Tongue mechanoreceptors: comparison of afferent fibers in the lingual nerve and chorda tympani

In contrast to cutaneous tissue, which contains a variety of organized nerve endings, the lingual mucosa contains only one, the mucocutaneous end organ, with possibly two variations. Mucocutaneous end organs occur in parallel with a free-ending nerve plexus and are located in the bases of fungiform, foliate and filiform papillae and in the intervening epithelium[10,11,14]. Sensory axons from the anterior two-thirds of the tongue project in the lingual nerve; a short distance posterior to its exit from the tongue a small branch, the chorda tympani, diverges, which carries mainly taste fibers, some somesthetic fibers, and efferents to the salivary glands. In the cat, diameters of myelinated axons in the chorda tympani range from 1 to 6 μm (ref. 4). The diameter spectrum of the lingual nerve extends from 1 to 15 μm (ref. 2) and carries mainly mechano- and thermosensitive fibers[1,6]. Thus, the sensory capacity of the tongue provides the central nervous system with information on thermal, mechanical and chemical properties of ingested substances. The following data on tongue mechanoreceptors were obtained incidental to a study of taste mechanisms.

In 11 cats, under Nembutal anesthesia, the lingual nerve and the chorda tympani were exposed posterior to their exit from the tongue. Both nerves were cut, the perineural sheaths removed and, by microdissection, the cut, distal ends were teased into fine fasciculi. Single unit potentials were recorded by placing a fasciculus on a macroelectrode and the reference electrode on adjacent soft tissue. The potentials were first fed through a preamplifier, then into an audiomonitor and an oscilloscope. They were also recorded on magnetic tape for later analysis.

Twenty-eight mechanoreceptors in the lingual nerve and 17 in the chorda tympani were investigated. Those in the lingual nerve were much more easily obtained than were those in the chorda tympani, possibly because the lingual nerve contains axons with larger diameters and a greater fraction of mechanosensitive fibers than does the chorda tympani. The location and size of the receptive field for each mechanosensitive fiber were determined by manual exploration of the tongue surface with small glass probes. Conduction velocities were estimated from conduction distances and latencies of unit potentials. An electrical stimulus was delivered through a bipolar electrode, placed on the receptive field of a mechanoreceptor, and the evoked unit potential recorded. At the end of several experiments, after further dissection, a thread was laid from the tip of the tongue along its ventral surface following the lingual nerve to the recording site, giving a measurement of about 62 mm. Then, for a given unit, the receptive field distance posterior to the tip of the tongue was subtracted to yield the conduction distance. All along the tongue, axons turn from the ventral surface vertically to end in the dorsal mucosa. This short vertical distance, proportional to the thickness of the tongue, was not included in our measurements; thus, all our conduction velocities are probably somewhat underestimated. However, this error is expected to be similar for both lingual nerve and chorda tympani fibers and should not interfere with establishing differences in conduction velocities between the two nerve populations.

Brain Research, 35 (1971) 584–588

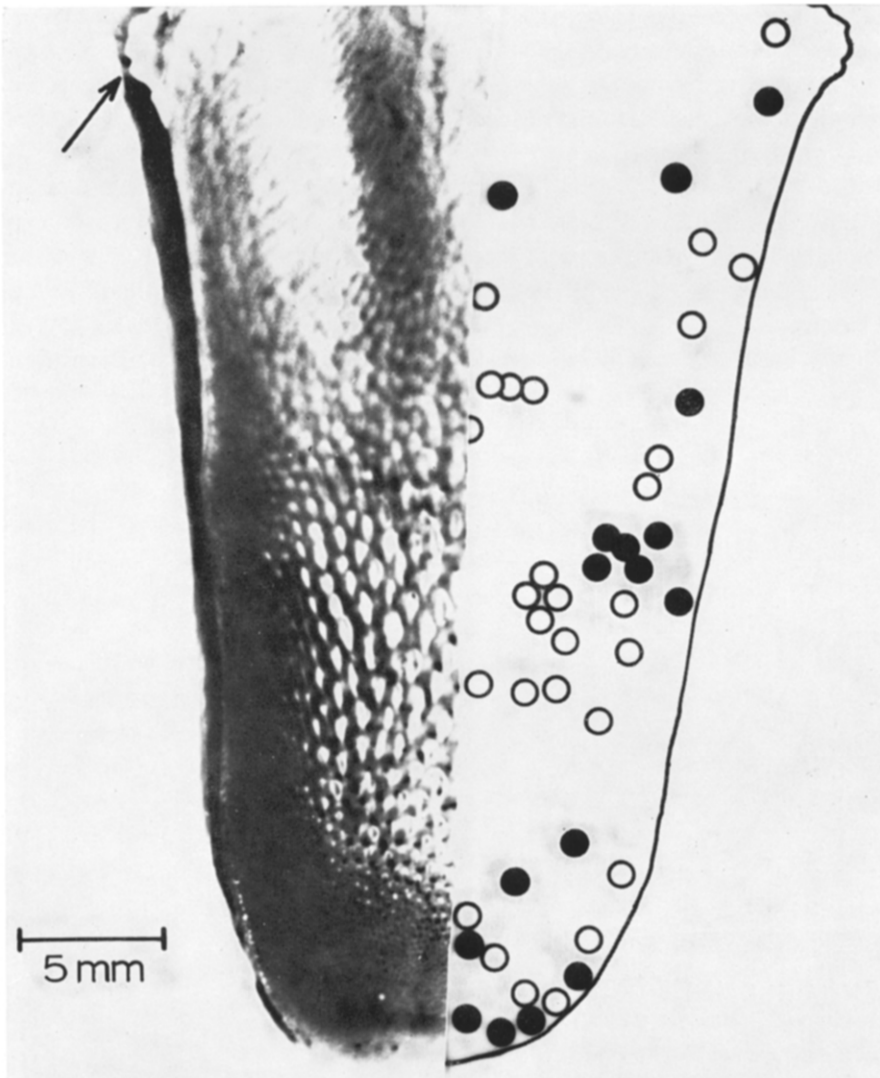

Fig. 1. Dorsal surface of anterior portion of tongue; on right half receptive fields of mechanosensitive fibers projecting in the lingual nerve (○) and in the chorda tympani (●). Arrow points to foliate papillae on lateral border of tongue.

Resulting conduction velocities of lingual nerve fibers ranged from 11 to 53 m/sec with a mean of 30 m/sec and those of chorda tympani fibers ranged from 9 to 38 m/sec with a mean of 19 m/sec. Although there is considerable overlap, as a whole the population in the chorda tympani is more slowly conducting than that in the lingual nerve.

The spatial distribution of the mechanoreceptors is shown in Fig. 1. From each receptive field, the distances to the midline and to the tip of the tongue were measured and entered on a photograph of the tongue. Lingual nerve and chorda tympani receptors were intermingled, with the greatest density on the tip and lateral border, and with least density on the ventral surface, where only two receptors were found. These observations are in agreement with histological studies on innervation density[11], physiological studies on the sheep's tongue[8], and two-point discrimination studies in humans[12].

Of the 45 units studied, 41 on the dorsal surface of the tongue had small receptive fields. Tests with near-threshold stimuli showed these fields to be approximately 1–4 sq. mm. Most fields increased in size somewhat with application of stronger mechanical stimuli. The remaining 4 units had larger receptive fields and will be described below.

On the basis of the adaptation rate to maintained mechanical stimulation,

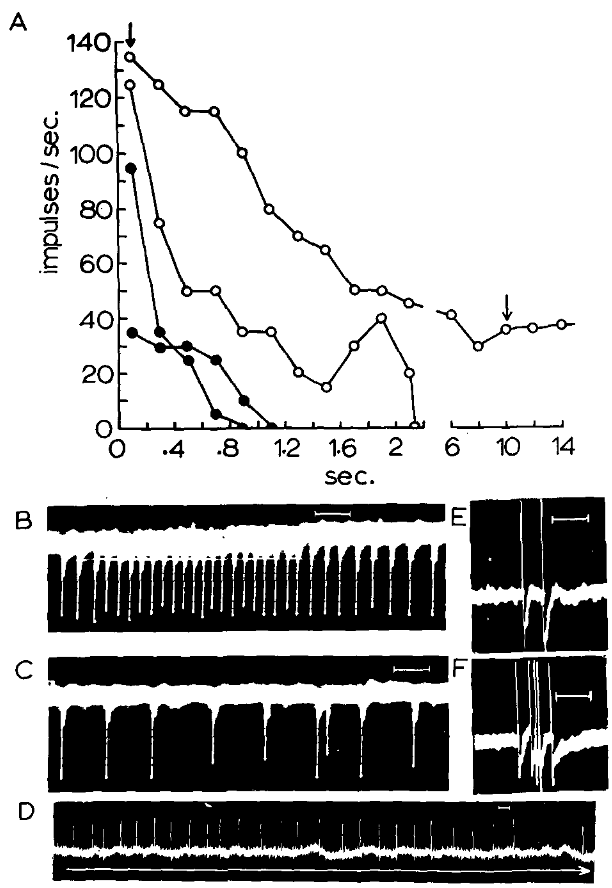

Fig. 2. A, Poststimulus time histograms of slowly adapting units. Stimulus, light pressure (○) and light squeeze (●), applied at time zero and maintained beyond the time indicated on the abscissa. B, Response of slowly adapting chorda tympani unit, section of record obtained at first arrow in A. C, Same unit, section obtained at second arrow in A. D, Lingual nerve unit, plotted in lowest graph in A; response to light squeeze lasts 1.1 sec. Stimulus was maintained beyond duration of response, as indicated by arrow on lower horizontal line. E, Rapidly adapting unit, response to touch. F, Same unit, response to light stroking. Positive up, horizontal bars 20 msec.

receptors in the tongue can be grouped, as in other tissues[3,7,9], into slowly adapting (24%) and rapidly adapting units (76%). Slowly adapting units were further divided into 3 subgroups: those firing for many minutes, SA_a; those firing for several seconds, SA_b; and 'squeeze' units, firing for about 1 sec, SA_c. The uppermost curve in Fig. 2A shows the response of a member of SA_a to maintained stimulation. The recorded spike trains were divided into 200 msec bins, the number of spikes/bin converted into impulses/sec and plotted on the ordinate. The initial firing rate was high, then declined to a lower steady rate and, in this unit, continued for at least 20 min. Sections of the original spike train obtained in Fig. 2A at the first and second arrows are shown in Figs. 2B and 2C. This unit fired at almost the highest rates observed; most other units fired at lower rates both during the initial and steady state phases. The second curve in Fig. 2A was plotted from a member of SA_b which stopped firing after approximately 2 sec. The lower two curves are from members of SA_c which were located along the anterior and lateral border of the tongue. They were much more effectively excited by a delicate squeeze applied with fine forceps, one tip on the dorsal, the other on the ventral side on the edge of the tongue, than by simple touch. The lowest curve in Fig. 2A was plotted from the 'squeeze' response shown in Fig. 2D.

The second main group, rapidly adapting units, discharged a short burst of spikes, occasionally lasting up to 200 msec, in response to a maintained stimulus. Rapidly adapting units were divided into 2 subgroups, RA_a and RA_b, on the basis of what comprised an adequate stimulus. Members of RA_a discharged a burst of spikes in response to simple touch by the probe (Fig. 2E). A light, stroking movement over the receptive field evoked a burst with higher spike frequency (Fig. 2F). Members of RA_b did not respond to simple touch; only a stroking movement over the receptive field was effective. Some of them were excited by movement of a few horny papillae which protrude from the dorsal surface of the cat's tongue.

Although a unit had a certain receptive field size, excitation did not necessarily require that the probe be applied to the whole field. Mechanical distortion of a certain minimal area was required; in some units this comprised the whole field but only portions thereof in others. Although all unit subgroups contained a range of sizes of minimal areas, the largest minimal areas definitely clustered in group RA_b (excited by stroking over the receptive field rather than by simple touch).

Comparison of the chorda tympani with the lingual nerve showed a clear difference in the distribution of the RA units: 12% of chorda tympani mechanoreceptors were RA_a, 64% were RA_b; among lingual nerve fibers 41% were RA_a, 33% RA_b. No difference in distribution of SA units was apparent, although this might be shown by study of a larger sample. Four fibers which projected to the lingual nerve did not fit into the above groups. The receptive fields of two were on the ventral surface of the tongue and extended over 1 to 2 sq. cm. Touch applied anywhere within the field evoked a brief burst of spikes, but a light stroking movement was more effective. The receptive fields of the other two units were difficult to delineate because the only effective stimulus was a strong rolling movement of the probe over the tongue. This suggested that receptors were located in the tongue musculature, rather than in the mucosa[8].

After study of properties of isolated receptors it is legitimate to ask how these function in the normal life of the animal. On food intake, mechanical and taste stimuli initiate salivation and mastication, continuing until coarse, dry food is converted into a fine, fluid mass. Evidently the mechanical consistency of food is continuously monitored until it is fine enough for swallowing, at which point the swallowing reflex is triggered; in fact, motor components of mastication–swallowing reflexes were described recently[5,13]. The slower conduction velocities of mechanoreceptors in the chorda tympani closely approached those of taste fibers in the same nerve[8]. Similar conduction velocities could result in the excitation of a central neuron population dependent on summation of convergent mechanosensory and taste inputs.

This study was supported by U.S. Public Health Service Grants DE 02152 and DE 00248.

Department of Physiology and Biophysics, University of Washington, Seattle, Wash. 98195 (U.S.A.), and Department of Physiology, University of Malaya, Kuala Lumpur (Malaysia)

M. A. BIEDENBACH
K. Y. CHAN

1 BENSING, H., HENSEL, H., AND WURSTER, R., Integrated static activity of lingual cold receptors, *Pflügers Arch. ges. Physiol.*, 311 (1969) 50–54.
2 BLOM, S., Afferent influences on tongue muscle activity, *Acta physiol. scand.*, Suppl. 170, 49 (1960) 3–97.
3 BURGESS, P. R., PETIT, D., AND WARREN, R. M., Receptor types in cat hairy skin, *J. Neurophysiol.*, 31 (1968) 833–848.
4 FOLEY, J. O., The sensory and motor axons of the chorda tympani, *Proc. Soc. exp. Biol. (N.Y.)*, 60 (1945) 262–267.
5 GOLDBERG, L. J., AND NAKAMURA, Y., Lingually induced inhibition of masseteric motoneurons, *Experientia (Basel)*, 24 (1968) 371–373.
6 HENSEL, H., AND ZOTTERMAN, Y., The response of mechanoreceptors to thermal stimulation, *J. Physiol. (Lond.)*, 115 (1951) 16–24.
7 IGGO, A., Electrophysiological and histological studies of cutaneous mechanoreceptors. In D. R. KENSHALO (Ed.), *The Skin Senses*, Thomas, Springfield, Ill., 1968, pp. 84–111.
8 IGGO, A., AND LEEK, B. F., The afferent innervation of the tongue of the sheep. In T. HAYASHI (Ed.), *Olfaction and Taste II, Symposium Publications*, Pergamon Press, New York, 1965, pp. 493–507.
9 KNIBESTÖL, M., AND VALLBO, A. B., Single unit analysis of mechanoreceptor activity from the human glabrous skin, *Acta physiol. scand.*, 80 (1970) 178–195.
10 KUNZE, K., Die Papilla filiformis des Menschen als Tastsinnesorgan, *Ergeb. Anat. Entwickl.-Gesch.*, 41 (1969) 3–64.
11 MARLOW, C. D., WINKELMANN, R. K., AND GIBILISKO, J. A., General sensory innervation of the human tongue, *Anat. Rec.*, 152 (1965) 503–511.
12 MCCALL, G. N., The assessment of lingual and tactile sensation and perception, *J. Speech Dis.*, 34 (1969) 151–156.
13 PORTER, R., The synaptic basis of a bilateral lingual-hypoglossal reflex in cats, *J. Physiol. (Lond.)*, 190 (1967) 611–627.
14 SPASSOVA, I., On the structure of encapsulated nerve endings in the tongue of the cat and its functional significance, *Z. mikr.-anat. Forsch.*, 72 (1965) 366–382.

(Accepted September 24th, 1971)