

Right handed Neandertals: Vindija and beyond

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Summary - Seven Vindija (Croatia) Neandertal teeth, dated ~32,000 years ago, were analyzed to determine patterning of scratches on the anterior teeth. Oblique scratches exclusively on the labial faces of incisors and canines represent a distinctive pattern, characteristic of hand directed, non-masticatory activities. At Vindija and elsewhere these scratches reveal activities, which were performed primarily with the right hand. The late Neandertals from Vindija, combined with other studies, show that European Neandertals were predominately right-handed with a ratio 15:2 (88.2%), a frequency similar to living people. Studies of teeth from *Atapuerca* extend this modern ratio to more than 500,000 years ago and increase the frequency of right-handers in the European fossil record to almost 94%. Species-wide, preferential right-handedness is a defining feature of modern *Homo sapiens*, tied to brain laterality and language with the ~9:1 ratio of right- to left-handers - a reflection of the link between left hemispheric dominance and language. Up-to-date behavioral and anatomical studies of Neandertal fossils and the recent discovery of their possession of the *FOXP2* gene indicate Neandertals (and, very likely, their European ancestors) had linguistic capacities similar to living humans.

Keywords - Handedness, Labial striations, Language capability, Croatia.

Introduction

The Vindija cave in the Hrvatsko Zagorje of northwest Croatia has provided much information about late Neandertals and the people who followed them. The multilayered site has a scattering of Neandertal fragmentary bones and isolated teeth in levels G3, G1 and F_d (Wolpoff *et al.*, 1981; Smith *et al.*, 1985; Smith & Ahern, 1994; Ahern *et al.*, 2003). The latest Mousterian G1 Neandertals are especially important since they appear to be associated with a split-based bone point and other tools connected in Europe to earliest Upper Paleolithic cultures (Karavanić, 1995; Karavanić & Smith, 1998). Specimens from G3 provide mtDNA and nuclear DNA

documentation of the Neandertal genome (Green *et al.*, 2010; Noonan *et al.*, 2006).

The schoolteacher Vukovic first excavated Vindija in the 1950s, and then the site was more extensively worked in the 1970's by Malez of the Institute of Archaeology in Zagreb (Malez, 1975; Malez, *et al.*, 1980). All the fragmentary remains attributable to Neandertals come from the Malez excavations and are located in levels G3-G1, and probably, F_d. Of these, only G1 is directly dated, initially at ~28,000 years ago (Smith *et al.*, 1999), but now revised to at least 32,000 years ago (Higham *et al.*, 2006). While somewhat deeper, G3 cannot be much older nor the continuous superior level F_d much more recent, given the two levels are separated by less than a

meter. We maintain the G3- F_d sequence spans probably less than 10,000 years. Level G3 represents a warmer period, while G1 and F_d, full of cryoclastic materials, are considerably colder. For the specimens from these levels it is important to recognize the effects of cryoturbation, solifluction and other factors at Vindija, which have moved at least tools vertically (Bruner, 2009; Karavanić, 1995; Wolpoff *et al.*, 1981). There is no reason to assume the teeth did not similarly move. Except for one lower canine located in a mandible (Vi206), all the anterior teeth are isolated and none come from the same individual.

The specimens were formally described by Wolpoff *et al.* (1981) and we concur with their assessments. One is attributed to the G3 Mousterian (Vi206), and two (Vi287, Vi290) are from G1, the latest Mousterian/earliest Aurignacian based on the mixed tool assemblages found in the level (Karavanić, 1995). As Wolpoff *et al.* (1981) and Karavanić (1995) argue the small number of tools make this level difficult to assess, but based on the split-base bone point (a signature tool of the early Aurignacian; Teyssandier 2008), an engraved baculum and the small lithic assemblage, this is apparently a Mousterian/Aurignacian complex (Karavanić, 1995). Despite the 'transitional' nature of the archaeological materials, all authors identify the human remains from G1 as Neandertals (Karavanić & Smith, 1998; Smith & Ahern, 1994; Wolpoff *et al.*, 1981). Three teeth (Vi286, Vi288, Vi289) come from F_d, an early Aurignacian context (Karavanić, 1995). Of these Vi289, a right, maxillary lateral incisor, is remarkable in its expression of typical Neandertal features, especially the degree of shoveling, expression of the basal tubercle and crown curvature (Wolpoff *et al.*, 1981). This is either a Neandertal tooth originally deposited in a lower level, a Neandertal surviving into the Aurignacian or an Upper Paleolithic tooth with strong Neandertal morphological characters. As we discuss below, Vi289 has a very heavily scored labial surface, typical of Neandertals at Krapina and elsewhere and, this coupled with the distinctive morphology, makes it unlike any other,

currently known Upper Paleolithic or modern specimen. We suspect the tooth is from G1 or even G3, making it a late Neandertal. Vi286 and Vi288 may be upwardly displaced too, since they also show Neandertal features, such as a well-developed basal cingulum in Vi286 and strong marginal ridging in Vi288. Given these features, we consider these Neandertal teeth. For the remaining tooth (Vi201), the archeological level is unclear, but since its morphology closely resembles Vi286, following Wolpoff *et al.* (1981) it is included in the Neandertal sample.

Hand preference and dental striations

The consistent use of the right hand in tasks is a unique, species-wide characteristic of modern *Homo sapiens*. Some geographic variation exists (Cashmore 2009; McManus 2009; Raymond & Pontier, 2004), but modern humans are primarily right-handed, showing a frequency of about 90% world-wide (Cashmore, *et al.*, 2008; Hardyck, *et al.*, 1975). In contrast, numerous studies demonstrate that most primates express no consistent pattern of species-wide handedness (Corballis 2003; McGrew & Marchant, 1997; Marchant & McGrew, 2007; McManus, 2004; Uomini 2009). In these species hand preference tends to be an individual option or differs by the kind of task performed. There are some exceptions to this in primates as reviewed by Papademetriou *et al.* (2005), but consistent, species-wide right-handedness is not found outside *Homo*. After surveying studies of chimpanzees and bonobos, Harrison and Nystrom (2008:266) concluded "that amongst extant apes species level handedness is unique to humans."

Hand preference in the living humans is measured by direct observation of manipulation or analysis of writing patterns, and, while not as straightforward as sometimes presumed (Faurie & Raymond, 2003), worldwide patterns are consistent. The same techniques obviously cannot be applied in the fossil record (Cashmore *et al.*, 2008; Uomini, 2009). Various methods

have been proposed for identifying preferred hand use in the fossil record. These range from stone tool flaking patterns (Toth, 1985; Cornford, 1986), cutmark orientation on bones (Bromage & Boyde, 1984, Bromage *et al.*, 1991; Pickering & Hensley-Marschand, 2008), brain lateralization and petalial patterns judged from endocasts (Begun & Walker, 1993; Falk, 1987; Holloway & de la Coste-Lareymondie, 1982), left/right asymmetry in hominid upper limb skeletons (Cashmore, *et al.*, 2008; Walker 1993), and scratches piercing the labial surface of anterior teeth (Bermúdez de Castro *et al.*, 1988; Bromage, *et al.*, 1991; Lalueza-Fox & Frayer, 1997; Puech, *et al.*, 1989). All have some drawbacks, but the most direct method, yielding the largest samples, is determination of hand preference from scratches scored into the labial surface of anterior teeth. Produced when stone tool edges come into contact with the face(s) of incisors and canines, these striations preserve a history of how an individual used his/her teeth during their lifetime and what type of action was performed in the production of the marks.

Lozano *et al.*, (2008, 2009) analyzed 163 incisors and canines from Sima de los Huesos (Atapuerca, Spain) for handedness. Five individuals showed no pattern of scratches or a vertical orientation, with the remaining 15 individuals exhibiting a common right-hand scratch pattern. This is much more than the number of Neandertals with preserved left and right humeri for analyzing skeletal asymmetry and inferring handedness. At Krapina, Lalueza-Fox & Frayer (1997) analyzed 82 anterior teeth, accounting for at least 19 individuals and found seven specimens with significant patterning of scratches to determine preference. None of the 21 Krapina humeri can be identified as antimeres, so without the teeth, there would be no possibility of estimating handedness in the sample. Sampling multiple teeth also provides an independent check on the assignment of hand preference. Wolpoff (1979) re-assembled many of the isolated Krapina teeth into tooth sets without regard to scratches on the labial faces of any teeth. This allows for a separate

assessment of the scratch patterning since individual teeth can be independently assessed. The presence of a common pattern among these isolated teeth (Lalueza-Fox & Frayer, 1997) supports the contention that the scratches were produced by a consistent action with the right (or left) hand. At Krapina or Atapuerca (Lozano *et al.*, 2008) there was never a case when two adjacent teeth or occluding teeth had opposite patterns, one left and one right.

There are some drawbacks in determining hand preference from tooth scratches. These are primarily analytical, such as what angle to use for the division between an oblique striation and a vertical or a horizontal mark? Or, how many scratches are necessary to describe a tooth as representing a right- or left-handed pattern. There are also problems separating dietary scratches (Ungar & Spencer, 1999) from manipulative ones. Yet, these problems are easily overcome by light microscopy, SEM and statistical techniques. And, while the frequency and heavy scoring of fossil canines and incisors are more common in fossils than living groups (Lozano *et al.*, 2008; Bax & Ungar, 1999), there are hunter-gatherer teeth which indicate the scratches are likely associated with anterior dental manipulation (Lozano *et al.*, 2008).

Labial scratches identical to the fossil examples have been experimentally reproduced and these are identical to scratches on fossil teeth. Bermúdez de Castro *et al.* (1988) and Lozano *et al.* (2008, 2009) experimentally produced labial scratches on human teeth inserted into athletic mouthguards. Using the *stuff and cut* technique, they determined that the angled pattern of striations in left- and right-handed individuals produced distinctively different scratch patterns, closely matching the scratches in the Atapuerca (and the Vindija) fossils. We find these experiments compelling and found no reason to repeat them. To extend experimental work we scored several prehistoric ovicaprid teeth with hand-held chert tools to compare with the Vindija scratches and with studies of cutmarks on bone. We found that the experimental cuts on the enamel preserve the same basic features as found on bone

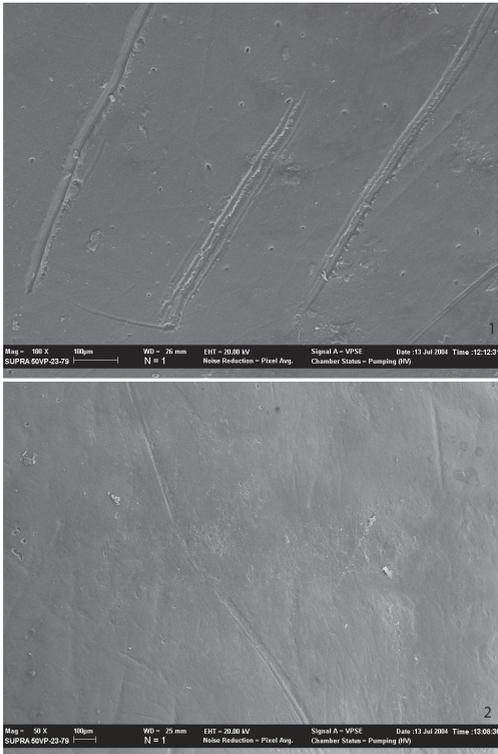


Fig. 1 - Stereomicroscopic images of striations from experimental stone tools on sheep/goat teeth (Araldite replicas).

(Cilli, *et al.*, 2000; Fischer, 1995; Giacobini, 1995; Lyman, 1994; Olsen & Shipman, 1988). Under SEM, the striae on the ovicaprid teeth have a V-shape form with secondary striae and microridges inside the scratch (Fig 1). These are produced by the edge of the stone tool, but compared to cutmarks in bone are less distinct, likely related to the hardness of the enamel and the less direct force applied to the tooth surface (Fig. 1). The main difference between the experimental scratches and those on the Vindija teeth relate to (1) premortem saliva erosion with the rounding and smoothing of the scratch edges and (2) post-mortem weathering of surface details. They show little evidence for secondary striae and microridges, but the overall morphology of the marks on the Neandertal teeth closely resembles the experimental marks on the ovicaprids.

Methods

Initially, non-occlusal surfaces of all 22 Vindija anterior and posterior teeth were examined, but concentrations of scratches were found on the only incisors and canines. Thus, our analysis focused on the seven anterior teeth, each representing a separate individual (Wolpoff *et al.* 1981:520). The striae were documented initially by eye and with a magnifying glass on the original specimens, housed in the Institute for Paleontology and Quaternary Geology, Zagreb. Since marks do not appear on the mesial, lingual or distal faces, only the labial faces of the seven anterior teeth were molded. We used silicon elastomers (Provil Novo), then epoxy resin (Araldite LY-554 and hardener Hy 956) for producing high resolution, positive casts. All analyses were done on the Araldite replicas. Separate transparent sputter coated replicas were produced for SEM analysis. The SEM work was performed on a Leo Supra 50 VP-23-79 in Rome.

Two types of scratches appear on the labial surface. Dietary scratches are present on most teeth and are distinctively different than the manipulative scratches in their small size, very narrow width and apparent shallowness (Ungar & Spencer, 1999). We traced only the more distinct manipulative scratches to the image, ignoring these much thinner and fainter dietary scratches.

Tooth surfaces were digitally photographed with a binocular microscope coupled to a digital camera. At 20x magnification striations were traced manually and saved in a vector format, which was used for measuring quantity, angle and scratch length. To avoid interobserver error, all striation identifications were done by one person (I.F.) and repeated, then revised a second time at least one month later. After tracing the scratches the image was calibrated with mesial-distal length used to derive the pixels per cm (pcm) scale and the image was converted to black and white to enhance contrast. Then, the original background image was eliminated, leaving only the lines. We utilized NIH freeware ImageJ: version 1.4g, using the morphological particle analysis routine, enabling the calculation of many morphological

parameters (among them length and angle) for each particle (the scratches in this case).

This software demanded no line crossovers, so we made two images --- one with the main striations and another with only crossover lines. These were tabulated separately by the software, and then combined in the statistical analysis, which counted the number of lines and calculated the length and angle of each line relative to the occlusal plane. Data for each tooth were uploaded to a database for statistical analysis. Because ImageJ picks up small, insignificant portions of lines, all marks less than 0.1mm were eliminated. Scratch breadth and depth were not measured.

Previous studies have made arbitrary decisions about the number of scratches necessary for accepting consistent right/left hand preference (Lalueza-Fox & Frayer, 1997). We attempted to avoid this by accepting hand preference only when statistically significant differences occurred among categories. First, for each tooth a sample was composed where all the vectors were separated into either $<90^\circ$ (right) or $>90^\circ$ (left) categories. This maximized sample size and was the first screening test for hand preference. If there was no significant difference ($p < .01$) with χ^2 , this implied the marks were randomly distributed. Second, we followed the approach initially developed by Bermúdez de Castro *et al.* (1988), and divided the scratch angles into five categories (horizontal $0-22.5^\circ$, right oblique $>22.5-67.5^\circ$, vertical $>67.5-112.5^\circ$, left oblique $>112.5-157.5^\circ$, horizontal $>157.5-180^\circ$). By χ^2 ($p < .01$) we tested the differences in right and left oblique and lack of significant difference rejected evidence for hand preference. While we formerly used this procedure (Lalueza-Fox & Frayer, 1997) and Lozano *et al.* (2008, 2009) recently applied the same divisions to the Atapuerca teeth, it is too conservative and arbitrary in its categorization of scratch angle. For example, why is a scratch angled at 22° determined to be horizontal, when it is clearly angled to the occlusal plane? With the addition of a single degree it would be considered as "right oblique" at 23° . New cutoffs were made for the degree ranges in each category, expanding the ranges and categorizing right-

handed marks as falling between $5-85^\circ$, and left between $95-175^\circ$ and the significance tested with χ^2 . Future research might follow these cutoffs. While still making arbitrary divisions, the expanded divisions better reflect the pattern of scratch angulations on teeth and provide larger samples for statistical testing. However, because all previous research has used the more restrictive degree ranges first proposed by Bermúdez de Castro *et al.* (1988), we use only these in our comparative data.

Results

Maxillary teeth

Vindija 287. Maxillary right canine. Level G1 (Figure 2:1)

Of the three canines, Vi287 has the least number of scratches (46) and these are not arranged in a consistent pattern. The scratches are mostly straight ranging between 0.16 and 0.86 mm and tend to be very short (0.45 mm) compared to the other Vindija teeth. They are primarily found in two areas, in the center of the tooth and adjacent to the large chip removed from the mesial-central occlusal border. The rather fresh appearance of the break and the abrupt termination of the marks at its edge indicate the chip is postmortem. That these marks do not extend into the fractured enamel is independent confirmation they are *postmortem*. The 46 striations are nearly equally divided in left (25) and right (21) directions, with a χ^2 of $p < .54$, so there is no evidence for hand preference.

Vindija 289. Maxillary right lateral incisor. F_d (Figure 2:2)

This is a remarkable tooth with a typical Neandertal-like morphology of marked shoveling and a strong lingual tubercle. Numerous small and large postmortem chips have been removed from the occlusal border and a complex of striations distinctly extend across the center of the labial face. The total of 129 scratches is the second highest at the Vindija, ranging between 0.13 and 2.67 mm

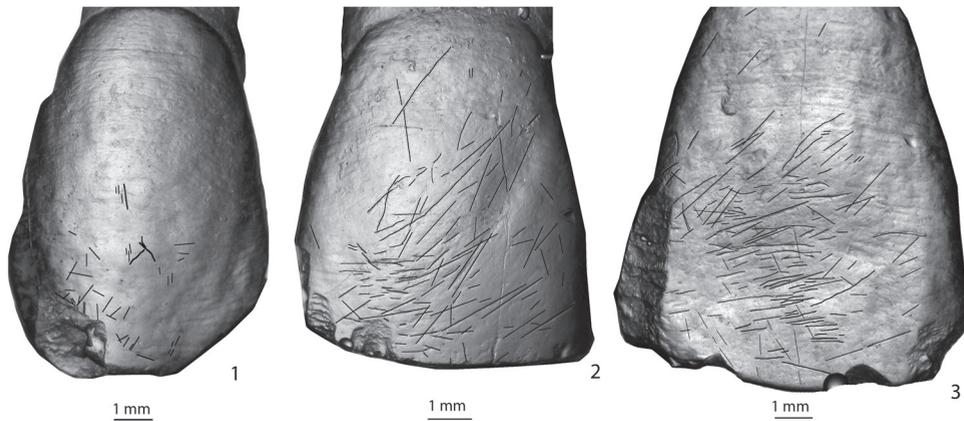


Fig. 2 - Striations as mapped on Vindija maxillary teeth (1. Vi 287; 2. Vi 289; 3. Vi 290).

(\bar{X} = 0.66 mm). Striae are mostly straight and concentrated more in the center of the crown than at the cervical or occlusal borders.

SEM images (Figure 3:1) show preservation of the marks similar to other Vindija specimens. The striation furrows are eroded, with rounded margins and presence of microfractures along the edges. These marks were made by repeated actions over the lifetime of the individual.

Angle analysis shows the marks are primarily of the right hand type. 95 of 129 marks are $<90^\circ$ accounting for 73.6%. Those between $5-85^\circ$ represent 74.3%, (81/109) and the ratio in the narrowest range is 52:6, or 89.7% of the right type. All these are highly significant ($p < .001$) and indicate the tooth was scored by a dedicated right-handed individual.

Vindija 290. Maxillary right I1. Level G1 (Figure 2:3)

With 163 scratches on its labial surface, this tooth has the highest number of striae of the seven teeth and may represent the most scratched of any Neandertal tooth studied thus far. The striae, with a length between 0.16 and 2.97 mm (\bar{X} = 0.67 mm), are mostly straight and concentrated in the center/distal portion of the tooth. Numerous, nearly horizontal scratches are located, just superior to the occlusal border. There is large chip spalled from the distal/occlusal surface, with a few striae ending at this

border, but the majority of striations are located in the center of the labial face. The superior third of the labial face is virtually devoid of marks. Striae in the crown's mesial half are fewer and located more toward the occlusal margin. SEM analysis shows that many furrows are eroded with rounded edges and a plethora of microchips (Figure 3:2). Some of these are due to postmortem weathering, but others are related to tooth damage while the Neandertal was alive.

Of the 163, 123 striations (75.5%) are less than 90° indicating a predominant right-hand pattern, which is significant at $p < .001$. 102 striations are between $5-85^\circ$ with only 28 between $>95-175^\circ$. These give an even higher right/left ratio of 78.5%. For the more conservative $>22.5-67.5^\circ$ and $>112.5-157.5^\circ$ categories, the ratios are 49 right (75.4%) and 16 (24.6%) left. Thus the right marks are more than three times as frequent in all breakdowns and in every case the differences are significant with χ^2 at the $p < .01$ level or better. The scratches on this tooth show the individual primarily used the right hand.

Mandibular teeth

Vindija 201. Mandibular left second incisor. Level? (Figure 4:1)

The lower incisor is not allocated to a level, but based on size and morphology Wolpoff *et*

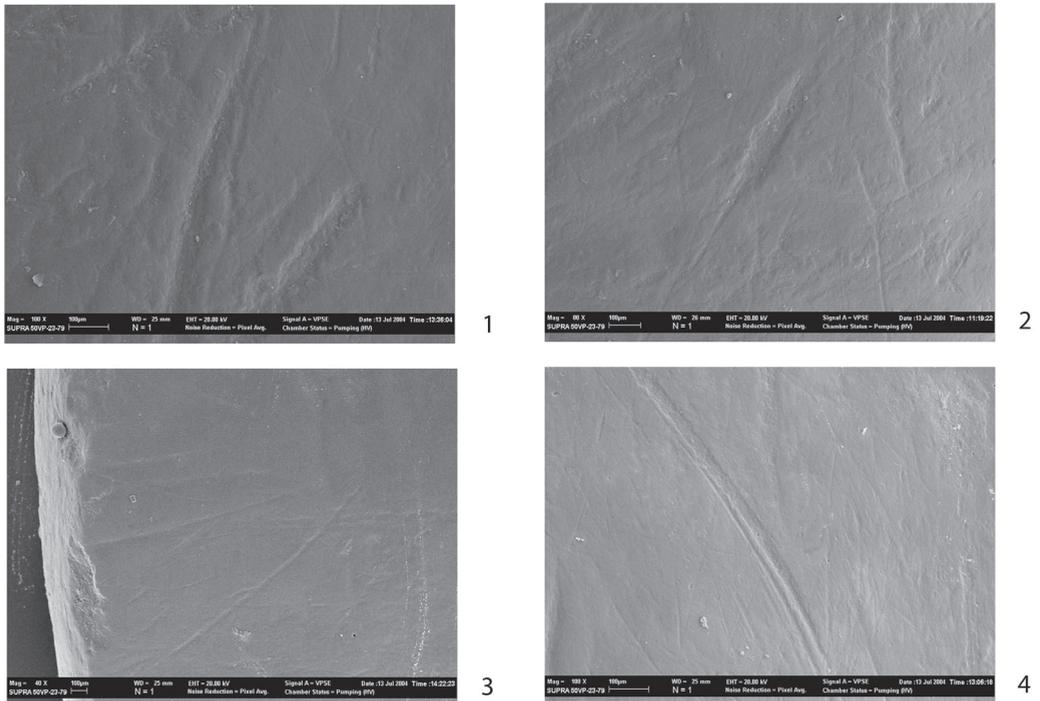


Fig. 3 - SEM images of scratches present on the labial aspect of four Vindija teeth: 1. Vi 289 – vertical striations with rounded margins and microfractures along the edges (magnification -100x); 2. Vi 290 – oblique striations with rounded margins and microfractures along the edges (magnification -40x); 3. Vi 201 – the image shows narrow oblique striations (upper central portion) near micro chipping of the occlusal border (magnification -80x); 4. Vi 206 – relatively long and deep striations showing a clear V shaped section and with secondary striations (magnification -100x).

al. (1981) considered it a Neandertal incisor. Like Vi 286, there are few marks on the labial surface and no consistent pattern is found. 21 marks are located at or near the occlusal margin, mostly on the distal half of the tooth. Lengths vary between 0.31 – 1.13mm with an average of 0.70mm. Many of the striations are associated with microchips removed from the occlusal surface (Figure 3:3).

For the angle analysis, ~50% are of the right type (10/21) with no statistical significance. In fact, all but four (19.0%) of the marks are greater than 85°, either vertical (38.1%) or left (42.9%) oriented. Unlike all the other Vindija anterior teeth there are no horizontal scratches, but there are not many scratches on the tooth surface. While the labial scratches resemble those on the other Vindija teeth, hand preference could not be determined.

Vindija 206. Mandibular right canine. Level G3 (Figure 4:2)

This canine possesses 110 striae with lengths ranging from 0.24-2.91mm, averaging 0.66mm. The scratches are mostly straight, interspersed with a few curved ones. Striations are located over the entire labial surface with some short marks near the cervical-enamel junction, longer marks in the center of the tooth and near the occlusal border. Most scratches are found in the tooth's center, especially along a slight ridge just off the distal border. Nearly everywhere, the marks are roughly parallel to each other, except for along the perpendicular ridge. In this region the striations range between 60°-85° and 95°-160°, with frequent crossovers. All but three of the over-markings are of the left-hand type, tend to be shorter and are more closely packed together compared to most

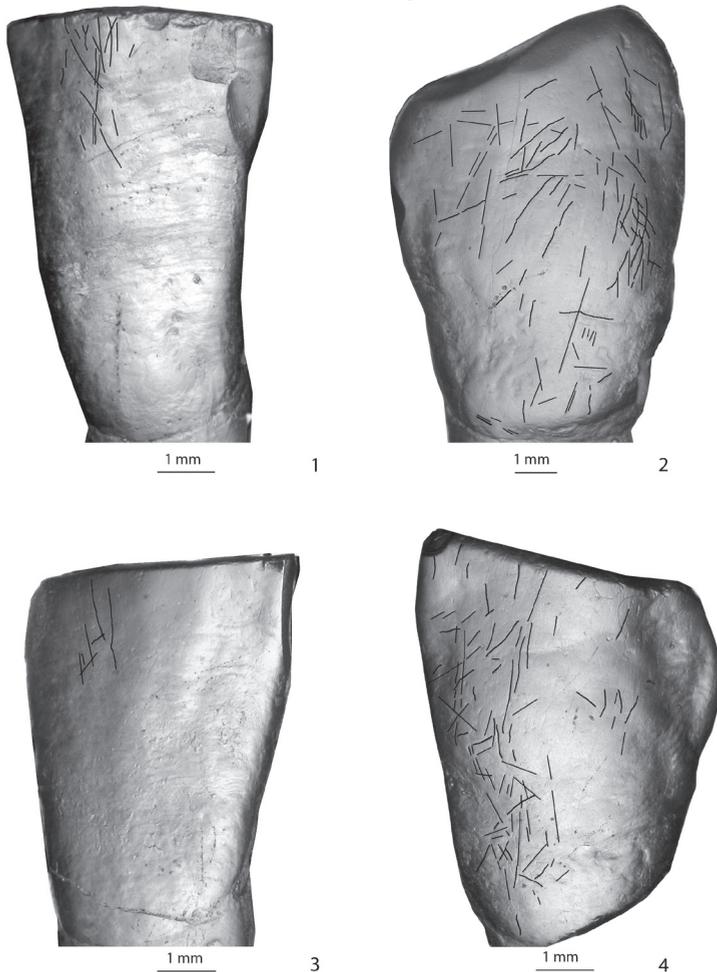


Fig. 4 - Striations as mapped on Vindija mandibular teeth (1. Vi 201; 2. Vi 206; 3. Vi 286; 4. Vi 288).

others on the labial face. Actions performed here appear to be different than on the main part of the tooth surface. SEM analysis (Figure 3:4) reveals relatively long, deep and well-defined striae.

Overall, 71 striations (62.7%) are less than 90° and with χ^2 significant at $p < .01$. Breaking down the categories further: 60 (65.2%) striations are between $5-85^\circ$ and 32 (34.8%) between $>95-175^\circ$. A total of 29 (61.7%) are in the $>22.5-67.5\%$ range. Each of the latter is significant at $p < .01$ with χ^2 . Thus, all data indicate a consistent pattern of right-handedness.

Vindija 286. Mandibular right second incisor. Level F_d (Figure 4:3)

With only 16 scratches this tooth has the fewest striae of any at Vindija. Lengths vary between 0.31 and 1.49 mm with an average of 0.73 mm. In only four cases do the scratches exceed 1mm in length. These are relatively deep and well defined compared to the others, which are more eroded and superficial. The scratches are mostly straight, located near or on the occlusal border and all, but one are on the distal half of the tooth. In this region are some small, enamel

fractures and most scratches are near the microchips. Angle analysis shows no consistent left/right orientation with the $<90^\circ$, $>90^\circ$ comparison not significantly different ($p < .134$). Given the small number of scratches a side preference cannot be determined.

Vindija 288. Mandibular left canine. Level F_d
(Figure 4:4)

Vi 288 has 93 scratches with lengths ranging from 0.15-1.60 mm, averaging 0.53 mm. Compared to other Vindija teeth the scratches are short and, while more numerous, similar to the upper canine Vi287. Scratches are primarily located along the mesial half of the tooth, especially in the tooth's central face. Of the 93 scratches, 60 (64.5%) are less than 90° . A similar frequency right-handed marks (63%: 51/81) occurs in the $5-85^\circ$ range and 73.5% (25/34) in the $22.5-67.5^\circ$ range. Each is significant at the .01 level or better with χ^2 , indicating the marks were produced by right-handed actions.

Discussion

Handedness in fossils and the implications

In these seven Vindija teeth, four (Vi206, 288, 289, 290) can be identified as belonging to individuals who consistently used their right hand to process material on tooth surfaces. Both upper and lower canines and incisors are involved and one tooth (Vi 290) is very heavily scored with mainly right hand marks. All these teeth show minimal occlusal wear, but often have microchips along the crown margin indicating that teeth were heavily used in oral processing. In many respects they resemble the heavily scored Neandertal teeth from Krapina (Lalueza-Fox & Frayer, 1997), even though dated nearly 100,000 years younger.

Data compiled for European Neandertals and the Sima de los Huesos individuals from Atapuerca show that right-handedness is the predominant pattern in the Paleolithic. While these data come from different investigators, using different criteria for measuring and counting

scratches on the labial faces of anterior teeth, the overall pattern is consistent. Currently there are 17 European Neandertals from Krapina (Lalueza-Fox & Frayer, 1997), Hortus and Cova Negra (Bermúdez de Castro, *et al.*, 1988), La Quina (Lalueza & Pérez-Pérez 1994) and Vindija, and all but Hortus 8 and Krapina KDP 4 are right-handed. For these European Neandertals, 88.2% are right-handed. Adding the 15 individuals from Sima de los Huesos (all right-handed) increases the frequency to 93.8%. As additional specimens are analyzed it is likely more left-handers will be identified, but the right dominant pattern is not likely to be significantly altered to the percentages seen in non-human primates. Thus, it is apparent that European Neandertals possessed dominant right-handed frequencies identical to modern humans and, based on the Sima de los Huesos pattern that this extended deep into the past.

Scratches, handedness and language capacity in Neandertals

It has long been contended that European Neandertal language capability was inferior to modern *Homo sapiens*. Original arguments stretch back to the earliest discoveries, when de Mortillet maintained in 1883 that the La Naulette Neandertal lacked linguistic ability because the mandibular genial tubercles were absent. In the early 20th century, a similar argument was made by Boule (1913) in his description of La Chapelle-aux-Saints, where he cemented in the concept of nonspeaking Neandertals. Almost four decades ago, Lieberman and his colleagues (Lieberman & Crelin, 1971; Lieberman *et al.*, 1972) extended this argument, arguing from anatomical reconstructions of the supralaryngeal vocal tract and formant extrapolations from it that Neandertals lacked the ability to produce essential vowels (*a*, *i*, *u*) and therefore lacked language capacity (Laitman *et al.*, 1979; Lieberman, *et al.*, 1992). In Lieberman's words (1975: 170):

"The most likely assessment of the encoding abilities of Neandertal man thus would be that his language was encoded but not nearly so much as that of modern Homo sapiens, because the Neandertal supralaryngeal vocal tract was

not suitable for fully encoded speech. The neural structures of the brain that play so crucial a role in the perception of encoded speech in the dominant, left hemisphere of the brain, therefore, may not have been as well developed in Neandertal man”.

The Lieberman and Crelin anatomical reconstructions and their inferences continue to be cited by him and others as evidence for Neandertal linguistic shortcomings (Lieberman & McCarthy, 2007; Klein, 2009; Tattersall, 2006). This interpretation persists, despite the fact that much criticism has been levelled at the accuracy of the Neandertal vocal tract evidence (Arensburg, 1994; Arensburg *et al.*, 1990; Arensburg *et al.*, 1989; Boë *et al.*, 2002; Burr, 1976; Carlisle & Siegel, 1974; Duchin, 1990; Falk, 1975; Frayer, 1993; Frayer & Nicolay, 2000; Gibson, 1994; Houghton, 1993, 1994; LeMay, 1975, 1976; Schepartz, 1993; Wolpoff *et al.*, 2004) as well as an accumulation of considerable evidence for Neandertal cultural and symbolic behavior (Hayden, 1993; Zilhão, 2006; Zilhão *et al.*, 2010). Lieberman now argues for changes in subcortical brain circuits of the basal ganglia as key to determining language origins and linguistic ability (Lieberman, 2007, 2009), but this is untestable in the fossil record with no anatomical area preserved for discerning this region.

There have now emerged numerous new reasons from different data sources, some quite unexpected, like nuclear DNA, to reject the notion that Neandertals lacked linguistic competence. New studies have documented complex behavior in Neandertals including evidence for incorporating seafood into their diet (Stringer *et al.*, 2008), open water seafaring (van der Geer, Dermitzakis & de Vos, 2006), the use of extensive plant remains (Lev *et al.*, 2005), the use of pigment (Cârciumaru *et al.*, 2002; Cârciumaru & Țuțuianu-Cârciumaru, 2009; d’Errico & Soressi, 2006), complex site utilization (Henry *et al.*, 2004; Vallverdú *et al.*, 2010) and evidence for advanced cultural behavior (Bednarik, 2006; Frayer *et al.*, 2008; Vandermeersch, 2008). All these indicate much more sophisticated adaptive and social behaviors in Neandertals than previously assumed, which would be impossible without complex language skills.

Right-handedness is long known to be highly correlated with left cerebral dominance and language (*e.g.*, Chance and Crow, 2007; Frost, 1980; McManus, 2004, Stubbe-Dräger & Knecht, 2009). There is not an “obligatory relationship between handedness and cerebral lateralization” (Holloway & de la Coste-Laremondie, 1982) since the left/right relationships are sometimes reversed, but for the most part language is strongly left cerebrally lateralized in both sexes (Frost *et al.*, 1999; Sommer & Kahn, 2009). This pattern seems related to the “non-allometric widening of the anterior cranial fossa,” most likely related to the differential increase in Broca’s cap in Neandertals and modern humans (Bruner & Holloway 2010). Most neurologists and paleoneurologists accept the relationship between language, lateralization and handedness (*e.g.* Knecht *et al.*, 2000; Falk, 1987). As Stubbe-Dräger & Knecht (2009, p. 68) conclude for humans “on the population level there is a strong tendency for left-hemispheric lateralization and handedness.” In the same vein, Chance and Crow (2007, p. 94) maintain:

“Lateralisation is central to both language and handedness in Homo sapiens ...[and] ... although the evidence is incomplete, and some[times] contradictory, most can be interpreted as consistent with the conclusion that directional handedness on a population basis and the form of cerebral asymmetry distinguish modern Homo sapiens from the great apes and other primates. These indices are putative correlates of the capacity for language”.

Demonstration of right-handedness in Neandertals and their European precursors is strong evidence for lateralization in these humans. Previous work has documented brain asymmetry in Neandertals, so it should not be surprising that Neandertals, like modern humans, are predominately right-handed. Another perspective on this issue is the discovery of the FOXP2 gene sequence in two male Asturian Neandertals dated about 40,000 years ago (Krause *et al.*, 2007; Torres *et al.*, in press). This gene, strongly implicated in speech and language development along with a host of other anatomical targets (Newbury, *et al.*, 2010; Konopka *et al.*, 2009),

shows no differences between Neandertals and moderns, indicating that at least this genetic component of normal language development was present in Neandertals.

Scientific evidence cannot confirm that Neandertals spoke like modern *sapiens*, but all the evidence now indicates that language capacity did not emerge recently in human evolution. Data for hand preference from Vindija, other Mousterian and earlier sites consistently points to a common pattern of right-handedness extending deep into European prehistory. These results have important implications for theories about language capability and language origins. Coupled with the ancient DNA and increasing evidence of cultural sophistication in the Middle Paleolithic, there are many independent lines of evidence confirming language capacity of Neandertals.

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