Handedness in the Krapina Neandertals: A Re-Evaluation

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ABSTRACT

Dominant right-handedness is well-established in European Neandertals and their likely ancestors with ratios indistinguishable from modern humans. Based on a previous analysis of oblique scratches into the enamel, the Krapina Neandertals represent a large portion of the Neandertal sample with six right-handers and one left-hander. These scratches are produced when stone tools etch the tooth face in repeated oral manipulations. In this update, the Krapina sample was blindly re-analyzed by re-casting the teeth and re-cataloguing the scratches. Done by a different researcher (IF) from the original study (Lalueza and Frayer 1997), this was an independent test of the determination of handedness from scratch patterns in the Krapina sample. We confirmed the earlier results of a predominant right-handed pattern from the striations' obliquity on the incisors and canines. Further, we identified the first deciduous tooth with a right-handed pattern, two more right-handers and added a second left-hander to the Krapina sample. Overall, our most up-to-date sample of all European Neandertals produces a frequency of about 90% right-handers. Handedness is a proxy for brain lateralization, and by extension, language capability. Coupled with other evidence from paleoanthropology to paleogenetics, it is apparent that Neandertals had all the capabilities of modern humans for language production.

INTRODUCTION

Labial scratches on a Neandertal incisor were initially documented by Martin (1923) at La Quina and subsequent researchers noted scratches on the labial faces of incisors and canines. The first systematic analysis of these scratches was done by Bermúdez de Castro et al. (1988), who documented a consistent right-handed pattern at Sima de los Huesos (Atapuerca) and provided the first experimental evidence to account for scratch patterning. Their categorization of the scratches into horizontal, vertical, left oblique, and right oblique intervals is now the established protocol for inventorying labial scratches. Frayer et al. (2010) provided a statistical procedure to more systematically predict when a set of labial scratches indicates the hand used to produce them.

The advantage of using labial scratches for estimating handedness is that much larger samples can be generated in place of using skeletal or cerebral indicators. For example, because at Krapina there are no associated left and right bones of the arm chain, it is not possible to estimate handedness based on skeletal asymmetry. This is why scratches on the labial face of incisors and canines are so valuable. A disadvantage is that labial scratches are not common in the Upper Paleolithic or Mesolithic people following Neandertals in Europe or in more recent populations (Bax and Ungar 1999). This makes finding examples from subsequent European populations or ethnohistoric parallels difficult. Although a few cases of scratches in modern teeth have been documented (Lozano et al. 2009), no cases in modern groups show the degree of scratching found in Neandertals. We suspect that the often highly scratched labial faces in the anterior teeth of Neandertals and earlier Europeans are related to using flake tools. Once blade tools became the dominant method of the tool kit, the "stuff and process" habit became less prevalent.

In 1997, Lalueza and Frayer documented labial scratch-

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es in the Krapina Neandertal teeth following categorizations established by Bermúdez de Castro et al. (1988). A total of 82 mandibular and maxillary incisors and canines were surveyed and six right-handed individuals and one left-handed individual were identified. Scratches were found only on the labial face and no teeth other than the incisors and canines were involved. We have sampled again many of these 82 teeth and documented scratch patterns with different techniques. Our new research was a blind study without reference to the earlier work. While the new survey does not exactly replicate the earlier identifications, mainly because some teeth from the earlier sample were not re-molded while a few different teeth were sampled, in the comparison of the earlier to the later samples, no contradictions were found.

THE KRAPINA NEANDERTALS

The Krapina Neandertals are represented in part by a large sample of fossil teeth, excavated by Gorjanović-Kramberger between 1899–1905 (Frayer 2006; Radovčić 1988). Dated to ~130,000 years ago (Rink et al. 1995), the sample consists of isolated primary and permanent teeth and teeth still in mandibles and maxillas. Wolpoff (1979) assembled many of the isolated teeth into tooth sets, based on morphological similarity, size, wear and fitting together interproximal wear facets. All Wolpoff's dental associations were made without regard for labial face scratches and some of these associated teeth have an identical scratch pattern, confirming his groupings. There are no cases in any Krapina Dental Person (KDP), as defined by Wolpoff (1979), where an isolated right incisor has a predominance of right-handed scratches and an associated left incisor has the opposite pattern. There are cases where the intensity of scratches varies in associated teeth, so that a right-handed scratch pattern is not duplicated in an antimere tooth or in one it occludes with, but in every case we have studied, the obliquity of the scratches in a set of individual teeth is consistent. For our analysis we followed the KDP designations in Radovčić et al. (1988). Some modifications in these tooth sets have appeared over time and are updated in an unpublished catalog (Radovčić and Wolpoff n.d.). None of these changes affect the teeth described here. Wolpoff (1979) estimated ages for most KDPs based on tooth wear and we include these assessments, except for Krapina 198, which was added to the sample after Wolpoff's inventory was published. As reviewed in Table 1, the Krapina Neandertals died very young—the youngest Neandertal in our sample aged 7 and the oldest aged 23, with a mean of 15.8 years. Labial striations occur across all age classes and begin early once the permanent teeth have erupted. We have no way to determine if there are differences between the sexes.

METHODS

In 1997 most of the Krapina anterior teeth were studied by Lalueza and Frayer and patterns of right-handed scratches were identified in six KDPs (5, 6, 17, 18, 29, Q) and lefthanded scratches in one KDP (4). In the original study, epoxy replicas made of Reichhold Epotuf were analyzed by Lalueza in Barcelona using a stereoscopic light microscope at 30–40x magnification. The locations and angulations of the striations were recorded with a semi-automatic Image Analyser System (IBAS) program at the University of Barcelona, using the occlusal plane as the x-axis. In 1997 we did not conduct statistical tests, but a predominant right or left pattern was identified when more than 50% of the scratches were either the right or left type.

In this re-study, the scratches were documented initially with a magnifying glass on the original specimens. Since the striations do not appear on the mesial, lingual or distal faces, only the labial faces were molded. All available dental remains were preliminarily observed with a stereo microscope. Teeth were selected when they showed multiple striae, which were relatively deep and obliquely oriented to the mesial-distal axis of the tooth. Further inspection of the microfeatures with an evaluation of the concentration, length, depth, orientation and microfeatures of the scratch's floor and walls allowed us to rule out specimens showing only striations possibly associated with other processes, such as mastication and sediment damage. The teeth selected for the quantitative analysis showed unequivocal microdamage produced by the impact with the cutting edge of stone tools. Our ultimate sample is smaller than the 1997 study, in part because we did not mold every tooth with a scratch and in part because not all teeth were available for study. For molding we used silicon elastomers (Try Novo). High resolution, positive casts were made with epoxy resin (Araldite LY-554 and hardener Hy 956). All quantitative analyses were done on the Araldite replicas, using a light transmitted stereomicroscope and on transparent, sputter-coated replicas for SEM analysis. SEM work was performed on a Leo Supra 50 VP-23-79 in Rome.

From the epoxy casts we analyzed scaled images, magnified at 20 times in Photoshop. Only manipulative scratches were traced on the image, ignoring the much thinner and fainter dietary scratches. Dietary scratches are present on the surfaces of most teeth (Kreuger and Ungar 2012) and are distinctively different than the manipulative scratches in their small size and shallowness. Our criteria for eliminating them were similar to a recent study of the Sima de los Huesos (Atapuerca) teeth by Lozano et al. (2009). There are some diagenetic alterations, but these are generally easy to distinguish from the scratches resulting from manipulation. In every case, cataloguing the scratches was conservative. For the re-study, each cast was photographed with a binocular microscope coupled to a digital camera. Magnified striations were traced manually and saved in a vector format, which was used for measuring quantity, angle and scratch length. We do not describe scratch length in this paper, but they are included in the Excel files for each tooth in the Supplemental Information (SI). To maintain consistency and to avoid inter-observer error, all striation analyses were done by one person (I.F.). After tracing the scratches, the image was calibrated with maximum mesial-distal crown length used to derive the pixels per cm scale. The image was converted to black and white to enhance contrast and the original background image was elimi-

TABLE 1. INVENTORY OF TEETH STUDIED, INDIVIDUAL ESTIMATED AGE, AND OUTCOMES FROM LALEUZA AND FRAYER (1997) AND THIS RE-ANALYSIS.

KDP	Tooth #	Tooth ID	Age*	Lalueza/Frayer	This Re-Study
1	13	Lt di$_2$	7	no	yes, Rt
3	119	Lt C$_1$	11	no	no
	131	Rt I^2		no	yes, Rt
4	153	Rt I^2	15	yes, Lt	yes, Lt
	154	Rt I^1		yes, Lt	yes, Lt
	160	Lt I^2		no	yes, Lt
5	Max 49	Lt I^1	15–16	yes, Rt	yes, Rt
	Max 49	Rt I^1		yes, Rt	yes, Rt
6	125	Lt I^2	23	no	no
	142	Lt C^1		no	no
	Mand 58	Lt I$_1$		yes, Rt	not studied
	Mand 58	Rt I$_1$		yes, Rt	not studied
	Mand 58	Lt I$_2$		yes, Rt	not studied
17	147	Lt C^1	18	yes, Rt	not studied
	156	Lt I^2		yes, Rt	not studied
	157	Rt I^1		yes, Rt	yes, Rt
	158	Lt I^1		yes, Rt	yes, Rt
18	127	Rt I^2	20	yes, Rt	not studied
	129	Rt I^1		yes, Rt	not studied
23	70	Rt $_1$	16	no	no
29	122	Lt I^2	13	no	no
	123	Lt I^1		yes, Rt	yes, Rt
30	92	Rt I^1	14	no	yes, Rt
35	126	Rt I^1	10	no	yes, Lt
	130	Rt I^2		no	no
Q	132	Rt I^1	19	yes, Rt	yes, Rt
	148	Rt I^2		yes, Rt	not studied
No KDP Designation					
	37	Lt C^1	15	no	no
	144	Lt C^1	22	no	no
	198	Rt I$_2$	-	not available	no

*ages are from Wolpoff 91979, Appendix 1)

nated, leaving only the lines. The morphological particle analysis routine, NIH freeware ImageJ: version 1.48j, was used to determine length and angle for each scratch. The 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. Because ImageJ picks up small, insignificant portions of lines, all marks less than 0.1mm were eliminated.

In both studies, the scratch angles for each tooth were divided into four classes dependent on their deviation from the 0±180º (occlusal) line (Bermúdez de Castro et al. 1988). The four categories were: horizontal (from 0º to 22.5º and from >157.5º to 180º), right oblique (from >22.5º to 67.5º), vertical (from >67.5º to 112.5º), and left oblique (from >112.5º to 157.5º). The horizontal and vertical categories are neither perfectly parallel nor vertical to the occlusal plane and small degree differences can shift a scratch from one category to another. We have advocated using a wider range for determining side type (Frayer et al. 2010), but, since nearly the entire literature for Neandertal scratches is based on the Bermúdez de Castro et al. (1988) categories, we continue to use them.

For the most part, in this study, we ignore vertical (>67.5º to 112.5º) and horizontal (0º to 22.5º and >157.5º to 180º) scratches. In some perspectives (Frayer et al. 2010), it is subjective to classify them as vertical or horizontal based on a single degree of deviation from the established Ber-

TABLE 2. CHI² SIGNIFICANCE LEVELS FOR THE RE-STUDY OF KRAPINA TEETH.

KDP	Tooth #	Side and Significance Chi²
1	13	Rt: 0.00
3	119	0.77
	131	Rt: 0.04
4	153	Lt: 0.00
	154	Lt: 0.00
	160	Lt: 0.00
5 Max 49	no #	Rt: 0.00
	no #	Rt: 0.00
6	125	0.15
	142	0.83
17	157	Rt: 0.00
	158	Rt: 0.00
23	70	0.12
29	122	0.12
	123	Rt: 0.00
30	92	Rt: 0.00
35	126	Lt: 0.00
	130	0.75
Q	132	Rt: 0.00
No KDP Designation		
	37	0.81
	144	0.31
	198	0.15

múdez de Castro et al. (1988) intervals. On the other hand, widening the intervals results in the inclusion of scratches that may be related to different kinds of activities. For example, Bax and Ungar (1999) found labial striations in modern dentitions, which were primarily vertical. Lozano et al. (2009) argue that vertical striations are produced by a different action and have a different etiology than the oblique marks. Horizontal marks can be viewed similarly. In any scenario, the Krapina Neandertals were heavily using their anterior teeth, leaving traces of different actions and different habits permanently etched in their anterior teeth. We interpret the angular scratches related to activities reflecting handedness and the vertical and horizontal marks a consequence of an undetermined activity.

KRAPINA SCRATCHES RE-STUDY

In this inventory of the re-studied material, we include images of the teeth, a graph of the counts (x-axis) of the horizontal, vertical, left, and right categories (y-axis), and a SEM enlargement of each tooth showing some of the scratches. Data for each tooth are included in the supplementary Excel files. With chi² for contingency tables we tested differences between left and right scratches. These are reported in Table 2.

KDP 1

Originally designated as Maxilla A, the specimen represents an upper left, fragmentary jaw of 5–6 year old child and associated lower primary teeth. The right dI_2 (#13) shows scratches, which fit the designation of right-handedness (Figure 1) and represents the first specimen where enough scratches appear to define handedness in a primary tooth. A total of 69 striations appear on the labial face accounting for 44.9% of the total. Right-handed marks are the most common followed by vertical marks. Only 8 left-handed marks are present, accounting for 11.6% of the total. When only right and left marks are considered, right-handed marks make up 79.5% of the total. These differences are significant with chi² (see Table 2) and we classify KDP 1 as a right-hander.

KDP 3

This individual is represented by two teeth, an upper right lateral incisor (#131) and a lower right C (#119) (Figure 2). For the lower canine most of the marks are vertical, so that only the lateral incisor shows enough right-handed scratches to designate KDP 3 as a right-hander (chi²=0.04, see Table 2). Of the total of 13 scratches, 8 are right, accounting for 61.5% of the total marks. Only 1 mark is the left type

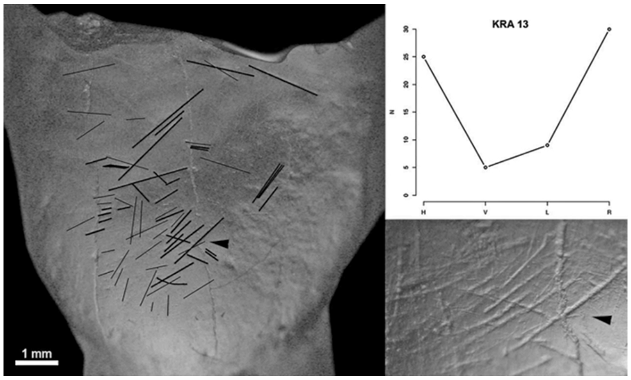

Figure 1. KDP 1.

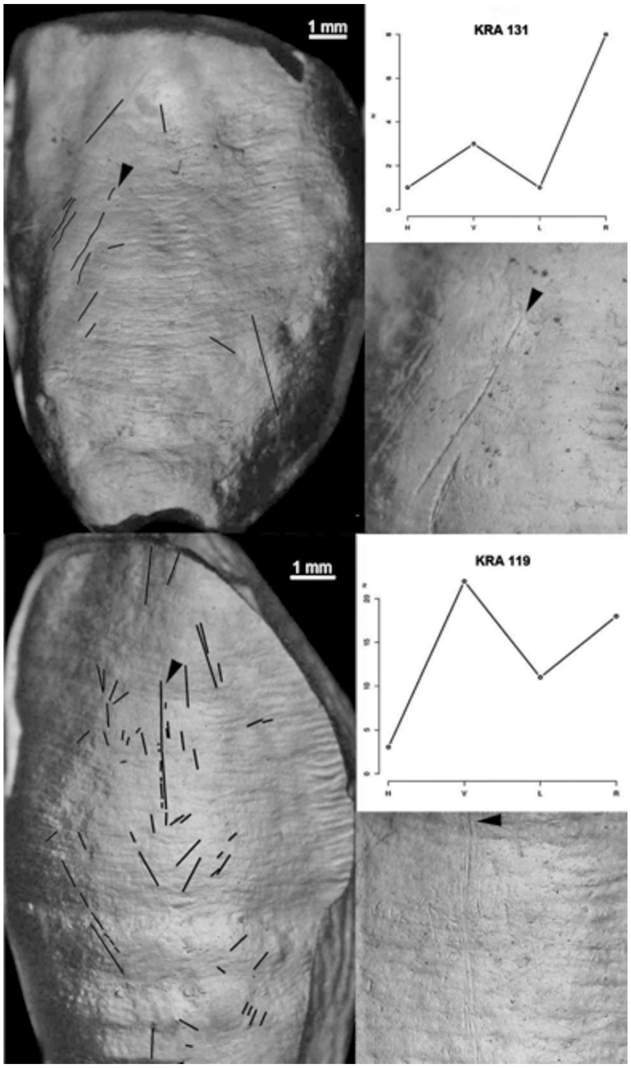

Figure 2. KDP 3.

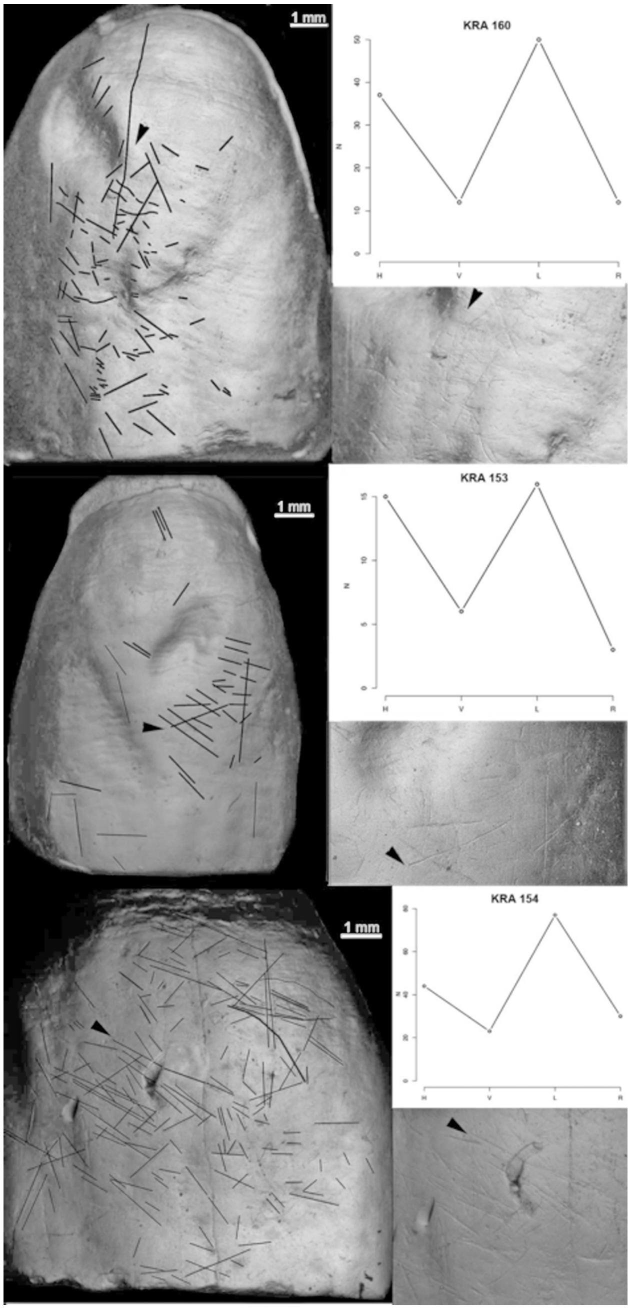

Figure 3. KDP 4.

so that the ratio or right to left scratches is 8:1 or 88.5% of the right-handed type.

KDP 4

This individual is represented by three maxillary teeth, a right I^1 (#154), a right I^2 (#153) and a left I^2 (#160). For each tooth, left oblique scratches predominate, never less than 40% of the entire sample of scratches per tooth (Figure 3).

Compared to the right-hand type, left-hand scratches make up 84.2%, 72.0%, and 80.6%, respectively, for the three teeth. These differences are each highly significant (see Table 2) indicating KDP 4 was a left-hander.

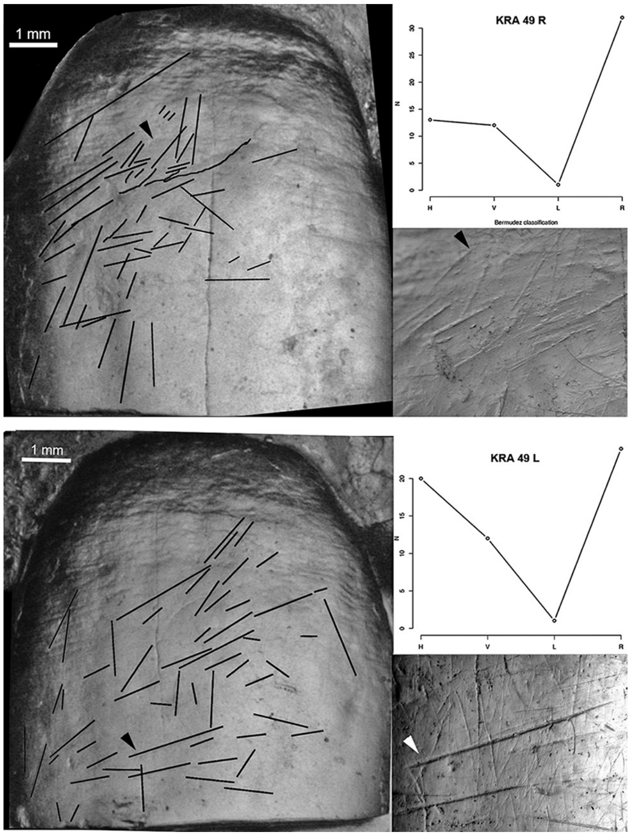

Figure 4. KDP 5.

KDP 5

Consisting of two right and left maxillary I¹s, right-hand scratches are markedly more common (Figure 4). For the totals, they constitute 55.2% of all marks on the right I¹ and make up 42.1 % on the left I¹. When just right or left type scratches are considered, over 95% of the scratches are of the right type. In both cases these differences are highly significant (see Table 2) and KDP was a right-hander.

KDP 6

Sampled teeth from KDP 6 include a left C¹ (#142) and left I¹ (#125). Mandible 58 associated with KDP 6 was not available for study. The two upper teeth do not show a significant left or right pattern (see Table 2), but both teeth have a high number of vertical scratches (Figure 5). In tooth #142, there are 104 vertical striations, representing the most scratches per type of any tooth in our sample. Overall for tooth #142 vertical marks account for 74.8%.

KDP 17

These right (#157) and left (#158) maxillary central incisors represent two teeth in KDP 17 (Figure 6). Both incisors show a high percentage of right scratches. For #157, 56.0% of all the scratches are right oblique and compared only with the left scratches, 90.3% are the right type. Similar results are found in the left central incisor (#158) where overall 39.0% are the right type, compared to the left scratches, 100% are of the right orientation. With chi² the differences with the

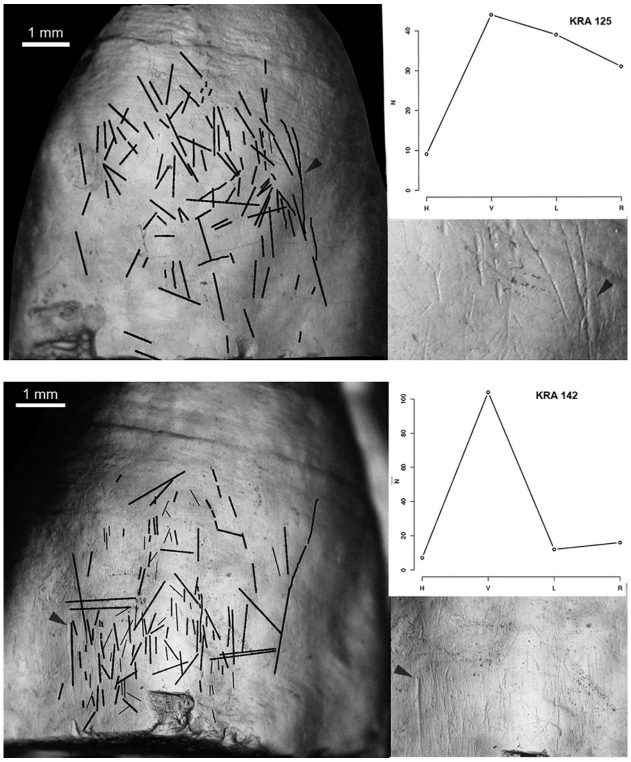

Figure 5. KDP 6.

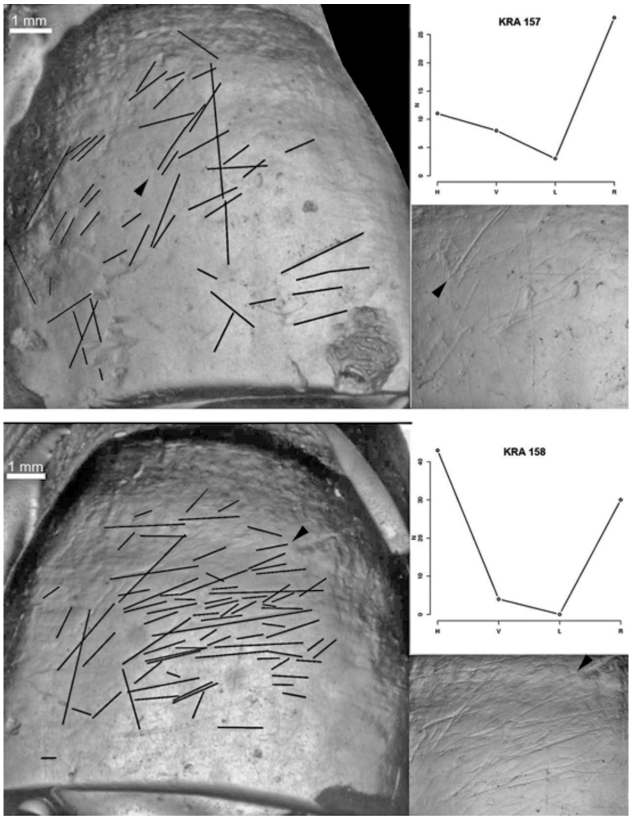

Figure 6. KDP 17.

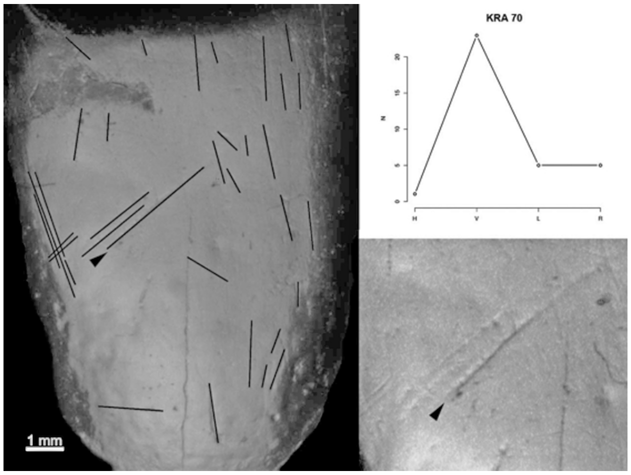

Figure 7. KDP 23.

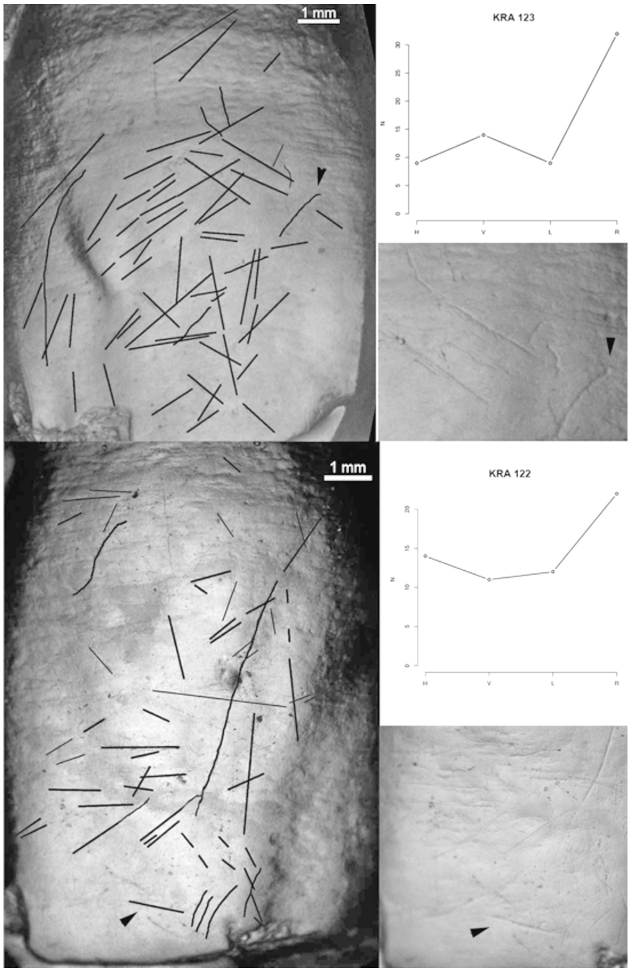

Figure 8. KDP 29.

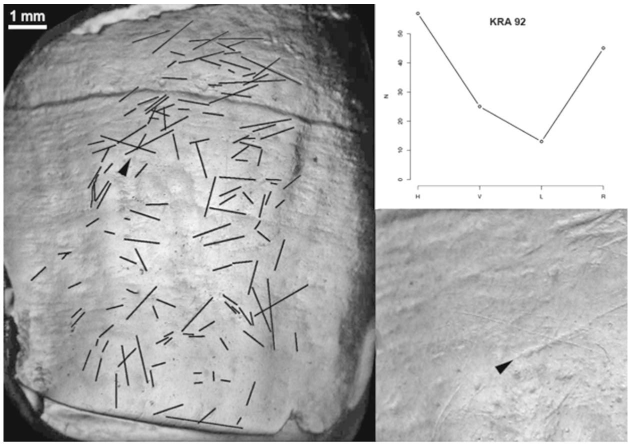

Figure 9. KDP 30.

frequency of left scratches are highly significant (see Table 2). KDP 17 was a right-hander.

KDP 23

Represented by a single upper right central incisor (#70), the tooth preserves a total of 34 striations (Figure 7). Two-thirds are vertical and no pattern for a right- or left-handed action is preserved.

KDP 29

An upper left central incisor (#123) and upper second incisor (#122) are the two teeth making up KDP 29 (Figure 8). Both show a predominance of right-handed striations. For #123 right-handed striations make up 48.4% of the total scratches and 76.9% are the right type compared only to the left. For tooth #122, a total of 59 scratches are preserved and 22 are the right type, 12 the left type. From the total, 37.3% of all scratches are the right type, while when only left and right scratches are counted, 64.2% are the right type. KDP 29 was a right-hander (see Table 2).

KDP 30

A single right maxillary I^1 incisor comprises this individual and it is dominated by a high frequency of horizontal scratches with a rate of 34.5% (Figure 9). However there are also a high number of right-handed scratches and, when only right and left striations are considered, 78.9% are of the right type. These represent significant differences with chi^2 (see Table 2) and KDP 30 was a right–hander.

KDP 35

This individual is comprised by two teeth, left and right maxillary central incisors. The left I^1 preserves only seven scratches and no significant differences exist between scratch types. It is not illustrated. However, #126 shows a high percentage of left marks (68.6%) overall and no right oblique marks (Figure 10). With significantly more left scratches (see Table 2) this individual represents the second left-hander at the site.

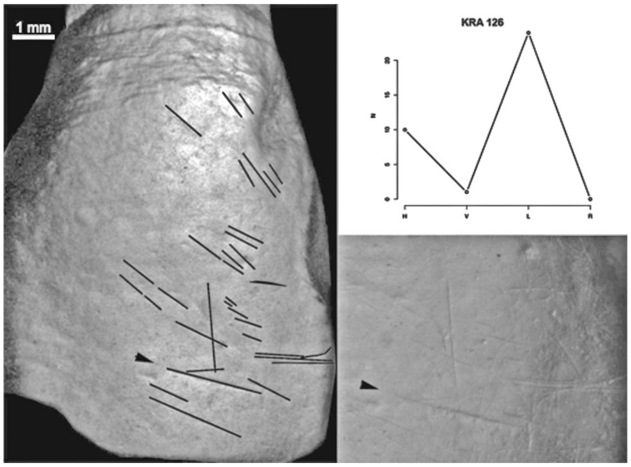

Figure 10. KDP 35.

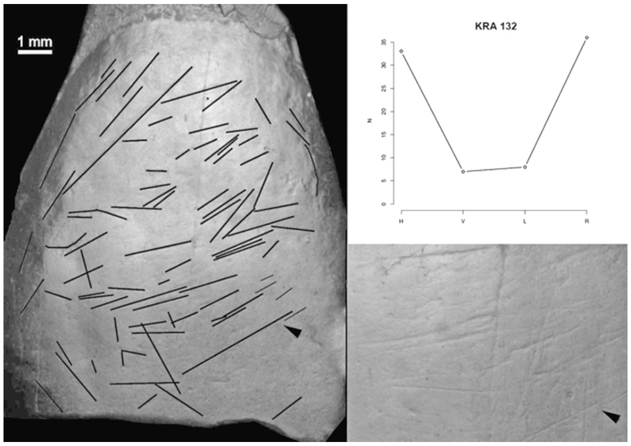

Figure 11. Individual Q.

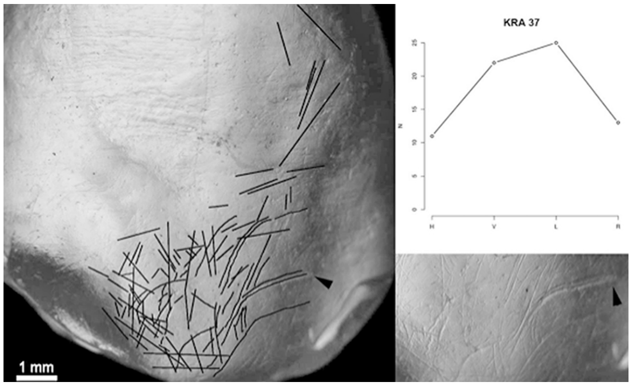

Figure 12. Tooth #27.

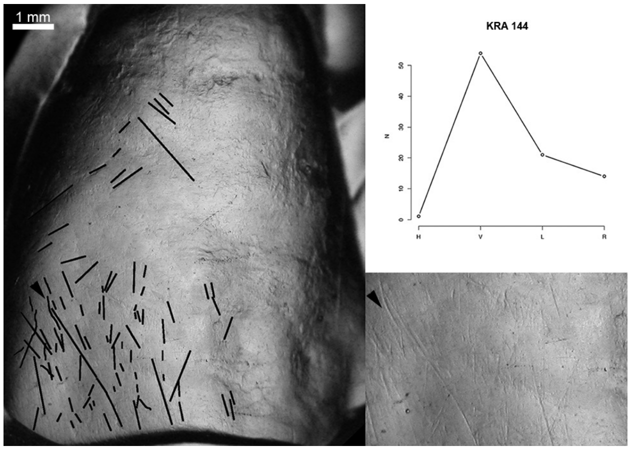

Figure 13. Tooth #144.

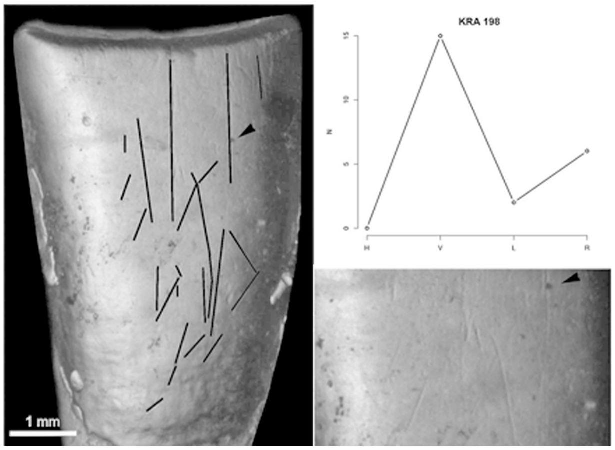

Figure 14. Tooth #198.

INDIVIDUAL Q

A right maxillary central incisor (#132) with a high percentage of horizontal scratches (39.3%) and an equally high number of right oblique marks (42.9%) characterize individual Q (Figure 11). Left scratches are poorly represented, so 81.8% of the scratches are of the right oblique type. These differences are statistically significant (see Table 2) and this specimen was a right-hander.

NO KDP DESIGNATION

Three isolated teeth were analyzed for labial scratches, which have no KDP designation. #37 is an upper left canine, #144 is another upper left canine, and #198 a lower right incisor (Figures 12–14). On all three teeth vertical striations predominate and no evidence for handedness is found.

Overall, we have added a right-handed juvenile (KDP 1) with a deciduous incisor, two more right-handers (KDP 3 and KDP 30), and another left-hander (KDP 35).

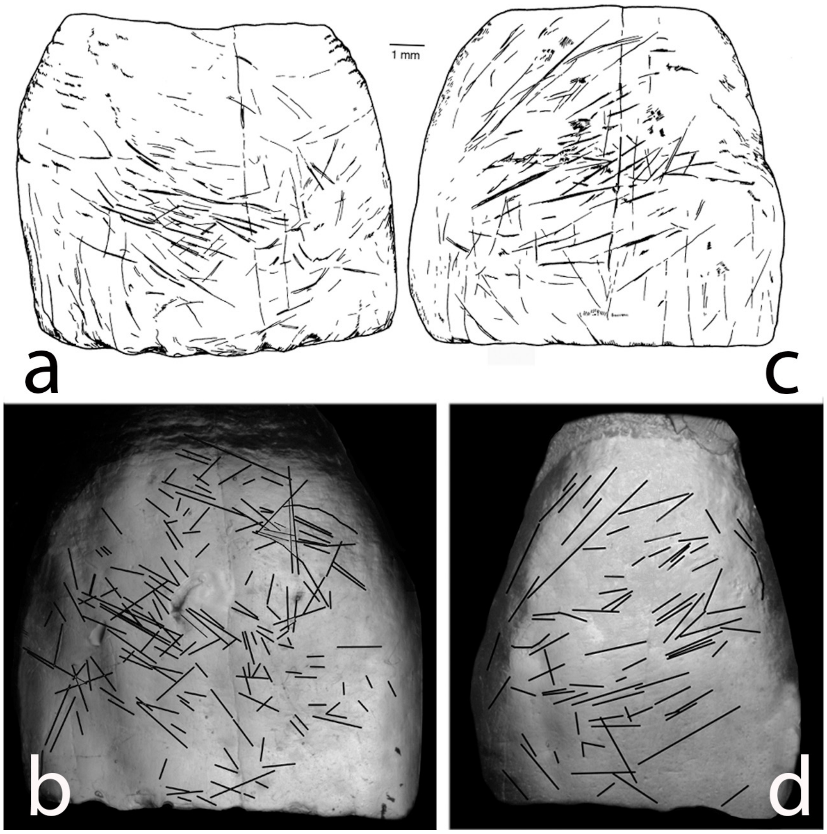

Figure 15. Teeth #154 (a, b) and #132 (c, d) from 1997 and this study.

COMPARISONS

Figure 15 illustrates two teeth from the 1997 study compared to the same teeth in this re-analysis. KDP4 is represented by tooth #154, a right I^1 and Q by #132, a right I^1. The upper two images are from Lalueza and Frayer (1997) and are microscopic renderings. The lower images are the original epoxy casts with the cut marks defined electronically. The teeth were drawn or photographed at different angles, which accounts for some of the distortion, especially in #132 where the occlusal margin is tilted upward in comparison to the earlier image. Despite the differences in perspective and the different techniques for identifying the cut marks, visualization of striation angulation is similar in the two studies, with clearly a predominant left-handed pattern in #154 and a right-handed pattern in #132. We conducted chi^2 tests on these two teeth comparing all four categories and just left/right counts. For all four comparisons, the counts are significantly different at >.001 level. But if just the left and right counts are considered for each tooth, there are no significant differences between the earlier and this re-study (Table 3). Identifying striations on teeth is not an exact science with different eyes categorizing the scratches for length and definition, but the patterning of left and right scratches produces similar outcomes and in no cases did the results in this study vary from the earlier study—that is, where the earlier study identified the scratches as a right-handed pattern and the re-study as a left-handed pattern (or the reverse). In short, the count of left- and right-handed scratches may vary, but the overall patterning was consistent.

ORIGIN OF SCRATCHES

Different types of scratches occur on the labial surfaces of the anterior teeth. The fact that these are exclusively limited to the incisors and canines suggests they are related to operations and functions performed as these teeth were used to hold and manipulate objects (Brace 1967). Here, we are concerned with oblique scratches as defined by Bermúdez de Castro et al. (1988), but some teeth are dominated by vertical (e.g., Krapina tooth #198) or horizontal marks (KDP 30). We note that in mandible from Régourdou, the four incisors are dominated by oblique scratches, while the canines have mostly vertical striations (Volpato et al. 2012). This suggests that sometimes different types of activities were done on the incisors compared to the canines. We consider vertical and horizontal scratches a consequence of a different actions, but it is important to consider that the cut-offs of the Bermudez de Castro et al. (1988) categories can change a vertical or horizontal scratch into an oblique one by a few degrees of angulation (Frayer et al. 2010). Like any categorization, there are gray areas of overlap, complicated by the variable ways the teeth were used in manipulating different types of materials.

As we and others have argued in a number of publications (Bermúdez de Castro et al. 1988; Frayer et al. 2010; Lozano et al. 2009; Volpato et al. 2012), all these scratches were

TABLE 3. SCRATCH COUNTS AND SIGNIFICANCE LEVELS FOR TWO TEETH EVALUATED BY LALUEZA AND FRAYER (1997) AND THIS RE-STUDY (Monte Carlo 10,000 iterations).

Tooth	Horizontal	Vertical	Left	Right	
132	33	7	8	70	this re-study
	26	27	10	38	Lalueza and Fox (1997)
all categories: chi^2 =11.41 Monte Carlo p=0.009; left/right comparison only: chi^2 =0.103 Monte Carlo p=0.8					
154	44	23	77	30	this re-study
	40	43	45	10	Lalueza and Fox (1997)
all categories: chi^2 =20.77 Monte Carlo p=0.0001; left/right comparison only: chi^2 =0.89 Monte Carlo p=0.18					

produced when the tooth enamel came into contact with a stone tool during some kind of oral manipulation. European Neandertals generally show differential wear, where the primary and permanent anterior teeth are generally more heavily worn than the posteriors. Some have ascribed this to the stuff and cut mode of eating (Brace 1967), but it may involve any activity where the mouth is used as a vise to hold an object and a stone tool is used to modify it. These could include hide processing, woodworking, or fiber processing, all known to be part of the Neandertal behavioral repertoire (e.g., Soressi et al. 2013; Vaquero et al. 2001; Hardy et al. 2013). For the oblique scratches, as a right-hander pulls with the left and cuts with the right in a downward motion, characteristic striations can etch the crown surface if the stone tool comes into contact with it. The opposite-angled, oblique scratches are produced by a left-hander, pulling with the right and cutting downward with the left hand. Bermúdez de Castro et al. (1988) conducted experiments using plastic mouth guards and Lozano et al. (2009) used mouth guards embedded with teeth. Both were able to produce similar scratch patterns as found in Neandertals or the Sima de los Huesos humans. Based on this experimental evidence, the type of oblique scratches can indicate the dominant hand used in prehistoric contexts.

DETERMINING HANDEDNESS

A number of different ways have been proposed to estimate prehistoric handedness and laterality. In living humans, handedness is measured by direct observation of manipulation, analysis of writing patterns, or other hand preference activities (Annett 2009; Peters 1995). While not as straightforward as sometimes presumed, worldwide patterns are consistent (McManus 2003), with a fairly steady ratio of 9 right-handers to every 1 left-hander. Techniques developed for assessing handedness in living populations obviously cannot be applied in the fossil record (Cashmore et al. 2008; Uomini 2009a, b), but various methods have been proposed for identifying preferred hand use in the fossil record. Closest to modern determinations are negative hand prints on prehistoric cave walls, but these are primarily limited to European Upper Paleolithic or equivalent age sites elsewhere in the world. Faurie and Raymond (2003) tallied the number of right and left hand stencils in French/Spanish Upper Paleolithic caves and report a ~8 : ~2 predominance of left hands, indicating the left hand was held against the wall and the right hand was used to produce the negative image. Other approaches range from stone tool flaking patterns (Toth 1985; Cornford 1986) to cut mark orientation on bones (Bromage and Boyde 1984; Bromage et al. 1991; Pickering and Hensley-Marschand 2008), but these remain controversial.

For limb bones, Auerbach and Ruff (2006) collected 14 measurements from the radius, humerus, femur, and tibia on a large sample of worldwide modern skeletons. They found that "upper limb bones show a systematic right bias in all dimensions in the radius and humerus, while lower limb elements have biases closer to zero" (2006: 203). A subsequent study of torsional bending strength and cross-sectional bone area in midshafts of the humerus and ulna of living males shows that the dominant limb has significantly greater values than the opposite side (Shaw 2011). Bones of the hand seem to be less reliable for determining handedness, based on a work by Plato et al. (1980) who revealed that right/left difference in various measures of metacarpal 2 were not related directly handedness. They concluded that "(i)t seems that there is an inherent tendency for larger bone in the right side regardless of lateral dominance" (1980: 31). Steele (2000) and Steele and Uomini (2009) have argued for a skeletal association with handedness, especially since people of the past used their limbs in more strenuous ways than living moderns. Their study points to the value of computed tomographic work in fossils (e.g., Volpato et al. 2011) where torsional and strength variables can be assessed. Whatever the evaluative technique, the number of nonpathological Neanderthal skeletons with associated left and right upper limb bones is restricted to just a few European and Levantine specimens (Frayer et al. 2012), so this approach is of limited value. It is important to note that determining handedness in recent populations from left/right arm chain bones is not reliable

TABLE 4. RESULTS COMPARISON OF LALUEZA AND FRAYER (1997) AND THIS RE-STUDY.

	Lalueza and Frayer, Hand?	This Re-Study, Hand?
KDP 1	Rt, but ns	Rt
KDP 3	Rt, but ns	Rt
KDP 4	Lt	Lt
KDP 5	Rt	Rt
KDP 6	Rt	not significant
KDP 17	Rt	Rt
KDP 18	Rt	not analyzed
KDP 23	no	no
KDP 29	Rt	Rt
KDP 30	no	Rt
KDP 35	no	Lt
Q	Rt	Rt
tooth #37	no	no
tooth #144	no	no
tooth #198	not available	no
right/left ratio	6Rt : 1Lt 85.7%	7Rt : 2Lt 77.8%
combined	9Rt : 2Lt 81.8%	

(Komar and Buikstra 2008; Schulter-Ellis 1980).

Others have documented endocast morphology, lateral asymmetry from petalial variation, and the preservation of language areas on the brain's left side (Holloway 1985; LeMay 1977). Holloway also has documented brain asymmetry and left occipital/right frontal petalial asymmetries (Holloway 1981; Holloway and de la Coste-Lareymondie 1982). In European Neandertals, there is a preponderance of the right-handed, modern pattern. Feldhofer 1, La Ferrassie 1, Forbes Quarry 1, Le Moustier 1, Saccopastore 1, Spy 1, and Spy 2 all show left hemisphere dominance, with only La Chapelle-aux-Saints 1 showing an opposite pattern (Holloway and de la Coste-Lareymondie 1982). While informative, samples of brain endocasts are limited, restricted to just a few fossils and it unlikely future samples will ever be very large. In any event these samples are small, but none of the studies from various parts of the skeleton contradict each other—all support the contention that Neandertals were lateralized like modern *Homo sapiens.*

NEANDERTAL LATERALITY

New handedness evaluations for Krapina are presented in Table 4. Unlike the earlier study we were able to identify a single primary tooth with a significant number of right-handed scratches. In addition, we found another left-hander in the collection bringing the right/left ratio at Krapina to 7 : 2 in this re-study. We also found a general concordance between this re-study and the 1997 review. From Table 4, there were no cases where either study identified a pattern as right-hander and the other as a left-hander, although several teeth in the two studies were not attributed to a left or right designation. A few differences exist between the two studies. (1) While the 1997 study recognized right oblique scratches on the di_2 tooth (#13), these did not attain the threshold for identifying it as right-hander. In the re-study, these differences reached statistical significance. (2) KDP 6 (mandible) and KDP 18 (teeth #127 and #129) were not available in the re-study, but were identified by Lalueza and Frayer (1997) as right-handers. (3) For KDP 17, two teeth (#147 and #156) were not molded in the re-study, but teeth #157 and #158 were analyzed in both studies and were consistent in identifying KDP 17 as a right-hander. (4) In the 1997 study KDP 30, represented by tooth #92 was not identified as a right-hander, but the differences between right and left oblique reached statistical significance here. (5) For KDP 35, tooth #126 in this study we found a predominance of left-handed scratches, making it the second left-hander at Krapina.

Given the overall consistency between the two studies, we feel justified in combining the results ending in a ratio of 9 : 2 for the site. Adding these results to the larger European Neandertal sample, in Table 5 we document a strong right-handed preference in European Neandertals with a ratio of 30 right : 3 left or 90.0% right-handed. Adding the

TABLE 5. HANDEDNESS FREQUENCIES IN NEANDERTALS AND THEIR LIKELY ANCESTORS FROM SIMA DE LOS HUESOS*.

KDP 1	Rt	
KDP 3	Rt	
KDP 4	Lt	
KDP 5	Rt	
KDP 6	Rt	
KDP 17	Rt	
KDP 18	Rt	
KDP 29	Rt	
KDP 30	Rt	
KDP 35	Lt	
Q	Rt	
Régourdou 1	Rt	
Cova Negra	Rt	
Hortus 7	Rt	
Hortus 8	Lt	
Hortus 9	Rt	
Hortus 11	Rt	
Hortus 12	Rt	
La Quina 5	Rt	
Vindija 206	Rt	
Vindija 288	Rt	
Vindija 289	Rt	
Vindija 290	Rt	
El Sidrón	+10Rt	
Sima de los Huesos	+12Rt	
	count	**ratio**
European Neandertals	30 : 3	90 : 10
Fossil Europeans	42 : 3	93 : 7

*data from Estalrrich and Rosas (2013), Frayer et al. (2012), and Volpato et al. (2012)

12 individuals from Sima de los Huesos, the ratio of fossil Europeans is 42 right : 3 left or 93% right-handed. From these data, we maintain that Neandertals and their predecessors in Europe were strongly lateralized.

SIGNIFICANCE OF A PREDOMINANT RIGHT-HANDED PATTERN

Brain laterality in modern humans has long been considered associated with language capacity and handedness (e.g., Corballis 2003; Galaburda et al. 1978; Stubbe-Dräger and Knecht 2009). While there are some studies which document cerebral asymmetries in chimpanzees (Gannon et al. 1998; Glissen and Hopkins 2013), humans represent the extreme of lateralization and left hemispheric specialization as part of a continuum from monkeys to apes (especially chimpanzees) to humans (Smaers et al. 2011).

Since the identification of Broca's and Wernicke's areas in the mid/late 1800s, left side brain areas in addition to these have been implicated as language processing areas in right and left handers (Keller et al. 2009; Price 2010; Samara and Tsangaris 2011). While many animals show some degree of lateralization, among mammals, only humans show the high frequency of right-handedness at about 90% species-wide (Corballis 2009; Coren and Porac 1977; Gilbert and Wysocki 1992; McManus 2009a, b). This contrasts with apes and other primates, which vary at the population level in their degree of handedness (McGrew and Marchant 1997). In non-human primates, left-handedness sometimes predominates, such as in orangutans or snub-nosed monkeys (Zhao et al. 2012), but species- or population-level right-handedness for combined tasks never reaches the 9 : 1 human pattern. Generally the ratios are closer to 5 : 5 (McGrew and Marchant 1997) and in many nonhuman primates there is a high incidence of task related ambidexterity (Hopkins et al. 2011). For example, Hopkins (2013) reviewed different handed activities in wild chimpanzees and 7/8 were right-handed. However, frequencies of right-handedness never reached 80%, ranging between 34.3% – 78.9%. Considerable hand inconsistency was present; in pestle pounding, "reach action" was significantly right-handed at 78.9%, while "pound action" was only 58.9%. So a sequential task was first right-handed, then not (Hopkins 2013: Table 1). Anecdotally, this seems the opposite of a typical human right-hander who would likely reach and pound with only the right or reach with the left and consistently pound with the right. In the same review, throwing had a right-handedness frequency of 75% in 3 of 4 populations, but the activity was most commonly bimanual in 12 of the 16 samples (Hopkins 2013). No study of humans has documented this level of ambidexterity in human throwing (Calvin 1982) or other handed activities, so that living humans are overwhelmingly right-handed from tennis to tooth brushing to finger pointing (van Strien 2002; Mathews et al. 2012).

Right-handedness begins in the womb (Hepper et al. 1991, 1998), continues consistently into adolescence and adulthood (Hepper et al. 2005; Hepper 2013), and likely corresponds to early fetal brain lateralization (Kasprian et al. 2011; Hepper 2013). Unlike other primates, handedness frequencies do not differ between human subadults and adults, although the frequency of left-handedness decreases in old age (Gilbert and Wysocki 1992). Yet, for the majority of people, once handedness is established, it is fixed in humans.

Language capacity in fossils has had a long history of debate and contention, in part because there are few direct biological indicators of language ability. Early attempts in Neandertals focused on the expression of morphological features, like the genial tubercles as an signal of tongue musculature and language incompetence (de Mortillet 1883; Boule 1913). These anatomical projections at the base of the internal symphysis were shown to be variable in modern humans (Weidenreich 1904), sometimes present, sometimes absent, so they were deemed to have no relationship to language competence. Others attempted to reconstruct vocal tract dimensions and sound production (Lieberman and Crelin 1971) for Neandertals, initially from the *flat* cranial base of La Chapelle aux Saints. Their assertions were strongly criticized by numerous researchers (e.g., Burr 1976; Carlisle and Siegel 1974; Duchin 1990; Falk 1975; Houghton 1993; LeMay 1975) and equally strongly defended (Lieberman 1976, 1978; 1987; Lieberman et al. 1992; Lieberman 1994). Subsequently, Boë et al. (2002) convincingly demonstrated that some of the basicranial anatomy of the La Chapelle aux Saints fossil was incorrectly reconstructed in the original work by Boule (1913), which was also strongly contested by Lieberman (2007a). Yet, it is clear that Boule's reconstruction of the flat, chimpanzee-like cranial base was incorrect (Heim 1989), resulting in a fatal flaw for the Lieberman and Crelin reconstruction since they relied on a cast of the La Chapelle aux Saints cranium based on the original Boule reconstruction (Boë et al. 2007). Furthermore, their own work showed that some Neandertals had a flexed cranial base (e.g., La Ferrassie 1) like modern humans (Laitman et al. 1979). Barney et al. (2012) made a virtual reconstruction the Neandertal supralaryngeal vocal tract and modeled the formants "a," "i," and "u." Neandertal production of these three vowels was not significantly different from modern sound production, especially for "i" and "u." Differences in the "a" formant are equivalent to dialect variants.

While there are no perfect correlations among handedness, brain laterality, and language, the fact that Neandertals are right-handed like modern people lends credence to the argument that they were brain lateralized in the same way as us. Proving that Neandertals had language is not possible, but there is a conjunction of various types of evidence from a wide variety of non-overlapping sources, which makes it difficult to deny a linguistic equivalency to moderns (Dediu and Levinson 2013). For Neandertals, there are paleoanthropological signs of complex site utilization (e.g., Hayden 1993, 2012; Speth et al. 2012; Vallverdú et al. 2010), systematic, sophisticated use of fire (e.g., Cabanes et al 2010; Courty et al. 2012; Roebroeks and Villa 2010), many new examples of faunal subsistence patterns in common with modern groups (e.g., Cortéz-Sánchez et al. 2011; Stringer et al. 2008), use of floral components in the diet (Henry et al. 2010; Lev et al. 2005), and inclusion of plants of no nutritional, but likely medicinal, value (Hardy et al. 2012). There is now incontrovertible evidence for symbolic capacity, represented by pigment collection (e.g., Cărciumaru, et al. 2002; Dayet et al. 2014; Peresani et al. 2013; Roebroeks et al. 2012; Soressi and d'Errico 2007), feather procurement (Finlayson et al., 2012; Hardy and Moncel 2011; Peresani et al. 2011), ornament use (Fiore et al. 2004; Morin and Laroulandie 2012; Zilhão et al. 2010), and even some evidence for art (Pike et al. 2012; Rodríguez-Vidal et al. 2014). Ritual treatment of the dead (Frayer et al. 2006), intentional primary (e.g., Hayden 2012; Maurielle and Vandermeersch 2007) or secondary burials (Russell 1987) are documented for a variety of Mousterian sites, including Krapina. Almost certainly as time passes, more, not less evidence, for Neandertal complex behavior and symbolic communication will be found. In addition to cultural evidence, a variety of the modern FOXP2 allelic sequence is found in Neandertals (Krause et al. 2007; Hawks 2013), linking them to modern humans and separating them from non-speaking apes. We recognize that this genetic sequence is linked to systems other than language, but it clearly is involved in the facilitation of language (e.g., Schreiweis et al. 2014) and people with a non-normal FOXP2 sequence inevitably have linguistic deficiencies (Lai et al. 2001). We agree with Lieberman's assessment (2007b: 52) where he proposed, "The FOXP2 gene provides a means to date the evolution of the human brain and emergence of …speech … in a time frame associated with the emergence of anatomically modern *H. sapiens*." We only would modify this to read "with the emergence of Neandertals."

CONCLUSIONS

Speth (2004) argued against the use of negative evidence for denying biological or cultural capabilities to Neandertals. His ideas were prescient, published before the discovery of Neandertal nuclear DNA and before most of the new evidence cited above for Neandertal cultural complexity. It is now clear that multiple lines of evidence point to a much more complex life for Neandertals, where they reveal their own behavior, which could not have been copied from modern humans. It is difficult to imagine they could have accomplished this behavior without a language. We now know they produced the essential formants and had genetics in place for grammatical and articulatory expression. They were also strongly lateralized based on a large sample the teeth from Krapina and elsewhere. For all these details there is not a single piece of contradictory evidence pointing to any kind of deficiency in Neandertal linguistic capacity. And, it is important to consider that lateralization, as measured by handedness, extends back to, at least, Sima de los Huesos, or more than one-half million years ago. Future discoveries will better define when the first modern linguistic capacity emerged, but for now there is little doubt that Neandertals spoke like us.

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