Computer simulations show that Neanderthal facial morphology represents adaptation to cold and high energy demands, but not heavy biting.

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1. Introduction

Neanderthals (Homo neanderthalensis) are an ‘archaic’ human species which persisted through multiple glacial–interglacial cycles in mid-late Pleistocene Eurasia. A number of craniofacial features distinguish Neanderthals from other human species, including a thickened nasal septum, a robust mandible, and a deep facial profile. These characteristics have been interpreted as adaptations to cold and high energy demands, but the underlying mechanisms remain poorly understood. In this study, we use computer simulations to test three adaptive hypotheses that have been proposed to explain the distinctive Neanderthal face: (i) an improved ability to accommodate high anterior bite forces, (ii) more effective conditioning of cold and/or dry air, and (iii) adaptation to facilitate greater ventilatory demands. We test these hypotheses using three-dimensional models of Neanderthals, modern humans, and a close outgroup (Homo heidelbergensis), applying finite-element analysis (FEA) and computational fluid dynamics (CFD). This is the most comprehensive application of either approach applied to date and the first to include both. FEA reveals few differences between H. heidelbergensis, modern humans, and Neanderthals in their capacities to sustain high anterior tooth loadings. CFD shows that the nasal cavities of Neanderthals and especially modern humans condition air more efficiently than does that of H. heidelbergensis, suggesting that both evolved to better withstand cold and/or dry climates than less derived Homo. We further find that Neanderthals could move considerably more air through the nasal pathway than could H. heidelbergensis, suggesting that both evolved to better condition cold, dry air, and, to move greater air volumes in response to higher energetic requirements.
modern humans, including a wide, tall nasal aperture, a
depressed nasal floor, a wide projecting nasal bridge, a
retro-molar gap, ‘swept back’ zygomatic arches, and a
depressed nasal floor [1,2]. Whether, or to what degree,
some of these features may represent adaptations to heavy
para-masticatory activity (teeth as tools), better conditioning
of cold, dry air, increased ventilatory flows in response to
higher energetic demands, genetic drift, or simply retained
pleisiomorphies shared with earlier Homo has been the subject
of longstanding debate [3–5], but the Neanderthal cranium is
certainly distinctive [6].

Of the three adaptive hypotheses offering explanations
for Neanderthal craniofacial evolution, the anterior dental
loading hypothesis (ADLH), suggesting that the Neanderthal
face incorporates adaptations to sustain high loads applied to
the incisors and/or canines, has perhaps received the most
attention. It has been underpinned by evidence of heavy
wear on the anterior teeth in Neanderthals, although compar-
able wear may exist among contemporaneous modern
humans [7]. Early arguments for the ADLH theorized that the
Neanderthal face was better able to oppose rotation
under loading on the anterior teeth around either transverse
been that facial prognathism in Neanderthals represents a
trade-off between demands for high bite force at the anterior
teeth and increasing the functional surface area of the molars
for the mastication of resistant foods, while maintaining com-
pressive forces at the temporomandibular joints during both
anterior and postcanine loading [9]. Other studies have
rejected the ADLH outright [10].

Similarly, the argument that the Neanderthal face incor-
porates adaptation to life in cold climates through an
improved capacity to condition cold, dry air also
remains controversial. The proposition that their large nasal
cavities would have served to warm and humidify cold air
more effectively [5] has been difficult to test quantitatively
[11,12]. The hypothesis that their well-developed paranasal
sinuses [13] are a cold-adaptation has also been questioned.
Some have asserted that Neanderthal paranasal sinuses are
not particularly large [14], others have argued that paranasal
size is largely irrelevant in the conditioning of inspired air
[15]. Recent studies based on modern human samples have
concluded that it is the shape, not the size of the nasal
cavity, that primarily determines the capacity to warm and
humidify inspired air [16]. It has been proposed that airway
size likely relates to the energetics of the organism, whereas
airway shape might be more indicative of physiology and
climate [17].

A third hypothesis that might in part explain Neanderthal
facial morphology is that it represents adaptation to facilitate
greater ventilatory demands driven by high energy expendi-
tures [18,19]. High respiratory demands have been proposed
for Neanderthals and other ‘archaic’ humans, such as H. heidelbergensis, based on evidence for relatively high
body masses and routinely strenuous hunting/oraging behav-
aviours [20]. Regarding Neanderthals, selective pressure
may have been further increased by high cold resistance
costs [21] as well as energetic hunting strategies [22].

Although considerable effort has been expended on
addressing these explanations for Neanderthal facial mor-
phology, no extensive quantification of facial stress or strain
regimes during biting have been performed. Regarding the
modelling of heat transfer and humidification, computational

fluid dynamics (CFD) has previously been applied in ver-
tebrate palaeontology and to some extant hominids [23,24].
Most recently two modern humans have been compared to
a partial model of a Neanderthal nasal passage [25]. Results
showed that the partial Neanderthal was less efficient at con-
ditioning cold, dry air than a modern north-eastern Asian,
but slightly more efficient than a southern European. How-
ever, unlike the present study, this previous study only
incorporated differences in external nasal aperture mor-
phology and the Neanderthal’s internal nasal passage was not
reconstructed. Moreover, no previous CFD analyses have
included modelling of a close outgroup to modern humans
and Neanderthals, or compared respiratory flow rates, mean-
ing that CFD results have yet to be placed in a broader
evolutionary context.

The application of quantitative 2D beam theory to craniofa-
cial biomechanics represents a major advance over qualitative
general comparisons, but 3D computer-based approaches,
such as finite-element analysis (FEA), allow the biomech-
anics of whole structures to be modelled and compared based
on a range of performance metrics [26–28]. In recent years FEA
has been increasingly applied in palaeoanthropology [26,29–
32], boosted by improvements in virtual reconstruction
methodologies (figure 1) and integration with geometric
morphometrics (GMM) [33–35]. Importantly, FEA also
allows the researcher to directly predict mechanical perform-
ance in great detail and consider it in comparative contexts
[26]. Similarly, while CFD is a time-consuming process
which limits sample sizes, it is the only means available that
allows researchers to directly test the effects of geometry on
fluid and heat flow in living and extinct taxa, whereas
morphometric-based approaches are restricted to identifying
correlations between morphology and variables such as diet
or climate [24].

2. Material and methods

(a) Materials

Models are based on computed tomography of the following
specimens: Broken Hill 1, Mauer 1 (Homo heidelbergensis); La
Ferrassie 1, La Chapelle-aux-Saints 1, Gibraltar 1, Le Moustier 1,
Regourdou 1 (H. neanderthalensis); Mladěč 1 (Pleistocene Homo
sapiens); NMB 1271 Khoe-San female, ULAC210 European
male; AMNH 99/7889 Asian female, PM 0003 Asian male,
AMNH 19.33 European female, AMNH 99.1/511 Inuit male,
PM 1702, Inuit female DO.P.004 European male, PM 1532 Paci-
fic male, PM 0084 Peruvian female, UNC002 European male, and
UNC013 African American male (recent Homo sapiens).

These latter two modern human specimens (CFD analyses
only) were chosen because they represented a more polar-
adapted (European) and more tropical (African) adapted nasal
morphologies [16,36].

Broken Hill 1 was selected as our outgroup because it is the
most complete specimen commonly assigned to H. heidelbergensis
[37]. Our selection of Neanderthal material was based on com-
pleteness. Remaining modern human specimens reflected the
widest ethnographic range available.

(b) Virtual reconstructions

Fossil specimens were variably damaged or fragmentary. Where
morphology was missing or damaged on one side of a specimen,
but complete on the other, virtual reconstruction (step 1)
was relatively straightforward [38] (electronic supplementary
material, figure S1), i.e. for Broken Hill 1 and Mladéč 1. In all three Neanderthals at least some bone, including internal portions of the nasal cavities were damaged or missing altogether. For these, a second step, ‘warping’, was applied after step 1 reconstruction, following established protocols [33,39] (figure 1 and electronic supplementary material, figures S2–S4). The source mesh for warping was a recent modern Homo sapiens chosen for its particularly regular and symmetrical internal nasal morphology (ULAC-210).

(c) Finite-element analyses

(i) Model generation

For our FEA, 3D volume meshes were generated and loads applied on the basis of computed tomography, largely using previously described protocols [26,29,40,41]. Segmentation was conducted in Mimics v17 (Materialise) and finite-element models (FEMs) were generated in 3-matic v8 (Materialise) based on a previously described approach [26,41]. FEMs were kept at approximately 2 million tet4 elements and assigned a homogeneous property set [40]. Results can be influenced by differences in the distribution of materials [31,42] and proportions of cortical and cancellous bone may vary across large size ranges [43]. However, size differences are not great between specimens included in the present study and the assignment of multiple properties would have introduced further assumptions.

(ii) Muscle forces and constraints

Application of jaw adductor muscle forces followed published protocols [29,40]. Forces were based on muscle physiological cross-sectional area (PCSA) [44], corrected for pennation and gape [45], such that 1 cm$^2 = 30$ N [46]. Muscle forces were scaled on the basis of cranial volume to the two-thirds power [40,47] and applied using Boneload [48]. Traction were applied to plate elements modelled as a 3D membrane (thickness = 0.0001 mm; $E = 20.6$ GPa). We subjected all models to: a bilateral anterior tooth bite applied to the left and right incisors and canines, a unilateral anterior tooth bite at the left I1, and a unilateral molar bite at the left M2. Models were oriented and constrained following previous methods [40].

(iii) Automated collection of finite-element analysis results

Comparison of the VM micro-strain at 203 landmarks for each of the models in this study results in an expected 3045 individual landmark cases. To automate the process, a function was developed to rapidly extract micro-strain results.

(d) Computational fluid dynamics

We used La Chapelle-aux-Saints 1 because it had the most complete nasal passage among Neanderthals. Assumptions remain of course and accuracy will ultimately be tested by the

Figure 1. La Chapelle-aux-Saints 1 Neanderthal mesh-mesh metric comparison of initial fossil material (a) with final reconstruction, (b) (performed in Cloud Compare). The models are superimposed (c) and the original-reconstructed mesh-mesh metrics are computed. (d) Regions where the final reconstruction lies further out (from the model centroid) than the original fossil material are shown in blue. Regions where the final reconstruction lies further in (from the model centroid) than the original fossil material are shown in red. Regions of the original fossil material that lie further than $\pm 1.875$ mm (3 voxel edge lengths) from the final reconstruction have been clipped from the image. Regions that overlap almost exactly are shown in off-white.
Figure 2. Results of finite-element analysis under an anterior bite simulation (loading via muscle force scaled to volume^{2/3}, restraints applied to incisors and canines) for 10 recent \((a–j)\) and one Pleistocene \((k)\) modern human, as well as \(H. \) heidelbergensis \((l)\), and three \(H. \) neanderthalensis \((m–o)\). Number of elements for each models also given for: \(a\) Khoe-San female, 1 571 213; \(b\) Caucasian male, 1 602 686; \(c\) European female, 1 651 738; \(d\) Chinese male, 1 593 342; \(e\) Malay female, 1 608 934; \(f\) Inuit male, 1 625 463; \(g\) Inuit female, 1 700 708; \(h\) Pacific Islander male, 1 701 642; \(i\) Peruvian female, 1 619 268; \(j\) European male, 1 651 945; \(k\) Mladěč 1, 1 724 664; \(l\) Broken Hill 1, 1 611 994; \(m\) La Ferrassie 1, 1 618 373; \(n\) La Chapelle-aux-Saints 1, 1 625 022; and \(o\) Gibraltar 1, 1 609 723.

3. Results and discussion

(a) Finite-element analysis

We solved three load cases, comparing von Mises (VM) micro-strain generated in a: (i) bilateral anterior bite restrained at all upper incisors and canines [4], (ii) a unilateral anterior bite restrained at the left upper first incisor [9] and, (iii) a unilateral bite restrained at the left upper second molar for each of our 15 finite-element models (FEMs) (figure 2; electronic supplementary material, figures S3 and S4). Muscle forces (electronic supplementary material, table S1) were scaled to cranial volume following a 2/3 power rule [29,40]. VM micro-strain was analysed from 203 homologous craniofacial landmarks grouped into 24 curves and 16 surfaces (electronic supplementary material, figures S3 and S4). Bite reaction forces, mechanical advantage, and reaction forces at the temporomandibular joints were also computed (electronic supplementary material, table S1).

From FEA of both bilateral and unilateral anterior biting, Broken Hill 1 (\(H. \) heidelbergensis) exhibited the least mean micro-strain for all facial landmark groups (electronic supplementary material, figures S3 and S7). Statistical comparisons between the mean recent modern \(H. \) sapiens and mean \(H. \) neanderthalensis (electronic supplementary material, figure S3) showed significant differences. Where differences were found, the mean Neanderthal was 37°C and assigned 100% relative humidity. CFD results are given in figure 3 and see electronic supplementary material.

discovery of complete Neanderthal crania. However, our reconstruction and CFD clearly shows that the internal morphology of the Neanderthal nasal passage is very different to that of any of the modern humans modelled (including ULCA210, the warp source), or Broken Hill 1 (figure 3).

Estimated energy savings were calculated for a single breath in each species. We also calculated maximal airflow through the nasal passages prior to the onset of extensive turbulence through the nasal passage (and see electronic supplementary material). We simulated nasal passages prior to the onset of extensive turbulence through the nasal passage [51,52] (electronic supplementary material, table S4). A second, mass-dependent flow rate was also tested (electronic supplementary material, table S5). We simulated 0°C air at 20% relative humidity. Nasal mucosa of the CNP was 37°C and assigned 100% relative humidity. CFD results are given in figure 3 and see electronic supplementary material.
typically showed lower micro-strain than the mean recent modern human, however, in most instances one or more recent modern humans fell within the Neanderthal range (electronic supplementary material, figure S7). The late Pleistocene modern human, Mladec 1, fell within or below the Neanderthal range in almost all instances (electronic supplementary material, figures S3 and S7).

In unilateral anterior biting, mechanical advantage was consistently higher in modern humans (mean = 0.37) than in any of the Neanderthals (mean = 0.32), which in turn recorded slightly higher mechanical advantage than *H. heidelbergensis* (0.29). This is reflected in the bite reaction forces (BRF) at the anterior teeth in loadings where muscle forces were scaled to the volume$^{2/3}$ of bone in the cranium. In *Homo heidelbergensis* (Broken Hill 1), which exhibited the highest cranial volume and muscle forces, BRF was 428 Newtons (N), above either the mean (371 N) or any individual result for the three Neanderthals. However, the distinction
was less clear compared to the modern human sample, which, despite much lower muscle forces (70% that of Broken Hill 1) recorded a mean of 399 N.

Our predictions of mechanical performance during a unilateral bite at M2 revealed even fewer significant differences in micro-strain between the mean recent modern human and mean Neanderthal (electronic supplementary material, figure S4). Mechanical advantage in molar biting is slightly lower for Broken Hill 1 (0.48) than for the mean Neanderthal (0.50), although within the Neanderthal range (electronic supplementary material, table S1). For all modern humans mechanical advantage (mean = 0.67) is well above that of either Broken Hill 1 or any of the Neanderthals (electronic supplementary material table S1). Again this is reflected in the M2 BRF data. BRF at M2 for Broken Hill 1 (719 N) was above either the mean or any individual BRF at M2 for the three Neanderthals (mean = 581 N). While, despite much lower muscle forces, mean BRF at M2 for modern humans (719 N) was identical to that computed for Broken Hill 1 and four of the modern humans generated higher BRFs at M2 than did Broken Hill 1 (electronic supplementary material, table S1).

Considered together with the VM micro-strain results, we find no clear support for the argument that the facial morphology of Neanderthals is an adaptation linked to heavy anterior biting. Although we found that Neanderthals have higher average mechanical advantage in biting at the anterior teeth than Broken Hill 1, differences were minor and micro-strain was relatively high in the Neanderthals, despite higher bite reaction forces in H. heidelbergensis. In unilateral biting at M2 H. heidelbergensis fell within the Neanderthal range for mechanical advantage, but again generated higher bite reaction forces while exhibiting less micro-strain.

Reaction forces at the temporomandibular joint (TMJ) were uniformly in tension in unilateral M2 biting for the modern humans, suggesting that they cannot exert maximal muscle forces concurrently on working and balancing sides in biting at M2 without generating distinctive forces on the working side [53,54]. The functional significance of this remains uncertain because a relatively modest reduction in muscle force on the balancing side brings the working side back into compression, with only a slight reduction to BRF [54]. Working-to-balancing-side asymmetry in muscle recruitment is commonly observed in primates [55].

There is a potential trade-off in unilateral molar biting, in that increased mechanical efficiency allows a more powerful BRF for any given muscle force, and, a reduced need for heavy supporting structures for any given BRF [26], but beyond the point at which the balancing side TMJ goes into tension some reduction in muscle recruitment and hence reduction in BRF is required. The real cost of this increased mechanical efficiency in modern humans might be a loss of available molar occlusal area rather than reduced bite force. The potential benefit is a reduction in the musculature, bone, and energy required.

(b) Computational fluid dynamics

It is important to note that the modern European (ULCA210) used to generate the source CFD mesh in our Neanderthal reconstruction, behaved in all respects most like the other ethnic European (UNC002) and was very distinct from either the Neanderthal or Broken Hill 1 (figure 3).

All three species effectively conditioned inspired air. However, modern humans were the most efficient, recovering 84–96% of energy used. The La Chapelle-aux-Saints 1 nasal passage was 8–10% less effective than those of the modern humans, and Broken Hill 1 was the least efficient (5–15% and 9.5–25% less efficient than La Chapelle-aux-Saints 1 and the modern humans, respectively) (figure 3 and electronic supplementary material, tables S3–S4). Our CFD results are not necessarily inconsistent with recently published data for a Neanderthal and two modern humans [25], but cannot be directly compared because of differences in material and approach. Notably the previous results were based on analyses which only considered the external morphology of the nasal passage. The ensuing model based on 11 landmarks did not address internal nasal passage geometry. Our Neanderthal model nasal passage was based on a ‘warped’ model which included 103 landmarks, 54 of which were internal landmarks. Previous studies have shown that using a higher number of landmarks across warped source models will produce more accurate target models [33,39].

At 18723 mm³, the reconstructed Neanderthal nasal passage was approximately 29% larger than the average volume of the modern humans (14487 mm³), which were in turn considerably greater than that of Broken Hill 1 (11751 mm³). However, total volume of the nasal passage is not the sole predictor of maximal airflow rates, which are also influenced by the interaction of lung tidal volume, breathing frequency, and the calibre of the conducting portion of the respiratory system. In humans, the size of the nostril and nasal valve are the strongest determinants of flow rate limits. Although smaller calibre air spaces are found deeper in the nasal passage (e.g. the olfactory slit/superior meatus), their effect on flow rate can be offset by larger calibre openings located within the same cross-sectional plane, allowing more air to pass by without requiring excessive air speeds to maintain continuity. In contrast, all inspired air must pass through the nostril and choana, making these the prime choke points for airflow within the nasal passage. As the nostril is the smaller of the two openings, it will impose a greater limit on airflow. Based on predicted nostril sizes for La Chapelle-aux-Saints 1 and Broken Hill 1 (see electronic supplementary material), our CFD analyses predicted that the Neanderthal could move almost twice the volume of air through their nasal passages under laminar conditions than modern humans (approx. 50 l min⁻¹ in Neanderthal versus approx. 27 l min⁻¹ in modern humans). Despite its lower total nasal volume, predicted nostril size in Broken Hill 1 (see electronic supplementary material) gave a maximum airflow rate of approximately 42 l min⁻¹, lower than for the Neanderthal, but still substantially higher than in the modern humans.

Our results indicate that nasal passage shape, rather than total nasal cavity size, is the critical factor here (and see electronic supplementary material). Results are in agreement with the proposition that Neanderthals, and to a lesser extent, Broken Hill 1, may have had considerably higher energetic demands than modern humans, a finding consistent with predictions of both Neanderthal and H. heidelbergensis physiology [20,21,56] and lung volume [57]. A further point to consider is that this capacity to move more air through the nasal cavity would have conferred a higher nasal to oral breathing threshold on Neanderthals, allowing them to benefit from the air conditioning and pathogen/pollutant
filtering capacity [58] of the nose over a wider range of flow rates than other hominin species.

4. Conclusion

Our results show that, compared to either the likely more ‘primitive’ condition in H. heidelbergensis, or the independently derived condition in modern humans, Neanderthals are not clearly better adapted to sustain high loads on the anterior teeth and Hypothesis 1 is rejected. However, relative to the likely pleisiomorphic condition, Neanderthal nasal passage morphology may represent an adaptation to cold that improves conditioning of inspired air, albeit a less efficient solution to that found in modern humans. These findings are consistent with Hypothesis 2. Our results further suggest that the Neanderthal capacity to move greater air volumes than either Broken Hill 1, or modern humans, may also represent an adaptation to cold, insofar as it could support a cold climate physiology [56]. An alternative, not mutually exclusive explanation, is that this ability reflects a more stenuous, energetically demanding lifestyle demanding high calorific intakes. It has been calculated that Neanderthals used 3360 to 4480 kcal per day to support winter foraging and cold resistance [21]. Consequently, we conclude that Hypothesis 3 is also supported and that the distinctive facial morphology of Neanderthals has been driven, at least in part, by adaptation to cold, both regarding the conditioning of inspired air and a greater ventilatory capacity demanded by cold resistance.

Ethics. Research conducted for this study was largely performed on skeletal and fossil specimens that are reposited in accredited museums. The protocols for collection and use of scans for UNC013 and UNC002 were reviewed and approved by the Duke University and University of North Carolina Institutional Review Boards. IRB numbers are DUMC IRB 4881-03 and UNC-CH IRB 03-Surg-372.

Data accessibility. All data, code, and results needed to replicate this study are available from Dryad (https://doi.org/10.5061/dryad.39272). Additional results and supplemental methods have been uploaded as part of the electronic supplementary material. CT scan data are reposited with the museums/institutes that hold copyright; requests to use scan data should be made directly to those museums/institutes.


Competing interests. We declare we have no competing interests.

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References

3. Trinkaus E. 2003 Neandertal faces were not long; modern human faces are short. Proc. Nat. Acad. Sci. USA 100, 8142 – 8145. (doi:10.1073/pnas.133023100)