

CHAPTER 11

The Evolution of Human Speech: Comparative Studies

HUMAN SPEECH HAS traditionally been identified as a unique defining characteristic of *Homo sapiens*. A discussion of the evolution of human speech thus necessarily involves the question of human uniqueness. The particular path that I shall take in following the possible evolution of human speech, however, touches on some broader questions regarding human uniqueness and the nature of the mechanisms of evolution. I have argued throughout this book that human linguistic ability is based on rather general neural mechanisms that structure the cognitive behavior of humans as well as other animals, plus a set of species-specific mechanisms that structure the particular form of human speech. Whereas the enhanced cognitive ability of modern *Homo sapiens* involves the gradual elaboration of neural mechanisms that can be found in other living animals, the species-specific aspects of human speech are unique and follow from anatomical specializations and matching neural mechanisms that are not present in other living animals. I will focus on the evolution of the human ^{supralaryngeal} vocal tract, using data derived by the methods of comparative anatomy.

These data are consistent with what I shall term a "functional branch-point" theory for natural selection. This theory differentiates between evolutionary change at the structural, anatomical level and the possibility for abrupt, qualitatively different functional selective advantages. A functional branch-point theory for evolution by means of natural selection claims that a process of gradual anatomical change can at certain points yield "sudden" functional advantages that will lead to qualitatively different patterns of behavior in a species. A functional branch-point theory accounts for the tempo of evolution, which, as Gould and Eldridge (1977) note, is not always even. Long periods of stasis marked by little change can occur, "punctuated" by intervals of rapid evolutionary change. The anatomical and fossil data relevant to the evolution of the human vocal tract, however, refute

Gould's (1977) claim that a special, "unique" evolutionary mechanism—neoteny—was operant in hominid evolution. Human uniqueness thus does not involve any unique evolutionary mechanism or the higher directing force implicit in Gould's model.

I will not here discuss in detail the evolution of other aspects of human language. I have already discussed such aspects as automatization, critical periods, the status of words as markers for fuzzy concepts, the role of pragmatic context, and the possible evolution of the neural bases for rule-governed morphophonemic and syntactic processes. Comparative data on the linguistic and cognitive ability of apes using modified versions of American Sign Language and other symbolic systems are relevant to the discussion of the evolution of these aspects of language since they reveal the cognitive base from which hominid evolution probably departed. Studies of the acquisition of language by human children likewise are relevant. I will note some of the features of hominid culture that are consistent with the presence of language. We know something about the tool kit of early hominids because they worked stone to make tools, and stones can survive thousands or millions of years. We also know a little about their burial rituals, habitation sites, and diet. Some aspects of the pattern of archaic hominid culture are apparent in the record of the fossil bones themselves, which show that the infirm were cared for. However, we have no record whatsoever of their actual utterances, which makes discussions of syntax, morphophonemics, word forms, and the like rather speculative, to say the least. Many discussions of the possible syntactic ability of early hominids have attempted to make use of the indirect evidence of hominid culture. Certainly the presence of burial rituals and of a fairly complex tool technology is consistent with the presence of language. However, at present I would not agree with even my own previous inferences (1975a, pp. 163–170) that posit a definite connection between a Lavalloisian tool culture and a transformational grammar. There are simply too many other cognitive strategies that could account for the steps that are necessary to make a stone tool for any conclusion on the precise nature of the syntax of the language of some archaic, extinct hominids to be anything but speculative.

CULTURE AND THE EVOLUTION OF LANGUAGE

Many discussions of the evolution of language have likewise attempted to key the "invention" or "appearance" of words or some putative "unique" quality of the syntax, morphology, semantic structure, and so on, of human language to some aspect of human culture.

Various aspects of human culture have been noted that hypothetically demonstrate a particular level of syntactic or morphophonemic complexity—for example, the division of labor in human societies, hunting, the nuclear family, cave painting, thin-bladed stone tools, burial rituals, manufactured objects that have hinges. I do not see how these proposals are particularly relevant in light of the cultural diversity of human society throughout even the historical period. Human linguistic ability did not change with the introduction of the wheel into different cultures, nor have changes in the structure of the American family had any significance with respect to our linguistic ability.

I also doubt that there is any single aspect of human culture that in provided the key to language or even yielded the factor that gave a selective advantage to variations that would enhance human linguistic ability. Cultural patterns like the division of labor that hypothetically provides a selective advantage for the evolution of human language also occur in nonhuman primates like baboons. Though a phenomenon like mother-to-infant communication may be a factor that will enhance the selective value of communication, it likewise can be observed in the behavior of modern chimpanzees (Goodall, 1974). Markers like the presence of a stone-tool technology appear to be exclusively hominid patterns of behavior, though we can see similar but simpler parallels in animals like the California sea otter (Kenyon, 1969). However, how can we possibly test the inferences that we may draw regarding the syntactic or morphologic ability of hominids who made stone axes? Would any linguist dare to predict the syntactic system or morphology of a present-day human culture if he or she had only a sample of bowls, pots, pans, and knives to work with? We could arrange a test of such speculations using the comparative method. Linguists who thought that they could deduce the form of syntax or inventory of words from indirect cultural evidence could be presented with the artifacts of contemporary human isolates. If they were able to predict the different linguistic forms from the evidence of pots, pans, arrows, baskets, agriculture, and the like, their theories would

have some merit.

The data that we need to study the evolution of language are those of language. We do not have any record of the sentences or words that archaic, extinct hominids or our more immediate ancestors uttered 1 million, 100,000, or 30,000 years ago. We therefore cannot say much about how they put words together (their syntax) or how they modified words (their morphology). If we knew more about the neural bases of syntax and morphology, we might be able to make some inferences through reconstructions of the brains of fossil

that would be difficult since the soft tissue of the brain is never preserved long after death. However, I believe that we can derive some insights regarding the evolution of human language by studying the evolution of human speech.

As I have noted throughout this book, human speech is an integral element of human language. The species-specific aspects of human language indeed may be at the level of speech production, specialized speech perception, which appear to reflect the presence of neural devices that interface with a cognitive, general-purpose neural "computer." The properties of human speech, if this view is correct, then must reflect the neural devices that govern the production and perception of speech. By studying speech, we can derive some insight into the function and organization of the brain. Although hominids have no direct evidence of the speech of various fossil hominids, the physiology of speech production is known, and so we can deduce some aspects of the nature of the sounds that various fossil hominids could have produced if we can determine their speech-producing anatomy. This last problem is not trivial, but we can make use of the supralaryngeal comparative anatomy to derive the general form of the

geal airways of fossil hominids.

RECONSTRUCTING THE SUPRALARYNGEAL VOCAL TRACTS OF EXTINCT HOMINIDS

The supralaryngeal airways of animals are defined by soft tissue muscles, ligaments, and so on, as well as by some bones. Soft tissue sometimes is preserved long after death, as when an animal's body rests in a peat bog or in ice. Soft tissue can also be indirectly preserved when an animal's body leaves an impression in mud that subsequently hardens. However, we at present lack any material supralaryngeal indicates the morphology of the soft tissue of the

airway of extinct hominids. Despite the lack of direct evidence, it is possible to reconstruct these supralaryngeal airways. The process of reconstruction and the problems are similar to those involved in the reconstruction of other soft tissue. The muscles of dinosaurs, for example, can be reconstructed even though we have no samples of dinosaur muscle tissue. The methods of comparative anatomy and the overall continuity of evolution make these reconstructions possible. First of all muscles, as Campbell (1966) notes, "leave marks on bones." You can easily feel, for example, the facets or points of attachment where your digastric muscles are attached to, or inserted into, the lower border of the

inside of your mandible (lower jaw). The facets are shallow nubbled pits. Since muscles are essentially "glued" to the bones or cartilages, a greater surface area yields a stronger gluejoint. A shallow pit yields a greater surface area than would be the case if it did not exist. The larger the surface area of the facet, the bigger the muscle that is glued to the facet. When electrically stimulated, muscles pull on the bones or cartilages that they are attached to. A big muscle will exert a greater force on the bones than a smaller muscle; hence the facets of bigger muscles have greater surface areas. Thus we can deduce the size of a muscle that once was attached to a bone by looking at the surface area of its facet. Small bumps, nubbles, also increase the area of the "glue joint." The principle is again quite similar to that relevant to carpentry, where the surface of a joint frequently is roughened to yield a stronger glue joint.

Note that the digastric muscle in Figure 11-1 runs down and back from the mandible to the hyoid bone. The hyoid bone is a small semicircular bone that supports the larynx. Note, for the moment, that the "tilt" of the facets by which the digastrics are attached to the mandible lines up with the direction in which the digastrics run between the mandible and the hyoid. This arrangement represents good engineering since the force that the digastrics apply to the mandible is exerted in the direction in which they run. The gluejoint at the facet thus is oriented perpendicular to the direction in which the muscle exerts a force. Figure 11-1 sketches this relationship. The strength of the glued muscle-to-mandible joint therefore is its *tensile* strength. The tensile strength of most materials is substantially greater than their shear strength. If you, for example, attempt to pull apart a stick of chalkboard chalk *along* its length, you will not succeed because its tensile strength is too high. But you can easily snap it in two *across* its long dimension because its shear strength is much lower. The situation is similar for muscles and their gluejoints. Muscles and their facets tend to be lined up so that shear forces are minimized in the normal action pattern of the muscles. Muscles and ligaments are often "pulled" when they are stressed in some odd direction—a direction in which large shear forces pull the bone-to-muscle joint asunder. We thus can infer the probable direction in which a muscle was inserted into a bone by examining the geometry of the facets and bones.

These general observations about the arrangements of bones and muscles are, however, only one aspect of the comparative method. Animals are functional complexes of bones and soft tissue. All living animals are related; they are, moreover, related in various degrees to all extinct animals, of which extinct hominids form a subclass. We can

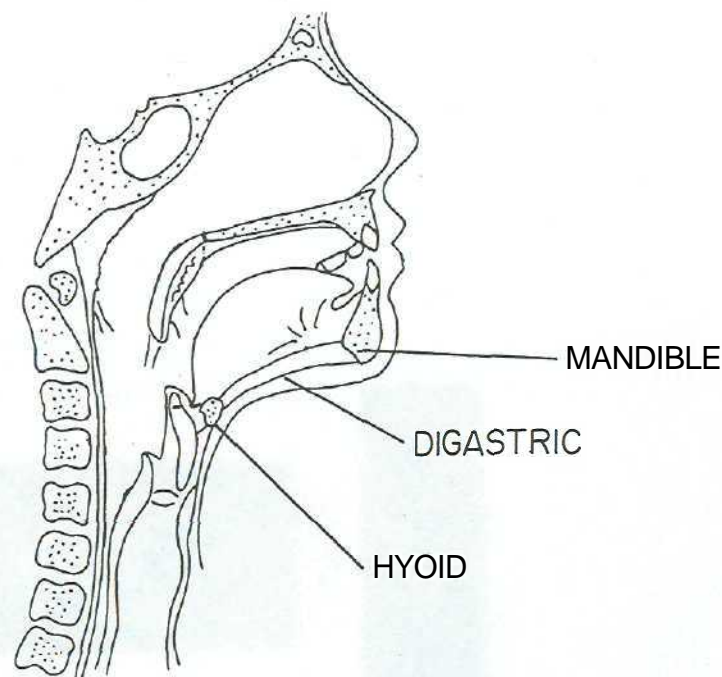


FIGURE 11-1.

The anterior belly of the digastric muscle in relation to its insertion in the mandible and the hyoid bone. The digastric runs down and back from the mandible to the hyoid. The lower inside surface of the mandible where it is attached is angled to minimize shear forces.

derive reasonably certain reconstructions of the soft tissue structures of extinct hominids by comparing the bones of extinct forms with the bones and soft tissue of related, living animals. The problem of reconstructing the *supralaryngeal* airway of an extinct hominid, say *Australopithecus africanus*, is similar to the problem of reconstructing the neck or the legs of a dinosaur. We can look at the bones and facets for the muscles of the fossilized extinct animals. If we are reconstructing dinosaurs, we can also look at the bones and muscles of *living* lizards that have bones which resemble those of extinct dinosaurs and that are closely related to these extinct animals. The bones and muscles of lizards "go together" in a consistent pattern; there are

variations in the pattern, to be sure, but there is an overall "normal" pattern that has been optimized through the process of natural selection. We thus can make a reasonable reconstruction of an extinct dinosaur.

ONTOGENY AND PHYLOGENY

The living animals that give us an insight into the relation of the soft tissue of the supralaryngeal vocal tract to the fossil remains of australopithecines and other extinct hominids are the living nonhuman primates and newborn human beings. Human neonates are qualitatively different from human adults. The ontogenetic development of all animals necessarily proceeds from the simple stage that exists after conception to the complexity of the adult stage. The process of development is not complete at birth. The situation is similar for all primates. Newborn chimpanzees, gorillas, and the like, all differ from adult members of their species. Human neonates likewise differ from adult human beings.

The adult forms of virtually all animals differ from the newborn and late embryonic stages. Darwin (1859, pp. 439-450) discusses the similarities between related species in their embryonic stages in detail. Haeckel's (1866) "Biogenetic Law: Ontogeny Recapitulates Phylogeny" was actually formulated by Darwin, who attributes the observation to Louis Agassiz:

In two groups of animals, however much they may at present differ from each other in structure and habits, if they pass through the same or similar embryonic stages, we may feel assured that they have both descended from the same or nearly similar parents, and are therefore in that degree closely related. Thus community in embryonic structure reveals community of descent.

As the embryonic state of each species and group of species partially shows us the structure of their less modified ancient progenitors, we can clearly see why ancient and extinct forms of life should resemble the embryos of their descendants,—our existing species. Agassiz believes this to be a law of nature; but I am bound to confess that I only hope to see the law hereafter proved true.

(1859, p. 449)

Darwin characteristically tested this "law" by experiments using the data of artificial selection. We know that the different breeds of domestic dogs have similar ancestors, that different breeds of pigeons

have similar ancestors, and so on. Darwin compared greyhounds and bulldogs, which, though they appear so different in their adult state, "are most closely allied, and have probably descended from the same wild stock" (1859, p. 445). He measured old dogs and their 6-day-old puppies and "found that the puppies had not nearly attained their full amount of proportional difference." Similar measurements involving horses and their foals and the nestling birds of different varieties of domestic pigeons replicated these data. Human adults and human newborn infants differ in their own special way as much as newborn chimpanzees or nonhuman primates differ from their parents.

It is apparently difficult for people to notice that familiar animals that they *know* are similar are really different. Thus when Darwin measured dogs and puppies as well as full-grown cart horses and racehorses and their foals, he was told by breeders that the puppies and foals of different breeds differed from each other as much as their parents did. The claim that human adults resemble newborn infants more than is the case for other primates probably rests on this same lack of objectivity regarding familiar animals that we know are the "same." Who could be more human than our infant sons and daughters? It is furthermore easy to overlook the anatomical and physiologic data that demonstrate that we differ from newborn human infants. The first comprehensive anatomical atlas of the human newborn, Crelin's, for example, was published in 1969.

The theory of neoteny that has been revived by Gould (1977) and Gould and Eldridge (1977) claims that human evolution involves a unique process: neoteny. We supposedly retain the morphology and physiology associated with the newborn. In contrast, all other primates grow up. Gould and Eldridge claim that the rapid pace of human evolution follows from modification of the regulatory genes that govern human development. They thus explain the rapid changes that have occurred in the last ten million years of hominid evolution by the process of "neotenization." We, however, do not resemble newborn infants; adult human beings diverge from newborn infants as much as, if not more than, other adult primates diverge from their newborns. Human newborn infants conform to the general principle noted by Darwin: they are closer to the newborn forms of nonhuman primates; they reveal our common ancestry. Human newborn infants, in particular, retain the supralaryngeal airways and associated skeletal morphology that occur in living nonhuman primates. We can use the skeletal similarities between newborn human infants, adult and juvenile nonhuman primates, and extinct fossil hominids too as a guide to the reconstruction of the fossil supralaryngeal airways.

Living human newborn infants and nonhuman primates thus serve the same function in the reconstruction of a hominid fossil's supralaryngeal airway as a lizard does for the leg muscles or neck of a dinosaur. The lizard is not a dinosaur, but it is closely related to extinct dinosaurs and has a similar skeleton. Newborn human infants likewise are not australopithecines or Neanderthal men or women, but they are closely related to these hominids and have similar skeletal structures. The process of reconstruction involves four steps.

1. We must note the correspondences between soft tissue and skeletal structure that occur in human neonates and nonhuman primates.
2. We then must evaluate the generality of these relationships by looking at the total range of nonhuman primates and other animals.
3. We must determine the functional significance of supralaryngeal morphology with respect to that of human neonates, nonhuman primates, and adult humans.
4. We can then extend our inferences concerning soft tissue, skeletal structure, and physiologic function to the reconstruction of the fossil supralaryngeal vocal tract, using the total skeletal complex as an anchor point for our reconstruction.

COMPARATIVE ANATOMY AND PHYSIOLOGY

Comparisons between the skeletal structure, brains, hands, and so on of humans and other primates date back to the first anatomical studies of apes at the end of the seventeenth century. Victor Negus's comprehensive study of the comparative anatomy and physiology of the larynx is, however, the primary model for the comparative study of the upper respiratory system. Negus's data and conclusions are presented in two works, *The Mechanism of the Larynx* (1928) and *The Comparative Anatomy and Physiology of the Larynx* (1949). Negus traces the evolution of the larynx from its appearance in ancient fish, who, like similar living fish such as the African lung fish and the mud fish of the Amazon, could breathe air (1949, pp. 2-8). Negus points out the selective advantage of the larynx in these air-breathing fish vis-a-vis still more "primitive" air-breathing fish like the climbing perch, which lack a larynx. The function of the larynx in air-breathing fish is to prevent water from entering the lung. The larynx in these animals is essentially a valve that is positioned in the floor of the pharynx. When the fish is in the water, the laryngeal valve closes; when the fish is out of the water, the larynx opens and allows air to be swallowed and

forced into the fish's lung. The laryngeal valve in these fishes consists of a simple sphincter. It is interesting to note in this regard that the human embryo, when it is about 5 mm long, shows a slit in the pharyngeal floor "much like that of the Lung Fish" (Negus, 1949, p. 6).

The origin of the larynx was to facilitate air breathing in fish that *already* could breathe air. The initial developments that allowed primitive fish which resembled living forms like the climbing perch to breathe air follow from the process of "preadaptation"—"the highly important fact that an organ originally constructed for one purpose, namely flotation, may be converted into one for a wholly different purpose, namely respiration" (Darwin, 1859, p. 190). The swim bladders of fish, which are homologous with the lungs of vertebrates, evolved for flotation. Fish can extract dissolved air from water by means of their gills. The swim bladders of fish are elastic sacs that can be filled with air extracted from water by a fish's gills. Air-breathing fish instead filled their swim-bladder/lung by swallowing air, which then was transferred to their bloodstream from the swim bladder serving as a lung. The change in *function* of the swim bladder constitutes a *functional branch-point*. The new behavior is disjoint with the previous behavior of fish. Life out of water is quite different and novel compared with a watery existence.

Given these new conditions of life—life out of water—there are selective advantages for the further development of the larynx. *The presence of the larynx itself yields the possibility for further changes.* As Negus points out, the next stage in the evolution of the larynx was the development of fibers to pull the larynx open to allow more air into the lungs during breathing. Further stages of evolution yielded cartilages that facilitate the opening movements of the larynx. The elaboration of the larynx yields a second functional branch-point when it can act as a sound-generating device. The process of phonation, in which the vocal cords move rapidly inward and outward to convert the steady flow of air from the lungs into a series of "puffs" of air, can occur in the larynges of animals like frogs. Negus's (1949, pp. 40-42) comparative studies again demonstrate that many of the larynges of many animals are specialized for phonation at the expense of respiration.

FUNCTIONAL BRANCH-POINTS

Figure 11-2 illustrates these functional branch-points in the evolution of the upper respiratory system. A branch-point marks the point at which the course of evolution can potentially be changed by virtue of selection for a new mode of behavior that is of value to a group of

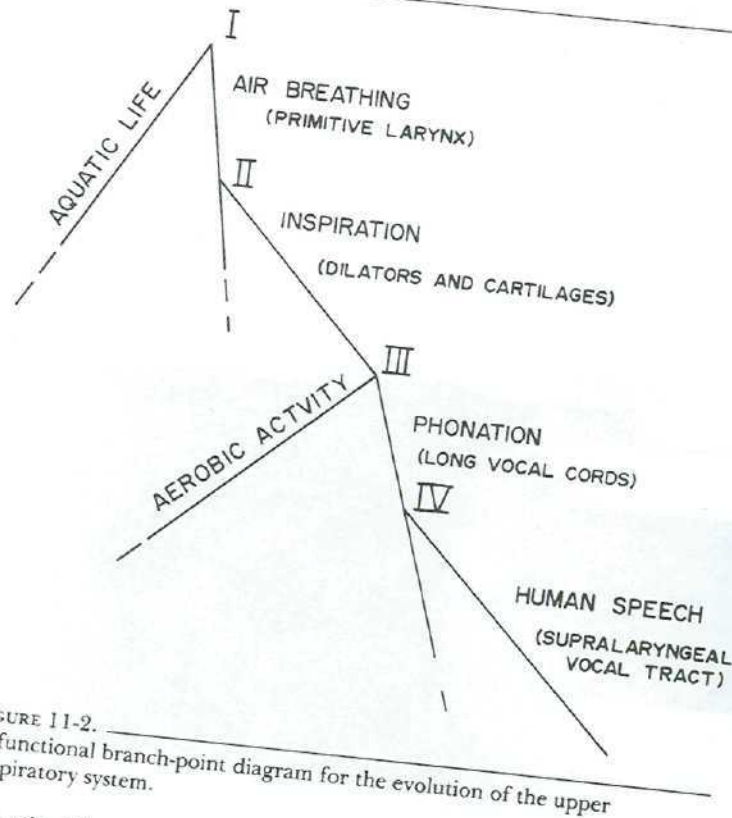


FIGURE 11-2.
A functional branch-point diagram for the evolution of the upper respiratory system.

animals. The new function may conflict with the old function, and rapid divergence can occur that ultimately will result in speciation as different populations retain different genetically transferred anatomical structures that have a selective advantage for either the new or the old function. The divergence can become quite extreme, as specializations for a given behavioral function can themselves lead to new functional branch-points. The concept of evolution by means of natural selection is often overlooked. A theory of natural selection that incorporates functional branch-points accounts for both the even tempo of evolution (Gould and Eldridge, 1977) and the value of small changes.

The selective value of small steps is apparent in the gradual changes that occur within a functional continuum, such as the differences in the dilators of the larynx (Negus, 1949, p. 7). Darwin's eloquent comment on the value of small changes holds true within a functional continuum:

For as all the inhabitants of each country are struggling together with nicely balanced forces, extremely slight modifications in structure or habits of one inhabitant would often give it an advantage over others; and still further modifications of the same kind would often still further increase the advantage. No country can be named in which all the native inhabitants are now so perfectly adapted to each other and to the physical conditions under which they live, that none of them could anyhow be improved.

(1859, p. 82)

Although I do not advocate a neo-Darwinian model for economic development, it is obvious that the branch-point model holds true for the marketplace. For example, in the "struggle for existence" that occurs in the development and sale of automobiles, small differences yield a selective advantage. The differences between competing cars is often so small that slight differences in cost, performance, or reliability have profound effects. The changes that occurred in the American marketplace in the 1970s derive from small advantages in the price and fuel efficiency of imported Japanese cars. The trend toward higher sales of Japanese cars can probably be arrested by similar small changes in the design and price of American-made cars. The competition between car makers represents a contest in which they are "struggling together with nicely balanced forces." In contrast, earlier in the century there was a rapid change when automobiles began to compete with horse-drawn carriages. The nature of the contest was inherently different. Finely designed carriages would not compete, no matter how well made or how durable they were. Automobiles were qualitatively different; a functional branch-point occurred, and new selective forces entered into the competition.

An observer charting the evolution of conveyances would see a long period extending over centuries in which gradual changes improved horse-drawn carriages. The period of horse-drawn carriage improvement would appear to be a "static" period compared to the "sudden" introduction and improvement of the automobile. However, the evolution of the automobile also was long and had its roots in the gradual improvements in engines that had been going on for several centuries. Improvements in metallurgy, manufacturing, and

the like that also had occurred gradually were all necessary factors for the invention of the automobile. A branch-point theory for natural selection accounts for the tempo of evolution. It differentiates between the slow, gradual process of change within a functional modality and the abrupt shifts in function that occur at a branch-point with the consequent opportunity for rapid change. Within a functional modality *slight* structural changes yield small selective advantages. At a branch-point small *structural* changes, such as alterations of the cartilages of the larynx that yield phonation, can produce an abrupt, *great functional* advantage by virtue of the selective advantage of the new mode of behavior.

LARYNGEAL MODIFICATIONS FOR RESPIRATION

A branch-point diagram captures phylogenetic divergence. The data of Negus (1949) are consistent with the four functional branch-points sketched in Figure 11-2. Negus discusses the anatomical bases of the first three stages in detail. The anatomical modifications that yield more efficient and controlled phonation at branch-point III, for example, impede efficient respiration. Different species went their own way with regard to the modifications of the larynx that would yield either more efficient respiration or phonation. Negus, for example, demonstrates that animals like horses have a larynx that is "designed" to maximize the flow of air to and from the lungs. In contrast, the human larynx is designed to enhance phonation for the process of vocal communication. Canids, which are social animals that also communicate by using vocalizations but that run down their game, represent an intermediate solution to the competing selective forces deriving from respiratory efficiency and phonation.

Figure 11-3 shows the relative area of the trachea, or windpipe, compared with the maximum opening of the larynx for a horse, a dog, and a human being (Negus, 1949, p. 31). The larynx acts as a valve with respect to the flow of air through the trachea, which leads to the lungs. Obviously a valve that can be opened wider will offer less resistance to the flow of air through the airway that leads to the lungs. All other things being equal, a wider opening will result in a greater airflow. You can demonstrate this to your own satisfaction by using a hydraulic analogy — opening the faucet of your kitchen sink. Animals that run long distances at a fast speed have to maintain aerobic conditions; that is, they have to transfer enough oxygen to their lungs to maintain the higher metabolic rate of sustained running. Horses thus have to

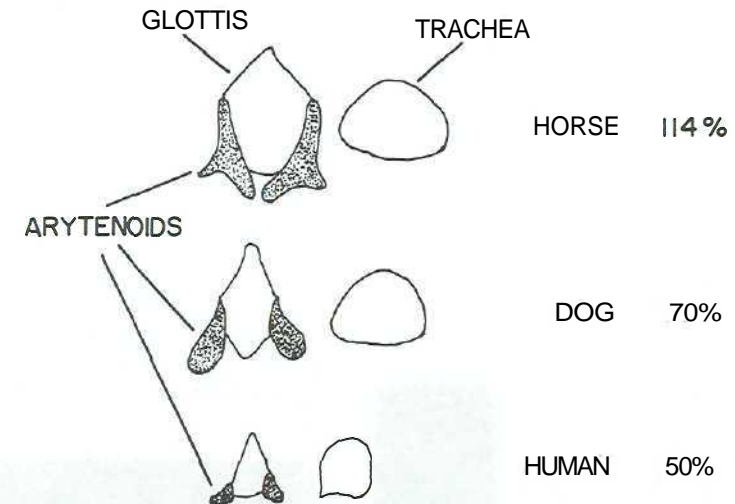


FIGURE 11-3. Relative opening of the larynx and trachea in horse, dog, and human being. The arytenoid cartilages are stippled in these transverse views looking down on the larynx. Note that the maximum opening of the larynx is smaller than that of the trachea in human beings, where it is 50 percent of the tracheal area. The human and canid larynges thus obstruct the airflow to the lungs even when they are wide open.

maintain a high flow rate of air to their lungs. The larynx of the horse and of other ungulates that use the strategy of running for long distances to escape from predators thus has evolved to open wide to yield the minimum resistance to airflow.

Figure 11-3 also shows the mechanics of the larynx that affect its maximum opening. Horses have a larynx that has long arytenoid cartilages. These cartilages swing apart to open the larynx for respiration. The sketch shows the two arytenoid cartilages abducted to the maximum open position. The cross section of the trachea immediately below the larynx is sketched to the right of the diagram of the open larynx. Note that the opening of the horse larynx is larger than the cross-sectional area of the trachea. The horse's larynx thus does not impede the airflow to the horse's lungs during respiration. Horses, in a sense, are optimally designed

for sustained long-distance running. Their hooves, legs, and larynges have evolved with the selective value of running as the crucial parameter in natural selection.

The sketch of the larynx of a dog (a staghound), in contrast, shows that the dog's larynx presents an obstacle to airflow even when it is at its maximum opening. The airway to the dog's lungs is restricted to 70 percent of the tracheal cross section. The sketches of the human larynx in its open respiratory state in Figure 11-3 shows that our airway also is restricted, to 50 percent of the tracheal cross section. The relative deficiencies of the dog and human larynges with respect to respiration follow from the short length of the arytenoid cartilages. The larynx opens for respiration by swinging the arytenoid cartilages outward from their posterior pivot point. Negus (1949, pp. 40-42) demonstrates that the optimum length of the arytenoid cartilages for maximizing the opening of the larynx relative to the trachea is about 0.7 times the diameter of the laryngeal opening. The nearest approach to this optimum length occurs in the Persian gazelle. The Persian gazelle can sustain speeds of 60 miles per hour. Human beings, in contrast, have almost the shortest arytenoid cartilages of any mammals relative to their tracheal cross section. Short arytenoid cartilages, however, have a functional advantage for phonation. High-speed motion pictures of the larynx show that phonation usually involves the anterior vocal cords, which run from the ends of the arytenoid cartilages to the thyroid cartilage (Timcke, von Leden, and Moore, 1958; Lieberman, 1967).

LARYNGEAL MODIFICATIONS FOR PHONATION

The soft parts of the larynx—the vocal cords, which consist of the vocal ligaments, and the thyroarytenoid and cricoarytenoid muscles—move during phonation. The heavy arytenoid cartilages normally do not move during steady-state phonation. In human beings phonation involving a heavy arytenoid cartilage usually yields a low-frequency "fry" or "creaky" laryngeal source. The average glottal (laryngeal) opening is large in fry phonation; airflow thus is high compared with the acoustic energy of fry phonation. Given the high mass of the arytenoid cartilages, fundamental frequency also is not so easy to control as it is in the normal registers for human phonation (Van den Berg, 1958). The functional trade-off therefore is between respiration and phonation. Animals who take the right branch-point at level III in Figure 11-2 thus retain changes that yield smaller

arytenoid cartilages and more efficient phonation. These animals, as Negus notes, are social animals that rely on vocal communication. The leftward branch at level II takes the direction of selection for more efficient respiration as part of a total behavior complex that stresses sustained, high-speed running.

THE STANDARD-PLAN SUPRALARYNGEAL VOCAL TRACT

The functional branch-point at level IV denotes the modifications of the supralaryngeal vocal tract that typify anatomically modern *Homo sapiens*. Negus, in his comprehensive *Comparative Anatomy*, noted the differences between the supralaryngeal vocal tract that is typical of modern human beings and the vocal tract characteristic of all other terrestrial mammals. Negus also noted some of the selective disadvantages of the adultlike human supralaryngeal tract, and in collaboration with Sir Arthur Keith he reconstructed the supralaryngeal vocal tract of a Neanderthal fossil (1949, p. 195). However, he was not able to evaluate the functional significance of the differences between the human and nonhuman supralaryngeal vocal tracts. This deficiency was not Negus's; the physiologic and perceptual studies of human speech production and perception that are germane to assessing this difference were carried out long after Negus's active days. In brief, the functional divergence at branch-point IV involves the competing demands of selection for vegetative functions like breathing, swallowing, and chewing versus phonetic efficiency for high data-rate communication. I will attempt to demonstrate that the "unique" supralaryngeal airways of anatomically modern *Homo sapiens* evolved to enhance vocal communication at the expense of these vegetative functions. I will also argue that until comparatively recent times, 50,000 years before the present, there were different groups of hominids, some of whom retained the primitive standard-plan supralaryngeal airway.

The peculiar deficiencies of the adult human supralaryngeal airways with respect to swallowing have long been noted. We simply are not very well designed with respect to swallowing, and thousands of deaths occur every year when people asphyxiate because a piece of food lodges in the larynx. Charles Darwin, for example, noted "the strange fact that every particle of food and drink which we swallow has to pass over the orifice of the trachea, with some risk of falling into the lungs" (1859, p. 191). These deficiencies do not occur to the same degree with the standard-plan supralaryngeal airway, which is also better adapted for breathing and chewing. Negus's primary contribu-

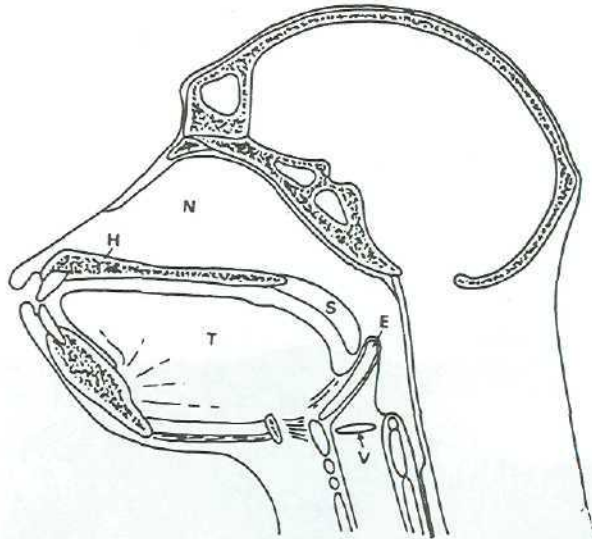


FIGURE 11-4.

Midsagittal view of the head of an adult chimpanzee: *N*, nasal cavity; *H*, hard palate; *S*, soft palate; *E*, epiglottis; *T*, tongue; *V*, vocal cords of larynx. (Adapted from Laitman and Heimbuch, 1982.)

tion with respect to our view of the physiology and evolution of the human supralaryngeal airway was his demonstration that there is a standard-plan airway from which we diverge in both an ontogenetic and a phylogenetic sense.

Figure 11-4 shows a schematic midsagittal section of the head of an adult chimpanzee and is a reasonable introduction to the anatomy of the nonhuman standard-plan supralaryngeal airway. If we were to slice a head in two on a plane midway and perpendicular to a line between the eyes, we would be able to see a midsagittal view. You can see the nasal and oral cavities of the supralaryngeal airway in the sketch. The animal's tongue is long and thin compared with that of an adultlike human being, and it is positioned entirely within the oral cavity, the animal's mouth. The larynx is positioned *behind* the tongue and is close to the roof of the nasopharynx, which leads into the nasal cavity. The roof of the nasopharynx consists of the bones that form part of the base of the skull. This fact is crucial to the reconstruction of

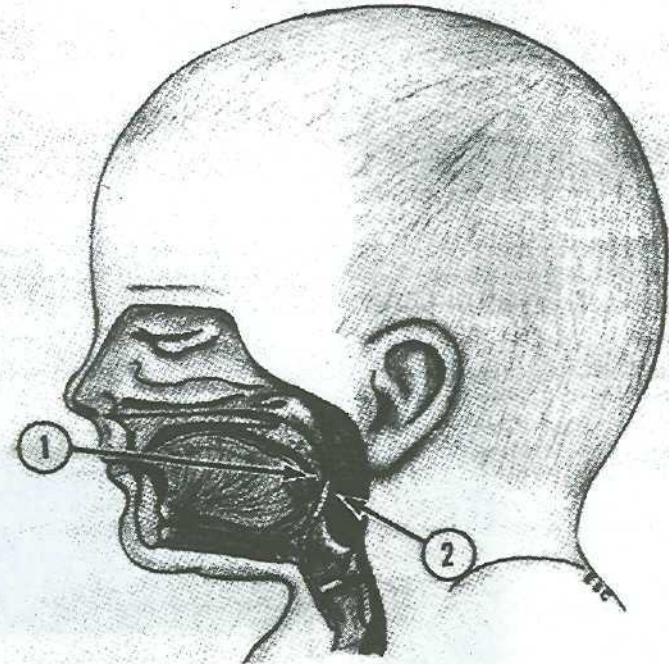


FIGURE 11-5.

Diagram of human newborn showing the larynx locked into the nasopharynx during quiet respiration. The soft palate "1" and epiglottis "2" overlap. (After Laitman, Crelin, and Conlogue, 1977.)

the supralaryngeal airways of fossils. The hard palate, which is also a bony structure that is often present in hominid fossils, forms the anterior (front) part of the roof of the animal's mouth. The posterior (back) part of the roof of the mouth is the soft palate, or velum. The velum can be pulled upward and backward by levator and tensor muscles (Bell-Berti, 1973).

The functional logic behind the morphology of the standard-plan supralaryngeal airway is apparent when we look at the position of the larynx during respiration. Figure 11-5 is a diagram of a human newborn showing the larynx locked into the nasopharynx during quiet respiration. The newborn infant moves the larynx upward into the nasopharynx. The high position of the larynx relative to the

nasopharynx of the standard-plan supralaryngeal airway allows the newborn to do this. Note that the epiglottis and soft palate overlap and form a double seal. The diameter of the larynx of the newborn is small in relation to the distance between the end of the bony hard palate and the base of the spinal column. There is also room for food or water to pass on either side of the elevated larynx. The larynx, in effect, functions as a tube that extends upward from the trachea into the nasopharynx. The soft palate, epiglottis, and pharyngeal constrictors seal the airway that is formed through the nose into the larynx and trachea and to the lungs. Newborn infants can simultaneously swallow fluids while they breathe. The fluids enter their mouths, pass to either side of the elevated larynx, and enter the pharynx and esophagus positioned *behind* the larynx. Since their airway for breathing runs from the nose through the larynx-to-nasopharynx seal, liquids cannot fall into the larynx and trachea to choke the newborn infant. The neural mechanisms that control respiration are also matched to the standard-plan supralaryngeal morphology of the human newborn. Human newborns are obligate nose breathers. As Crelin notes, "Obstructions of the nasal airway by any means produces an extremely stressful reaction and the infant will submit to breathing through the mouth only when the point of suffocation is reached" (1973, p. 28).

The standard-plan morphology of the human newborn is typical of *all* other mammals, adult and young, which can elevate their larynx to form an airway through the nose to the lungs that is sealed from the mouth. Ibexes, horses, dogs, monkeys, apes—all can simultaneously breathe and drink (Negus, 1949; Laitman, Crelin, and Conlogue, 1977). Figure 11-6 shows the supralaryngeal airways of an ibex and a dog. Note that both have long, flat tongues that are positioned entirely within the mouth. The larynx is positioned high close to the base of the skull. The epiglottis of the larynx thus is positioned so that it can easily make contact with the soft palate. These animals are obligate nose breathers. The ingestion of fluids and small, solid objects can take place while these animals breathe; the fluid is routed around either side of the larynx.

Two other vegetative functional differences that distinguish adultlike human beings from other mammals can be correlated with the morphology of the standard-plan airway. The first difference is in respiration—the larynx exits directly into the nose. Compared with the adultlike human supralaryngeal airway, there is less of a bend in the airway. As Negus (1949, p. 33) notes, this results in a lower airflow resistance. The second vegetative functional difference is in chewing.

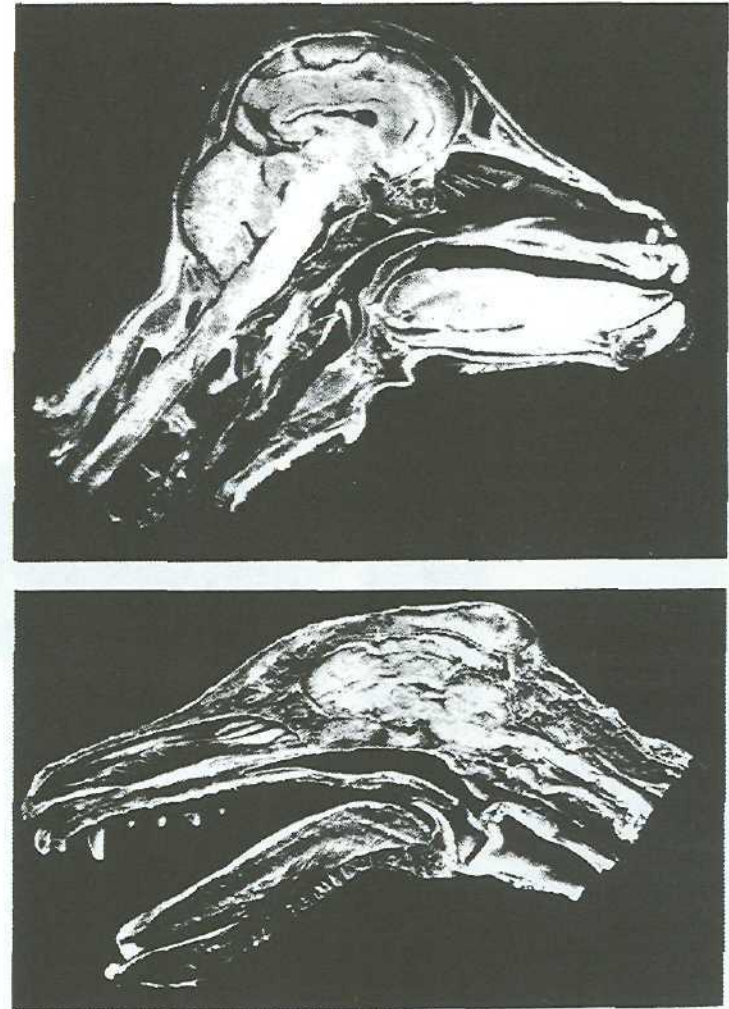


FIGURE 11-6. Sections of the heads of an ibex (above) and a dog (below) showing the nonhuman standard-plan supralaryngeal airway. The high position of the larynx and the tongue's location in the oral cavity are apparent. (After Negus, 1949.)

The body of the mandible is relatively long compared with its ramus, consistent with the long, thin tongue. There is more room for teeth in the standard-plan morphology. Efficiency of chewing, all other things being equal, is a function of the tooth area that comes into contact during chewing. Studies of the efficiency of chewing that were directed at perfecting dentures show that a "swept tooth area" is the most important determinant of chewing efficiency (Manley and Braley, 1950; Manley and Shiere, 1950; Manley and Vinton, 1951). I will return to this topic in connection with the anatomical specializations of classic Neanderthal hominids (Trinkaus and Howells, 1979), which I think represent a hominid line that specialized for chewing at the expense of phonetic efficiency at branch-point IV.

THE HUMAN SUPRALARYNGEAL VOCAL TRACT

Figure 11-7 shows a midsagittal view of an adult human supralaryngeal vocal tract. The restructuring of the supralaryngeal vocal tract in human beings is quite pronounced by age 3 months (George, 1978). Negus again noted that the human supralaryngeal vocal tract gradually takes form in the course of ontogenetic development:

There is a gradual descent [of the larynx] through the embryo and foetus and child. The reason for this descent depends partly on the assumption of erect posture, with the head flexed on the spine, so as to bring the eyes into a line of vision parallel to the ground . . . But this alone would not account for the position, since similar changes have occurred in the higher Apes without a corresponding descent of the larynx. The determining factor in Man is recession of the jaws; there is no prognathous snout . . . The tongue however retains the size it had in Apes and more primitive types of Man, and in consequence it is curved, occupying a position partly in the mouth and partly in the pharynx. As the larynx is closely approximated to its hinder end, there is of necessity descent in the neck; briefly stated the tongue has pushed the larynx to a low position, opposite the fourth, fifth and sixth cervical vertebrae.

(1949, pp. 25-26)

Negus, in other words, does not treat the descent of the larynx as an isolated event. It is necessarily related to the total skeletal support system and the tongue. Still x rays and cineradiographic data derived from many normal speakers (a total sample size in excess of 200 subjects) show that the tongue body moves as an almost undistorted

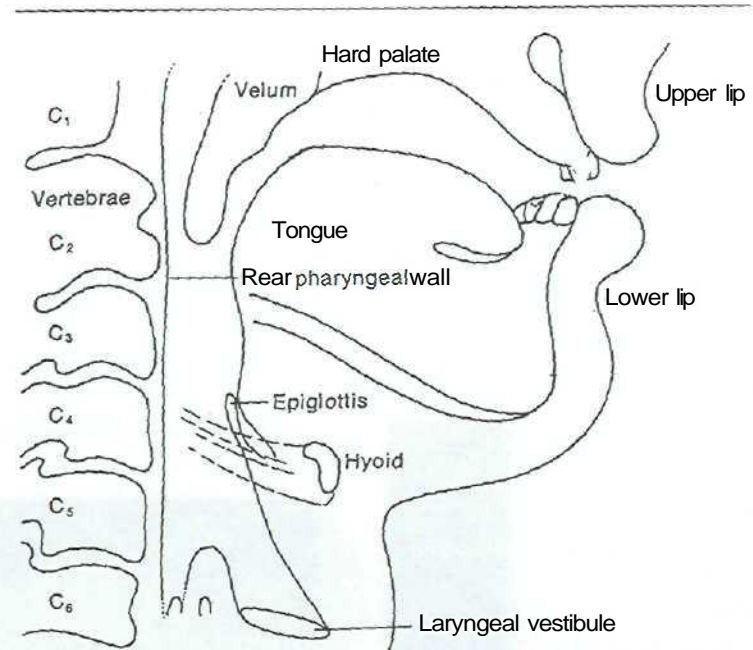


FIGURE 11-7. Midsagittal view of the adult human supralaryngeal vocal tract.

body during the production of speech. The contour of the tongue body that forms the floor of the mouth and anterior wall of the pharynx, moreover, is, as Negus noted, curved. Its shape can be closely approximated by an arc of a circle (Nearey, 1978).

Human speakers, when they produce the vowels of a language like English (where tongue blade maneuvers are not used), move their tongue about in the space defined by the roof of the mouth and the spinal column. Figure 11-8 shows the position of the tongue for the production of the vowels [i] and [a] of American English. Nearey derived these data from cineradiographic x-ray movies of normal adult speakers. The tongue contours and center points for all the vowels of American English were derived by Nearey. The "horizontal" top part of the tongue body effectively determines the cross-sectional area of the mouth; the vertical back part of the tongue determines the cross-sectional area of the pharynx. The intersection

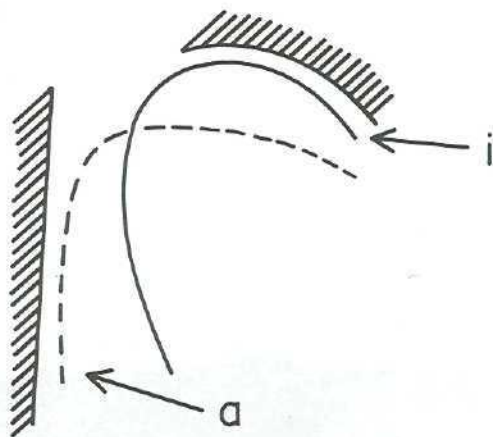


FIGURE 11-8.

Midsagittal view showing the contour of the tongue with respect to the hard palate and rear pharyngeal wall during the production of the vowels [i] and [a]. The contours were traced by Nearey from a cineradiographic film of an adult speaker of American-English. (After Nearey, 1978.)

of the planes defined by the vertebral column and the palate of the mouth yields an approximate right angle. The angle at which the pharynx and oral cavity intersect does not change when you bend your neck. X rays of people bending their necks forward and backward to the extreme limits of flexion (Shelton and Bosma, 1962) show that the bend takes place below the pharynx to the oral cavity bend, between the third and the fifth cervical vertebrae.

The speaker moves the tongue within this space. If the tongue is moved upward and toward the lips to produce the vowel [i], the tongue will yield the two-tube airway sketched in Figure 11-9. The cross-sectional area of the oral cavity will be constricted. In contrast, the cross-sectional area of the pharyngeal cavity will be quite large. The discontinuity at the approximate midpoint of the supralaryngeal airway will generate a vowel sound that has the *quantal* properties identified by Stevens (1972). The vowel [a] likewise is produced by a two-tube airway in which the pharyngeal tube is constricted and the oral tube expanded. The speaker in this case moves the tongue downward and back toward the vertebral column.

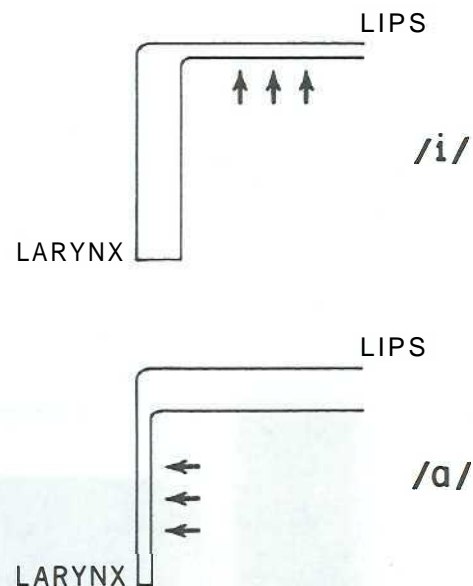


FIGURE 11-9.

Schematized adult human two-tube supralaryngeal airway.

THE PHONETIC DEFICIENCY OF THE STANDARD-PLAN AIRWAY

Computer-modeling studies in which the supralaryngeal airways of rhesus monkeys (Lieberman, Klatt, and Wilson, 1970), chimpanzee, and newborn human beings (Lieberman, Crelin, and Klatt, 1972) were systematically perturbed through the possible range of area-function variation show that the standard-plan supralaryngeal airway cannot produce vowels like [i], [u], and [a]. This deficiency follows from the fact that ten to one area-function variations are necessary to produce these vowels (Stevens and House, 1955). As I noted above, these area-function variations can be generated at the midpoint of the human supralaryngeal vocal tract by simply shifting the curved "fat" human tongue around in the right-angle space defined by the spinal column and palate. It is not possible to generate these abrupt area-function discontinuities in the *nonhuman* standard-plan supralaryngeal vocal tract. The standard-plan vocal tract is essentially a single-tube system in which the long, thin tongue defines the floor of the mouth. There is

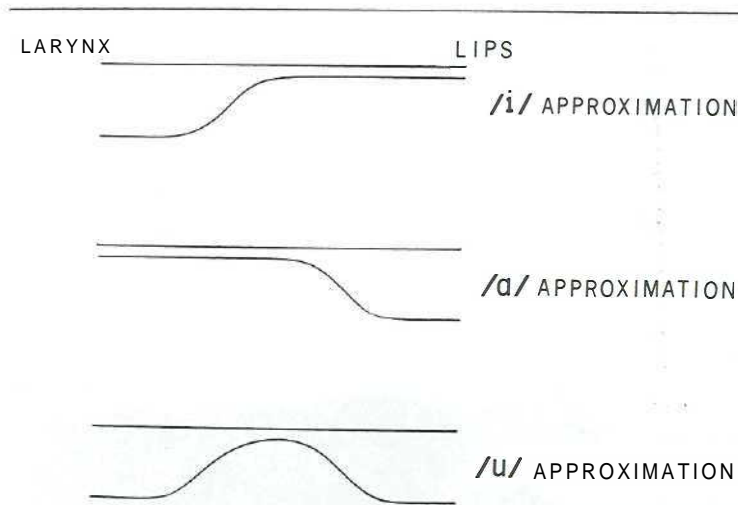


FIGURE 11-10. Schematized nonhuman one-tube supralaryngeal airway in approximations to human vowels [i], [a], and [u].

no natural discontinuity in the system at which an abrupt area-function change can be generated along the tube. Figure 11-10 perhaps makes this point clear. A constriction necessarily must gradually give way to an unconstricted area of the single tube since the tongue muscle cannot itself form an abrupt discontinuity. Cineradiographic studies of newborn cry show this to be the case (Truby, Bosma, and Lind, 1965).

BREATHING, SWALLOWING, AND CHEWING

Human adults, unlike other adult mammals, are not obligate nose breathers. Negus connects this change in our breathing pattern with the descent of the larynx. Using the method of comparative anatomy, he compares the human airway with the airways of fast-running animals. In these animals the airways are relatively straight. In deer, for example, the nasal passage has only a slight curve "so designed as to cause no interference with the rapid passage of air" (Negus, 1949, p. 33). In contrast, the human airway is "a tortuous channel, the nasopharynx failing to reach the larynx and the air current turning through two right-angles; any disability due to angulation can, how-

ever, be partly overcome by opening the mouth" (Negus, 1949, p. 33). Negus is, of course, correct when he notes that mouth breathing is useful when we want to optimize airflow through the human supralaryngeal airways. Anyone who has run more than a mile knows that mouth breathing is necessary for strenuous aerobic exercise. It is interesting to note that human infants usually begin to breathe through their mouths at age 3 months (Laitman, Crelin, and Conlogue, 1977), after the first major restructuring of the supralaryngeal vocal tract toward its adult configuration (George, 1976, 1978; Goldstein, 1980). Whether mouth breathing is a consequence of adaptations for human speech or is a precursor of changes in the supralaryngeal airway that ultimately yielded human speech is an interesting question that I shall return to.

The pattern for swallowing that occurs in adultlike human beings is also quite different from that of other primates. We pull the larynx up and forward by tensing muscles like the anterior digastrics. If you refer back to Figure 11-1, you will see that in an adult human the hyoid bone, from which the larynx is suspended, is positioned below the mandible. In order to avoid having food fall into our larynx, we pull the larynx forward and upward, tucking the opening of the larynx behind the pharyngeal section of the tongue as we simultaneously push the bolus of food toward the opening of the esophagus. The food is rapidly pushed past the critical point at which it could lodge in the pharynx, which is a common food-and-air pathway (Negus, 1949, pp. 176-177; Bosma 1975; Laitman and Crelin, 1976). Figure 11-11 shows the food and air pathway of an adult human being.

The powerful pharyngeal constrictor muscles aid in propelling the bolus of food down the pharynx into the esophagus. Unfortunately the adult human pharynx is also part of the respiratory airway, owing to the ontogenetic descent of the larynx into the pharynx. An error in timing can propel the bolus of food into the larynx with results that are often fatal. It is not uncommon to find cadavers in a medical school dissection with a preserved piece of steak blocking the larynx. In the standard-plan airway, the pharynx lies behind the larynx (see Figures 11-4 and 11-5). Food that is being propelled down the pharynx thus cannot block the respiratory airway. Claims like those of Falk (1975, 1980) to the effect that fossil hominids could not have had nonhuman supralaryngeal airways because they supposedly would *not* be able to swallow in an upright position are thus wrong. The nonhuman supralaryngeal airways are *better* adapted for swallowing in any position; chimpanzees and monkeys habitually swallow food while they sit upright (Lieberman, 1982a, 1982b).

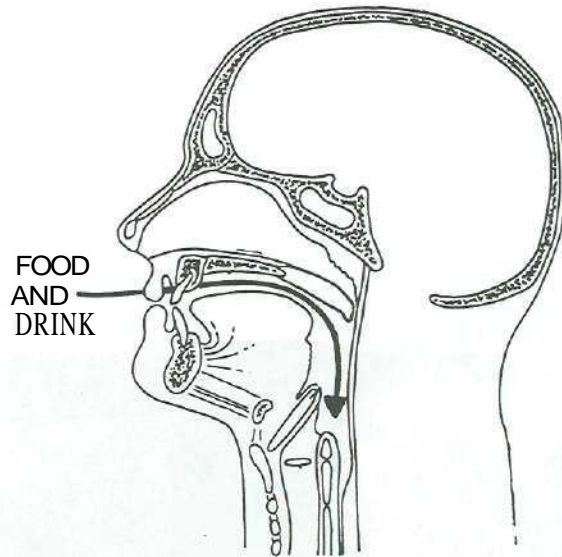


FIGURE 11-11.

Diagram of adult human being showing pathway for the ingestion of food. The food must pass over the opening of the larynx.

The manner in which adult human beings open and close their jaws is also somewhat different from that of other primates. DuBrul (1976, 1977) points out that adult human beings open their jaws by pulling the mandible down and back with the anterior digastric muscles. If you refer back to Figure 11-1 again, you will note that the anterior digastric muscles, which run between the hyoid bone and the mandible, can pull the mandible downward if the hyoid bone is simultaneously stabilized by the sternohyoid muscle, which runs between the hyoid and the sternum (collarbone).¹ The opening motion of the human mandible is different from that of standard-plan airways where the digastric muscles exert a backward force on the mandible because the hyoid bone is positioned close to the base of the skull. The hyoid bone supports the cartilages of the larynx, and so its position depends on that of the larynx relative to the base of the skull.

The pattern of forces that open the mandible is quite different in animals who have standard-plan vocal tracts. Their mandibles open by a "camming" action in which the force generated by the pull of the anterior digastric muscles is opposed by an equal and opposite force

from the bone structure of their tempromandibular joint, the joint into which the mandible fits on the skull. Apes consequently have a massive tempromandibular joint that is quite different from that of an adult human being. The apes' tempromandibular joint has to be more massive to cope with the force generated in the camming action. The presence of an apelike tempromandibular joint in a fossil hominid thus is consistent with the fossil's having a nonhuman standard-plan supralaryngeal airway. DuBrul (1976, 1977) argues that fossil hominids like the La Chapelle-aux-Saints classic Neanderthal could not have had a standard-plan vocal tract because they would not be able to open their jaws like modern adult human beings. DuBrul, however, overlooks the pongid character of the La Chapelle-aux-Saints fossil's tempromandibular joint, which Boule (1911-1913) noted in the original descriptions of this fossil. DuBrul thus is "hoist with his own petard"; the pongid characteristics of the classic Neanderthal tempromandibular joint are consistent with its opening and closing like a gorilla's or a chimpanzee's. The massive brow ridges of classic Neanderthal fossils are also consistent with the pongidlike tempromandibular joint. Gorillas are not very pretty by human standards, but they have powerful jaw muscles and massive jaws that can exert a powerful bite. Neanderthal fossil hominids also have massive jaws and doubtless had powerful masseter muscles, whose presence we can infer from the facets on their skulls and mandibles. Though they too probably would not win any beauty contests today, their bites were undoubtedly more powerful than ours.

The long body of the mandible that is a characteristic of the standard-plan supralaryngeal airway is necessary to keep the tongue within the oral cavity. As Negus noted in his comparative studies, all animals except adult human beings have long mandibles with long bodies. There is plenty of space along the nonhuman mandible and upper jaw for teeth. This increases the efficiency of chewing. As I noted earlier, studies of the efficiency of chewing demonstrate that, all other things being equal, a greater tooth area will yield more effective chewing (Manley and Braley, 1950; Manley and Shiere, 1950; Manley and Vinton, 1951). The reduction in the length of the mandible that Negus first noted in connection with the movement of the tongue down into the pharynx is thus counterproductive for chewing.

The picture that emerges with regard to the vegetative functions of breathing, swallowing, and chewing is that the adult human supralaryngeal airway, and its associated skeletal structure, is less effective in these functions than the nonhuman standard-plan arrangement. This conclusion is not very surprising, given the ubiquitous occurrence of the standard-plan morphology.

NEOTENY

The superiority of the standard-plan supralaryngeal airway in these vegetative functions also explains the retention of this airway in newborn human infants. There is a selective advantage in being able to breathe and suckle simultaneously. Vocal communication is not as important in the first months of life as weight gain, efficient respiration, and avoidance of asphyxiation. Newborn human infants thus retain the "base form" mammalian supralaryngeal airway. As they develop, they deviate from the mammalian standard-plan airway. The nonhuman primates, in this regard, retain their functional "neoteny," so they are examples of "neotenus" development, not we. Adult nonhuman primates differ from their infants in other ways (Schultz, 1968; Laitman, Heimbuch, and Crelin, 1978; Laitman, 1983). In general, as Louis Agassiz and Charles Darwin observed over a hundred years ago, the adult forms of animals deviate from their infantile states. The theory of neoteny as propounded by Gould (1973, 1977) is refuted by the data of human and primate ontogenetic development, as well as by those of phylogenetic evolution.

THE SKELETAL CORRELATES OF THE SUPRALARYNGEAL AIRWAY

I have already noted some of the skeletal correlates of the standard-plan and adult human supralaryngeal airways. The base of the skull and the jaw, the basicranium and the mandible, are the skeletal features that support the soft tissue of the supralaryngeal vocal tract. The basicranium, moreover, itself defines the upper (superior) border of the supralaryngeal airways. Negus obviously saw the connection between the morphology of the skull base, mandible, and soft tissue of the supralaryngeal airway. The reconstruction of the airways of a Neanderthal fossil that he attributes to Sir Arthur Keith (Negus, 1949, pp. 195–200) is quite similar to recent reconstructions (Lieberman and Crelin, 1971; Laitman, Heimbuch, and Crelin, 1978; Grosman, 1979). Negus unfortunately does not discuss in detail the anatomical features that are the bases of the reconstruction. His discussion of the anatomical principles for reconstructing the fossil supralaryngeal airway is limited to the comment that I noted earlier, that the low position of the larynx in modern human beings derives from "the recession of the jaws" (Negus, 1949, p. 25) and to the comment that the larynx descends in human infants after birth "as a result of alteration in the vertebro-occipital and pituitary angles, together with downward movement of the tongue in the pharynx" (1949, p. 175).

Recent studies indicate that the basicranium is appreciably different from the other bones of the skull and is an extremely reliable guide both for the reconstruction of the supralaryngeal airways of fossils and for the assessment of phylogenetic relationships. The basicranium is first a very conservative region of the skull in an evolutionary sense. As Laitman (1983) notes, the numerous openings in the basicranium (the basicranial foramina) through which the cranial nerves and blood supply of the brain enter and exit the skull preclude drastic, uncoordinated changes in its form. Whereas deformations of the other bones of skull are usually not life threatening, abnormalities of the skull base frequently either are not viable (Bosnia, 1975) or have profound behavioral consequences (Pruzansky, 1973). The special status of the basicranium is reflected in its composition. It is largely derived from cartilage. In contrast, the greater part of the rest of the skull is derived embryologically from membranous bone. Recent studies have shown that cartilage cells are more sensitive to growth-regulating hormones. This increased sensitivity to regulatory hormones is consistent with the restructuring of the skull base that occurs in the ontogenetic development of infants and children. It allows the precise changes that must occur if life is to be sustained as the basicranium changes its shape. As Laitman concludes,

The basicranium is thus appreciably different from other components of the skull both in its largely endochondral development and its involvement with inviolable nervous and vascular structures. Due to these factors the basicranium is an evolutionary conservative area. Unlike the more plastic bones of the face or vault the configuration of the mature mammalian basicranium shows comparatively little variation within, or even among species. This evolutionary conservatism and stability has implications both for interpretation and reconstruction of fossil remains and for the assessment of phylogenetic relationships. The constant and predictable relationships among foramina and landmarks permit basicranial reconstruction with a degree of accuracy not possible for the more variable facial or neural bones. Similarly, phylogenetic change can often be monitored through the use of the basicranium as a guide. Since the basicranium is such a conservative feature, any alteration may indicate change of a more substantial nature than the more frequent, and easily achieved, changes in the more plastic parts of the skull. (1983, p. 9)

As we shall see, whereas there is little difference between the basicraniums of human newborns and other infantile or adult pri-

mates, who all have standard-plan supralaryngeal airways, there are profound differences between these skulls and the basicraniums of normal adult human beings. The selective forces that led to the restructuring of the human basicranium thus must have had extremely high selective value. In short, two facts emerge at this juncture.

1. The evolution of anatomically modern *Homo sapiens* does *not*, as Gould (1973, 1977) claims, involve the putative process of neoteny. Whereas adult apes differ from the juvenile "base" form with respect to differences involving the more plastic bones of the skull, we differ with respect to the basicranium.

2. The selective value of the functional consequences of the restructuring of the human basicranium must have been extremely high. The selective value of encoded, high-speed vocal communication is the factor that I think was involved. High-speed vocal communication coming together with the enhanced cognitive power of the hominid brain in the late *Homo erectus* stage of human evolution probably yielded human language. In more advanced cultural settings the communicative language of modern *Homo sapiens* may have yielded the selective advantage that outweighed the vegetative advantages of the nonhuman supralaryngeal airway.