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052141265X - Nonverbal Vocal Communication: Comparative and Developmental  
Approaches - Edited by Hanus Papousek, Uwe Jurgens and Mechthild Papousek

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PART I

**Systems of communication**

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## Introduction and review

UWE JÜRGENS

Part I provides the reader with some general information about the biological foundations of nonverbal vocal communication. It starts with an anatomical description of the phonatory apparatus. In accordance with the aims of this book, the description follows a phylogenetic line, delineating the changes and specializations that have taken place in the development of the larynx and supralaryngeal tract from lungfish to humans. It thus recapitulates the morphological transformation of the larynx from a pure respiratory organ (lungfish) to a respiratory organ with some vocal capability (amphibian, reptiles, lower mammals) and finally to that highly sophisticated instrument that we use when singing or producing variegated emotional intonations. This description makes clear the degree to which the rich vocal repertoire typical of humans and of nonhuman primates (squirrel monkeys, for instance, with their extraordinary vocal range of more than eight octaves) depends upon specific morphological prerequisites.

As chapter 1 further points out, the phonatory apparatus, as it evolved toward its form in humans is paralleled not only by an increase in vocal repertoire but also by an increase in voluntary control over vocalization. At the lowest level at which vocal communication can take place, a subject reacts innately to a specific stimulus, with a specific call. In ethological terms, this is called a vocal "fixed action pattern," activated by an "innate releasing mechanism." In such a case, neither the vocalization, which represents a genetically preprogrammed motor pattern, nor the eliciting stimulus, which elicits vocalization without any prior experience, has to be learned. At this lowest level of vocal communication, voluntary control is absent. Instead, the vocal repertoire corresponds to a reflex reaction, comparable to coughing as a response to an irritating stimulus in the pharynx. Nevertheless, such completely genetically determined vocal reactions occur not only in submammalian verte-

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brates but, as chapters 1 and 2 show, also in primates, including humans.

The next-highest level of communication is represented by a situation in which a subject reacts with a genetically preprogrammed vocal motor pattern, but the eliciting stimulus is learned. In other words, the subject has to learn in what adequate context to use a particular vocal utterance which until then has been called for more or less indiscriminately. Most of the monkey calls and a number of the nonverbal emotional vocal utterances of humans seem to belong to this category. The alarm calls of the vervet monkey and the squirrel monkey are the most intensively studied examples of this kind; consequently, they will be discussed in the following chapters in greater detail. In some mammalian species, such as the cat, the dog, the sea lion, the dolphin, and several monkey species, it has been shown that these animals can be trained to master a vocal conditioning task, that is, to emit a species-specific vocalization for a food reward when a conditioned stimulus is presented (and to refrain from vocalizing during presentation of a different stimulus). Such animals clearly have some voluntary control over vocalization. This control, however, is limited to the initiation and suppression of vocalization; it does not extend to the acoustic structure – which still is genetically determined.

The highest level of vocal communication is represented by learned vocal motor patterns uttered in response to learned stimuli. In this case, there is not only voluntary control over initiation and suppression of an utterance, but also voluntary control over the acoustic structure of the utterance. This type of communication is the common communicatory mode in humans. In nonhuman primates and other mammals, it seems to be the rare exception.

As chapter 2 shows, depending on the level at which vocal communication takes place, the brain structures involved differ. For the production of learned vocal motor patterns, a number of brain structures are necessary that are not needed for the production of innate vocal utterances. Furthermore, the capability of initiating or suppressing vocalization volitionally depends upon brain structures not needed for the production of unconditioned vocal reactions. The message of the second chapter thus is that, parallel to the behavioral hierarchy of complexity in vocal communication, there is a hierarchy of brain structures underlying the different forms of vocal communication.

The last chapter of part I deals with the functional properties of nonverbal vocal utterances. It is asked, what type of information is transferred by such utterances and how do they influence the partner. With

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respect to the first question, it is shown that the information transmitted carries a subjective and an objective component. The subjective component consists of the vocal expression of the momentary emotional state. This component signals the preparedness of the vocalizer to react in a specific way. As acoustic analyses reveal, different emotional states are represented by different acoustic patterns. This holds especially for non-human primates and humans: Both possess a rich vocal repertoire of nonverbal emotional utterances enabling them to express a wealth of emotional shades. In man, this is not limited to nonverbal utterances: By way of emotional intonation superimposed on the linguistic component of speech, it extends to verbal utterances as well. As chapter 3 points out, there are first indications that the acoustic features characterizing specific emotional states are similar across species. In other words, there seem to exist universals of emotional vocal expression. This again argues for a genetic – more specifically, phylogenetic – basis of emotional vocal utterances.

The second, objective component in the information transmitted by nonverbal vocal utterances relates to states outside of the vocalizer. Vocalizations often are reactions to specific situations. In these cases, vocalizations reflect specific external events in their acoustic structure – provided that the partner is able to decode the signal. According to Scherer, this may be regarded as a symbolic component inherent in nonverbal vocal utterances. In this sense, not only learned but also innate vocal patterns may have a symbolic function.

With respect to the question of how nonverbal vocal utterances can influence a partner, again two principal modes can be distinguished. The better-known mode is that of the vocalizer trying to provoke a reaction in the partner(s) that is different from the vocalizer's own; for instance, when the partner is forced to retreat by the emission of a threatening call or, conversely, when the aggression of a dominant partner is dampened in response to a flattering utterance. The other mode is characterized by a process that might be called "emotional infection," or emotion transfer by identification. In this case, the vocalizer attempts to evoke a response in the partner(s) that is identical to the vocalizer's own. A well-known example from the animal kingdom is the mobbing response found in many species against potential predators. Here, one animal starts to emit alarm calls against the predator. This serves to draw attention of other group members to the source of excitation. They join the first animal in uttering alarm calls, thus forming a louder and louder chorus. Corresponding examples from the human sphere are presented in chapter 3.

# 1. The evolution of vocal communication

DETLEV W. PLOOG

It is our interest in the evolution of human language and speech that inspires our interest in the evolution of vocal communication. Around the middle of the nineteenth century, this topic met with so much abuse that in 1866 the Paris Société de Linguistique enacted its famous ban against papers dealing with the topic. The subject of dispute then was – and it still is – the question of whether early humans used gestures for communicating before they learned to use the voice, or whether vocal sounds formed the primordial language (Harnad, Steklis, & Lancaster, 1976). I would like to show that comparative biology of the mammalian voice clearly points to a process of natural selection leading to an optimization of audiovocal communication.

The voice is, and most probably always was, an outstanding means of social signaling in nonhuman primates and in humans. Hence, it is promising to study the physical structures and functions of the organism which produces and controls vocal behavior. Phylogenetic comparison will, to a substantial degree, compensate for the missing fossil records of the nonbony tissue involved in vocalization; that is, not only parts of the larynx, tongue, and the like, but also of the brain. Moreover, it is the whole system which is involved in audiovocal communication that must be considered in an evolutionary context.

From a neuroethological point of view, a signaling system must consist of at least four parts: (1) the peripheral apparatus, which generates the species-specific signal; (2) the cerebral motor system, which produces the patterning of the signal; (3) a sense organ, which receives the species-specific signal; (4) the cerebral decoding apparatus, which transforms the signal into a message that may or may not produce a modification of behavior on the receiver's side – for example, a vocal response to a vocal signal. The way in which the cerebral motor patterning and the decoding systems are linked seems to be the key to understanding

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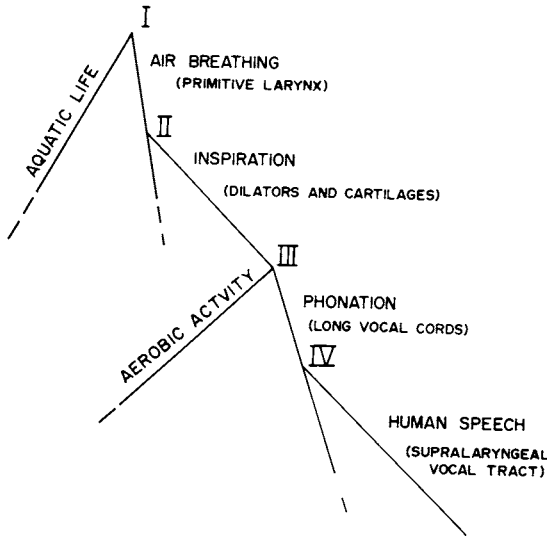


Figure 1.1. A functional branch-point diagram for the evolution of the upper respiratory system (Lieberman, 1984, p. 266).

communication processes in general. The four subsystems function as an interdependent system in communication processes. Therefore they should be studied together in order to appreciate the evolutionary progress in regard to the behavior achieved, that is, the audiovocal mode of communication.

### The peripheral signal generator

Let us first consider the peripheral apparatus which generates the species-specific signal. During evolution a gradual transformation of the larynx and the supralaryngeal tract took place (Fig. 1.1). The first appearance of the larynx can be traced back to the ancient lungfish. Here, it is essentially a valve that is positioned in the floor of the pharynx. In the water, the simple sphincter closes. Out of the water, the sphincter opens and allows air to be forced into the fish's swim bladder, which is homologous with the lungs. A first functional branch-point was the new condition of life out of the water. A *branch-point* is that 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 animals (Lieberman, 1984; Mayr, 1942). The next stage in the evolution of the larynx was the development of fibers to pull the larynx open to allow more air

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into the lungs during breathing. Later stages of evolution yielded lateral cartilages that facilitated the opening movements of the larynx. The elaboration of the larynx enabled it to act as a sound-generating device and marked a second functional branch-point.

Negus's (1949) comparative studies demonstrate that the larynges of many animals are specialized for phonation at the expense of respiration, whereas other animals like horses maximize the flow of air to and from the lungs. The human larynx is designed to enhance phonation for the process of vocal communication. Canids – vocalizers and hunters – represent an intermediate solution to the competing selective forces deriving from respiratory efficiency and phonation (Lieberman, 1984).

The evolutionary condition of the sound-producing apparatus corresponds with the organism's vocal behavior. For instance, frogs have an early tripartite primary larynx skeleton, consisting of arytenoid cartilages and tracheal cartilages. Male frogs are provided with a vocal repertoire of only up to five calls, chiefly the mating call that is to attract a female and the release call that serves to repel other males. Other calls signal territorial defense, warning, and distress (Capranica, 1968). The calls are innate; the mating call, especially, is strictly species-specific and has a selective effect on the female.

In contrast to the primitive condition of the sound-producing apparatus in amphibians with only a few calls, the highly evolved larynx of nonhuman primates corresponds with a rich vocal repertoire used not only for the purpose of procreation but for differentiated vocal communication in complex social interactions. The vocal repertoire of the squirrel monkey will serve as an example (Fig. 1.2). Five classes of calls, first described in 1966 (Winter, Ploog, & Latta), are shown as graded signals from the center toward the periphery. The individual sounds are depicted in frequency by time sonagrams, with shrieking close to white noise in the center of the circle. Each class – and probably innumerable graded signals – are associated with a certain function.

From this example it is obvious that the evolution of the sound-producing apparatus from the amphibians to the nonhuman primates has led to an enormous range and diversity of communal vocal communication. How did this materialize? In the scaffolding of the mammalian larynx, the fourth cartilage, the thyroid emerges and hinges on the cricoid cartilage, which facilitates the opening and shutting of the laryngeal aperture. The definite secondary laryngeal skeleton, then, consists of four parts: the thyroid, the cricoid with superadded aryte-

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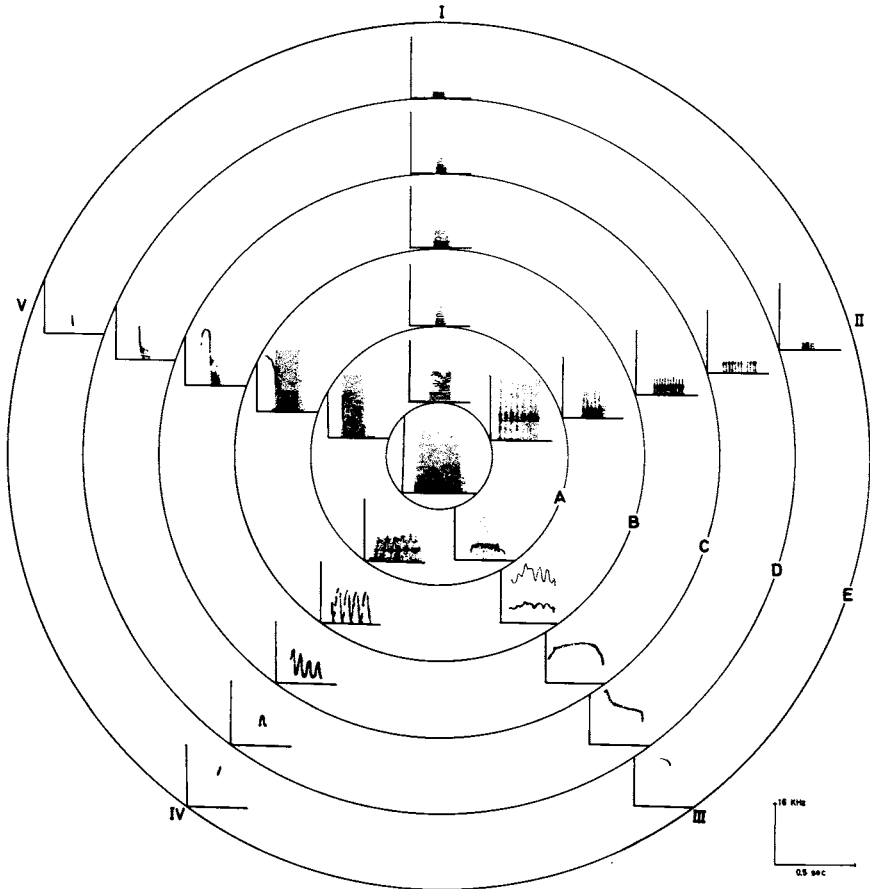
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Figure 1.2. Vocal repertoire of the squirrel monkey. Calls represented as frequency–time diagrams. *Class I* (groaning–cawing–shrieking): Calls of this group act as protest calls. With increasing spectral energy (toward the center), their function changes from an expression of slight uneasiness to one of intense defensive threat. *Class II* (purring–growling–spitting): Calls of this group express a challenging or self-asserting attitude. With increasing spectral energy, there is an increasing probability that a directed aggressive action will ensue. *Class III* (chirping–isolation peep–squealing): These calls serve a number of cohesive functions to express the desire for social contact. *Call IIIc* is the isolation peep, sometimes also called “separation peep.” *Class IV* (twittering–chattering–cackling): The function of these calls is to confirm social bonds and to create companionship; with low energy, pleasurable events are announced; with high energy, intraspecific mobbing against one or several outsiders is set about. *Class V* (clucking–yapping–alarm peep): Its function is warning, ranging from disagreement with a conspecific to alarm calls against aerial VC or terrestrial predators VB. (Jürgens & Ploog, 1976.)



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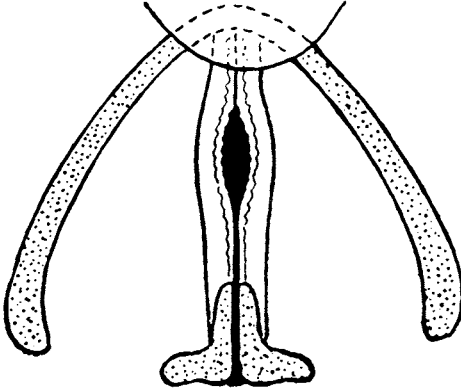


Figure 1.3. Function of the vocalis muscle in humans only. Falsetto mechanism. The central part of the glottis is blown open (*black*), and only a short length of vocal fold is in vibration. The thyroid cartilage and the arytenoid cartilage are stippled (Negus, 1949).

noid cartilages hinged on the cricoid, and the tracheal ring. The epiglottis is also a new formation (Negus, 1949; Paulsen, 1967).

Further evolutionary differentiation in higher mammals developed in the shapes of the cartilages, in humans especially the arytenoids, and in the laryngeal musculature. The arytenoid transversus muscle is singularly observed in all primates. In apes, an oblique interarytenoid muscle detaches itself as a separate unit, becoming increasingly conspicuous along the line orangutan – chimpanzee – gorilla – human (Kelemen, 1963). The thyroarytenoid muscle is located in all nonhuman primates at the base of the vocal cords (vocalis muscle). Only in humans does it reach into the medial part of the vocal cords, thus making a finer vocal adjustment possible. The glottis became a perfect vocal organ with the insertion of muscle fibers at the vocal cord (Fig. 1.3). It grows a considerable length during ontogeny, from 3.0 mm at 3 days of age, to 5.5 mm at 1 year, and to 9.5 mm at 15 years. The adult male has a vocal fold of 17–23 mm and the adult female, of 12.5–17 mm (Negus, 1949).

For humans, the most important change concerns the supralaryngeal tract (branch-point IV in Fig. 1.1). The functional divergence at this point involves the competing demands of selection for vegetative functions like breathing, swallowing, and chewing as opposed to nonvegetative functions like phonetic efficiency. Lieberman (1984) demonstrated that the supralaryngeal airways of anatomically modern *Homo sapiens* evolved to enhance vocal communication at the expense of these vegetative func-

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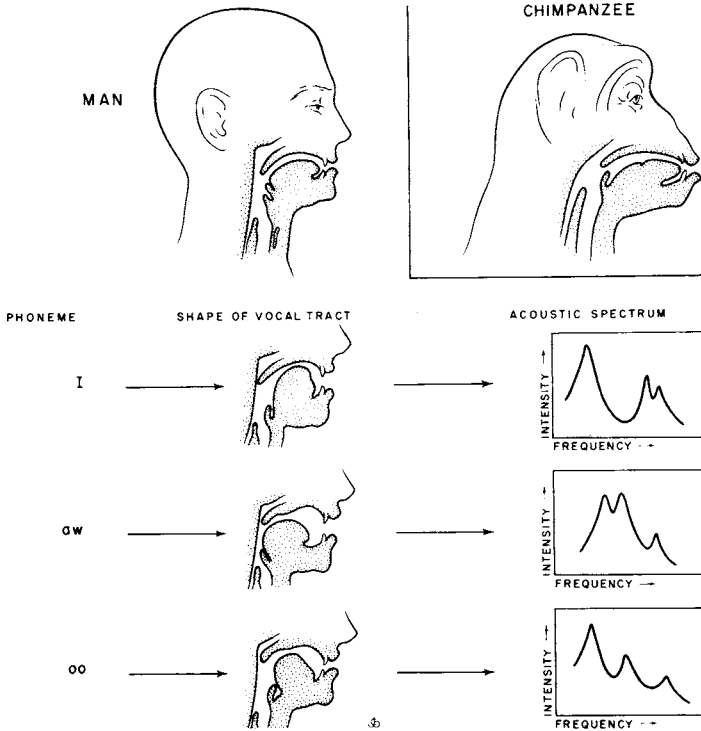


Figure 1.4. The phonatory apparatus of humans and chimpanzees. The configuration of the mature human vocal tract enables him or her to produce sounds that the chimpanzee (and the human infant) cannot produce, e.g., the three vowels presented in their articulatory positions and their intensity–frequency spectrum (Wilson, 1975).

tions. Interestingly enough, Darwin already noted “the strange fact that any 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” (1859/1964, p. 191). Thousands of deaths occur every year when people, especially children, asphyxiate because a piece of food lodges in the larynx. Swallowing the wrong way, however, does not occur in newborn infants. They can simultaneously swallow fluid and breathe. They are obligate nose breathers. The high position of the larynx relative to the nasopharynx allows them to do this. The epiglottis and soft palate overlap and form a double seal. The larynx, in effect, functions as a tube that extends upward from the trachea into the nasopharynx.

This situation changes drastically within 3 months, at which age the descensus of the larynx is almost completed, an age at which the vocal