

Neandertals and the Anterior Dental Loading Hypothesis: A Biomechanical Evaluation of Bite Force Production

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Absolutely large anterior occlusal loads have been frequently postulated as the driving mechanism behind the evolution of the Neandertal face. Bite force production capabilities of Neandertals are estimated via mathematical models to test this anterior dental loading hypothesis. Biomechanical analysis in the lateral and frontal projections indicates that even moderate occlusal loading would have been very costly for Neandertals in terms of condylar reaction force. In the Neandertal model, reaction force at the condyles is always greater than bite force. Absolute bite force values determined from muscular force estimates are smaller in Neandertals than in modern humans despite absolutely larger muscle force estimates. These results suggest that the typical Neandertal pattern of relatively great anterior dental attrition is not due to absolutely heavy occlusal loading but to continuous loading over time. Likewise, degenerative joint disease of the Neandertal temporomandibular joint is an expected outcome of moderate dental loading given the geometry of the Neandertal masticatory system. Emphasis on the anterior dental loading hypothesis as the driving force in the origin and evolution of Neandertal facial morphology is therefore unwarranted.

INTRODUCTION

The specific designation of Neandertals and their phylogenetic relationship to *Homo sapiens* continues to evoke heated debate. Recently, several workers have approached the question of Neandertal phylogenetic positioning via biomechanical and functional analyses of the Neandertal face (Smith 1983; Rak 1986; Demes 1987; Trinkaus 1987). The relative continuity or discontinuity of structure, function and ultimately niche envisioned for the two morphs (Neandertal and modern human) provides fuel for the question of phylogenetic continuity or discontinuity. Smith (1983) and Trinkaus (1987) tend to see continuity while Rak (1986) envisions discontinuity.

These studies differ on the specifics of modelling bending moments in the Neandertal face. However, each author agrees that these moments are in part due to heavy occlusal loads at the Neandertal anterior dentition. Both Smith (1983) and Rak (1986) propose anterior tooth loading to be the driving factor in the evolution of Neandertal facial morphology. This hypothesis is referred to as the Anterior Dental Loading Hypothesis. Smith (1983) clearly refers to absolutely large occlusal loads as opposed to continuous use over time. Rak (1986) is not as clear in his definition of heavy anterior dental loading. The assumption of large anterior tooth loading in Neandertals has been based on: 1) heavily worn anterior dentition with respect to the degree of wear on the posterior teeth; and 2) consistent appearance of degenerative joint disease (DJD) of the articular eminence of the temporal bone.

To test the supposition of absolutely high occlusal loading in Neandertals, the probable maximum force production at the anterior teeth in Neandertals was determined via two-dimensional mathematical models. These models allow for the analysis of the external forces active at the temporomandibular joint (TMJ) and occlusal surfaces and are frequently used to analyze modern human masticatory forces (Smith 1978; Pruim *et al.* 1980; Hylander 1985; Osborn and Baragar 1985). The results (possible force production of Neandertals) are then compared with the force production capabilities of extant humans.

MATERIALS AND METHODS

Materials

Casts of cranial and mandibular remains of Amud I from Israel were used to determine cross sectional areas, orientations and moment arms for the Neandertal model (see below). Cranial remains from La Ferrassie, France were used in determining the cross-sectional area of the temporal fossa due to damage in this area of the Amud specimen. These specimens were chosen on the basis of their relatively complete states and their reasonably close approximations to one another in size and form.

Methods

The mandible was modelled as a lever with its fulcrum at the condyle. Because the total mus-

cle force vector (**Fm**) is positioned posterior to the bite point, in static equilibrium both useful bite force (**Fb**) and condylar reaction force (**Fc**) are produced (Figure 1; Hylander 1985). In order to estimate the absolute **Fb** production in Neandertals it is therefore necessary to understand the relationship between **Fb**, **Fm** and **Fc** and to be able to estimate **Fm**.

Muscle Force Determination

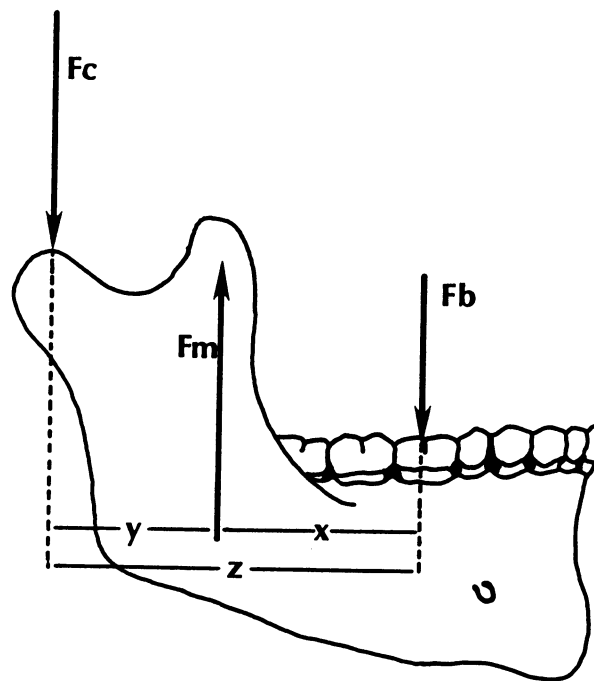
Force is a vector quantity. In order to estimate muscle force it is therefore necessary to define both the direction and the magnitude of the force for each muscle modelled.

The muscles used here (superficial masseter, medial pterygoid and temporalis) to model the external forces at the TMJ are considered power muscles (Osborn and Baragar 1985). Power

muscles produce **Fb**. Control muscles (lateral pterygoid and parts of the temporalis) have poor moment arms for producing useful **Fb**. Instead, they act to stabilize the condyle. Hence, the lateral pterygoid muscle was not used in this model.

Experimental studies indicate that the muscles modelled here are all functionally heterogeneous pinnate muscles (Moller 1966; Herring *et al.* 1979). Depending on its fiber angle, a pinnate muscle may produce a different contractive force than is predicted from its cross-sectional area (Gans and Bock 1965; Josephson 1975; Gans and de Vree 1987). However, due to the complex nature of the pinnation, the inherent difficulties of determining fiber angle from fossil remains, and, most importantly, the lack of determination of fiber angle of the masseter, medial pterygoid and temporalis muscles in modern humans, these muscles have been modelled as simple parallel-fibered muscles. If parallel-

Figure 1. Lateral projection analysis.



Schematic representation of lateral projection of external forces acting on the human mandible during biting. **Fc** equals condylar reaction force. **Fm** equals total muscle resultant force (summed left and right muscle forces of the medial pterygoid, temporalis and masseter). **Fb** equals bite force. **X** equals distance between **Fb** and **Fm**. **Y** equals **Fm** moment arm. **Z** equals **Fb** moment arm. In conditions of static equilibrium these forces are related in the following manner:

$$F_m = \frac{(F_b)(z)}{y} \quad F_c = \frac{(F_m)(x)}{y} \quad \text{or} \quad F_c = \frac{(F_b)(x)}{z}$$

Twisting and bending moments due to the more lateral placement of **Fm** relative to **Fb** are not considered in determination of **Fb**. Therefore, **Fb** is likely to be overestimated. (Redrawn from Hylander 1975).

fibred muscles are assumed, muscular orientations and force vector directions can be inferred from bony morphology (Klaauw 1963; Gans and de Vree 1987).

Muscle Force Vector Direction

Muscle force vector direction was modelled as a single vector for each of the three muscles. This vector was positioned as the central fiber (essentially the centroid; Hiiemae 1971) within the body of the muscle. Vector direction was then determined by joining the areas of origin and insertion by this central line (Figure 2).

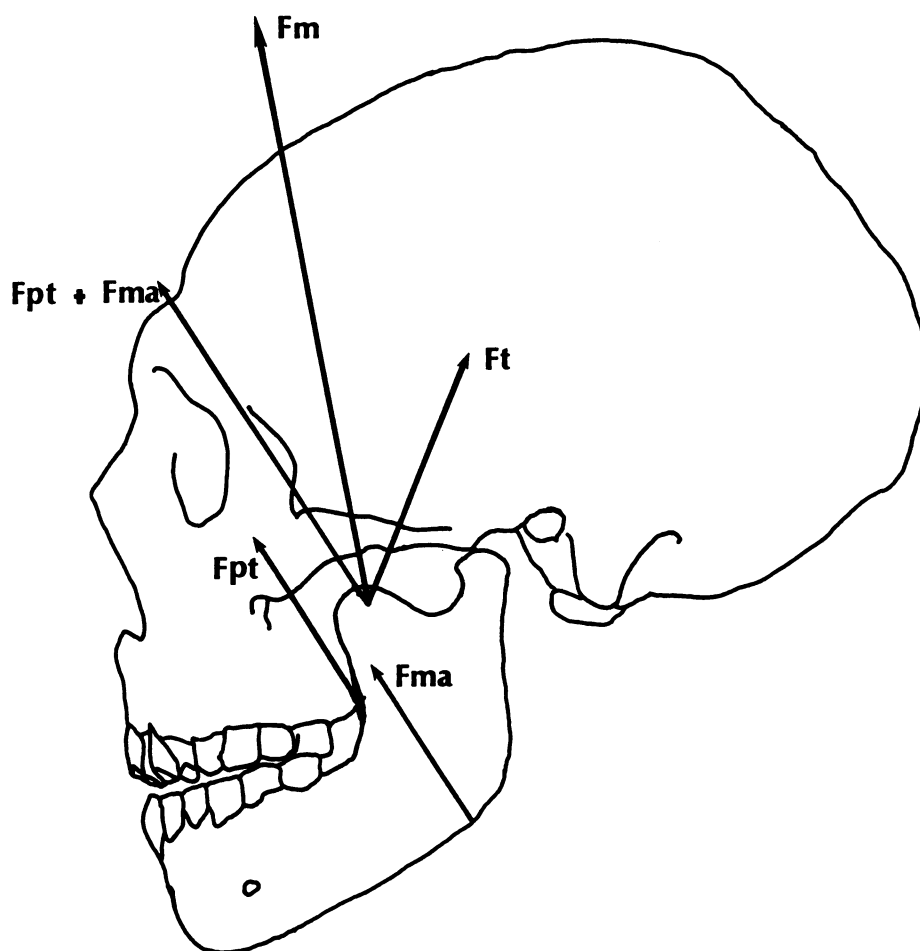
The greater surface area under the temporal line and the further posterior extension of this line indicates a larger posterior temporalis component in Neandertals than in modern humans. The temporal fossa is similarly elongated posteriorly,

providing an increased advantage to some of these posterior fibers over the condition in modern humans. For these reasons the resultant temporalis muscle vector direction has been placed slightly more obliquely than in modern humans (Figure 2). This placement is not critical to the determination of maximum occlusal and condylar reaction force magnitudes. The direction would, however, significantly affect the direction of the condylar reaction force vector (Throckmorton 1985). The resultant vectors of the masseter and medial pterygoid muscles are quite similar to those of modern humans.

Reconstruction of Muscle Force Vector Magnitude

Assuming simple muscle architecture, the maximum force a muscle can exert is equal to the

Figure 2. Estimated Neandertal muscle force vectors.



Vectors represent combined right and left muscle forces for the masseter (F_{ma}), medial pterygoid (F_{pt}), and temporalis (F_t). F_m equals the sum of F_{ma} , F_{pt} and F_t . 1 mm = 20 N and $F_m = 2010$ N. (Neandertal silhouette after Trinkaus 1983).

physiological cross-sectional area of that muscle (i.e., an estimate of the number of muscle fibers firing in unison) multiplied by the stress in the muscle (Weijs 1980; Dul *et al.* 1984). Muscle cross-sectional areas (Table 1) were determined from bony insertions as follows: 1) the area enclosed within the temporal fossa was used as an estimate for temporalis cross-sectional area; 2) the triangular area formed by the mandibular corpus and ramus at the gonial angle and the mylohyoid groove was used as an estimate for medial pterygoid cross-sectional area; 3) the product of the length of the masseteric origin on the zygomatic arch and the distance between the lateral edge of the zygomatic arch and the lateral edge of the mandibular ramus was used to estimate cross-sectional area for the masseter. Cross-sectional areas for these muscles in Neandertals are given in Table 1.

These same measurements were taken on a modern human skull and compared to physiological cross sections for these muscles (Table 2). Correction factors were determined by assuming a linear relationship between physiological cross-sectional area and bony cross-sectional area. The correction factor was greatest for the temporalis. The cross-sectional area of this muscle was overestimated by a value of 6. The medial pterygoid was overestimated by the bony cross section by a factor of 1.5. The masseter value was not corrected. The Neandertal cross-sectional areas were corrected using the same correction factors.

The force and cross-sectional areas reported by Schumacher (1961) for modern humans were used to calculate the stress in each muscle (Tables 1 and 2). Given the close phylogenetic relationship of Neandertals and modern humans, stress

was assumed to be the same in both groups.

Individual muscle force magnitude was calculated using the product of the corrected cross-sectional areas for Neandertal muscles and the modern human muscle stresses. Empirically derived modern human muscle forces are given in Table 3. Position, direction and magnitude of the combined muscle force (**F_m**) was determined by simple vector analysis after projecting all vectors onto the same plane (Figure 2).

Biomechanical Analysis

External forces at the TMJ were analyzed by determining moments about the mandibular condyle, assuming static equilibrium, in lateral projection with the jaw in closed position and with a fixed center of rotation. Simple lateral projection analysis is adequate only when the forces on the two halves of the mandible are equal (Hylander 1975, 1985; Smith 1978). Such conditions are met during bilateral biting. During unilateral biting, the working (biting) side and the balancing side condylar reactions are not equal. In order to completely analyze unilateral biting, an analysis in the frontal projection was also performed (see Hylander 1985). In both analyses, bending and twisting moments produced by the positioning of the **F_m** lateral to the **F_b** were not considered. As such, **F_b** is likely to be overestimated, as all components of **F_m** were considered to produce useful **F_b**.

Lateral projection analyses derive two of the three variables (**F_m**, **F_b** and **F_c**) from the third (known) variable. In the model used here, Neandertal **F_b** is determined from **F_m** (see below and

Table 1. Estimated Neandertal muscle cross-sectional areas and forces (for one side).

Muscle ^b	Uncorrected Cross section (cm ²)	Corrected Cross section (cm ²)	Human Stress ^a (kgm ⁻¹ s ⁻²)	Force (N)
T	3.2	5.5	8.4 x 10 ⁵	4.6 x 10 ²
Ma	3.7	3.7	8.4 x 10 ⁵	3.1 x 10 ²
MPt	5.5	3.8	9.3 x 10 ⁵	3.5 x 10 ²

^a Human muscle stress determined from Schumacher (1961).

^b T = Temporalis, Ma = Masseter, MPt = Medial Pterygoid.

Table 4). For the system to be in static equilibrium, the summation of the moments around any point is equal to zero (Figure 1; Hylander 1975; Smith 1978). That is:

$$(\mathbf{Fb}) (z) = (\mathbf{Fm}) (y)$$

where: \mathbf{Fm} = muscle force

\mathbf{Fb} = bite force

y = muscle moment arm

$(\mathbf{Fb}) (z)$ = bite force moment arm

From these conditions it follows that:

$$\mathbf{Fb} = \frac{(\mathbf{Fm}) (y)}{z}$$

and from analyzing moments about \mathbf{Fm} it follows that:

$$\mathbf{Fc} = \frac{(\mathbf{Fb}) (x)}{y}$$

where: \mathbf{Fc} = condylar reaction force

x = the distance between \mathbf{Fb} and \mathbf{Fm}

\mathbf{Fm} and \mathbf{Fc} represent the sum of left and right muscular and condylar reaction forces, respectively. \mathbf{Fb} is measured perpendicular to the occlusal plane. Forces were calculated for both molar (first molar, M1) and incisal (lateral incisor, I2) biting and the forces were considered point loads (Table 4).

To analyze unilateral biting, a frontal projection analysis followed the lateral projection analy-

sis for both molar and incisal biting. In such an analysis (Table 5):

$$\begin{aligned} \mathbf{Fc} &= \mathbf{Cw} + \mathbf{Cb} \\ \mathbf{Fm} &= \mathbf{Fmw} + \mathbf{Fmb} \end{aligned}$$

where \mathbf{Cw} and \mathbf{Cb} are \mathbf{Fc} on the working and balancing sides, respectively, and \mathbf{Fmw} and \mathbf{Fmb} are \mathbf{Fm} on the working and balancing sides, respectively. The \mathbf{Fm} resultant was positioned as if the working and balancing side musculature were equally active.

The mandible was analyzed as a stationary beam with a point load applied to it (Figure 3). Given conditions of static equilibrium it follows that:

$$\mathbf{Cw} = \frac{(\mathbf{Fm}) (d) - (\mathbf{Fb}) (z)}{w}$$

$$\mathbf{Cb} = \frac{(\mathbf{Fm}) (w-d) - (\mathbf{Fb}) (w-z)}{w}$$

where: w = bicondylar width

d = distance from \mathbf{Fm} to \mathbf{Cw}

z = bite force moment arm

RESULTS

Muscle Force Determination

Neandertal muscle force vector direction is shown in Figure 2. Corrected muscle cross-sectional areas for Neandertals are slightly larger

Table 2. Modern human muscle bony and physiological cross-sectional areas.

	Bony Cross Section (cm^2)	Physiologic Cross Section ^a (cm^2)	Correction Factor
Muscle ^b			
T	2.4×10^1	4.2	6
Ma	3.4	3.4	----
Mpt	2.8	1.9	1.5

^a Physiological cross-sectional areas taken from Schumacher (1961).

^b Muscles abbreviated as in Table 1.

than the values determined by Schumacher (1961) for modern human muscles (Tables 1 and 2). The largest difference in cross-sectional area is in the medial pterygoid, which is twice as large in the Neandertal estimates as in modern humans. Consequently, muscle force magnitude estimates are slightly larger for Neandertal masseter and temporalis muscles and two times as large for the medial pterygoid estimates than those of Schumacher (1961).

Several authors have calculated individual muscle forces in modern humans from F_m and physiological cross-sectional area. In all cases the combined force of the masseter and medial pterygoid was slightly greater than that of the

temporalis (Carlsoo 1952; Schumacher 1961; Pruim *et al.* 1980). This is also the case with the Neandertal results.

Muscle force magnitude estimates calculated here are comparable to those of Pruim *et al.* (1980) and lower than those of Carlsoo (1952). Pruim *et al.* (1980) explained the difference between their force estimates and those of Schumacher (1961) and others as being due to the fact that Pruim *et al.* (1980) did not take into account soft tissue inhibitions to force production. This was also the case with this study. Carlsoo's (1952) larger force determinations were due largely to his use of a higher muscle stress value ($1.1 \times 10^6 \text{ N/m}^2$) than used here.

Table 3. Modern human muscle forces (in Newtons).

	Temporalis	Masseter	Medial Pterygoid
Pruim <i>et al.</i> 1980	5.6×10^2		6.4×10^2
Carlsoo 1952	8.2×10^2	6.1×10^2	3.0×10^2
Schumacher 1961	3.6×10^2	2.9×10^2	1.8×10^2

Table 4. External forces (in Newtons) at the TMJ in molar and incisal biting determined in the lateral projection. (See text for abbreviations).

<u>Molar Biting</u>			
	Fb	Fm	Fc
Modern Human (Pruim <i>et al.</i> 1980)	9.6×10^2	1.6×10^3	7.1×10^2
Neandertal	7.8×10^2	2.0×10^3	1.2×10^3
<u>Incisal Biting</u>			
	Fb	Fm	Fc
Modern Human (Pruim <i>et al.</i> 1980)	7.0×10^2	1.6×10^3	9.9×10^2
Neandertal	5.5×10^2	2.0×10^3	1.5×10^3

Biomechanical Analysis

Lateral Projection Analysis

Bite force production at both molar and incisal bite points is absolutely smaller in Neandertals than in modern humans (Table 4). This is despite the more than 15% increase in muscle force production capability in Neandertals as compared to modern humans. At I2 the values are 550 Newtons (N) for Neandertals and 700 N in modern humans. The **Fb** values at M1 are 780 N in Neandertals and 960 N in modern humans. However, the relative proportion of **Fb** at I2 relative to **Fb** at M1 is nearly identical (approximately 70%; Table 5).

Condylar reaction force is substantially greater at both molar and incisal bite points than bite force in the Neandertal model. At M1 the **Fc**

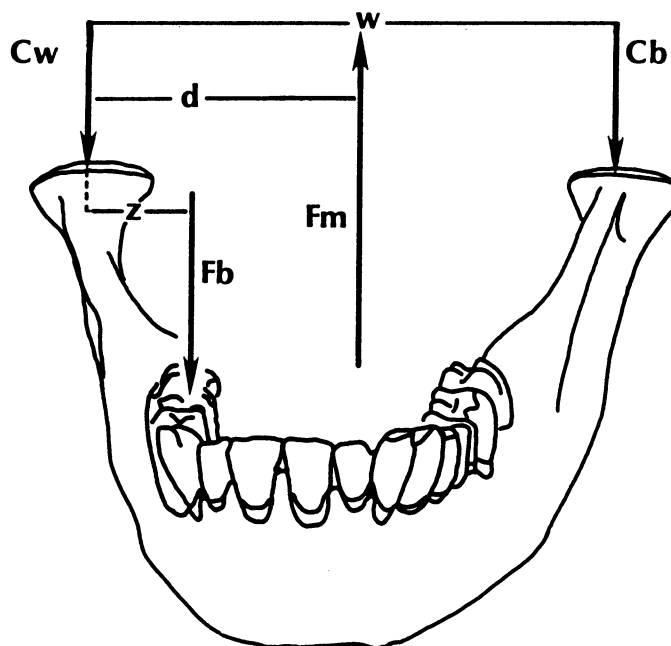
is 158% of **Fb** and at I2 the **Fc** is 264% of **Fb** (Table 5). In contrast, **Fc** in modern humans is 74% of **Fb** at M1 and 145% at I2. The absolute values of **Fc** are 30% to 40% greater than those for modern humans (Table 4).

In Neandertals, bite force is only 39% and 28% of **Fm** at M1 and I2, respectively, while it is 57% and 42% of **Fm** in modern humans (Table 5). Likewise, **Fc** is 61% and 72% of **Fm** at M1 and I2, respectively, in Neandertals. **Fc** is only 42% and 59% of **Fm** in modern humans. Thus, Neandertals are producing much less useful **Fb** per **Fm** than modern humans at a much greater expense to the TMJ.

Frontal Analysis

Frontal projection analysis showed that in Neandertals the balancing side condyle is more

Figure 3. Frontal projections analysis.



Schematic representation of external forces acting on the mandible in the frontal projection. **Fm** and **Fb** are defined as in Figure 1. **Cw** and **Cb** are **Fc** on the working and balancing sides, respectively. **W** equals becondylar width. **Z** equals **Fb** moment arm and **d** equals **Fm** moment arm (distance to working side condyle). In static equilibrium:

$$Cw = \frac{(Fm)(d) - (Fb)(z)}{w}$$

$$Cb = \frac{(Fm)(w-d) - (Fb)(w-z)}{w}$$

Cb is greater than **Cw**. (Redrawn from Hylander 1985).

heavily stressed than the working side condyle (Table 6). This is also true of modern humans (Smith 1978) and is corroborated by clinical evidence in which patients with diseased TMJs chew on the diseased side (Hylander 1975). The greater Fc in Neandertals than in modern humans is reflected in the greater percentage of Fb represented by Fc (Table 6). In molar biting in modern humans, Fc is 62% of Fb at the working side condyle and 92% of Fb at the balancing side condyle. During incisal biting Fc is 87% of Fb on the working side and 171% of Fb at the balancing side. Thus, incisal biting is extremely costly.

DISCUSSION

Neandertal facial prognathism has been suggested to be the result of the rearrangement of the infraorbital plates and the anterior migration of the tooth row with respect to the mandibular ramus (Rak 1986). Masticatory muscular relations

with respect to the TMJ are not greatly altered by this facial arrangement. However, the Fb moment arms are elongated resulting in the production of a less useful bite force and a very large condylar reaction force.

The consistent appearance of DJD in Neandertals is most likely due to the proportionally larger Fc produced at the TMJ. Even moderate occlusal loading at either the molar or incisal regions inflicts large reaction forces at the condyles leading, over time, to this degeneration.

The physiological restrictions imposed by the production of large Fc make it unlikely that the attrition of the anterior dentition is related to absolutely greater occlusal loading. This absence of large anterior occlusal loads is corroborated by the presences of only minor trauma (enamel microfracture and flaking) in Neandertal anterior teeth (Smith 1983). This conclusion contradicts Smith's (1983) idea that the small amount of trauma was due to absolutely larger teeth which were better able to bear greater loading.

Heavy anterior dental attrition may more

Table 5. Relationships between masticatory forces for modern humans and Neandertals.

	Modern Humans		Neandertals	
$\frac{Fb @ I2}{Fb @ M1}$	73%		71%	
	Molar	Incisal	Molar	Incisal
$\frac{Fc}{Fb}$	74%	145%	158%	264%
$\frac{Fb}{Fm}$	57%	42%	39%	28%
$\frac{Fc}{Fm}$	42%	59%	61%	72%

Table 6. Working and balancing side condylar reaction forces as a percentage of useful bite force. (Modern human data from Smith 1978).

	Molar		Incisal	
	Work	Balance	Work	Balance
Modern Human	15%	63%	71%	71%
Neandertal	62%	92%	87%	171%

likely be due to repetitive usage of the anterior dentition in food preparation or other cultural behaviors. Similar wear patterns are observable in prehistoric Californian groups which have heavy anterior dentition usage (personal observation). These patterns exist without the elongated facial geometry typical of the Neandertal face. Such paramasticatory behavior is also suggested by microwear studies of the Neandertal anterior dentition which show labial wear striae indicating the use of the anterior dentition in a vice-like grip (Trinkaus 1983).

The assumption that absolutely large anterior occlusal loads contribute to bending moments of the Neandertal face cannot be supported. However, bending moments in the sagittal plane due to increased Fb moment arms are greater than those in modern humans. Additionally, forces generated by continuous use of the anterior dentition over time may be a factor in the evolution of facial morphology (see Hylander 1979).

The unique facial morphology of the Neandertals certainly affected their masticatory force production capabilities. However, the supposition that masticatory forces were the driving forces in the evolution of facial morphology begs the question of the origin of the morphology (see Rak 1986). Force production capabilities of Neandertals are disadvantageous compared to those of less prognathic hominids. Facial elongation (with or without the rearrangement of the infraorbital plates typical of the Neandertal face) is not an effective method of counter-balancing high anterior dental loading and sagittal bending moments when compared to forces incurred by less prognathic hominids. Therefore, it seems unlikely that facial prognathism would have developed as a direct result of heavy anterior dental loading unless the prognathic position of the face were advantageous for some separate reason.

CONCLUSIONS

The geometry of the Neandertal masticatory system makes the production of even moderate occlusal loads very costly in terms of condylar reaction forces. It is likely that the level of these reaction forces may provide an upper limit to the level of Fb production possible.

Estimates of Fb production capabilities for Neandertals are well below modern human capabilities. This is true despite greater muscle force production capabilities for the Neandertals.

In sum, the attrition of the Neandertal anterior dentition is not likely to be related to absolutely greater occlusal loads but to consistent usage of the anterior dentition through time, use

which might have entailed paramasticatory behaviors such as food, tool or leather preparation. Thus, the central role which the heavy anterior dental loading hypothesis has been given in the origin and evolution of the Neandertal face appears unwarranted.

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