Anterior dental microwear textures show habitat-driven variability in Neandertal behavior

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Abstract

The causes of Neandertal anterior tooth wear patterns, including labial rounding, labial scratches, and differential anterior-posterior wear, have been debated for decades. The most common explanation is the "stuff-and-cut" hypothesis, which describes Neandertals clamping down on a piece of meat and slicing a portion close to their lips. "Stuff-and-cut" has been accepted as a general aspect of Neandertal behavior without fully assessing its variability. This study analyzes anterior dental microwear textures across habitats, locations, and time intervals to discern possible variation in Neandertal anterior tooth-use behavior.

Forty-five Neandertals from 24 sites were analyzed, represented by high-resolution replicas of permanent anterior teeth. The labial surface was scanned for antemortem microwear using a white-light confocal profiler. The resultant 3D-point clouds, representing 204x276 μm for each specimen, were uploaded into SSFA software packages for texture characterization. Statistical analyses, including MANOVAs, ANOVAs, and pairwise comparisons, were completed on ranked microwear data. Neandertal descriptive statistics were also compared to ten bioarchaeological samples of known or inferred dietary and behavioral regimes.

The Neandertal sample varied significantly by habitat, suggesting this factor was a principal driving force for differences in Neandertal anterior tooth-use behaviors. The Neandertals from open habitats showed significantly lower anisotropy and higher textural fill volume than those inhabiting more closed, forested environments. The texture signature from the open-habitat Neandertals was most similar to that of the Ipiutak and Nunavut, who used their anterior teeth for intense clamping and grasping behaviors related to hide preparation. Those in more closed habitats were most similar to the Arikara, who did not participate in non-dietary behaviors. These Neandertal individuals had a broad range of texture values consistent with non-

dietary and dietary behaviors, suggesting they varied more in anterior tooth-use behaviors and exploited a wider variety of plant and animal resources than did those from open habitats.

Introduction

Using the anterior dentition as a tool is often associated with Neandertal subsistence strategies. This is due largely to the variety of anterior wear patterns found singularly or in various combinations; these patterns include labial rounding, labial scratches, and differential anterior-posterior wear. Although various explanations for some or all of these patterns have been put forth (Martin, 1923; Koby, 1956; Stewart, 1959; Wallace, 1975; F. Smith, 1976; P. Smith, 1976; Puech, 1978, 1979, 1981; Wolpoff, 1979; Trinkaus, 1992), none have garnered as much support as that of "stuff-and-cut."

The "stuff-and-cut" hypothesis describes Neandertals clamping or grasping a piece of meat (or animal hide) between their anterior teeth and using a lithic tool to slice a portion close to their lips (Koby, 1956; Brace, 1967, 1975; de Lumley, 1973; Ryan, 1980; Brace et al., 1981; Trinkaus, 1983). This idea was taken from ethnographic accounts of Arctic peoples who used their anterior dentition in this manner (Beechey, 1831; Simpson, 1855, 1875; Ray, 1885). Although a range of non-dietary anterior tooth-use behaviors has been observed in modern human populations, such as sinew preparation, weaving tasks, wood softening, tool production, and lithic retouching (Man, 1883; Cybulski, 1974; Lukacs and Pastor, 1988; Foote, 1992; Mayes, 2001), the "stuff-and-cut" hypothesis has emerged as the most cited explanation for the combinations of Neandertal anterior tooth wear patterns. Consequently, many paleoanthropologists remain focused on the "stuff-and-cut" hypothesis, as well as on the idea that all Neandertals, regardless of habitat, location, or time, engaged in this behavior.

That said, recent studies point to significant variation in Neandertal tooth use and diet (Lalueza et al., 1993; Pérez-Pérez et al., 2003; El Zaatari et al., 2011, 2016; Fiorenza et al., 2011,

2015; Henry et al., 2011, 2014; Hardy et al., 2012). Data suggest that these hominins were not uniform in their actions, but could employ diverse adaptive strategies, including plant consumption, cooking, and possibly medicinal plant utilization (El Zaatari et al., 2011; Fiorenza et al., 2011, 2015; Henry et al., 2011, 2014; Hardy et al., 2012, but see Buck and Stringer, 2014). Such diversity, when combined with the range of non-dietary anterior tooth-use behaviors documented and inferred for modern human groups (Man, 1883; Cybulski, 1974; Lukacs and Pastor, 1988; Foote, 1992; Mayes, 2001), suggests that a single cause for Neandertal anterior tooth wear is unlikely. Moreover, while non-dietary anterior tooth use may have been a common Neandertal behavior, patterns of variation have not been adequately assessed.

The goal of the present study is to address this issue by focusing on a large sample of Neandertals ($n = 45$) using dental microwear texture analysis (DMTA) as the means to evaluate patterns of variation by habitat, geographic location, and time in anterior tooth-use behaviors.

Background

Neandertal anterior tooth wear: descriptions and explanations

Three specific anterior tooth wear patterns, labial rounding, micro- to macroscopic labial scratches, and differential anterior-posterior wear, have been documented on several Neandertal subadult and adult fossils across environment, space, and time (Sollas, 1908; Martin, 1923; Koby, 1956; de Lumley, 1973; Brace, 1975; Brace et al., 1981; Trinkaus, 1983, 1992; Lalueza Fox and Pérez-Pérez, 1994; Lalueza Fox and Frayer, 1997; Arsuaga et al., 2001; Compton and Stringer, 2012; Hlusko et al, 2013; Estalrich and Rosas, 2013, 2015; Fiore et al., 2015; Willman, 2016, *in press*.). Rounding is described as an abrasion of much of the overall tooth crown, with a pronounced rounding of the incisal edge on maxillary and mandibular incisors and canines. This

pattern is evident on the Shanidar 1, 3, 4, and 5, Forbes' Quarry 1, and La Ferrassie 1 individuals (Sollas, 1908; Brace, 1975; Brace et al., 1981; Trinkaus, 1983). Micro-level striations are those typically recorded in microwear analyses; however, macroscopic scratches are deeper and wider ($\geq 20 \mu\text{m}$) and found to be more common on the central aspect (mesial-distal plane) of the labial surface, especially for incisors (Bermúdez de Castro et al., 1988; Lalueza Fox and Frayer, 1997; Lozano-Ruiz et al., 2004; Lozano et al., 2008; Estalrich et al., 2015; Fiore et al., 2015). They also occur with greater frequency on maxillary incisors than on those in the mandible (Lozano-Ruiz et al., 2004). These striations are found on several subadult and adult Neandertal individuals, including those from Cova Negra, El Sidrón, Hortus, Krapina, La Quina, Moula-Guercy, Palomas, Pontnewydd, Regourdou, Saint-Brais, Shanidar, Spy, Tabūn, and Vindija (Martin, 1923; Koby, 1956; de Lumley, 1973; Trinkaus, 1983; Lalueza Fox and Pérez-Pérez, 1994; Lalueza Fox and Frayer, 1997; Arsuaga et al., 2001; Frayer et al., 2010; Compton and Stringer, 2012; Volpato et al., 2012; Hlusko et al., 2013; Estalrich and Rosas, 2013, 2015; Fiore et al., 2015; Willman, *in press*). Lastly, some Neandertals (e.g., Shanidar 1 and 2, Amud 1, and Tabūn C1) show a greater degree of anterior relative to posterior wear. This alone is not unusual and can be found among hunting and gathering groups (Clement et al., 2012, Willman, 2016). However, when crown size and occlusal wear gradients are considered together, the large incisor and canine crowns of Neandertals allow for more crown volume loss per unit of occlusal wear compared to anatomically modern humans (Trinkaus, 1992; Willman, 2016).

Examples of these wear patterns have been documented throughout the decades, and several explanations have been proposed to explain them. Martin (1923) recorded parallel and superimposed diagonal scratches on the La Quina 5 anterior teeth and attributed them to specialized chewing, similar to that of rodents. Koby (1956) noted similar striations on the Saint-

Brais II Neandertal maxillary anterior teeth. Although he recognized the likeness of the scratches to those of La Quina, he ascribed them to a combination of coarse food and "stuff-and-cut" behaviors.

This interpretation has been supported by experimental work in which stone tools were used on porcelain (Bermúdez de Castro et al., 1988), ovicaprid teeth (Frayer et al., 2010), and surgically extracted human teeth with pristine enamel (Lozano-Ruiz et al., 2004) during simulated "stuff-and-cut" activities. In each study, the authors noted the morphology of the labial striations found on the fossil samples closely matched those produced experimentally (Bermúdez de Castro et al., 1988; Lozano-Ruiz et al., 2004). Further support came from labial surface striation comparisons between the Sima de los Huesos fossils and those of a sample of aboriginal Australians (Lozano et al., 2008). The latter group has been ethnographically documented as using their anterior teeth for holding, pulling, and cutting different types of materials, resulting in vestibular-lingual striations on their anterior teeth. The same wear pattern was found on the fossil sample, suggesting to Lozano et al. (2008) that the Sima de los Huesos individuals engaged in similar teeth-as-tools behaviors.

The extreme labial rounding on Neandertal incisors and differential anterior-posterior wear have also provided fodder for interpretation. For example, these wear patterns, found on Shanidar 1, were suggested by Stewart (1959) to be from the dentition acting as a compensatory mechanism for an amputated arm. The wear patterns of La Ferrassie 1 and 2, among other Neandertals, was proposed by Puech (1978, 1979, 1981) to be from excessive mastication of grit-laden foods. Other researchers generally implicated jaw movements associated with the chewing cycle and a combination of diet and "stuff-and-cut" activities (Wallace, 1975; F. Smith, 1976; P. Smith, 1976; Wolpoff, 1979; Trinkaus, 1992).

Although alternative explanations have been proposed, the “stuff-and-cut” hypothesis has remained conventional wisdom, with Ryan’s (1980) dissertation work providing support. The microscopic gouging pattern found in his sample of European and Southwest Asian Neandertals appeared similar to that of the Ipiutak from Point Hope, Alaska. He attributed the similar pattern to both groups participating in power-grasping behaviors with the anterior dentition. He wrote that Neandertal anterior teeth were “specifically adapted for rigorous chewing and for paramasticatory activities”(Ryan, 1980:172), and suggested that microwear patterns point to the anterior teeth being used as a clamp for clothing manufacture and consuming gritty meat.

Considering the variety of non-dietary anterior tooth-use behaviors documented in recent modern humans (Man, 1883; Cybulski, 1974; Lukacs and Pastor, 1988; Foote, 1992; Mayes, 2001), it seems reasonable to conclude that “stuff-and-cut” behaviors were not the only agent potentially responsible for the distinctive patterns of Neandertal anterior tooth wear. Indeed, variation in anterior tooth-use behaviors is probable, especially considering the different habitats, geographic locations, and time intervals in which Neandertals lived. Differential access to animal and plant resources, as well as exposure to different abrasive agents, could be contributing factors to these distinct Neandertal anterior tooth wear patterns.

Henry et al. (2006) identified some variation in incisor microwear in a sample of early modern humans ($n = 8$) and Neandertals ($n = 12$) using scanning electron microscopy (SEM). While no significant differences were found by hominin or tool technology, the samples did differ by geographic location (Europe vs. Southwest Asia). These geographic differences were attributed to diet, suggesting that the European individuals may have had access to a broader variety of foodstuffs and that the southwest Asian individuals may have been exposed to heavier abrasive loads (Henry et al., 2006). They also noted, however, that their SEM-based approach

had limitations, including repeatability of microwear characterization and high error rates in measurement (Henry et al., 2006). In light of this and other past research, variation in Neandertal anterior tooth-use behaviors needs to be reassessed.

Challenges to previous research models

Previous research offers important insights regarding Neandertal anterior tooth wear, but some challenges remain. Primarily, we cannot assume behavioral uniformity; that is, that all Neandertals across habitats, time, and space were participating in "stuff-and-cut" behaviors. We also cannot ignore the potential contribution of other wear agents responsible for the patterns seen. Lastly, the most commonly used methods for characterizing and assessing anterior tooth wear, optical light and SEM, offer benefits, but have drawbacks too.

Specifically, measurement error and repeatability are the main concerns (Grine et al., 2002; Scott et al. 2008; Ungar et al., 2008; Fraser et al. 2009; Mithlacher et al. 2012; DeSantis et al. 2013). For instance, shadowing effects of light source-specimen geometry can change the apparent microwear signal. Similarly, SEM image quality and analyses can be impacted by electron beam-specimen-collector geometry, working distance, and the type of electrons used to generate an image (Gordon, 1988; Scott et al., 2006). Moreover, SEM user fees can be expensive and quantification of individual features time consuming. On the other hand, the more economical low-magnification light microscopic analysis may fail to detect subtle variation in diet, as well as taphonomically altered surfaces (Ungar et al., 2008.) As a result, dental microwear texture analysis is utilized to mitigate these methodological challenges (Scott et al., 2005, 2006).

Dental microwear texture analysis, an objective approach with much less observer measurement error, uses surface characterizations (Scott et al., 2006). Two approaches have developed, one using ISO standard measures (Schulz et al., 2010) and the other using scale-sensitive fractal geometry (Scott et al., 2006). Two measures from the latter approach have proven especially useful in describing anterior tooth wear patterns: anisotropy (*epLsar*) and textural fill volume (*Tfv*; Krueger and Ungar, 2010, 2012; Krueger, 2014, 2015). Anisotropy, or degree of texture orientation, has been shown in recent human samples to distinguish non-dietary from dietary anterior tooth use (Krueger and Ungar, 2010; Krueger, 2014, 2015). Previous studies have suggested that high anisotropy values reflect dietary uses, while low values indicate non-dietary behaviors. The high values evidently reflect endogenous and/or exogenous abrasives being dragged cervically on the labial surface during incision. On the other hand, low anisotropy suggests that the anterior teeth were used in a variety of ways, such as non-dietary anterior tooth-use behaviors.

Textural fill volume has been shown to reflect anterior loading in bioarchaeological samples (Krueger and Ungar, 2010; Krueger, 2014, 2015). High values are typically found in groups reported to engage in heavy loading of the anterior teeth, whereas low values are more commonly found in those that use light loading (Krueger and Ungar, 2010, 2012; Krueger, 2014, 2015). This attribute measures the depths of features in the 2–10 μm diameter size range (Scott et al., 2006). In comparative studies of recent humans, the combination of textural fill volume and anisotropy have together been effective in identifying distinct patterns of variation that can then be correlated to specific behaviors (Krueger and Ungar, 2010; Krueger, 2014, 2015).

For example, two high-Arctic populations sampled here, the Ipiutak and Nunavut Territory Sadlermiut, relied on caribou for food and hides and used their anterior teeth as a third

hand for preparing those hides for clothing, boots, and trade (Mathiassen, 1927; Larsen and Rainey, 1948; McCartney, 1977; Costa, 1980; Ryan, 1980; Merbs, 1983). Both show low anisotropy and high textural fill volume values, consistent with non-dietary anterior tooth-use behaviors with a heavy anterior loading regime (Krueger, 2014, 2015). Taken together, these values provide evidence for intense clamping and grasping behaviors associated with hide preparation. On the other hand, there is no evidence (e.g., ethnographic, archaeological, oral histories, skeletal and/or dental, etc.) to support non-dietary anterior tooth-use behaviors in the Arikara from the plains of South Dakota. This sample shows high anisotropy and low textural fill volume values, which indicate only dietary use of the anterior teeth (Krueger, 2015). These observed associations between texture pattern and tooth use in baseline groups will be used here to interpret the Neandertal microwear.

Materials and methods

Fossil sample

A total of 45 permanent Neandertal anterior teeth were used in this study. The sample ranges in time from MIS 7 to MIS 3 (240 to $\approx$ 30 kyr), and includes individuals from 24 sites in eight countries across Western Eurasia. The countries included, along with the number of sites in parentheses, are Croatia (2), Czech Republic (2), France (13), Great Britain (1), Hungary (1), Spain (1), Iraq (1), and Israel (3; Table 1).

Three different factors are used here to group the Neandertal sample: habitat, site location, and time interval. The challenge in grouping such a diverse sample is that each fossil site has a unique excavation history, with inconsistent information on stratigraphic context and associated faunal and lithic assemblages. Further, approaches to environmental and climate

reconstruction vary, and dating techniques differ. Every attempt has been made to standardize information and place each fossil in the most appropriate categories given the data available (see Supplementary Online Material [SOM]). To that end, our classifications are, by necessity, broad; however, this represents the best available approach to categorizing the samples given limitations inherent in comparability of the metadata for each site.

The habitat categories used here are open, mixed, and closed, and are based on vegetation cover. The "open" category is associated with sites that are reconstructed to be from colder, more steppe environments, where arboreal tree cover is sparse (less than 15%, if pollen analyses are available) and a variety of cold-preferred fauna are found (e.g., *Rangifer*, *Coelodonta*, *Mammuthus*). The "mixed" category encompasses a wide variety of habitats, from the temperate, woodland hills and cold, dry mountainous areas of Shanidar to the mostly open with some woodland environments at Pontnewydd. This grouping is associated with those sites that have approximately 20–50% arboreal pollen and/or have dominant fauna indicative of a variety of habitats (e.g., from both steppe and woodland environments, which may include *Rangifer*, *Equus*, *Sus scrofa*, *Cervus elaphus*, etc.). The "closed" category is associated with warmer woodland climates that include deciduous forest or Mediterranean woodland sites like Krapina and Zafarraya, respectively, where arboreal pollen is greater than 50% and/or woodland fauna dominate (e.g., *Cervus elaphus*, *Dicerorhinus kirchbergensis*, etc.). These habitat categories are similar to those used in Neandertal molar microwear texture studies (El Zaatari et al., 2011, 2016). Furthermore, our use of faunal habitat categories closely approximates those used in paleoenvironmental reconstructions from faunal remains for Pleistocene sites in Western Europe (e.g., Griggo, 1996; Delpech, 2003).

The location categories used here are Western Europe, Central Europe, and Southwest Asia. Although altitude is not taken into consideration, as all are <1,100 m above sea level, altitude for each site can be found in the SOM. Finally, the time intervals are “early” and “late.” The early category represents those Neandertals dated from MIS 7–5, while those in the late category are from MIS 4–3. Neither morphology nor interactions with modern humans were considered when creating these time categories. Instead, it was based simply on the time ranges for each fossil site. Some sites have very specific MIS designations (or even sub-stage designations) due to advanced or multiple dating techniques, while others span two MIS categories. As a result, these groupings represent the most cautious designation for each fossil and will help to mitigate inherent problems with using MIS categories in such a large-scale study.

Other factors that may affect within- and between-site differences in Neandertal DMTA relate to the age and sex categorization of fossils. However, the fossils analyzed here consist of individuals represented by single anterior teeth, partial to full dentitions, and associated skeletons. The assignment of sex to individual Pleistocene fossils, and especially dental fossils, is difficult without the use of ancient DNA (see Estalrrich and Rosas, 2015) or the presence of associated pelvic remains (see Trinkaus, 2016). Likewise, age is difficult to estimate in the present sample since dental macrowear cannot be used as an aging method on isolated anterior dental remains without associated dentitions or skeletal material. Regardless, studies of labial scratches suggest that Neandertals used their anterior teeth as tools throughout their lifespans, since both deciduous and permanent anterior teeth are known to present them (Lalueza Fox and Frayer, 1997; Compton and Stringer, 2012; Hlusko et al., 2013; Estalrrich and Rosas, 2015;

Fiore et al., 2015). Thus, sex- and age-related variation in DMTA is not assessed in the present study.

We acknowledge that some researchers may not agree with our categorization schemes, the assignment of certain fossils to specific categories, and/or the exclusion of age/sex sub-groupings. Future research will inevitably expand the spatiotemporal and eco-geographic distribution of the Neandertal DMTA sample used here. To that end, we have provided the *epLsar* and *Tfv* data for each specimen used in this analysis (see SOM), and others are welcome to categorize and assess the data using any category scheme they deem appropriate.

Bioarchaeological comparative sample

The recent human comparative baseline series is comprised of 222 individuals representing 10 different populations (Tables 2 and 3). These include the Aleut ($n = 24$), Andamanese ($n = 15$), Arikara ($n = 18$), Chumash ($n = 19$), Illinois Bluff ($n = 20$), Nunavut Territory Sadlermiut ($n = 27$), Ipiutak ($n = 22$), Tigara ($n = 34$), Coast Tsimshian ($n = 25$), and Puye Pueblo ($n = 18$; data from Krueger and Ungar, 2010 and Krueger, 2014, 2015). Individuals ranged in date from 5000 BP to the early 20th century, lived in a spectrum of environment types, subsisted on different diets, participated in a variety of non-dietary anterior tooth-use behaviors, and were exposed to multifarious abrasives. Datasets independent of the microwear textures were used to assign each group into these categories (see SOM). These datasets include ethnographic information for historic groups (usually in the form of early European explorer observations and notes), dental analyses (presence of anterior and posterior wear patterns, chipping, and/or gouging), archaeological remains (tools used for scraping, hunting, skinning, processing hides, etc.), stable isotope analyses, and indigenous oral histories.

Dental microwear texture analysis

High-resolution replicas were used for analysis of both the fossil and recent human comparative samples. All molds and casts were prepared following standard microwear analysis protocols. The labial surface of each specimen was gently cleaned with acetone using cotton swabs. President Jet regular body polysiloxane (Coltène-Whaledent) and Epotek 301 epoxy base and hardener (Epoxy Technologies) were used as the mediums for mold and cast production, respectively. Each tooth was examined for antemortem microwear on the labial surface, adjacent to the incisal edge, using a Sensofar Plu white-light confocal profiler (Solarius Development Inc., Sunnyvale, California).

It is important to note that large-scale, stone-tool induced labial striations described earlier were not targeted for sampling here. This was done to reduce sampling bias, as they tend to cluster in a more central position on the labial face, which is a different area from that sampled for the modern human comparative groups (Bermúdez de Castro et al., 1988; Lalueza Fox and Frayer, 1997; Lozano-Ruiz et al., 2004). Further, while it has been demonstrated experimentally that large-scale striations can be caused by “stuff-and-cut” behaviors (Bermúdez de Castro et al., 1988; Lozano-Ruiz et al., 2004), such behaviors are also the most cited explanation for anterior tooth rounding and differential anterior-posterior wear, and should be especially evident at the incisal edge, where microwear textures were sampled.

Four adjacent scans of the enamel surface were taken using a 100x objective lens, yielding a lateral point spacing of 0.18 μm and individual fields of view of 138x102 μm , following Scott et al. (2006). The total area sampled, 276x204 μm , is comparable to typical SEM analyses at 500x. The four scans representing each tooth were then leveled and examined for

postmortem damage (e.g., excavation tool marks) and/or adherent particles (e.g., preservative, glue, soil, or dust) using Solarmap Universal software (Solarius Development Inc., Sunnyvale, California). Any data points recording postmortem damage or adherent particles were removed prior to analysis using Solarmap. These deleted areas were ignored by the scale-sensitive fractal analysis software. Any one scan (out of four taken for each tooth) where more than 10% of the antemortem surface was obscured was cause to remove the individual from analysis. The scans were then uploaded into Toothfrax and SFrax scale-sensitive fractal analysis software packages (Surfract, www.surfract.com) for surface characterization. Two texture variables, *epLsar* and *Tfv*, are used here; their mathematical underpinnings are described in detail in Scott et al. (2006).

The recent human dataset consisted of maxillary central incisors only. The fossil dataset included these, as well as maxillary lateral incisors, mandibular central and lateral incisors, and maxillary and mandibular canines. The reason for the expanded range of tooth types for the fossil sample is to provide the largest possible sample of Neandertals; however, it was not known prior to analysis whether combining all anterior tooth types was appropriate given that possible variation in signal by tooth or jaw may exist. Consequently, statistical analyses (described below) were performed to elucidate whether tooth type and/or jaw affect anterior dental microwear texture signatures, at least in the fossil sample.

Statistical analyses

General Linear Models (GLM) were used for statistical analyses. All data were rank-transformed prior to analysis to mitigate violation of parametric statistics assumptions (see Conover and Iman, 1981). The first GLM compared the Neandertal microwear signatures to confirm that they do not differ significantly by tooth type (again, to maximize the fossil sample).

A two-factor multivariate analysis of variance (MANOVA) was performed with tooth type (central incisor, lateral incisor, and canine) and jaw (mandible and maxilla) as the factors and each texture attribute as dependent variables.

The second and third GLMs were a two-factor MANOVA (location and time) and a separate one-factor MANOVA (habitat) for the Neandertal sample. Insufficient data for habitat prohibited a single three-factor MANOVA. Analysis of variances (ANOVAs) for individual texture attributes and pairwise comparisons tests for the groups were used to determine the sources of significant variation as necessary. Both Tukey's post hoc HSD and Fisher's a priori LSD tests were used to balance risks of Type I and Type II errors (Cook and Farewell, 1996).

The Benjamini-Hochberg procedure, which similar to a Bonferroni correction, was performed on all MANOVA and ANOVA p -value results to control for the number of false positives associated with multiplicity (Benjamini and Hochberg, 1995). While this multiple comparisons problem is usually controlled using the familywise error rate (FWER), as in the Bonferroni correction, it is controlled in this method using the false discovery rate (FDR; Benjamini and Hochberg, 1995; McDonald, 2014). The Benjamini-Hochberg procedure works by comparing individual p -values (ranked from smallest to largest) with the Benjamini-Hochberg critical value. This critical value is calculated using the equation $(i/m)Q$, where i is the rank assigned to each p -value, m is the total number of tests, and Q is the chosen false discovery rate (McDonald, 2014). The FDR used here was 0.25.

Results

Anterior microwear signatures by tooth type and jaw

Results show neither significant interaction between anterior tooth type and jaw, nor significant variation in microwear textures for these two factors (Table 4A). This indicates that, regardless of the specific anterior tooth type, position in the jaw, or jaw itself, the microwear texture signal does not vary significantly between the various incisors and canines, at least not when examining the labial surface nearest the incisal edge. These results support the inclusion of different anterior tooth types in dental microwear texture analysis. Indeed, Brace (1967:812–813) commented that "canines have functioned as incisors throughout the known course of hominid evolution" and many discussions of Neandertal anterior wear patterns include canines and incisors (Stewart, 1959; Brace, 1967; Howells, 1975; Wallace, 1975; F. Smith, 1976; Wolpoff, 1979; Brace et al., 1981; Puech, 1981; Lalueza Fox and Frayer, 1997; Frayer et al., 2010; Estalrich and Rosas, 2013, 2015; Fiore et al., 2015).

Anterior microwear signatures by habitat, site location, and time interval

Results are presented in Tables 4-7 and illustrated in Figures 1–3. The MANOVA results indicate significant differences by habitat only (Table 4B). The three habitat categories, open, mixed, and closed, differ significantly in both *epLsar* and *Tfv* (Tables 5A, 6A, and 7, Figs. 2 and 3). The significant variation in anisotropy is attributed to the extremely low *epLsar* values of the open-habitat Neandertals and the higher values of the closed-habitat individuals. On the other hand, the significant variation in *Tfv* is due to the extremely high values of the open-habitat Neandertals and the lower values of the closed-habitat individuals.

Discussion

Comparison with modern human groups

Results show significant variation in Neandertal anterior dental microwear textures by habitat, offering clues regarding subsistence strategies and behavioral regimes. The open-habitat Neandertals are identified as having significantly lower *epLsar* and higher *Tfv* values than their closed-habitat counterparts (Tables 6A and 7, Figs. 2 and 3). The extremely low *epLsar* and high *Tfv* values suggest that these Neandertals were participating in non-dietary anterior tooth-use behaviors that required a heavy anterior dental loading regime. Both mean values are similar to those of the Ipiutak and Nunavut Territory Sadlermiut (Table 3, Fig. 3). This indicates that the open-habitat Neandertals may have used their anterior dentition in much the same way as these recent humans, which involved intense clamping and grasping behavior for the preparation and utilization of hides (Mathiassen, 1927; Larsen and Rainey, 1948; McCartney, 1977; Costa, 1980; Ryan, 1980; Merbs, 1983). Indeed, open (and indirectly, colder) environmental conditions would have required some form of protective covering, and these individuals most likely participated in a focused regimen of preparing hides for sustained or prolonged protection from the environment.

Inferences of Neandertal critical and minimum sustainable temperatures suggest protective coverings were a necessity. Even insulation resulting from increased muscle mass and dietary-related elevated basal metabolic rate (BMR) would not have been sufficient to survive the cool, open conditions (Aiello and Wheeler, 2003). Archaeological evidence for these behaviors is found at several sites, including Corbiac, Pech de l'Azé, La Quina, and Combe Grenal, where lithic microwear analyses indicated hide preparation (Anderson-Gerfaud, 1990; Hardy, 2004). Specialized bone tools, attributed to Neandertals at Pech-del-l'Azé and Abri Peyrony, are similar in use-wear to lissoirs, tools used to smooth and prepare hides (Soressi et al., 2013). Sites from southeastern France, northwestern Italy, and Wales evince skinning cut

marks on cave bear (*Ursus* sp.), lynx (*Lynx spelaea*), and cave lion (*Panthera leo spelaea*) bones indicative of the acquisition of fur resources (Valensi and Psathi, 2004; Aldhouse-Green et al., 2012). Lastly, several cold, open, steppe sites show a pattern indicative of reindeer intercept hunting (Mellars, 1996; Gaudzinski, 2000; Gaudzinski and Roebroeks, 2000; Costamagno et al., 2006). For example, the northern German site of Salzgitter-Lebenstedt contained the remains of 86 reindeer, with the majority taken during autumn (Gaudzinski, 2000; Gaudzinski and Roebroeks, 2000). This assemblage could represent the preferential hunting of reindeer, much like high-Arctic modern humans preferentially take caribou, for not only meat and marrow purposes, but also for hides to prepare for the approaching winter.

In contrast, the closed-habitat Neandertals show significantly higher anisotropy and lower textural fill volume values than those in more open environments (Tables 6A and 7, Figs. 2 and 3). The higher *epLsar* and moderate *Tfv* values suggest that these individuals were participating in predominantly dietary anterior tooth-use behaviors that required moderate anterior loading. Their *epLsar* mean value is the same as that of the Arikara (Table 3, Fig. 3). There is no evidence of the Arikara using their teeth as tools, but, instead, they most likely used them only for incising food items (Leigh, 1925; Denig, 1961; Lehmer, 1971; Meyer, 1977).

The *Tfv* values of the closed-habitat Neandertals are most similar to those of the Tigara and Aleut, suggesting a similar (albeit a slightly heavier) anterior dental loading regime. Both the Tigara and Aleut are documented to have participated in some clamping and grasping and wood softening anterior-tooth-use behaviors, which may account for the similar *Tfv* signal for the closed-habitat Neandertals (Simpson, 1875; Moorrees, 1957; Campbell, 1967; Merbs, 1968; Foote, 1992). However, a more parsimonious interpretation, when taking into account the higher *epLsar* values of this sample, is that the closed-habitat Neandertals were using their anterior teeth

predominantly for processing tough foods with endogenous and/or adherent exogenous dietary abrasives that required moderate loading, and, in some measure, also used their teeth as tools.

While these closed-habitat individuals may also have utilized a spectrum of non-dietary anterior tooth-use behaviors, it is clear that these Neandertals did not carry out intense clamping and grasping behaviors to the same degree or frequency as their open-habitat counterparts. Instead of focusing on preparing protective coverings, perhaps the closed-habitat Neandertals spent more time exploiting a wider variety of both animal and plant resources. Evidence for a broad resource base with both plant and marine exploitation is found at sites in the Levant (Madella et al., 2002), France (Anderson-Gerfaud, 1990; Hardy, 2004), Italy (Stiner, 1994), Portugal (Antunes, 2000a, b; Antunes et al., 2000), Spain (Vaquero et al. 2001), Gibraltar (Stringer et al., 2008), and numerous other sites across the Neandertal habitation range (Bar-Yosef, 2004; Patou-Mathis, 2004; Hardy et al., 2010; Henry et al., 2011, 2014).

It is important to note that variation between individuals exists within each habitat category. That is, while the majority of open-habitat Neandertals has very low *epLsar* and very high *Tfv* values, there are a few that do not. For example, Combe Grenal 5 has an *epLsar* value clearly in the range of comparative samples that tend to use their front teeth only for food ingestion. This same variation exists for those in the closed-habitat group. For instance, two of the individuals from Moula-Guercy (259 and 588) show *epLsar* and *Tfv* values indicative of intense clamping and grasping behaviors. It is clear that while the majority of individuals assigned to each habitat category are engaging in similar behaviors, there exists some variability in anterior tooth-use behaviors, especially within the closed-habitat Neandertal group.

Within-site variation also exists in this sample. For example, the 10 individuals from Krapina, four from Vindija, and three from Moula-Guercy show a range of *epLsar* and *Tfv*

values, indicating a variety of anterior tooth-use behaviors. It is plausible that the sexual division of labor could account for at least some of the within-site variation detected here. Indeed, this has been put forth as an explanation for wear pattern differences related to non-dietary anterior tooth use among Neandertals from Hortus, Spy, and El Sidrón (Estalrich and Rosas, 2015).

Comparison with Neandertal molar microwear textures

A more comprehensive picture of Neandertal dietary and behavioral strategies can be realized when the anterior microwear texture results are compared to those for the molars. El Zaatari et al. (2011, 2016) found significant differences between their paleoecological groups, which were also based on vegetation cover. The wooded-environment Neandertals showed greater complexity ($Asfc$) than those in mixed and open environments. Moreover, Neandertals from open environments had lower heterogeneity ($HAsfc$) than those from the other two vegetation categories. These results suggest that the wooded Neandertals had a more varied diet, most likely from an increase in plant foods, and that dietary flexibility increased with arboreal tree cover. On the other hand, the data from the open-habitat Neandertals indicated a more homogenous, meat-based diet.

A clearer picture forms of Neandertal subsistence and behavioral regimes when the anterior and molar microwear texture results are taken together. Habitat consistently stands out in distinguishing Neandertal diet and behavior, indicating that environment played an important role in determining adaptive strategies. As the vegetation cover changed, Neandertals modified their food exploitation tactics and anterior tooth-use behaviors to accommodate the changing resource availability, food supply, and, presumably, climate. In sum, different environmental

conditions required different behavioral strategies, and it appears from the microwear texture data that Neandertals were able to adapt.

Conclusion

Anterior dental microwear texture data offer evidence for variation in dietary and behavioral strategies of Neandertals. These hominins were not uniform in their behaviors, and were able to employ a spectrum of subsistence practices under different environmental conditions. These data suggest that open-habitat Neandertals focused on non-dietary anterior tooth use in the form of clamping and grasping activities, probably related to hide preparation. This included "stuff-and-cut" behaviors. However, the closed-habitat individuals varied more in their anterior tooth-use activities, but engaged in predominantly dietary behaviors. This included incising a variety of tough foods with abrasives, and perhaps some non-dietary behaviors. These actions may have led to the distinct anterior wear patterns recorded on many specimens. However, it is evident from the microwear texture data that not all Neandertals were participating in "stuff-and-cut" and/or other heavy non-dietary anterior tooth-use behaviors, especially those in more closed, forested habitats.

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Figure legends

Figure 1. Two- and three-dimensional point clouds of Neandertal anterior dental microwear surfaces. Each two- and three-dimensional image measures 204x276 μm and 102x138 μm , respectively. **A)** Biache-Saint-Vaast 1, **B)** Krapina 73, **C)** La Ferrassie 1, **D)** La Ferrassie 2, **E)** Combe Grenal 5, **F)** Kebara 2, **G)** Tabūn B, Series III, **H)** Shanidar 3, **I)** Vindija 290/12.4, **J)** Zafarraya Z23.

Figure 2. Box plots showing the distribution and central tendencies of anisotropy and textural fill volume by habitat.

Figure 3. Scatter plot of mean anisotropy (*epLsar*) vs. textural fill volume (*Tfv*) values with recent human groups (denoted with circles) and habitat (squares), location (diamonds), and time (stars) for Neandertal groups. AL = Aleut, AND = Andamanese, AR = Arikara, CH = Chumash, IL = Illinois Bluff, IP = Ipiutak, NT = Nunavut Territory, PRH = Prince Rupert Harbour, PU = Puye Pueblo, TIG = Tigara, OPEN = open-habitat Neandertals, MIX = mixed-habitat Neandertals, CLOSED = closed-habitat Neandertals, WEST = Western European Neandertals, CENT = Central European Neandertals, SWA = Southwest Asian Neandertals, EARLY = early Neandertals, LATE = Late Neandertals.

Figure 1a

5.1
 μm

3.7
 μm

4.9
 μm

5.6
 μm

5.9
 μm

Figure 1b

1.5
 μm

3.6
 μm

2.7
 μm

1.6
 μm

3.2
 μm

Figure 2

Figure 3