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Production of Vocalizations in Mammals

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Introduction

Mammals are an ancient and diverse lineage of vertebrates, and because humans are mammals, the study of mammalian vocal production provides a crucial context for understanding the evolution of human speech and singing. Conversely, from an acoustical and physiological viewpoint, the best understood mammalian vocalization is human speech, so theories and techniques from speech science have played an important role in increasing our understanding of the vocal production system (VPS) of other mammals. Despite a long tradition of believing that human vocal production is somehow highly distinctive from that of other mammals, converging data demonstrate that humans are using a relatively ordinary mammalian VPS to speak or sing. Indeed, in the context of the diversity of mammalian vocalizations that include ultrasonic sounds high above our hearing range (e.g., from bats or rodents) and infrasonic vocalizations far below it (e.g., from whales or elephants), along with a wide range of fascinating anatomical adaptations such as giant larynges or air sacs, humans appear

decidedly normal. What is quite unusual is the way we use this apparatus, particularly our capacity for vocal imitation, and the motor control underlying human vocal production. However, even this skill is shared by a few other mammal groups.

This article provides an overview of mammalian vocal production, attending both to themes (aspects of vocalization shared by most mammals) and to variations (unusual adaptations appearing in isolated groups). I adopt a comparative, evolutionary viewpoint, beginning by emphasizing that mammals are an ancient lineage (Carroll, 1988). The ancestors of mammals, the synapsids or mammal-like reptiles, were a diverse and successful group before the evolution of dinosaurs. The earliest true mammals arose simultaneously with early dinosaurs in the late Triassic, approximately 210 million years (MY) ago. The best known of these early mammals is *Morganucodon*, a small shrew-like mammal (approximately 3–10 cm long), preserved in numerous fossils on several continents. With the rise of the dinosaurs, however, mammals entered a long twilight. For 150 MY, dinosaurs dominated the world, and mammals eked out a peripheral existence, small in size and few in number. Some mammal groups survived the massive extinction event ~65 MY ago, at the end of the

Cretaceous, which wiped out the dinosaurs and many other groups. The surviving mammals then entered a phase of explosive adaptive radiation during the Cenozoic or 'Age of Mammals.' These early modern mammals quickly diversified into virtually all available niches, and by 55 MY ago all orders of extant mammals had evolved. Thus, despite the recency of mammalian dominance, the mammalian lineage itself is surprisingly old: more ancient than either birds or anurans (frogs and toads), the other large groups of highly vocal vertebrates. Thus, some basic traits of the mammalian vocal communication system (such as extra middle ear bones and laryngeal morphology) developed long ago, in the shadow of the dinosaurs.

Basic Themes in Mammal Vocal Production

All tetrapods (amphibians, reptiles, birds, and mammals) inherit from our common ancestor three key components: (1) a respiratory system with lungs; (2) a larynx that acts primarily as a quick-closing gate protecting the lungs, and often secondarily to produce sound; and (3) a supralaryngeal vocal tract that filters this sound before emitting it into the environment. Most mammals, amphibians, and reptiles have continued to use this system for vocalization, whereas birds and cetaceans (whales and dolphins) have developed novel vocal production mechanisms. The functioning of the basic mammalian VPS can be understood within the theoretical framework of the myoelastic-aerodynamic and source/filter theories developed by speech scientists (Titze, 1994).

The lungs and attendant respiratory musculature provide the pressure and air stream powering phonation. In primitive air-breathing vertebrates, the lungs were inflated by rhythmic compression of the oral cavity or 'buccal pumping,' a relatively inefficient system. Inspiration by active expansion of the thorax evolved later, powered originally by the intercostal muscles (in the common ancestor of reptiles, birds, and mammals). Mammals alone evolved a muscular diaphragm, which is a very efficient air-pumping system (Liem, 1985). Phonation is typically powered by passive deflation of the elastic lungs or, in some cases, by active compression of the intercostal and abdominal musculature. Phonation can also be powered by an inspiratory air stream (e.g., in donkeys or chimpanzees, and occasionally in ingressive human speech).

The trachea is protected by a larynx in all tetrapods, derived from the gill bars of our fish ancestors. Once our common tetrapod ancestor became terrestrial, gills were no longer useful, and their remains provided the 'spare parts' from which evolution built the larynx. This structure primitively includes sphincter-like musculature and a pair of bar-like cartilages that can be separated (for breathing) or pushed together (to seal the airway) (Negus, 1949). Although the larynx can support a wide variety of vocalizations, its function as a protective gateway remains primary. Expiration through the partially closed larynx creates a turbulent hiss, perhaps the most primitive vocalization, which virtually all tetrapods (and mammals) can produce. Very primitive mammals, such as the egg-laying echidna, can hiss. Phonation became possible after the innovation of elastic membranes within the larynx, termed 'vocal cords' in frogs and vocal reptiles (geckos, crocodilians) and 'vocal folds' in mammals. The mammalian vocal folds are unique in that they generally include within them a 'vocalis' or thyroarytenoid muscle, which results from the incorporation of additional gill bars (which make up the thyroid cartilage) and their attendant musculature (Schneider, 1964).

Although our knowledge of animal phonation is still limited, phonation in nonhumans seems to follow the principles of the myoelastic-aerodynamic theory of human phonation (Titze, 1994). The airflow from the lungs sets the vocal folds into vibration, and the rate of vibration is passively determined by the size and tension of these tissues. Vibration at a particular frequency does not typically require neural activity at that frequency. Thus, relatively normal phonation can be obtained by blowing moist air through an excised larynx in many species. However, cat purring relies on an active tensing of the vocal fold musculature at the 20 to 30 Hz fundamental frequency of the purr (Frazer Sissom et al., 1991). During phonation, the movements of the vocal folds can be periodic and stable (leading to tonal sounds) or highly aperiodic or even chaotic (e.g., in screams); though such aperiodic vocalizations are rare in nonpathological human voices, they can be quite important in mammalian vocal repertoires (Fitch et al., 2002).

Sounds created by the larynx must pass through the air contained in the pharyngeal, oral, and nasal cavities, collectively termed the supralaryngeal vocal tract or simply 'vocal tract.' Like any column of air, this air has mass and elasticity and vibrates preferentially at certain resonant frequencies. Vocal tract resonances are termed formants (from the Latin formare 'to shape'): they act as filters to shape the spectrum of the vocal output. Because all tetrapods have a vocal tract, all have formants. Formant frequencies are determined by the length and shape of the vocal tract, and large animals have long vocal tracts and low formants. Mammals are able to control the

configuration of the vocal tract. Raising the larynx into the nasal cavity, and sealing it with the mammalian epiglottis and velum, allows mammals to breathe through the nose while swallowing liquid through the mouth, an ability that is very useful during suckling (Crompton *et al*., 1997). Most mammals normally breathe in this position, exclusively through the nose. However, by varying the position of the larynx during vocalization, mammals can change the configuration of their vocal tract, producing nasal sounds (through the nostrils), oral sounds (through the mouth), or a combination of the two. Because the nasal passages are convoluted and filled with spongy absorptive tissue, nasal sounds are much quieter than oral sounds. Cineradiographic data indicate that loud sounds are thus produced through the mouth in all mammals studied thus far (e.g., dog barks, goat bleats, pig squeals, or monkey chatters), but some soft sounds (e.g., dog whines or pig grunts) are produced through the nose (Fitch, 2000b). Thus, the lowering of the larynx into the oral cavity to produce loud sounds appears to be a homologous trait shared by most mammals.

Finally, the motor neurons controlling the vocal production system are located in the cranial nerve motor nuclei and appear to be quite conservative and shared among mammals (Jürgens, 1998). The larynx is supplied by the recurrent and superior laryngeal nerves, branches of the vagus nerve, and their motor neurons are located in the nucleus ambiguus in the brainstem. The muscles controlling the vocal tract are supplied mainly by the hypoglossal and facial nerves, with motor neurons in the corresponding motor nuclei. In all mammals tested, including humans, vocalization can be elicited via electrical stimulation of the periacqueductal gray region of the midbrain.

In summary, mammalian vocal production is based on a rather conservative tetrapod vocal production system composed of lungs, larynx, and vocal tract. The basic anatomy and function of this system are shared by humans, down to the details of laryngeal anatomy and innervation. Derived traits, shared by mammals but different from other tetrapods ('mammalian synapomorphies'), include a diaphragm for efficient ventilation of the lungs, complex vocal folds that include a vocalis muscle, and an ability to lock the larynx into the nasal passages with an epiglottis and velum. Most mammals lower the larynx into the oral cavity during loud vocalizations, thus assuming a vocal tract posture resembling that used during human speech. Thus, the primary traits differentiating human speech or song from vocalization in other mammals appear to be at the level of central neural control rather than peripheral anatomy.

Variations in the Mammalian Vocal Production System

Laryngeal and Source Modifications

Because the length of the vocal folds determines the lowest frequency at which the folds can vibrate (Titze, 1994), and long folds are thus able to produce lower frequencies, one might expect that a low fundamental would provide a reliable indication of large body size. This is indeed true if we look across a large range of species (August and Anderson, 1987): mice have high fundamentals relative to dogs, and elephants very much lower. However, from an anatomical viewpoint, the size of the larynx is not tightly constrained by body size. Thus, a huge larynx has independently evolved in many mammal species, probably in response to selection for low-pitched voices. For example, in howler monkeys (genus *Alouatta*), the larynx and hyoid have grown to fill the space between mandible and sternum, giving these small monkeys remarkably impressive low-pitched voices (Kelemen and Sade, 1960). The most extreme example of laryngeal hypertrophy is seen in the hammerhead bat *Hypsignathus monstrosus*, in which the larynx of males expands to fill the entire thoracic cavity, pushing the heart, lungs, and trachea down into the abdomen (Schneider *et al*., 1967). A similar though less impressive increase in larynx dimensions is observed in human males and is responsible for their voice change at puberty (Titze, 1989). Even without greatly enlarging the larynx, a transformation of the vocal folds into massive vocal pads in large cats (Hast, 1989) and other mammals makes the production of very low-pitched roars possible in some large mammals.

Not surprisingly, the lowest pitched voices are possessed by the largest animals, which can produce infrasound (sounds with fundamental frequencies below the range of human hearing). Because low frequencies can travel further than high frequencies in some environments, infrasonic vocalizations probably represent the most widely broadcast animal signals in existence. Elephants produce and hear extremely low frequency 'rumbles' and other infrasonic vibrations (Langbauer *et al*., 1991). In certain environments (e.g., open savannah with temperature inversions), such sounds are able to carry more than 10 km, leading to unusually large vocally mediated communication networks in African elephants. However, even these long-distance communication systems are dwarfed by those of the large baleen whales, which are the largest animals to have ever lived. Both fin whales and blue whale males (*Balaenoptera physalis* and *B. musculus*) produce low-frequency vocalizations with 20 Hz fundamental frequencies (Croll *et al*., 2002), and under ideal conditions a

vocalization from a single animal can fill an entire ocean basin (Payne and Webb, 1971). The mechanism by which these low-frequency sounds are produced is unknown, but baleen whales possess a large larynx with a massive vocal fold and a laryngeal sac that allows air recirculation, making it possible that the aerodynamic/myoelastic theory applies even to these infrasonic vocalizations.

At the opposite end of the frequency spectrum, some rodents, primates, and bats can produce ultrasonic vocalizations with fundamental frequencies of 40 kHz and higher (Suthers and Fattu, 1973). Adaptations of the middle ear and cochlea allow most mammals to hear high frequencies (above 10 kHz) that are inaudible to birds or reptiles; the ability to produce sounds at those frequencies creates a 'private' communication channel for small mammals. This ability may have played a crucial role in the evolution of hearing and vocal production in early mammals during the Mesozoic, when birds and dinosaurs would have been the top predators. This 'private' channel is still exploited today by many rodents, particularly in courtship and mother–pup communication (Sales and Pye, 1974). Ultrasound is put to much more specialized use by echolocating bats, where the short wavelengths of ultrasonic vocalization make them ideal for picking out details from small objects (Griffin, 1958). The ultrasonic production mechanism has been best studied in bats, which have a highly specialized vocal membrane that extends upward from the vocal folds; when this membrane is cut experimentally, the bat becomes unable to produce ultrasonic calls (Novick and Griffin, 1961). Similar membranes exist in nonhuman primates, and the function of such membranes has been modeled computationally using the same principles as human speech (Mergell et al., 1999).

Echolocation evolved independently in another group of mammals, the toothed whales (odontocete cetaceans, e.g., dolphins, porpoises, killer whales, and sperm whales). However, the broadband click-like echolocation signals used by these marine mammals are produced by a novel mechanism, the nasal bursae, which is unique to this group and still imperfectly understood (Cranford et al., 1996). This complex organ system is present in all odontocetes studied, is housed in the nasal passages, and appears to require air movements to power vocal production, but can produce sound without emitting air so it must involve a system for air recirculation. It is unknown whether the nasal bursa system also produces the communicative whistles used by some odontocetes, e.g., bottlenosed dolphins, Tursiops truncates. Because whistles and clicks can be produced simultaneously, it remains possible (but unproven) that clicks are produced by the nasal complex, whereas whistles are produced at the larynx (Evans and Prescott, 1962).

Vocal Tract Modifications

Because the vocal tract in mammals rests within the confines of the head, and skull size and body size are tightly linked (Fitch, 2000c), the formant frequencies of the vocal tract provide a possible indicator of body size. Large animals generally have long vocal tracts and low formants. Together with demonstrations of formant perception by nonhuman mammals (Sommers et al., 1992), this suggests that formants may have provided a cue to body size in primitive vertebrates (Fitch, 1997) and thus represent an ancient aspect of vocal communication. However, once a perceptual link between formants and body size was established, it becomes possible to break the anatomical link between vocal tract length and body size, lengthening the vocal tract and thus duplicating the formants of a larger animal. Some intriguing morphological adaptations have arisen to elongate the vocal tract (presumably resulting from selection to sound larger). Elongations of the nasal vocal tract are seen in the long nose of elephants or male proboscis monkeys. Vocal tract elongation can also be achieved by lowering the larynx; this is seen in extreme form in red deer, Cervus elaphus, which retract the larynx to the sternum during territorial roaring (Fitch and Reby, 2001). Similar descended larynges have evolved repeatedly in separate mammal groups, including koalas and all big cats. Again, a similar change occurs in human males at puberty: the larynx descends slightly to give men a longer vocal tract, and lower formants, than same-sized women (Fitch and Giedd, 1999). Vocal tract elongation has also evolved separately in several nonmammal groups, e.g., tracheal elongation in birds (Fitch, 1999) or the impressive nasal crests of hadrosaur dinosaurs (Weishampel, 1981). Thus, the descended larynx of humans, a perennial topic of discussion in language evolution (Lieberman, 1984; Fitch, 2000a), is just one of many convergent adaptations among disparate vertebrate taxa that elongate the vocal tract.

Another interesting set of vocal tract modifications is found in echolocating bats. Echolocating bats are divided into oral and nasal emitters, and many of the nasal emitters have evolved elaborate 'nose leafs' that function to form the echolocation signal into a focused beam of sound (Suthers and Fattu, 1973). The bat can thus point its echolocation signal at a target of interest, like the beam of a flashlight. In the paca, a large South American rodent, the zygomatic arches are hollow and ballooned outward, but the acoustic significance of this is unknown (Hershkovitz, 1955). Other interesting modifications of the nasal region

include the dulaa of male camels (*Camelus dromedarius*), which is an elastic extension of the velum that is blown out through the mouth like a large wet balloon during mating vocalizations (Arnautovic and Abdul Magid, 1974), or the similar extension of the nasal septum blown out through the nostrils during mating displays of the male hooded seal (*Cystophora cristata*) (Terhune and Ronald, 1973).

A final class of vocal tract modifications, vocal air sacs, is very widespread among mammals but still very poorly understood from an acoustic viewpoint. Air sacs appear to have evolved independently among many different taxa, in a bewildering variety of locations. For instance, many primates have air sacs attached directly to the larynx (Hewitt *et al.*, 2002); in many well-known primates (e.g., chimpanzees, baboons, macaques, howler monkeys) the laryngeal air sac fills a modified balloon-like hyoid bulla (Negus, 1949). The function(s) of these air sacs remains imperfectly understood; the only experimental study on primate air sacs documented decreased loudness of calls when they were punctured (Gautier, 1971). Primate air sacs are of particular interest with reference to the evolution of human vocalization, because all of our great ape cousins possess laryngeal air sacs, suggesting that our ancestors had air sacs and we have lost them in our recent evolution (Fitch, 2000a). Other groups that possess laryngeal air sacs include viscachas, seals, the baleen whales, in which the air sac probably serves in air recycling (Hosokawa, 1950) but perhaps also plays a role in coupling sound production to the environment, and bats, in which tracheal and nasal air sacs play a role in the production of echolocation signal (Suthers *et al.*, 1988). This great diversity of air sacs suggests multiple functions. More research will be necessary to understand the function of air sacs in those species that possess them before the significance of their loss in human evolution can be properly evaluated.

Neural Modifications

Humans share the basic innervation patterns and cranial motor nuclei described above with other mammals. However, humans are unusual among mammals, and unique among primates, in our ability to learn new vocalizations after hearing them produced (vocal imitation or vocal learning). Complex vocal learning abilities are also found in seals, cetaceans, and perhaps bats (Janik and Slater, 1997). A possibly unique characteristic of humans that may at least partially underlie this capacity is provided by the direct connections between motor cortex and vocal motor neurons, found in humans but not other primates (Jürgens, 1998). Thus, whereas vocal control in most mammals appears subcortical, humans can exert cortical control as well (for discussion see Jürgens, 1998). Unfortunately, little is currently known about the neural basis of vocal control in other mammalian vocal imitators, like dolphins, whales, and seals, to know whether similar neural specializations underlie vocal learning in these other lineages.

Another recently discovered change in neural control of vocalization in humans is more peripheral: MacLarnon and Hewitt (1999) found that modern humans have a larger thoracic vertebral canal than other primates, presumably linked to greater control over the muscles that have motor neurons in this area (intercostals and abdominals, but not the diaphragm). Because this is a characteristic that can be measured in fossils, this character provides an exciting possible cue to the timing of increased vocal control in the evolution of the human lineage. MacLarnon and Hewitt found that early *Homo erectus* (= *Homo ergaster*) had a thoracic cavity similar in size to that of chimpanzees or earlier hominids and concluded that increased breathing control involved in speech occurred no earlier than later *Homo erectus*.

However, it is important to realize that these changes are equally, if not more, relevant to singing. Sundberg (Sundberg, 1987) has convincingly argued that singing requires finer respiratory control than that necessary for speech. In normal conversational speech, the rate of airflow is approximately 0.2 L/s (0.1–0.3 L/s) and approximately 2 L tidal volume is utilized. With no involvement of the intercostals, and simple passive lung deflation, this would give 10 s of normal speech. But speakers normally breathe every 5 s. In contrast, phrases over 10 s are common in song, and singers often use nearly all of their approximately 5 L vital capacity. Furthermore, much greater subglottal pressures are generated during singing than speech (30–70 cm water relative to 6–15 cm water in normal speech). Most importantly, the finer control over amplitude and pitch required in singing leads to singers using all available muscles (including both sets of intercostals, the diaphragm, and the abdominal muscles), whereas speakers typically use only one set of intercostals for compensatory maneuvers during speech. Thus, an increase in fine respiratory control would seem to be more important in singing (where maintaining a constant subglottal pressure for consistent amplitude and pitch is a necessity) than in speech (where pitch is in any case varying continuously over a wide range).

Summary

In conclusion, mammals are an ancient lineage, and the approximately 4000 species of mammals have

developed a wide and fascinating range of vocal adaptations. Some of these, like a permanently descended larynx or the capacity for complex vocal learning, have evolved in parallel in humans and in other species. Others, like the air sacs attached to the larynx in all of the great apes, were lost in human evolution, but their significance is still poorly understood. Still others, such as ultrasonic and infrasonic vocalization, are far more extreme and indeed exceed human auditory perceptual capacities. Human adaptations for vocalization, including both speech and singing, thus take their place among a wide variety of similar vocal adaptations in mammals.

See also: Alarm Calls; Animal Communication: Overview; Animal Communication: Vocal Learning; Bats: Communication by Ultrasound; Cognitive Basis for Language Evolution in Non-human Primates; Communication in Marine Mammals; Development of Communication in Animals; Non-human Primate Communication; Vocal Production in Birds.

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Productivity

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Introduction

Speakers of a language coin new words on the basis of other words or word-forming elements on a daily basis. For example, English speakers turn adjectives such as *blue* into nouns by adding the suffix *-ness*, yielding *blueness*, or form compounds by joining existing words, as in *computer screen*. Some of these words may eventually make it into the common vocabulary of the speakers, but many newly coined words are never more widely used.

Word-formation processes are to a large extent rule governed, but one observes that some of these processes (or affixes) are quite often used to coin new words, whereas others are less often used or not used at all for this purpose. For example, it seems that no new noun can be formed in Modern English with the help of the suffix *-th* (as in *depth* or *length*), whereas the nominal suffix *-ness*, which is similar in function, is found very often in new formations (cf. *eco-friendliness*, first attested in 1989, *Oxford English dictionary* (*OED*)).

In this sense, some morphological rules are called productive and other rules unproductive or less productive. Given the differences in productivity among different rules, several theoretical and empirical problems need to be addressed. First, what makes a given rule productive or unproductive? Second, how can the productivity of a given rule be measured and what mechanisms are responsible for the variability in the productivity of morphological processes? Third, should productivity be regarded as a theoretical primitive, i.e., a nonderivable property of word-formation rules, or an epiphenomenon, i.e., a property that results from other properties of the rule in question?

In the following, we first look at different definitions and measurements of productivity, then turn to the psycholinguistic mechanisms influencing the productivity of word-formation rules, and finally discuss pragmatic and structural restrictions on productivity.

Defining Productivity: Qualitative and Quantitative Approaches

One important theoretical question concerning the nature of productivity is whether productivity is a quantitative or a qualitative notion. Some scholars have argued that productivity is of a qualitative nature and that a process or an affix thus either has this property or not. Others view productivity as a gradual phenomenon, which means that morphological processes are either more or less productive than others and that completely unproductive or fully productive processes mark only the end-points of a scale.