The puparia resulting from such injections were opened at suitable intervals to check on pupal and adult development in the absence of the ring gland. Almost all specimens pupated but only a few evaginated the head to the "phanerocephalic" state, a process achieved by strong contractions of muscles (*7*) which are obviously weakened in operated specimens. At this point, irrespective of head evagination, development comes to a stop. According to Shaaya and Karlson's (*8*) curve of ecdysone titer during fly development, by the time the pupal molt takes place ecdysone has disappeared, to reappear again to initiate adult development.

In the absence of the ring gland, injected ecdysone carries development exactly to the state reached with the first natural release of ecdysone, but no further development is possible (*9*). Pupae lacking ring glands are therefore virtually identical with diapausing pupae in which the second production of ecdysone is delayed (*10*). Ecdysone also controls calcification in an aberrant case of puparium formation where hardening is not due to tanning but to calcification (*11*).

P. BERREUR
Laboratoire de Genetique Evolutive, 91 Gif-sur-Yvette, France

G. FRAENKEL*
Department of Entomology, University of Illinois, Urbana

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Taste Nerve Fibers: A Random Distribution of Sensitivities to Four Tastes

Abstract. *The numbers of rat glossopharyngeal and chorda tympani fibers responding to one, two, three, or four taste stimuli of different quality (sodium chloride, hydrochloric acid, quinine, and sucrose) and to each of the six possible pairs of these stimuli can be predicted if there are four independent sensitivities randomly distributed among innervating fibers.*

Mammalian chorda tympani taste neurons respond differentially to the quality of taste stimuli; that is, they respond more to some substances than to others. Substances to which a single neuron may respond can be classified into two categories: (i) those of similar quality (NaCl and LiCl) and (ii) those of dissimilar quality (NaCl and sucrose). Substances of similar quality will elicit responses in the same set of neurons, but substances of dissimilar quality may or may not (*1*). For example, a neuron which responds to NaCl will also respond to LiCl, but it may or may not respond to sucrose. It is typical for a single chorda tympani neuron to respond to stimuli of very different quality.

Many individual rat chorda tympani fibers respond to both NaCl and HCl (salty and sour substances); very few respond to both sucrose and quinine (sweet and bitter substances) (*2*). But the anterior tongue, which the chorda tympani innervates, is highly sensitive to salt and acid but poorly sensitive to sucrose and quinine. The posterior of the rat's tongue, innervated by the glossopharyngeal nerve, is more sensitive to quinine and sucrose (*3*). There are probably more receptors sensitive to these stimuli in the foliate and circumvallate papillae in the back of the tongue than there are in the fungiform papillae in the front. If the combinations of sensitivities to different qualities were probabilistic, dependent only upon the numbers of receptors sensitive to each quality in a receptive field, there should be more combinations of sensitivities to bitter and sweet stimuli in glossopharyngeal fibers.

Sensitivities of 27 rat glossopharyngeal taste fibers were determined (*4*). The animal was anesthetized with sodium pentobarbital, the back of the tongue was exposed surgically, and the nerve was dissected free and cut centrally. After removal of the sheath, groups of fibers could be separated and placed upon silver-silver chloride wick recording electrodes and their responses amplified. The criterion for a single fiber response was uniformity of recorded spike amplitude. Stimulus solutions flowed into the lumen of the circumvallate or foliate papilla through a small pipette (0.1 mm in diameter).

Test stimuli were 0.3*M* NaCl, 0.01*N* HCl, 0.001*M* quinine hydrochloride, and 0.3*M* sucrose. The stimulus intensities produce about 50 percent of the total nerve's maximum response to these common representatives of the four taste qualities (salty, sour, bitter, and sweet). A fiber was classified as responding to a stimulus if there were at least a 50 percent increase in response rate during the first 5 seconds of stimulation. Fibers which responded to several stimuli usually did not respond equally well to all; however, response rate increased at least 500

Table 1. Numbers of single fibers responding to each combination of two tastes.

Combination (x, y)	$(p_x)(p_y)$	Predicted	Observed
Glossopharyngeal fibers			
NaCl, HCl	(.6)(.6)	9.7	9
NaCl, quinine	(.6)(.4)	6.5	6
NaCl, sucrose	(.6)(.4)	6.5	7
HCl, quinine	(.6)(.4)	6.5	8
HCl, sucrose	(.6)(.4)	6.5	6
Quinine, sucrose	(.4)(.4)	4.3	3
Chorda tympani fibers			
NaCl, HCl	(.8)(.7)	14.0	14
NaCl, quinine	(.8)(.4)	8.0	8
NaCl, sucrose	(.8)(.2)	4.0	4
HCl, quinine	(.7)(.4)	7.0	6
HCl, sucrose	(.7)(.2)	3.5	2
Quinine, sucrose	(.4)(.2)	2.0	2

Table 2. Numbers of single fibers responding to 1, 2, 3, or 4 tastes; T represents the number of fibers in sample.

Responses (n) (No.)	Predicted ($P_{(n)} \cdot T$)	Observed
Glossopharyngeal (T = 27)		
1	7.1	8
2	11.2	12
3	7.1	5
4	1.7	2
Chorda Tympani (T = 25)		
1	5.4	5
2	11.3	13
3	7.2	6
4	1.0	1

percent to more than one stimulus in one-quarter of the fibers. The electrophysiological response of one fiber (larger spike) to sucrose and of another fiber (smaller spike) to sucrose and HCl acid is shown in Fig. 1. Glossopharyngeal taste neurons are similar to chorda tympani neurons; they are differentially sensitive to quality but do not usually respond to only one quality.

This sample of glossopharyngeal fibers and a comparable sample of chorda tympani fibers differ only in ways predictable from differences in the sensitivities of the posterior and anterior tongue. Responses of 25 chorda tympani fibers to 0.1*M* NaCl, 0.03*N* HCl, 0.01*M* quinine, and 1.0*M* sucrose (*5*) were available for comparison. Of the chorda tympani fibers, eight-tenths responded to NaCl, seven-tenths to HCl, four-tenths to quinine, and two-tenths to sucrose; whereas, six-tenths of the glossopharyngeal fibers responded to NaCl, six-tenths to HCl, four-tenths to quinine, and four-tenths to sucrose. These proportions reflect differences in the intensities of the test stimuli as well as differences in the sensitivities of the front and back of the tongue.

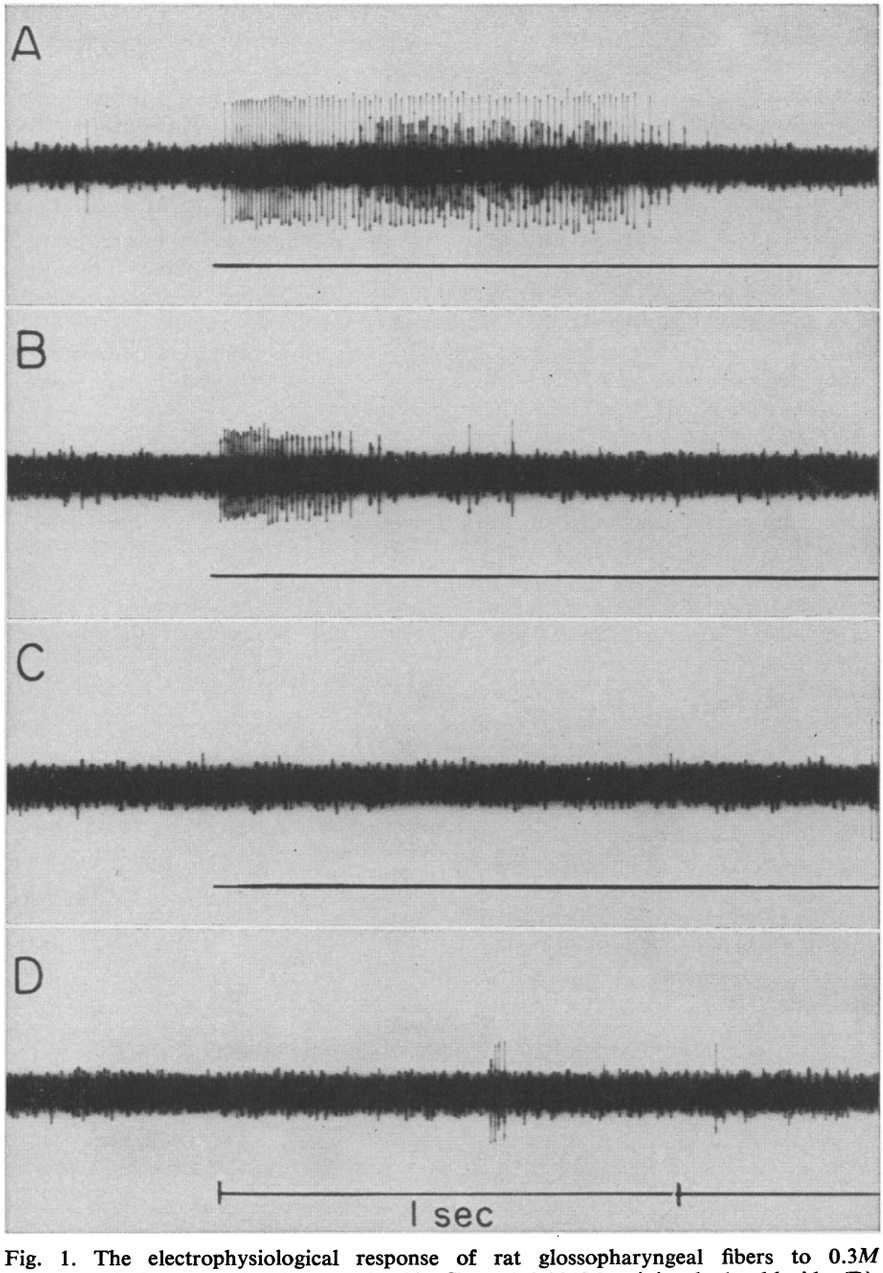

Fig. 1. The electrophysiological response of rat glossopharyngeal fibers to 0.3*M* sucrose (A), 0.01*N* HCl (B), 0.3*M* NaCl (C), and 0.001*M* quinine hydrochloride (D). Stimulation is indicated by the line beneath each record. One fiber (larger spike) responds to sucrose and the other (smaller spike) responds to sucrose and HCl; the former does not respond to acid and neither responds to NaCl or quinine.

If the sensitivities of these four stimuli are independent and randomly distributed among innervating fibers, the probability of obtaining responses to any pair of these four stimuli would be given by the product of the probabilities of obtaining responses to each stimulus of the pair. Probabilities of responses to the four stimuli (p_x) can be estimated by the proportions of fibers in a sample which respond to each of the stimuli. The probabilities for each of the six combinations of responses to two of the four stimuli ($p_x \cdot p_y$) and the predicted and observed numbers of fibers with each combination sampled from the glossopharyngeal and chorda tympani are given in Table 1. The proportions of taste fibers responding to each pair of stimuli can be predicted by assuming that four independent sensitivities combine probabilistically in innervating taste fibers.

Furthermore, if sensitivities to these four stimuli are mutually independent events ($N = 4$) with known probabilities (p_x) which are distributed randomly among taste fibers, the probabilities ($P_{(n)}$) of obtaining responses to 1, 2, 3, or 4 stimuli ($n = 1, 2, 3, 4$) are given by the successive terms of the binomial expansion [$(p_x + q_x)^N$, $q_x = 1 - p_x$, $P_{(0)}$ will not be considered]. Table 2 gives the predicted and observed numbers of glossopharyngeal and chorda tympani fibers responding to 1, 2, 3, or 4 stimuli. The proportions of fibers that are narrowly tuned (responding to 1 quality) or broadly tuned (responding to 2, 3, or 4 qualities) can be predicted given only the probability any fiber in the sample has of responding to each quality.

Invertebrate taste neurons respond exclusively to one class of chemical (*6*); mammalian taste neurons typically respond to several classes. But each mammalian taste neuron innervates a number of receptor cells. These cells vary in their sensitivities to different qualities (*7*). The broadening of the range of effective stimuli in mammalian taste neurons may result from random unions of a few independent exclusive chemosensitive receptors, similar to those found in invertebrates. Although there may truly be many varieties of taste receptors in mammals (*8*), there need only be a few, or as many as there are mutually independent stimuli. In any case, stimuli which have mutually independent effects on taste neurons,

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*).

M. FRANK
C. PFAFFMANN
Rockefeller University,
New York, New York 10021

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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

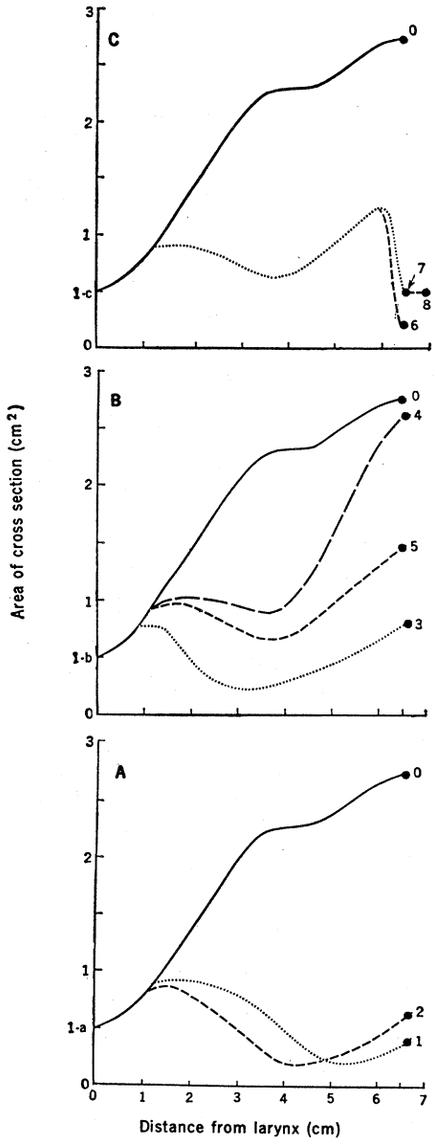

Fig. 1. Area functions of supralaryngeal vocal tract modeled by computer and corresponding vowel formant frequencies. Curve 0 is the unperturbed vocal tract of the rhesus monkey. The first formant frequency of this area function, F_1, is 1503 hz, F_2 is 4007 hz, and F_3 is 6287 hz. (a) Curves 1 and 2 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.