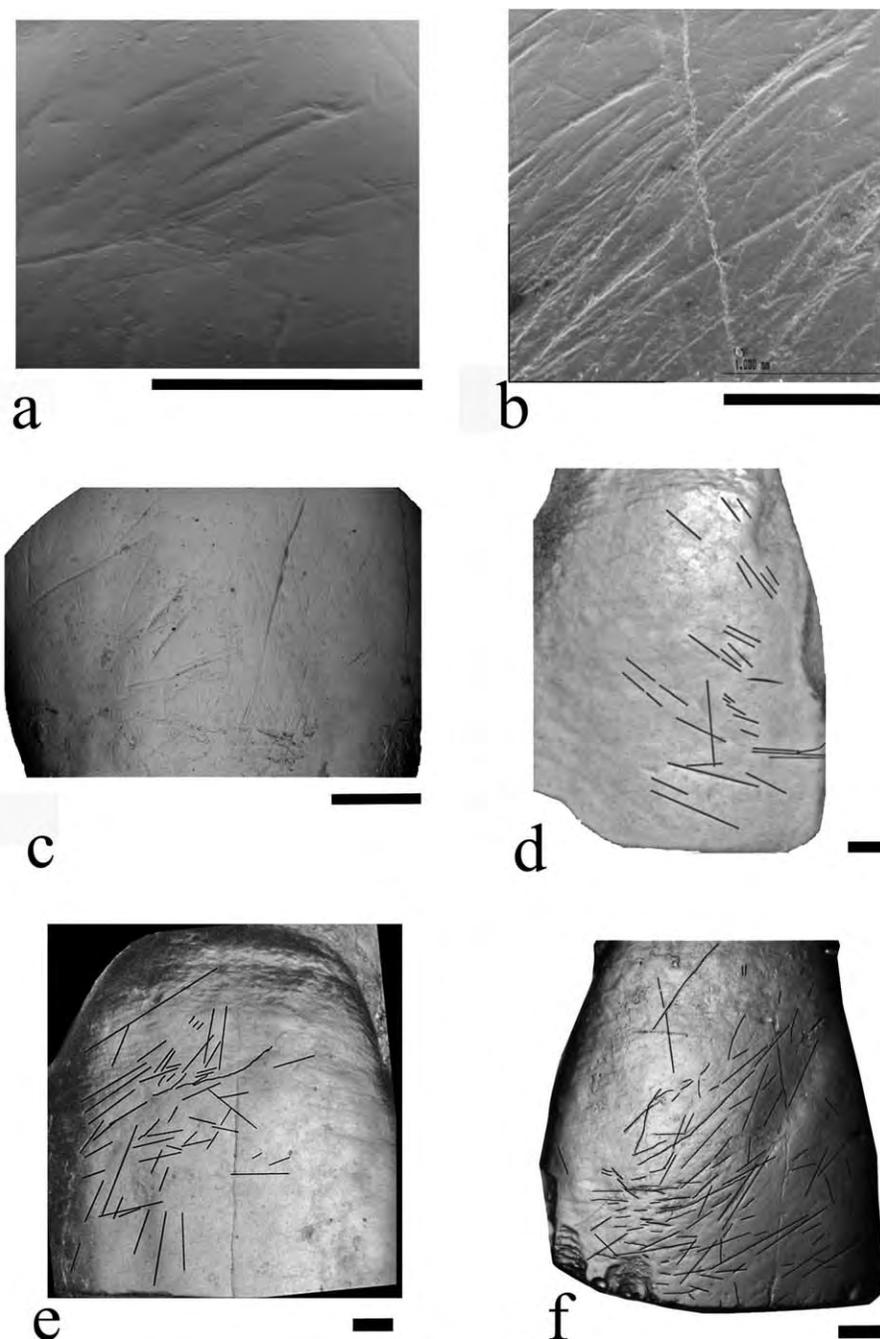


FIGURE 3 Labial scratches on permanent teeth: a. high magnification of a left I_2 of hominid 4 (18 years old) from Gran Dolina-TD6; b. high magnification of a left I^1 belonging to SH II (13-14 years old), a right-hander from Sima de los Huesos; c. high magnification of a right I_2 from El Sidrón adult 4, a right-hander; d. right I^1 from KDP 35 (10 years old), one of the two left-handers at Krapina; e. right I^1 of KDP 5 (15-16 year old) from Krapina, with a preponderance of right-handed striations; f. right I^2 (Vi 289) of a right-hander from Vindija

scratches in pre-Neandertals and Neandertals were not done in later groups.

A similar conclusion was reached by Bax and Ungar,⁸⁵ based on their analysis of different samples of recent groups. We have had the opportunity to restudy their casts and can confirm that the modern hunter-gatherer and agriculturalist groups in their sample lack concentrations of labial scratches like those found in Early and Middle Paleolithic human fossils. The patterns found in Neandertals, the earlier

European samples represented by Sima de los Huesos individuals, and a single example from *Homo habilis* extend this pattern deep into the prehistory of *Homo*.

There are too few specimens of *Homo habilis* to determine group tendencies, but a well-established pattern of handedness appears with the Sima del los Huesos paleodeme, where all individuals were right-handers. As documented in Table 1, Neandertals from various sites, including Krapina, Regourdou, El Sidrón, and Vindija, are consistently

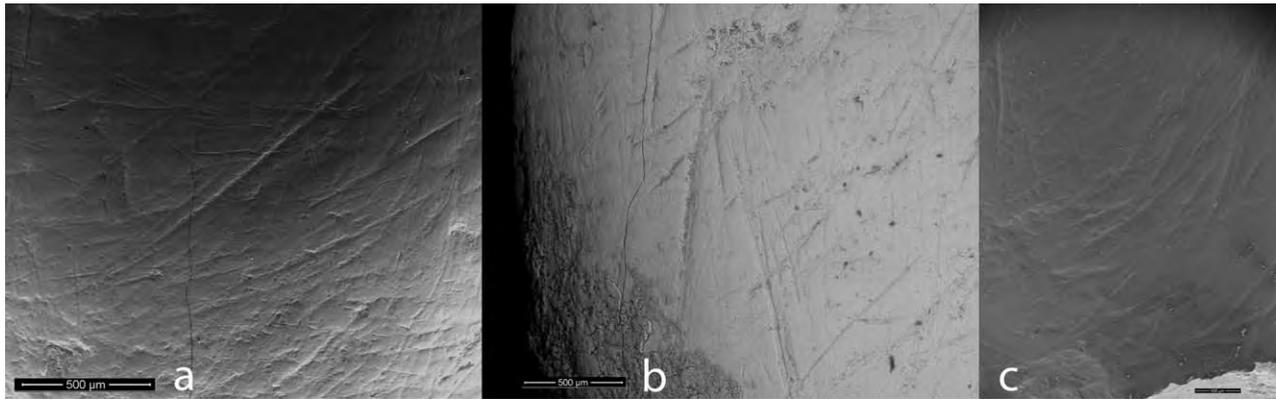


FIGURE 4 High-magnification images showing superimposed striations in three Neandertals as examples of continuous use of the mouth as a third hand. a: Vald M13, a left I_2 from Valdegoba; b: SD-599a, a right I_1 from El Sidrón; c: Vi 289, a right I_2 from Vindija

right-handed. There are only four left-handers in our Neandertal sample spanning about 130,000 years. We can also add Tabun 1, Kabwe, and Meipu, which show that specimens from the Middle Paleolithic of the Levant and Africa and a lower Pleistocene specimen from China

have the typical modern right-handed pattern. As more specimens are analyzed from all these areas and time periods, we expect more right-handers to be found.

TABLE 1 Handedness frequencies in Neandertals and their predecessors.^a

	Right-Handed	Left-Handed	
OH-65	1		

Sima de los Huesos 15			

Krapina	9	2	
Regourdou 1	1		
Vergisson 2		1	
Cova Negra	1		
Hortus	4	1	
La Quina 5	1		
Valdegoba	1		
El Sidrón	11		
Vindija	4		
	Count Rt Lt	Ratio Rt Lt	% Right-Handed
European Neandertals:	32 : 4	89 : 11	(88.9)
Fossil Europeans:	47 : 4	92 : 8	(92.2)
Tabun 1 (c)	1		
Kabwe	1		
Meipu	1		
	Count Rt Lt	Ratio Rt Lt	% Right-handed
All Fossils:	50 : 4	93 : 7	(92.6)

^aData for Kabwe and Tabun are from Lalueza and Pérez-Pérez¹⁴; those for Meipu are from Xing et al.⁸⁶

4 | HANDEDNESS AND ITS IMPLICATIONS

The connections between handedness and brain laterality are complicated, so that the “obvious” relationship between the two has been undermined by many studies over the past few years. The same is true for a direct connection between handedness and language areas of the brain. Contrary to earlier assertions by Annett⁸⁷ that handedness and language are controlled by a single gene, the capacity for language and handedness are not simply regulated.^{88–91} In living humans, gestural and spoken language is primarily a left hemisphere function; the same hemisphere directs the right hand.⁹² Yet simple models correlating the left hemisphere with both are complicated by the fact that 75% of left-handers have language in the left hemisphere and some right-handers have language in the right hemisphere.⁹³ The two traits appear to be determined by different gene complexes.^{94–97} It has recently been suggested that at least 40 genetic loci are involved in handedness.⁸⁸ Ocklenburg et al.⁹⁶ argue for “a spinal, not a cortical, beginning of hemispheric asymmetries Our data strongly suggest a multifactorial model for the ontogenesis of hemispheric asymmetries, including both multiple genetic and epigenetic factors.”

To complicate matters further, the preferred hand is also influenced by a host of nongenetic factors as wide-ranging as social stigmatization of left-handers to season of birth.⁹³ As Fitch and Braccini⁹⁸ maintain, “[h]uman handedness, rather than being a driving force, may be a by-product of more fundamental perceptual and cognitive asymmetries, particularly those involved in language evolution.” The paleoneurological evidence shows that Neandertal parietal lobes are different from those of *Homo sapiens*, especially in the areas related to processing visual and spatial information. Bruner and Lozano⁹⁹ linked the extended-mind theory and the use of the mouth as a third hand by Neandertals and their ancestors. For them, this behavior was the consequence of a mismatch between the neural structures and cultural

complexity in Neandertals, a problem that was solved in modern *Homo sapiens* by a more sophisticated technology, removing the need to use the mouth as a third hand and leading to a different parietal functional organization.

These implications are not inconsistent with the fact that early fossil humans and Neandertals show a similar pattern of hand lateralization. Today, wherever humans are found, the 9:1 right-to-left ratio never dips to the chimpanzee or bonobo levels, which show differences in direction of lateral bias or degrees of lateral bias in captive and wild settings^{30,31} (Box 1). In recent humans, the significance of this uniquely asymmetrical handedness is tied to brain laterality. It may also be related to language production,^{77,100,101} although, as noted earlier, there is considerable debate about the strength of this association. Perhaps, it is best to consider Stout and Chaminade's proposal that this a "co-evolutionary relationship"¹⁰² in which handedness, brain laterality, and language signal a pattern of organization that uniquely defines humans.

Handedness fits what Bruner and Lozano⁹⁹ label an "autocatalytic loop," in which biological and cultural factors interact to produce a more complex, enhanced brain. For now, samples are small for non-European fossils, but based on a few specimens from Asia and Africa, there is evidence that this right-hand dominant pattern occurs wherever *Homo* is found.

5 | CONCLUSION

We contend that the handedness data reviewed here shows that right-handedness extends deep into the past of our species. The modern right-handedness frequencies in earlier European human fossils from Sima de les Huesos and new specimens from the Early Pleistocene of China and Africa suggest that handedness stretches back well before the appearance of *Homo sapiens*. European Neandertals represent the biggest samples and continue this pattern, showing a right-to-left hand ratio identical to that among living *Homo sapiens*. In our view, the unique 9:1 ratio of right to left handers appears well before the emergence of modern *Homo sapiens* and is typical of our genus wherever and whenever it is found.

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