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Speculations About the Selective Basis for Modern Human Craniofacial Form

DANIEL E. LIEBERMAN

The last few decades have seen an explosion of knowledge about the time and place of origin of our species, *Homo sapiens*. New fossils, more sites, better dates, modern and fossil DNA, and scores of analyses have mostly disproved the multiregional model of human evolution. By and large, the evidence generally supports some version of the out-of-Africa model, according to which humans first evolved in Africa at least 200,000 years ago and then migrated to other parts of the world. Remaining debates about human origins primarily address if and how much hybridization occurred between modern humans and taxa of archaic *Homo* such as *H. neanderthalensis*.

Ironically, despite a growing consensus about when and where *H. sapiens* first evolved, we know little more today than we did 20 years ago about why we evolved. A key unresolved question is: What were the selection pressures that favored the evolution of modern humans in Africa around 200 Ka? We remain far from a definitive answer to this question, in part because of the substantial challenges of testing hypotheses about selection using archeological, genetic, and paleontological data. Of

these sources of information, the skull presents some especially interesting problems for several reasons. First, the skull is more derived in modern humans than is the postcranium,¹ and is thus a focal point for defining *H. sapiens* as a species and testing hypotheses about phylogenetic relationships within the genus *Homo*.^{2–5} Second, the skull participates in so many critical functions, among them cognition, vocalization, respiration, diet, and thermoregulation, that it is a valuable source of information for making inferences about behavior. And finally, the human skull is remarkably odd. To name just a few of our unusual craniofacial apomorphies, we are the only extant primate with an external nose, no snout, a spherically shaped (globular) braincase, a highly flexed cranial base, a face that is retracted almost entirely beneath the braincase, fur on just the top of the head, a chin, and so on. These and other features beg the question of what selective forces were at work to make our skull so especially derived in so many unique respects.

This essay is therefore an effort to review and speculate about some of the potential selective advantages that may be responsible for the origin of modern human craniofacial form. I undertake it with some trepidation.

Although it is always difficult to test hypotheses about natural selection from the fossil record, this problem is especially compounded for humans because of the detailed nature of the questions we ask, the complexity of human behavior, and our limited ability to conduct controlled experiments that test relationships among form, function, and fitness. Thus, the hypotheses presented here are difficult or perhaps impossible to test. Another problem is that hypotheses about natural selection in human evolution carry much emotional baggage. This is particularly true for hot-button topics such as language and cognition, in which deeply held preconceptions about what it is to be human lead to *a priori* viewpoints and strenuous objections to alternative hypotheses. At one end of the continuum are scholars who insist that humans are special (for example, that only humans can have language); at the other end are scholars who believe that all large-brained hominids are essentially human (for example, that Neanderthals are “human” too). Nevertheless, it is occasionally useful to speculate on controversial topics. What follows, then, is a review of some previous ideas and some further speculations about why the modern human skull may be unique. A few caveats. First, I admit that many of the ideas presented here really are just speculations that will be difficult to test definitively. Second, I have entirely avoided the topic of sexual selection not because it was unimportant in human evolution, but because I have no idea how to test for its occurrence. Finally, none of the following ideas are dear to my heart; I will be happy to see them all disproved.

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First, however, it will be useful to consider a few key pitfalls in trying to infer adaptation from morphological features.

SOME PROBLEMS WITH TESTING HYPOTHESES ABOUT ADAPTATION IN THE SKULL

One resurgent problem with testing hypotheses about possible adaptations in the skeleton is the issue of setting up and rejecting appropriate null hypotheses. Like many biologists, students of human evolution have tended to fall into one of two extreme camps. At one extreme is the “adaptationist” perspective, critiqued most famously by Gould and Lewontin.⁶ This perspective typically assumes a causal, adaptive relationship between form and function. As noted by Lauder,⁷ the adaptationist perspective is often characterized by a kind of “reverse engineering” approach in which one first identifies novel features such as chins or rounded cranial vaults and then assumes that these features might have been adaptive—that is, a heritable feature that has been selected because it improves survival and/or differential reproductive success. According to this approach, the null hypothesis for a feature is that it is an adaptation unless proven otherwise. This logic has led to many proposed adaptations in the human skull, including that the flexed cranial base is an adaptation for speech⁸ and that a chin is an adaptation for reducing wishboning of the mandible.⁹ Since Gould and Lewontin,⁶ however, there has been a reaction against adaptationism, leading to an opposite “spandrelist” extreme in which the null hypothesis for a morphological feature is that it is a spandrel unless proven otherwise. Lauder,⁷ for example, proposed a demanding set of criteria with which to test such evolutionary arguments from design, namely that proposed adaptations are derived, that they are tested experimentally in terms of their effects on performance, that alternative functions are also tested, and that the features have not been defined too strictly to exclude other related fea-

tures that may be part of the same morphological complex.

While laudable, the spandrelist approach also has its problems, because to prove rather than assume that a feature is a spandrel, one must first prove that it is not an adaptation. Such tests are especially difficult when applied to the fossil record or to species such as humans and other primates for which there are substantial experimental constraints. In reality, to assume that a feature is either an adaptation or a spandrel should be equally burdensome in terms of rejecting a null hypothesis.

A second problematic issue with testing functional hypotheses about human origins from the fossil record has been the assumption of independence among features. The *H. sapiens* skull,

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for example, is typically considered a mosaic of many independent or partially independent features, such as a large brain, a flexed cranial base, a canine fossa, highly curved cranial vault bones, and so on. Many developmental studies, however, indicate that these traits are not independent, but instead are highly integrated. Over-atomization of traits is a problem not only for phylogenetic analyses, but also for testing hypotheses about natural selection. Skulls are complex, strongly integrated structures characterized by high levels of covariation among multiple structures, even in different regions such as the face, basicranium, and neurocranium.^{10–14} Thus, when two or more features covary, it is no simple matter to determine which were targets of selection versus byproducts of selection. Consider, for example, the shape of the neurocranium. Many

interacting factors influence neurocranial shape, including the size and shape of the brain itself, as well as myriad interactions between the brain, its dural folds, the basicranium, the face, and the neurocranium (for review, see Lieberman, Ross, and Ravosa¹⁵). Consequently, multiple factors potentially can cause the braincase to become more spherical. In mice, for example, independent mutations that shorten either the face or the basicranium both lead to a relatively wider, more spherical neurocranium and a more flexed cranial base.¹⁶ Without knowing how these factors interrelate, it would be difficult to know which were targets of selection and which were spandrels.

Finally, just as there is a tendency to “atomize” the skull as a set of features that are assumed to be independent, there is also a tendency to atomize selective hypotheses. We may identify many *bona fide* adaptations in the skull that improve performance in different functional roles such as speech, locomotion, cognition, and thermoregulation. Yet these adaptations may not be independent at the level of the organism’s behavior. Thus, the selective forces behind the evolution of the human skull need to be considered in their general behavioral and cultural contexts: how early humans foraged, hunted, used the landscape, and interacted with each other. Put differently, good hypotheses about why humans have distinctively shaped skulls need to consider the selective advantages of the skull’s various derived features in the context of a larger behavioral and selective scenario.

Given these challenges, a useful strategy for thinking about selective hypotheses that may have driven the origin of modern human craniofacial form is to consider the skull as an integrated unit, then to work backward to generate hypotheses about particular functions and how these functions may be related. Formalized, this is a three-step, largely inductive process. The first step is to determine to what extent and how the features that changed at a given speciation event are integrated; in other words, what changed with what? The second step is to identify the functional

effects of these shifts and consider how they would have affected the function of other proposed modular shifts. The third step is to generate testable hypotheses about how selection might have acted, trying to reject simultaneously the alternative null hypotheses that a given feature is an adaptation and a spandrel.

MAJOR DERIVED FEATURES OF THE MODERN HUMAN SKULL

As argued, in order to test hypotheses about the functional implications of modern human cranial form it is first useful to ask what are the major integrated units of the skull that changed together in the transition from archaic to modern humans. Since various studies have already addressed this problem in depth, I will only briefly summarize their results here. Most notably, Lieberman and colleagues^{12,15,17,18} have shown that many of the derived features of the *H. sapiens* skull are not independent, but instead covary substantially both within adult and cross-sectional ontogenetic samples. Three integrated shifts between archaic *Homo* and modern humans account for a large proportion of the derived features of *H. sapiens*. First, the modern human skull has an absolutely and relatively smaller face, mostly in terms of anteroposterior length and superoinferior height. In Figure 1a, note, for example, that the orbits are relatively more rectangular in modern than archaic humans). Second, the modern human neurocranium, although similar in volume, is more spherical than that of archaic *Homo*, leading to more rounded contours of all the cranial vault bones. Third, the smaller modern human face is substantially retracted relative to the basicranium and neurocranium, contributing most obviously to a reduction in browridge size.¹⁹

Geometric morphometric (GM) analyses that compare archaic and modern human skulls^{17,18,20} corroborate these results, suggesting that a relatively small number of developmental shifts may be responsible for the integrated shape differences I have summarized. Three structural

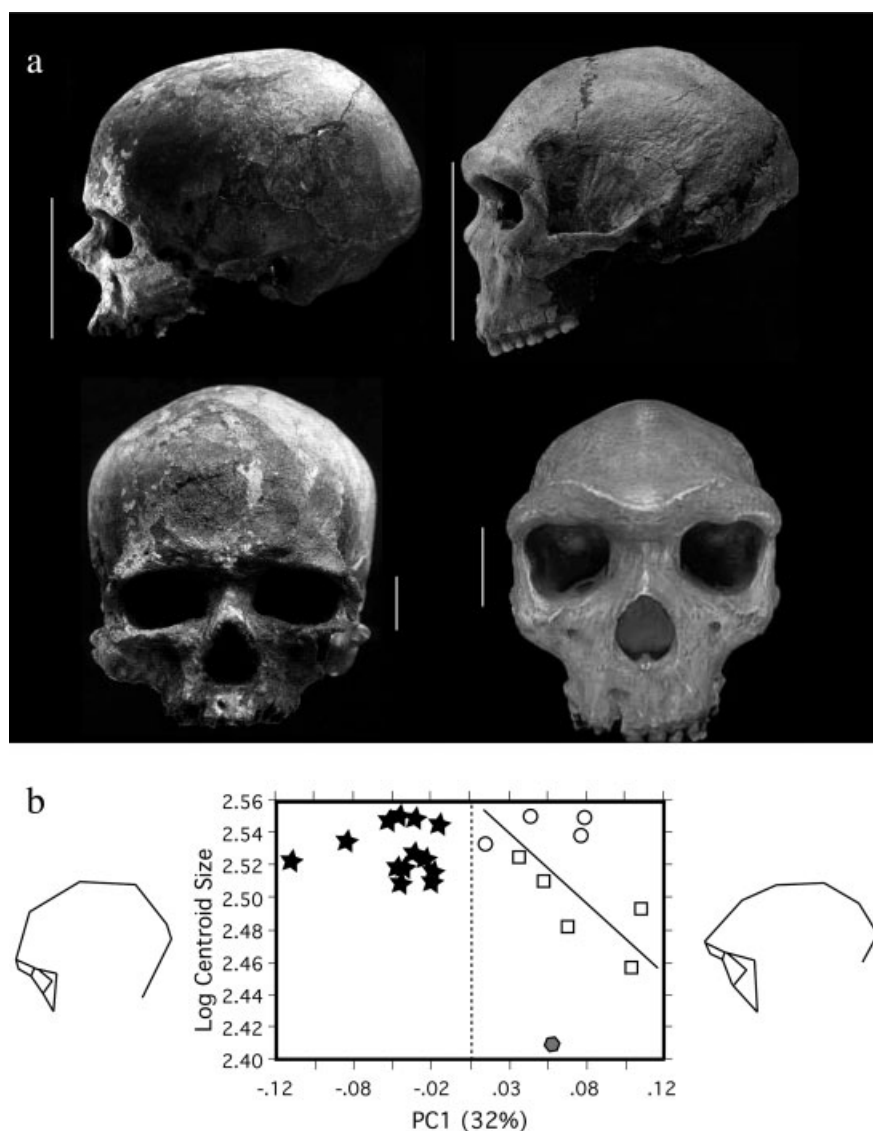


Figure 1. Comparison of modern *H. sapiens* and archaic *Homo* cranial form. A. Lateral and anterior views of Cro Magnon I (left) and Broken Hill (right), scaled to same height. Note the relatively longer face and orbits of the archaic human (as shown by white bars), which generates a more square-shaped orbit; the modern human face is also larger and more projecting, and the neurocranium is more spherical. B. Graph of centroid size versus the first principal component of cranial shape in Pleistocene modern *H. sapiens* (stars) and archaic *Homo* (circles), *H. erectus* (squares), and *H. habilis* (pentagon) following a Procrustes superimposition of the landmarks. Note that for this component of shape variation, which explains 32% of the variance, archaic *Homo* is largely a size-scaled version of *H. erectus*, but that *H. sapiens* falls off the allometry between size and shape. Line drawings to left and right show mean form along PC1 of modern and archaic humans, which comprises neurocranial globularity. Relative facial size and facial projection. See Lieberman and Bar-Yosef²⁰ for details of sample and analysis.

shifts (all evident in Figs. 1 and 2) appear to be particularly important. First, the modern human cranial base is about 15° more flexed. This flexion has several implications for skull shape, in part because the top of the face is the base floor of the anterior cranial base and also because the

back of the face is always roughly perpendicular to the anterior cranial base.^{21–23} The combined effect of these constraints is that a more flexed cranial base reorients the entire face as a block more ventrally beneath the anterior cranial fossa and decreases the length of the nasopharynx behind the



Figure 2. Midsagittal view of **a**, Skhul V (*H. sapiens*) and **b**, Broken Hill (archaic *Homo*). Note that in this particular comparison the angle of the cranial base is approximately 18° more flexed in the modern human. The Broken Hill scan is by courtesy of the Natural History Museum.

palate. Cranial base flexion may also contribute to neurocranial sphericity by decreasing the area of the platform on which the brain sits.^{24,25} A second major structural change is that in modern humans the anterior cranial base is relatively longer and wider, especially the more posterior part comprised of the middle cranial fossa.^{17,19,26} Elongation of the anterior cranial base probably contributes mostly to facial retraction by displacing anteriorly the upper (superior) part of the posterior margin of the face, known as the posterior maxillary (PM) plane. Because the PM plane is always nearly perpendicular to the top of the face, this displacement rotates the face as a whole ventrally (clockwise when viewed from the right).^{21,22} The third major shift is that the modern human face is relatively shorter both anteroposteriorly and superoinferiorly, but not narrower. Facial reduction, which has occurred more gradually than cranial base flexion and anterior cranial base elongation, contributes primarily to facial retraction, but may also be implicated in cranial base flexion (for discussion see Lieberman, Ross, and Ravosa¹⁵).

Note also that from a developmental perspective the differences between modern and archaic *Homo* skulls appear to be greater than those between *H. erectus* and archaic

Homo. As Figure 1b illustrates, large-brained taxa from the Middle Pleistocene, such as *H. heidelbergensis*, are in many ways scaled-up versions of *H. erectus*, different primarily in terms of relatively larger brains and faces.²⁰ In contrast, modern human skulls have an overall different architectural configuration. Put differently, the evolutionary transformation from a *H. erectus* skull into a *H. heidelbergensis* skull can mostly be explained by changes in the relative size of the brain and face. In contrast, the evolutionary transformation from an archaic *Homo* skull into a modern human skull is more complex, requiring a relatively longer middle cranial fossa, a more flexed cranial base, and a smaller face in terms of height and length.

POTENTIAL FUNCTIONAL CONSEQUENCES OF MODERN HUMAN CRANIAL APOMORPHIES

We can now speculate (and I emphasize that what follows are speculations, not tests) about how the preceding shifts might be adaptive in terms of their performance effects on craniofacial function. Of the many varied functions that a skull performs, five appear to be most relevant to neurocranial sphericity, and/or facial shorting and retraction: cogni-

tion, chewing, locomotion, respiration, and speech.

Cognition and Brain Shape

One longstanding topic of interest is whether modern humans had any cognitive advantages over archaic humans, perhaps related to the ability to create more complex technologies such as the Upper Paleolithic, generate more sophisticated language, and so on. However, it has been a challenge to find or test for any evidence of such adaptations. Most of the relevant archeological evidence is a record of absence (that is, the lack of Upper Paleolithic technologies and art made by archaic *Homo*) and does not explain why the archeological residues associated with modern and archaic humans are essentially identical for more than 150,000 years. Fossil evidence of neurological differences has also been hard to discern. Absolute and relative brain size in modern and archaic humans is approximately equal.²⁷ Also, there are few, if any, reliable endocranial features that point to major differences in brain structure, such as Broca's or Wernicke's areas, between archaic and modern humans.²⁸ However, another potential source of information is whether the contrasts in overall neurocranial shape reviewed earlier reflect some differences in the relative size of, and hence, selection on particular regions of the brain. The basis for such speculations is that the braincase and basicranium grow around the brain, largely in response to stimuli triggered by the growth of the brain itself.^{17,29,30} Thus, variations in the relative size of specific parts of the brain could generate differences in the shape of the cranium as a whole.

One such hypothesis is that the modern human brain has a relatively larger frontal lobe.³¹ Despite its appeal, this hypothesis has been disproved by comparative studies in hominoids. Measurements of the neocortex and other structures in the brain of extant primates using magnetic resonance imaging (MRI) have shown that the frontal, parietal, and occipital lobes in humans are about the same relative size as in other

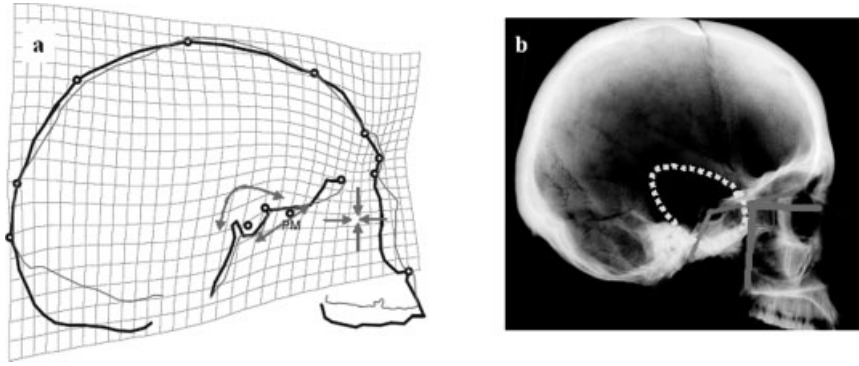


Figure 3. A. Geometric morphometric analysis of cranial shape differences between archaic and modern humans, from Lieberman, McBratney, and Krovitz.¹⁷ The red outline is an average of two archaic *Homo* crania (Broken Hill, Bodo) that have been warped to fit the same landmarks on four male modern humans (black outline). Grid deformations indicate the thin plate spline. Key differences, indicated by arrows, are the greater degree of cranial base flexion, the relatively longer anterior cranial base, and the relatively smaller face. B. Outline of lateral view of the temporal lobes relative to the cranial base. Note that the temporal lobes sit above the sphenoid, which is major site of cranial base flexion. Also shown (in red) is the 90° constant angle between the back of face (the posterior maxillary plane) and the neutral horizontal axis (NHA) of the orbits. Because this angle is constrained to be approximately 90° and the anterior cranial base is tightly correlated with the NHA, flexion of the cranial base causes the entire face to rotate underneath the anterior cranial fossa.

hominoids after scaling is taken into consideration.^{32–35} In contrast, the human cerebellum is proportionately smaller than in apes, by approximately 20%, and the temporal lobe is proportionately larger, by as much as 25%. Other, more fine-scale differences may also exist within lobes. Within the occipital lobe, the primary visual striate cortex is relatively smaller in humans³⁶; within the frontal lobe, the prefrontal cortex is about 6% larger, possibly because of more white matter.^{35,37,38}

Of these differences, evidence that the temporal lobe became relatively larger at some point in human evolution is the most intriguing because of the differences I have noted in cranial shape between modern and archaic humans. In particular, geometric morphometric comparisons of the cranial base (summarized in Fig. 3) indicate that in modern versus archaic humans the middle cranial fossa (MCF), which houses the temporal lobes, is approximately 15%–20% longer and 20% wider relative to overall cranial size.^{17,18,26} If MCF size correlates strongly with temporal lobe volume (an untested hypothesis), then it is possible that a proportional increase in temporal lobe volume was

coincident with the origin of modern humans.

Such a shift might also help explain some of the major derived aspects of modern human cranial shape. The anterior portion of the MCF comprises part of the anterior cranial base and, as noted earlier, the modern human anterior cranial base is relatively longer than that of archaic *Homo*, contributing to facial retraction (more of the modern human face is tucked below the anterior cranial fossa).¹⁹ Both GM data from fossil crania and the comparative MRI data from primate brains summarized earlier suggest that the increases in temporal lobe size are responsible for this anterior cranial base elongation. Another major factor that influences both neurocranial globularity and facial retraction is the angle of the cranial base, which is about 15° more flexed in modern than in archaic *Homo*. This difference, in conjunction with evidence of temporal lobe expansion, raises an interesting possibility. As Figure 3 illustrates, the temporal lobe sits on the center of the cranial base, just above the sphenoid synchondrosis, the major site of cranial base flexion. Various lines of evidence indicate that growth of the

brain relative to cranial base length influences cranial base flexion.^{15,39,40} While overall brain size cannot be the cause of more cranial base flexion in modern humans, a relatively larger temporal lobe is a possible cause, since it is the one portion of the brain that lies directly on the site where the cranial base actually flexes during the first few postnatal years.⁴¹

To reiterate, the hypothesis that relative increases in the temporal lobe were a factor in the evolution of modern humans remains speculative without further evidence. As initial tests of the hypothesis, it would be useful to determine whether the MCF and temporal lobe volume are correlated, and whether humans with larger temporal lobes have more flexed cranial bases. If so, however, then the hypothesis has intriguing implications for selection. The temporal lobe has many complex functions, including cognitive roles relevant to the organization of sensory input. These include language and various kinds of memory, such as the recognition of words, sounds, and visual images. In addition, the temporal lobe has been shown to be important during intensely spiritual and religious thoughts; for example, stimulation of the temporal lobe during surgery can induce spiritual emotions even in self-described atheists.⁴² It is thus interesting to speculate that religious and spiritual behaviors, so prevalent in all human societies, are a derived, emergent property of selection on other capabilities such as memory and language.

Bite Forces and Cooking

One intensely studied aspect of the relationship between form and function in the skull is the generation and resistance of bite forces. Thus, it is not for lack of looking that most researchers have found little reason to suspect that the modern human face has any particular derived adaptations for generating or withstanding chewing forces. Nevertheless, the human face presents an interesting paradox, as shown in Figure 4, which compares, in lateral view, the estimated mechanical advantages of bite-force production in the vertical plane

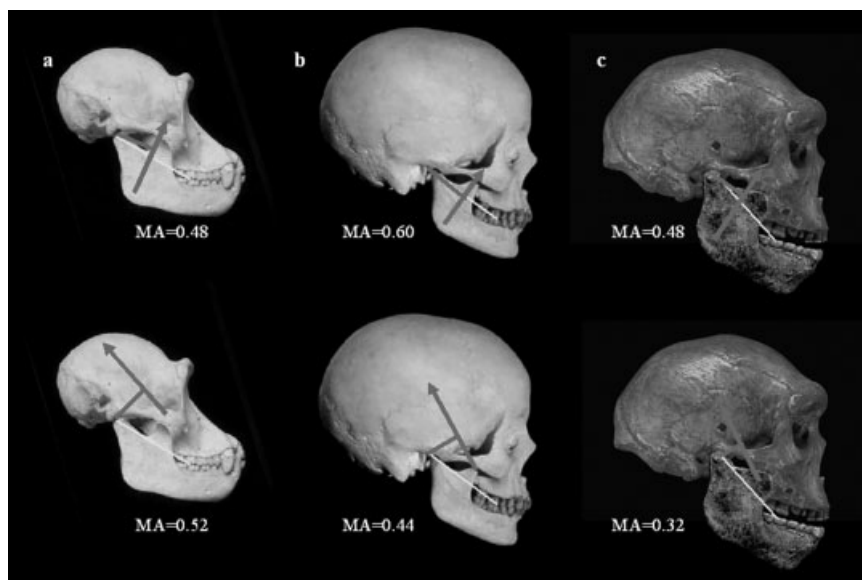


Figure 4. Mechanical advantages of the masseter (top) and temporalis (bottom) in a chimpanzee (a), *H. sapiens* (b), and a composite archaic *Homo* skull (c, a combination of the Broken Hill cranium and the Mauer mandible). Mechanical advantage (MA), the ratio of the lever to load arms, is calculated from the estimated average resultant of masseter and temporalis for a chew on M2. Note that resultant is an approximate estimate and will vary depending on factors such as bite location, food hardness, and other such factors. In spite of such variations, the modern human will have a higher MA for both muscles than did the archaic *Homo*, largely because of facial retraction and diminution.

of the masseter and temporalis muscles for a chew on the second molar in a chimpanzee, a modern human, and a representative archaic *Homo* (Broken Hill). Although the orientations of the muscle resultants are estimated and approximate, it is evident that by retracting and shortening the face, the human skull has a relatively shorter load arm for both the masseter and the temporalis, leading to an approximately 20%–40% higher mechanical advantage in modern versus archaic humans.

Although the human skull is more efficiently designed for producing bite forces, it would probably be unwise to hypothesize that the human face was selected to become shorter in order to increase masticatory efficiency. There is simply no corroborating evidence. Humans have small and thinly enameled tooth crowns that have become smaller rather than larger in the genus *Homo* during the last few hundred thousand years.⁴³ In addition, humans do not produce high bite forces relative to our body size for various reasons, including

smaller cross-sectional areas for some muscles⁴⁴ and relatively fewer fast-twitch (Type I) muscle fibers.⁴⁵ Consequently, most research on this topic has focused on how derived aspects of midfacial projection in the Neanderthal skull may have been adaptive. But the other side of the coin is to consider not the generation of bite force, but its resistance. As shown by Hylander and colleagues,^{46–49} chewing generates strains that are not only similar in magnitude to those generated in the limbs during locomotion, but also highly repetitive. A typical chimpanzee spends about 50% of the day chewing.⁵⁰ Thus, a key function of the face is to withstand masticatory strains, either through adding mass to decrease their magnitude or through repair mechanisms.

How the human face withstands chewing forces is incompletely understood, in part because we know relatively little about the nature of chewing-induced strains in the uniquely flat, short, retracted human face. Most *in-vivo* experimental data on craniofacial strain patterns comes

from nonhuman primates and other mammals with a somewhat tubular rostrum in which the maxillary tooth row is positioned well in front of the plane of the middle and upper face. Nevertheless, finite element modeling studies,⁵¹ as well as experimental data from mammals with retracted postcanine teeth, such as the rock hyrax (*Procavia capensis*), suggest that we can make at least two reasonable predictions.^{52,53} First, human facial strains probably resemble those of other mammals in following a strong gradient, with strains highest near the occlusal plane and regions of muscle attachments and diminishing away from these sites, with only tiny magnitudes in the upper face and browridge.^{48,49} In addition, unilateral mastication probably generates some combination of twisting around an anteroposterior axis plus shearing in the coronal plane.

As noted above, one of the most distinctive aspects of the *Homo* face is the lack of a rostrum, which in nonhuman primates and mammals such as swine partly functions to dissipate twisting and bending strains away from the rest of the face.^{54,55} Both archaic and modern humans therefore presumably resist such strains in an alternative manner by having a tall, wide, flat face in which most of the mass of the face is distributed in the coronal plane.^{52,56} If so, then one can hypothesize that the face in archaic *Homo* is larger, and especially taller than that of modern humans in order to withstand more and/or higher magnitude strains from twisting and shearing. Put differently, the modern human face may be superoinferiorly shorter not to generate higher occlusal forces, but because it has to withstand less strain. Indeed, in terms of its surface area in the coronal plane, the face is approximately 30%–50% smaller in modern than archaic humans, with substantial decreases having occurred in the last 12,000 years.⁵⁷ Moreover, some proportion of this size diminution is epigenetic and can be attributed to the mastication of softer, more processed foods.^{53,58,59,106}

This hypothesis needs to be tested but, if true, then one likely component of the selective equation behind

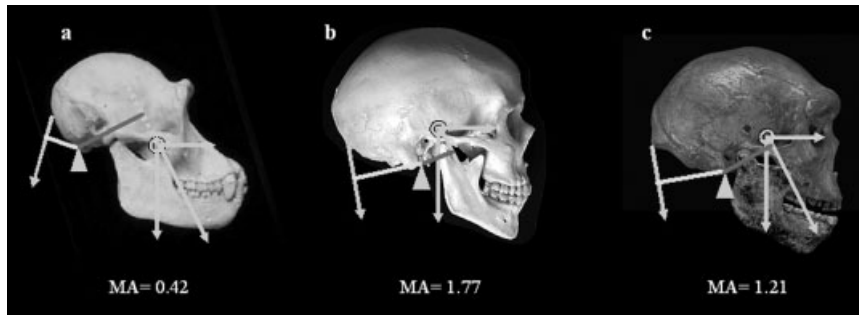


Figure 5. Mechanical advantage (MA) of the nuchal muscles for a chimpanzee (a), *H. sapiens* (b), and a composite archaic *Homo* skull (c, a combination of the Broken Hill cranium and the Mauer mandible). The center of gravity of each skull (bullseye) was estimated from the area centroid; the resultants of the nuchal and COG are based on unpublished experimental data. The combination of a relatively long nuchal plane, a centrally located foramen magnum, and a nearly balanced skull gives the nuchal muscles a higher MA in modern humans than in the other two species.

facial size reduction (why big faces were no longer adaptive) is most likely related to cooking and/or food preparation. As Wrangham and colleagues^{60,61} noted, cooking is not only a universal human behavior, but also may be a biological necessity for humans, even modern “raw-foodists” who intensively soak, grind, and otherwise process highly domesticated, high-quality foods. Cooking, of course has many advantages, including increasing nutrient accessibility and digestibility, inactivating toxins and parasites, and prolonging storage times.⁶² Cooking also makes food easier to chew. Cooking softens and tenderizes plants by breaking down cellulose; it makes meat stiffer and less tough, and thus easier to fracture.⁶³ There is much debate, however, about when cooking became prevalent in human evolution. On the basis of tooth size reduction, Wrangham and coworkers⁶⁰ and Lucas⁶³ have suggested that cooking first arose with the genus *Homo*. However, according to archeologists, the oldest evidence of cooking in the form of hearths is from the Middle Paleolithic/Middle Stone Age, about 250,000 years ago,^{64–67} approximately the same time as the evolution of *H. sapiens* (and the Neanderthals).

Further evidence is needed to resolve this problem, but one hypothetical possibility is that tooth size decreases and facial reduction constituted a two-stage process. The first stage, which occurred with the ori-

gins of the genus *Homo*, almost certainly involved a change in diet, with increased reliance on meat, which is easily and effectively tenderized by pounding. Thus, the regular addition of meat to the diet, combined with the adoption of simple food processing technologies such as pounding (a good use for Oldowan spheroids?), may have led to the initial diminution in tooth size, but not to smaller faces. Later, cooking evolved in the Middle Paleolithic, favoring further reductions in tooth size, as well as reductions in face size. In addition, although teeth have become smaller in both modern and archaic *Homo* since the Middle Paleolithic,¹⁰⁷ facial size decreases may have been less in Neanderthals for other reasons such as their expanded internal nasal cavities and their reliance on anterior dental loading.^{56,68,69}

Note that the invention or elaboration of cooking technologies in the Middle Paleolithic/Middle Stone Age may help account for why there was no longer a selective advantage to maintaining a large face, but it provides no selective advantage for reducing facial size. So any selective scenario needs to consider why a smaller, lighter face might be an adaptation. The modern human face is shorter both superoinferiorly, reducing its area in the coronal plane, and anteroposteriorly. The combined effect is to make the modern face absolutely less massive in modern versus archaic humans (assuming

that volume and mass are proportional). However, as I will discuss, a smaller face may have other functional advantages related to locomotion, respiration, and vocalization. So small faces cannot be explained by diet alone.

Locomotion

Although the role of the skull in locomotion is not often considered, one hypothesis to explore is that decreases in facial size played a unique role in humans to improve head stabilization capabilities during running. In all mammals, there is a tendency for the head to pitch in the sagittal plane during locomotion from a combination of vertical and horizontal accelerations (Fig. 5). These pitching forces need to be controlled in order to stabilize the gaze and avoid falling. This is not a trivial problem in inherently unstable, long-legged bipeds such as humans. Although minimal in walking, pitching forces increase several-fold in running gaits, especially at heel strike, when high ground reaction forces, the heel-strike transient (HST), travel almost instantaneously up the legs and the spine, delivering an impulsive load to the head that causes it to pitch forward rapidly.⁷⁰

Controlling head pitching forces is much more of a challenge for bipedal humans than for most quadrupedal mammals, which are well adapted for running (cursorial specialists). When walking and running, mammals typically hold their heads with their eyes directed forward and their horizontal semicircular canals within 20° of earth horizontal.^{71,72} Quadrupedal cursors effectively stabilize their heads during trotting and galloping by flexing and extending the neck, which has some degree of horizontal orientation.⁷³ This simple mechanism of stabilization, however, is not available to large-brained bipedal hominids, whose short vertical necks arise near the center of the skull. In this respect, human running is a bit like being on a pogo stick, because we have no mechanisms to control vertical fluctuations of the head's center of gravity (COG) and to dissipate the HST. Instead, hominids must stabilize the

head against pitching forces by flexing or extending the head almost entirely at the atlanto-occipital joint (AOJ). Yet even during running, humans usually manage to keep angular rotations of the head below 100°/sec following the HST, well below the 200° threshold at which the vestibulo-ocular reflex, which senses pitching movements and coordinates them with eye movements, becomes saturated.^{74,75}

As Bramble and Lieberman noted,⁷⁶ humans have several features that are not present in apes and possibly are also absent in australopithecines, which may help stabilize the head. These features include more sensitive anterior and posterior semicircular canals,⁷⁷ which sense accelerations in the pitching plane, and a nuchal ligament, which may act as a passive, elastic mechanism to stabilize the head.^{78,79} To this list we should probably add a more balanced head, because it reduces the moment arm of the pitching forces that need to be counteracted by head extension. Even though more balanced heads probably arose in *Homo* in part because of bigger brains, which extend more mass behind the AOJ, a smaller face also improves head stabilization performance in bipeds with short vertical necks, as shown in Figure 5. In modern humans, the head's COG is approximately 1 cm anterior to the AOJ.⁸⁰ Although it is difficult to calculate precisely the location of the COG in fossil crania, preliminary estimates using the area centroid as an approximation suggest that facial diminution in modern humans may be responsible for moving the COG approximately 1 cm closer to the AOJ than in archaic *Homo*. As shown in Figure 4, this small shift would halve pitching moments and increase the mechanical advantage of the head extensors by about 50%. In other words, modern humans may have been more effective than archaic humans at stabilizing the head because of a smaller face.

Of course the hypothesis that facial diminution was an adaptation for head stabilization during running is untested. However, as Bramble and Lieberman noted,⁷⁶ humans have spectacular endurance running (ER)

performance capabilities, better than those of most mammals, particularly over long distances in hot, arid environments. These capabilities derive from numerous features, some of which improve running performance but are irrelevant to walking, in which pendular mechanics are fundamentally different from the mass-spring mechanics of running. When ER capabilities arose is difficult to pinpoint, but they were probably present in *Homo* and may have played an important role in acquiring meat by scavenging, hunting, or both.⁷⁶ It follows that if ER capabilities improved modern human hunting performance, then morphological changes such as smaller faces that improved head stabilization might have been a selective advantage.

Respiration

Having a smaller face also has potential functional effects on the role of the pharynx in respiration, particularly in terms of thermoregulation during vigorous activities such as running. Superoinferior and anteroposterior shortening of the face decreases the length of several components of the pharyngeal airway (Fig. 6), including the nasal cavity and the nasopharynx above the soft palate, the oral cavity, and the oropharynx. If we assume that neck length has not changed much in the genus *Homo*, then the modern human pharynx is significantly shorter, possibly by about (12%–15%) relative to body mass than that in archaic *Homo*. This difference has several implications for the pharynx's role in thermoregulation. The epithelial lining of the nasal cavity and pharynx is highly vascularized and covered by hydrophilic mucosa. This lining functions to humidify and warm air to approximately 75%–80% humidity and 37° C, respectively; during expiration, the same tissues can act to recapture some of this heat and moisture. These thermoregulatory functions are particularly important in the nasal cavity, which has a much higher ratio of epithelial surface area to volume.

A shorter pharynx affects these functions by altering two interrelated parameters: the degree of turbulence

and the rate of flow. In a circular tube with laminar flow (characterized by no turbulence), resistance to flow, R , is quantified by the Hagen-Poiseuille equation:

$$R = 8nl/\pi r^4$$

where n is the viscosity of the gas, l is the tube's length, and r is the tube's radius.⁸¹ Because air viscosity is not species-specific, and the nasal and oral cavities are neither wider nor taller in modern humans (it is impossible to estimate the radius of the oropharynx in fossils), modern humans probably had slightly higher airflow resistance during conditions of laminar flow. However, most airflow through the human pharynx is not laminar, but turbulent, characterized by circulating vortices with no particular orientation relative to the tube's walls or the average direction of flow. Turbulence increases enormously during vigorous aerobic exercise. There is no simple equation to estimate R in turbulent flow, but turbulence itself is a function of the gas (or fluid's) Reynold's number, Re :

$$Re = 2rvd/n$$

where r is the radius of the tube, v is the average fluid velocity of the gas, d is the density of the gas, and n is the viscosity of the gas. As before, d and n are determined by the environment, and r is probably not much different in archaic versus modern *Homo*. However, the fluid velocity, v , is probably a little higher in modern humans because oxygen needs and lung volume scale isometrically with body mass.⁸² Consequently, the same volume of air per unit time (flow rate) flows through a shorter tube, leading to a higher average velocity. This difference in length, hence velocity, matters considerably during aerobic exercise. At optimal walking speed, about 5 kph humans breathe about 2.5 L/min. During moderate jogging, 15 kph, oxygen demands increase more than seven-fold to about 18 L/minute,⁸³ requiring both faster breathing rates and larger volumes per breath, from about 500 mL to 1,500 mL. Even faster flow rates are needed at higher speeds or higher altitudes. Consequently, turbulence in the mod-

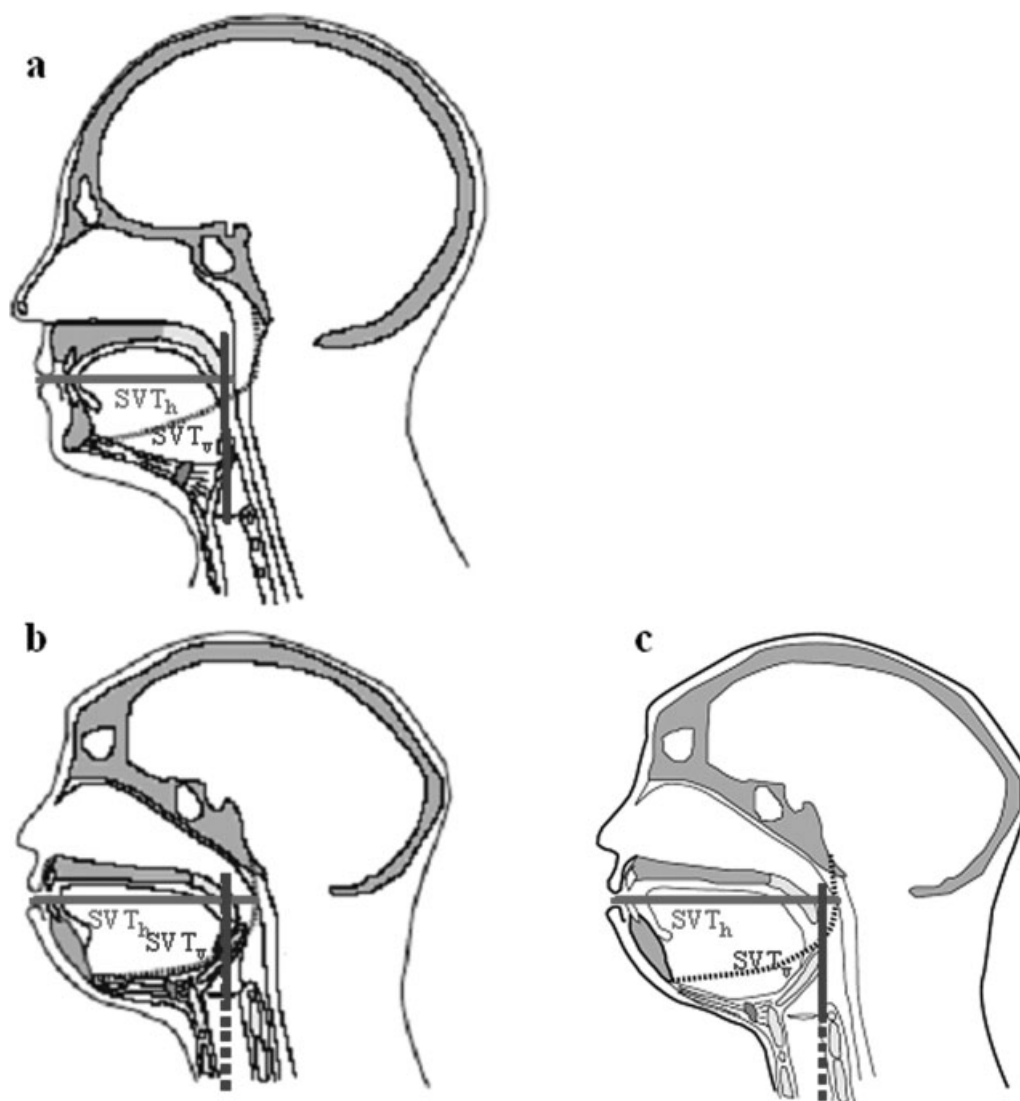


Figure 6. Midline view of the pharynx and supralaryngeal vocal tract (SVT) in a modern human (a) and two alternative reconstructions of an archaic *Homo* (b,c). SVT_h is shown in red and SVT_v in blue. The ratio of SVT_v to SVT_h in the modern human is 1:1. In version b, the archaic *Homo* has been reconstructed with an intranasal larynx and an intraoral tongue; in version c, the archaic *Homo* has been reconstructed with a descended (nonintranarial) larynx and a rounded human tongue. In both cases, the length of the SVT_v necessary to have a 1:1 SVT_v:SVT_h, is indicated by the dashed line.

ern human pharynx, already very high during conditions of exercise, must be higher for modern than archaic humans.

Turbulence and the resistance it causes lead to an important trade-off in thermoregulation. The advantage of turbulence is that it increases airflow contact with the epithelium in the pharynx, especially the nose. Within a cross-section, there is a velocity gradient in laminar flows, with flow rates approaching zero near the wall of the tube, creating a boundary zone estimated to be 0.25 mm wide in

modern humans.⁸⁴ Because such a boundary decreases effective heat and moisture exchange, it is not surprising that the nose in *Homo* has many adaptations to increase turbulence, including an external nasal vestibule, which is first evident in early *Homo*,⁸⁵ inferiorly directed nostrils, and a nasal valve.⁸⁶ However, the disadvantage of turbulence is that it generates considerable extra work for lungs. In laminar flow, pressure is a linear function of velocity, $P = kV$ (k is a constant). In turbulent flow, however, pressure increases to the power

of two relative to velocity, $P = kV^2$, thus generating much higher pressures. One well-known effect of this trade-off is that resistance is so high in the human nasal cavity during vigorous exercise that the pressures can be painful. Because airflow in the mouth is much more laminar than in the nose (r is an order of magnitude bigger), this may explain why humans are the only known mammal that is an obligate mouth breather during vigorous exercise.

Putting together the evidence, a shortened pharynx in humans may be

an adaptation for thermoregulation in the hot and arid environments in which modern humans appear to have evolved.

During normal activity levels such as walking, a shorter pharynx would help increase turbulent airflow in the nasopharynx, thereby increasing the efficiency of the respiratory epithelium, especially for recovering moisture. Moreover, during vigorous activity such as endurance running, when humans uniquely switch to oral breathing, a shortened oral cavity may help to improve the efficiency with which we dump heat.^{87,88} One cost of dumping heat, however, is a greater reliance on water.

Vocalization

A final function to consider is vocalization. I do so, however, with apprehension because the evolution of human speech is among the most contentious subjects in paleoanthropology. One problem is that there is no agreement on what null hypothesis to reject. To some, language and fully modern speech is a unique human apomorphy unless proved otherwise; others assume that large-brained hominids such as Neanderthals must have possessed human-like linguistic abilities unless proved otherwise. Given that neither speech nor the tissues that produce it fossilize, these are tough null hypotheses to reject.

That said, let's throw caution to the wind and consider how a shorter face and/or more flexed basicranium might influence speech production. To do so, it may be useful to begin with a short review of the acoustical and anatomical bases of speech. Speech sounds are essentially puffs of pressurized air from the lung that pass through the vocal folds of the larynx, which controls the vibrations. The frequency of the vibrations, typically between 250 and 4,000 Hz, determines the pitch, also known as the fundamental frequency (F0); the amplitude of the vibrations determines the volume. The sound waves are subsequently filtered by the airway, technically known as the supra-laryngeal vocal tract (SVT), to create

harmonics, known as formant frequencies. Importantly, each vowel has a unique, stable, distinct, and hence quantal combination of formant frequencies that derive from the shape of the SVT.⁸⁹ According to the quantal theory of speech,^{90,91} these formant combinations are stable over a range of tongue positions, requiring less muscular coordination because of two key properties of the SVT (Fig. 6). First, the SVT has two tubes of similar length: the horizontal tube, SVT_h, extends from our lips to the back of the oropharynx; the vertical tube, SVT_v, extends from the soft palate to the vocal folds. Second, movements of the tongue and jaw can modify the cross-sectional area of each tube independently by a ratio of approximately 10:1.⁹²

Although other mammals vocalize, only humans have an SVT with 1:1 proportions and in which the tongue can modify their cross-sections independently. In nonhuman mammals with snouts, the SVT_h is relatively long because the lower face is long; the SVT_v is short because the hyoid is positioned relatively high relative to the mandible. As Negus⁹³ noted, this configuration permits the epiglottis, which is suspended from the hyoid, to contact the soft palate, forming a "tube within a tube." The advantage of this configuration is that air can travel directly between the nasopharynx and the trachea through the portion of the pharynx in which food and liquids also travel, thereby minimizing the risk of asphyxiation or aspiration. But during human postnatal ontogeny, the hyoid descends relative to the soft palate, losing contact by about 3 months. The SVT_h/SVT_v ratio is 1.4 in a human infant, but reaches 1.1 by approximately 7–8 years.⁹⁴ As the ratio approaches 1.0, speech becomes more quantal and perception errors decrease.^{95,96} Because descent of the larynx leads to a trade-off between intelligible speech and risk of asphyxiation, the low human hyoid is evidence of selection for speech capabilities at the expense of other fitness costs.⁹²

Note that a 1:1 SVT_h/SVT_v ratio is not necessary for articulate, intelligible speech, but influences the degree to which speech is quantal.

Thus, considerable effort has been devoted to estimating the position of the hyoid and larynx in fossil hominids in order to make inferences about the evolution of speech capabilities. Most efforts have been disproved. Originally, it was suggested that the angle of the cranial base, both internal and external, was related to the position of the hyoid, based on evidence that the larynx descends postnatally relative to the soft palate as the cranial base flexes.^{8,97,98} This hypothesis, however, was disproved by evidence that there is no correlation during human ontogeny between laryngeal descent and cranial base angulation.⁴¹ In another effort, Arensburg and colleagues⁹⁹ suggested that, based on its human-like anatomy, the Neanderthal hyoid had a human-like position. This inference, however, is unjustified because there is no evidence to link hyoid shape with hyoid position in humans or other species.

One possibility, however, that remains untested is that an anteroposteriorly shorter face does improve speech performance capabilities in modern versus archaic humans by reducing SVT_h relative to the SVT_v. In a normal human with an SVT of approximately 17 mm, the length of each portion of the SVT is about 8.5 cm. In a modern human with a normally long neck, this places the hyoid about 2–3 cm below the lower margin of the mandible⁹⁴ and the larynx about the level of the 6th cervical vertebra. If the human SVT_h were about 2 cm longer, as is the case for a Neanderthal then the SVT_v would also have to be 2 cm longer to maintain a 1:1 SVT_h/SVT_v. This presents a potential anatomical problem because it would require a correspondingly longer neck with taller cervical vertebrae to prevent the larynx from being positioned in the chest below the 7th cervical vertebra. Such a position would prevent infrahyoid muscles such as the sternothyroid from being depressors of the hyolaryngeal complex. While it is theoretically possible that archaic humans had relatively longer necks than modern humans do, measurements of Neanderthal cervical vertebrae indicate that they had necks that were similar or possibly

even slightly shorter than those of modern humans.^{100,101}

In short, it is reasonable to hypothesize that two derived aspects of the modern human cranium would have improved modern human performance capabilities for producing more quantal vowels that would be more stable and less susceptible to errors of perception. First, the modern human oral cavity is absolutely shorter by at least a centimeter. Second, the modern human cranial base is more flexed, thereby rotating the whole face including the back of the palate ventrally underneath the anterior cranial base, decreasing the length of the pharyngeal space behind the palate by another centimeter.²² The combined effect of these two shifts is to shorten SVT_h by approximately 2 cm. Of course a longer SVT_h and a non-1:1 SVT_h/SVT_v ratio does not allow one to infer that archaic humans couldn't speak or even lacked sophisticated language. But, given constraints on larynx position in the neck, combined with the risks of asphyxiation that presumably increase with greater separation of the epiglottis and soft palate (a hypothesis that needs to be tested), it is not unreasonable to speculate that a shorter face might have been selected for speech performance. To test this hypothesis, however, we need better data on neck length in Neanderthals and other archaic humans, as well as more reliable indicators of the position of the hyoid and larynx in fossil humans. Also, estimates of SVT proportions do not address the various other neurological bases of language and speech that must also have been targets of selection at some point in human evolution.

FINAL SPECULATIONS

As noted, the various hypotheses I have discussed are only speculations; much research is necessary to test them. The list of needed tests is long and challenging, but a few are especially important. First, in order to test if temporal lobe volume is relatively larger in modern than archaic humans, data are needed on the strength of the relationship, if any, between temporal lobe volume and middle

cranial fossa size, as the latter is the only way to infer temporal lobe volume from fossils. Along the same lines, it would be useful to test if humans with relatively larger or smaller temporal lobes have more or less flexed cranial bases.

A second issue to test is the extent to which decreases in facial size may be related functionally and developmentally to changes in food preparation techniques. Testing this hypothesis more thoroughly will require more information on how strains are generated in the uniquely shaped human face and the extent to which pounding versus cooking influences the biomechanics of force resistance in the face. In addition, we need more data on the evidence of cooking versus other forms of food preparation from the archeological and fossil records. Another key source of evidence lies in teeth, the size of which may affect occlusal performance differently during the eating of cooked, pounded, and raw food.⁶³

A third issue that requires further analysis is endurance running, as this behavior may relate to both head balance and pharyngeal shortening. In addition to understanding more about the biophysics of airflow during respiration and its thermoregulatory effects, we need to understand more thoroughly the challenges that the heel-strike transient poses for head pitching during running, and how the unique configuration of the human head, neck, and upper body counteract these forces. In addition, more data are needed on the importance of running in human evolution. This is not an easy issue to address because, since the invention of the bow and arrow about 20,000 years ago, running has almost certainly become less important in human foraging societies. Modern human hunter-gatherers such as the Hadza and the Bushmen do run occasionally,^{76,102,103} but ER is no longer as necessary as it once may have been. Nonetheless, human ER performance, which is as impressive as or surpasses those of the best cursors, and relies on largely different biomechanics than walking, demands some explanation. We thus have to think creatively about the roles that run-

ning may have played in past hunter-gatherer behavior and the ways in which aspects of modern human skeletal morphology would have improved ER performance.

A fourth problem is speech, which may be the most intractable of all problems related to modern human origins. The biggest immediate problem is to find some reliable way to estimate the proportions of the SVT using skeletal data. The preceding analysis is not only informal and unquantitative, but also avoided making actual estimates of SVT_v length. Instead, it examined the effects of possible maximum SVT_v length on SVT proportions. Moreover, such analyses only address one aspect of speech, quantal vowel production, and have little to tell us about the other cognitive aspects of language that cannot be addressed using fossil data. Although the archeological record is frequently used to make inferences about language capabilities, it must be emphasized that such inferences are fraught with complications. Evidence of symbolism appears to be coincident with complex cognition, but only up to a point. The absence of evidence of symbolic art should never be used as evidence of the absence of abstract cognitive tasks such as language. Such logic might also lead us to conclude falsely that industrial modern humans have more complex cognitive capabilities than did Paleolithic hunter-gatherers or Neolithic farmers.

Finally, with regard to all the preceding hypotheses, there is the persistent problem of adaptations versus spandrels. Many of the features I have discussed are related to more than one function, and they have complex developmental bases. Thus, a persistent problem is to figure out ways to distinguish between spandrels and adaptations. As noted, one key issue is choosing appropriate null hypotheses to reject when testing whether features are adaptations, spandrels, or neither.

In spite of all these caveats and problems, let us conclude by assuming, blithely, that the foregoing speculations are corroborated. How, then, might they fit into a broader evolutionary scenario to explain how selec-

tion might have operated in the origin of *H. sapiens* some 200,000 years ago in Africa? Opinions on this question are likely to be varied, but the various major derived features of the *H. sapiens* skull all indicate some combination of changes in three aspects of behavior: improved running capabilities, including better head balancing and thermoregulation; increased reliance or dependence on cooking; and some suite of cognitive shifts in terms of speech and possibly other aspects of complex reasoning, perception, and/or knowledge (admittedly, this is highly speculative). To me, these shifts all point to a way of life, still evident in hunter-gatherer societies, that may have differed between modern and archaic *Homo*. Notably, modern human foragers rarely face starvation because they rely on social networks and cooperative relationships within a large group of nonkin that involves considerable sharing of meat, along with a diversity of other foods. Interestingly, many of the factors that underlie this overall strategy are linked, for several reasons, by endurance running, cooking, and language.

First, until the invention of modern technologies such as the bow and arrow, endurance running was probably useful in order to hunt and scavenge successfully with low risk of physical harm. Second, while hunting is critical for modern humans who require very high-quality diets relative to body mass, hunting is also a low-percentage endeavor; it cannot be accomplished without food sharing and cooking. Without the existence of reliable sharing, hunters who return to camp empty-handed would suffer reduced fitness, as would their families. In addition, there is a good argument to be made that cooking is an important complementary strategy to food sharing. Recall that chimpanzees, like many mammals, spend at least half their day eating, largely because they need to fill their stomachs regularly (about every two hours) with relatively high-fiber-content food. As Wrangham and Conklin-Brittain⁶¹ noted, cooking not only improves the nutrient content of food, but also decreases digestion time. Without cooked food, it is

doubtful that modern hunters could spend a large proportion of the day hunting and still satisfy their nutrient needs with a chimpanzee-like diet upon returning to camp. Cooking thus enables modern human hunters and their families to rely on meat, which has a lower probability of successful acquisition but a higher potential yield, and still be able to eat enough when they get back to camp empty-handed.

the various major derived features of the *H. sapiens* skull all indicate some combination of changes in three aspects of behavior: improved running capabilities, including better head balancing and thermoregulation; increased reliance or dependence on cooking; and some suite of cognitive shifts

Finally, this sort of way of life requires language and other cognitive skills in order to maintain social relationships and to foster among nonkin the cooperation necessary for food sharing. These cognitive skills, doubtless, were also advantageous for many other key tasks such as tracking animals and monitoring resources in complex changing habitats.

In short, although archaic humans may have done everything that modern humans did (hunt, speak, share, and even cook), it is interesting to speculate that modern humans may have invented a more intense, socially cooperative, and technologically based way of using these skills. This combination of hunting, sharing, cooking, communicating, and cooperating may have provided the behavioral context for selection on

human skull form that we first see in modern *H. sapiens* about 200,000 years ago,¹⁰⁴ and which appears more or less coincidentally in the archaeological record.¹⁰⁵ Testing this hypothesis and its components will be a serious but enjoyable challenge.

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