such as common examples of the classical psychophysical primary qualities (NaCl, salty; HCl, sour; quinine, bitter; and sucrose, sweet), might be defined as primaries of taste (*9*).

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10. Supported by an NSF predoctoral fellowship to M.F. and an NSF grant GB-4198 to C.P.

2 October 1968; revised 1 April 1969 ■

Vocal Tract Limitations on the Vowel Repertoires of Rhesus Monkey and other Nonhuman Primates

Abstract. *The vowel repertoire of a rhesus monkey* (Macaca mulatta) *was explored by means of a computer program that calculated formant frequencies from the area function of the animal's supralaryngeal vocal tract, which was systematically varied within the limits imposed by anatomical constraints. The resulting vowels were compared with those of humans and with recorded vocalizations of nonhuman primates. The computer model indicates that the acoustic "vowel space" of a rhesus monkey is quite restricted compared to that of the human. This limitation results from the lack of a pharyngeal region that can change its cross-sectional area. These animals thus lack the output mechanism necessary for production of human speech. Man's speech output mechanism is apparently species-specific.*

Vocalizations of captive rhesus monkey, chimpanzee, and gorilla have been recorded and analyzed by means of sound spectrograms and oscillograms (*1*). The acoustic analysis suggested that these animals lack the ability to produce the articulatory maneuvers necessary to produce the full range of human speech. The general assumption that the vocal mechanisms of these animals are sufficiently well developed to permit the articulation of words (*2*) would thus be wrong.

Human speech is essentially the product of a source (the larynx for vowels) and a supralaryngeal vocal-tract transfer function. The supralaryngeal vocal tract, in effect, filters the source (*3*). The activity of the larynx determines the fundamental frequency of the vowel, whereas its formant frequencies are the resonant modes of the supralaryngeal vocal-tract transfer function. The formant frequencies are determined by the area function of the supralaryngeal tract (*3*). The vowels /a/ and /i/, for example, have different formant frequencies though they may have the same fundamental frequency. The object of this study is to extend the acoustic analysis (*1*) that indicated that the nonhuman primates' vocalizations are restricted to schwa-like cries produced by means of a supralaryngeal vocal tract with a cross section that is uniform along its length. (An example of the schwa is the first vowel in the word *about.*) Our acoustic analysis was perforce limited to the sounds that animals actually uttered. Our present method makes use of a computer-implemented model of the supralaryngeal vocal tract of a rhesus monkey (*Macaca mulatta*) that we systematically manipulated. We thus were able to explore the full range of vowels that a rhesus monkey could produce if he exploited all the degrees of freedom of his supralaryngeal vocal tract. Our analysis of the possible range of monkey vocalizations thus can be independent of the restrictions inherent in the analysis of a limited set of actual utterances. There is, of course, no guarantee that a monkey will in fact use all of the articulatory maneuvers that we simulate. Itani (*4*), for example, reports that wild Japanese monkeys seldom use their lips during cries, though they are physically able to move their lips. However, we can explore the inherent limits of the output device.

A plaster casting was made of the oral cavity of a monkey soon after it died. The monkey's tongue and lips were positioned in an approximation of an aggressive "bark" (*5*). The plaster

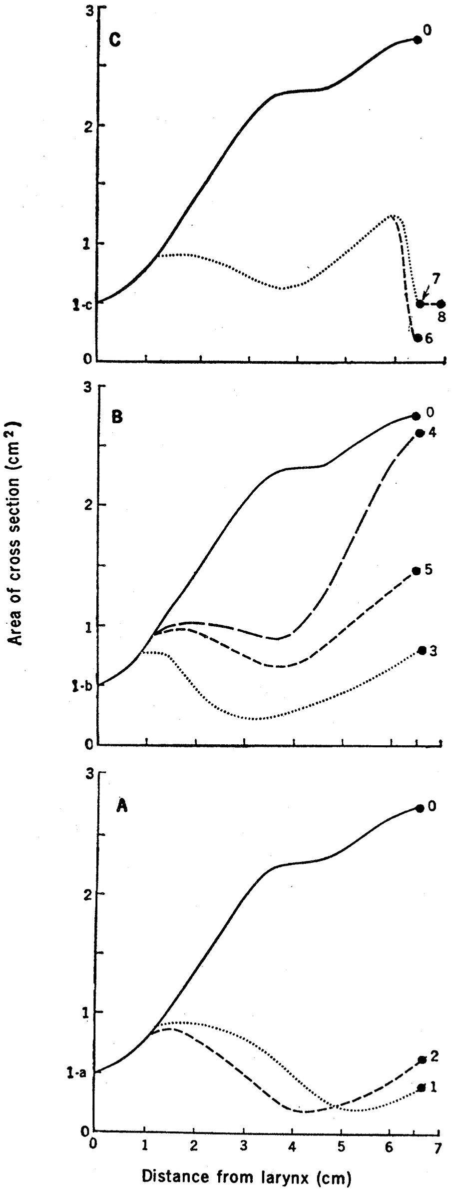

Fig. 1. Area functions of supralaryngeal vocal tract modeled by computer and corresponding vowel formant frequencies. Curve 0 is the unperturbed vocal tract of the rhesus monkey. The first formant frequency of this area function, F_1, is 1503 hz, F_2 is 4007 hz, and F_3 is 6287 hz. (a) Curves 1 and 2 are perturbed area functions analogous to human high, front vowels, and their formant frequencies, respectively, are 867, 4533, and 6816 hz and 971, 4475, and 6526 hz. (b) Curves 3, 4, and 5 are perturbed area functions analogous to human low, back vowels. Their respective formant frequencies are: 1144, 3867, and 6817 hz; 1542, 3816, and 6415 hz; 1354, 3918, and 6461 hz. (c) Curves 6, 7, and 8 are perturbed area functions analogous to human rounded, back vowels. Their corresponding formant frequencies are, respectively: 1010, 3103, and 6175 hz; 1212, 3465, and 6881 hz; and 1034, 3152, and 6093 hz.

casting was then sectioned at intervals of 0.5 cm and the cross-sectional areas were determined by weighing paper tracings of the sections on an analytical balance. This area is presented as the solid line in Fig. 1.

The acoustic waveform corresponding to a vowel can be regarded as the output of a vocal-tract filter system which is excited by vibrations of the vocal cord. It is the transfer function of the vocal tract that determines the vowel uttered because the volume velocity waveform at the vocal cords (the source) and the radiation impedance at the lips (the load) are relatively constant during vowel production and independent of the particular vowel.

The (frequency domain) transfer function of the vocal tract is determined by an area function which gives the cross-sectional area of the vocal tract as a function of position along the tract. For frequencies of interest, the vocal tract behaves as a linear system satisfying the one-dimensional wave equation (*6*). A closed-form solution to the wave equation for arbitrary area functions is not known; so it is necessary to use an algorithm to find an approximate solution for individual sample area functions.

The algorithm used in the computer program represents the vocal tract by a series of contiguous cylindrical sections, each of fixed area (*7*). Each section can be described by a characteristic impedance and a complex propagation constant, both being well-known quantities for uniform cylindrical tubes. Junctions between individual sections satisfy the constraints of continuity of pressure and conservation of volume velocity. The transfer function (magnitude and phase) is calculated directly as a function of frequency. Natural frequencies (formants) are determined from the phase spectrum.

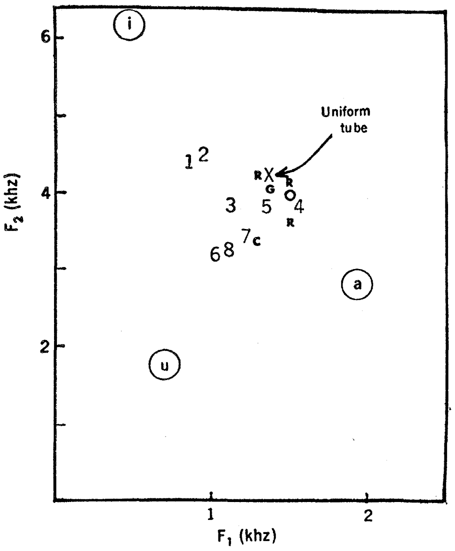

Fig. 2. Vowel "space" of simulated monkey vocal tract relative to human vowel space and natural ape and monkey cries (*1*). Chimpanzee cry noted by letter *C*, Gorilla by *G*, and rhesus monkey by *R*. The formant frequencies that would correspond to a uniform tube, 6.5 cm in length, terminated at one end are also plotted. All of the formant frequencies have been scaled toward those of the rhesus monkey to compensate for differences in overall vocal tract length.

In this fashion the computer program calculated the three lowest formant frequencies. (The lowest resonances are the perceptually most important aspects of a vocalization produced with a given supralaryngeal vocal tract configuration.) These formant frequencies are presented in Fig. 1.

We then systematically explored the possible range of supralaryngeal vocal-tract area functions that a rhesus monkey could make by moving his tongue, lips, and jaw. The computer program was used to determine the formant frequencies of the first three formants for each configuration. We estimated the range of articulatory maneuvers by manipulating the supralaryngeal vocal tract of an anesthetized monkey and by taking into consideration the continuity constraints imposed by the monkey's tongue as well as the effects of different jaw angles and lip rounding. In doubtful cases we allowed greater deviations from the "unperturbed" area function derived from the casting.

In Fig. 1a the dashed lines represent vocal tract configurations (for two different degrees of tongue height) that would be most likely to lead to the production of an unrounded high vowel. These result from changes in the tract toward that shape of a human vocal tract that is characteristic of the production of /i/. We note that F_1 decreases relative to the unperturbed vocal tract whereas F_2 increases. In Fig. 1b the three dashed lines represent vocal tract configurations analogous to low back vowels—that is, vowels produced with a tongue constriction toward the back of the mouth while the jaw is open or low, for example /a/. In Fig. 1c the dashed lines represent configurations for rounded back vowels—that is, vowels in which the lips are rounded, such as /u/. In configuration 8 we have tried to account for the lengthening of the vocal tract that can occur with lip rounding, as, for example, in the human vowel /u/.

The ratio of the maximum constrictions for these vocal tract configurations relative to the dimensions of the unperturbed vocal tract is similar to that measured by Fant (*3*) for human vowels. We have plotted the calculated first and second formant frequencies that correspond to our unperturbed and perturbed monkey vocal tract configurations in Fig. 2. We have also plotted the formant frequencies measured by Fant for a male human speaker for the vowels /a/, /u/, and /i/. These three vowels delimit the human "vowel space." The length of this speaker's supralaryngeal vocal tract was 17 cm for /a/. We have therefore multiplied the formant frequencies measured by Fant by the ratio 2.6 to take account of the fact that the tract length of the monkey is 6.5 cm, but that of the adult human who was measured by Fant was 17 cm. This procedure is valid for F_1 and F_2 of /a/ and F_2 of /u/ and /i/ where the behavior of the vocal tract can, as a first approximation, be represented by means of two or three tube models (*3*, *8*).

We have also plotted the previously analyzed formant frequencies of both ape and monkey cries that were produced with the vocal tract terminated

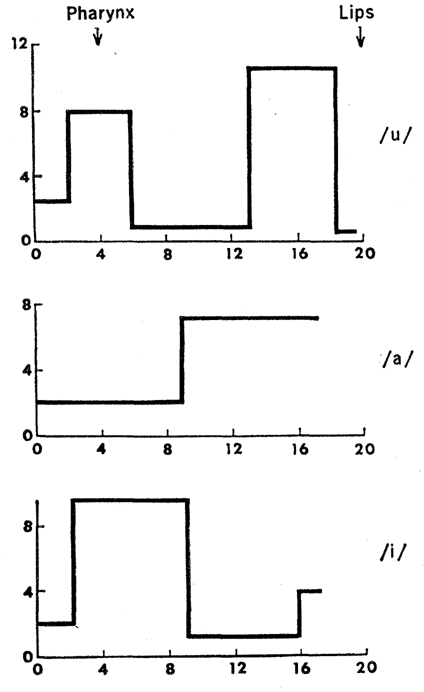

Fig. 3. Schematized area functions for the human vowels /a/, /u/, and /i/. Note that the area of the pharyngeal region is independent of the area of the front part of the supralaryngeal vocal tract.

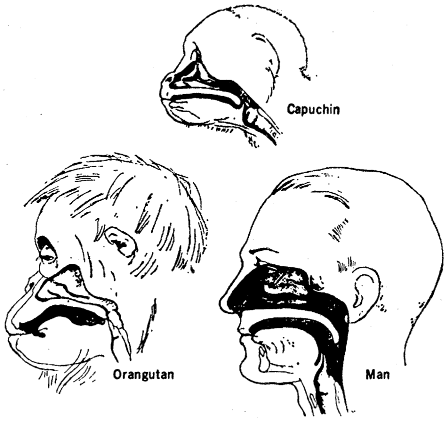

Fig. 4. Vocal tracts of monkey, ape, and man after Negus (*10*). The nonhuman primates lack a pharyngeal region where the root of the tongue forms a movable anterior wall. The nonhuman primates thus lack a speech-production mechanism where the area of the "back" pharyngeal region is variable and independent of the area of the "front" of the vocal tract.

by a high laryngeal impedance (*1*, *9*). We have also scaled up these formant frequencies to take account of the longer vocal tracts of these animals relative to rhesus monkey. The formant frequencies that would correspond to a uniform tube, 6.5 cm long, terminated at one end are also plotted in Fig. 2. The actual monkey and ape cries occupy only part of the vowel space of our computer-generated vowels. The only natural cry that is a signficant deviation from this schwa vowel is the chimpanzee cry which was produced by the animal with its lips rounded (*1*); the formant frequencies of this cry correspond most closely to configuration 7 of Fig. 1c, which represents the least rounded of our simulated rounded back vowels. Our computer-modeled configurations of the perturbed monkey vocal tract thus encompass and extend beyond the "acoustic vowel space" that was measured for actual utterances of nonhuman primates. The nonhuman primates previously recorded did not, in fact, use all of the articulatory maneuvers that we simulated for the rhesus monkey by means of the computer model.

The computer model further indicates that the possible acoustic vowel space of a monkey is quite restricted compared to the human range. Even if a rhesus monkey were able to manipulate his supralaryngeal vocal tract to make use of all of the possibilities that we considered in our computer model, he would not be able to produce the full range of human vowels. We can thus conclude that the vocal apparatus of the rhesus monkey is inherently incapable of producing the range of human speech.

In Fig. 3 we have presented schematized area functions for the human vowels /a/, /u/, and /i/ where we have approximated the vocal tract by means of uniform tubes for illustrative purposes. We have based these approximations on Fant's data (*3*). The supralaryngeal vocal tract can essentially be divided into an anterior and a posterior cavity. The cross-sectional area of the pharyngeal region in man can be constricted while the front of the mouth is open as in /a/. A large cross-sectional area can also be produced in the pharyngeal region with either a constricted anterior passage as in /i/ or a large cavity as in /u/. The nonhuman primates cannot produce vocal-tract area functions like man's because both the apes and monkeys lack a pharyngeal region like man's (*1*, *10*), where the body of the tongue forms a movable anterior wall. We have reproduced an illustration (Fig. 4) from Negus (*10*), indicating relative positions of the palate and larynx in the nonhuman primates and in man. The nonhuman primates lack a pharyngeal region like man's, where the cross-sectional area continually changes during speech. The inability of apes to mimic human speech (*2*) is thus an inherent limitation of their vocal mechanisms. Some of man's recent ancestors also may have been unable to produce the full range of human speech; the skeletal evidence of human evolution shows a series of changes from the primate vocal tract that may have been, in part, necessary for the generation of speech (*1*). The human speech-output mechanism thus should be viewed as part of man's species-specific linguistic endowment.

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9. Some of the ape and monkey cries were apparently produced while the animals' larynges were open wide (*1*). These cries are not plotted in Fig 2 because the vocal-tract boundary conditions do not correspond to the computer model. However the acoustic analysis indicated that the shape of the animals' supralaryngeal vocal tract when they produced these cries still appeared to approximate a uniform tube. These cries therefore would not change our conclusions concerning the range of supralaryngeal vocal-tract configurations that underlie these animals' vocalizations.
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23 December 1968

Chromosomal Location of MN Blood Group Locus

German *et al.* (*1*) have reported that an abnormal child with a translocation of a distal segment of the long arm of chromosome No. 2 to a point near the distal end of the long arm of chromosome No. 4 is hemizygous at the MN locus. They concluded that the evidence suggests that the MN locus is either in the middle of the long arm of chromosome No. 2 or near the distal end of the long arm of chromosome No. 4. In a study of the possibility of genetic linkage between a pericentric inversion on chromosome No. 2 and a number of genetic loci, Weitkamp *et al.* (*2*) reported a probability of free recombination between the MN locus and the inversion of 0.976. This calculation assumed an a priori probability of finding linkage between the MN locus and the inversion of 1 in 22, the number of autosomal pairs in man. However, if the MN locus is on either chromosome No. 2 or No. 4, then the probability that the MN locus is on chromosome No. 2 is $\Lambda/(\Lambda + 1)$, where Λ, the average probability ratio, was found to be 0.51. Thus, the probability that the MN locus is on chro-