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Single Unit Recordings from the Geniculate Ganglion of the Facial Nerve of the Cat[1]

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Summary. 1. Within the cat geniculate ganglion three distinct neural populations were definable on the basis of single unit recordings. These three neural populations were designated "ear units", "regular discharge units" and "tongue units." Units from these three populations tended to be located in different regions of the ganglion and were influenced by different types of stimulation to different parts of the body.

2. Ear units seemed to constitute a uniform functional population, with the major differences between units being the external locus of projection. Ear units typically had no spontaneous activity. They were discharged by dynamic displacements of hairs on the skin of the inner surface of the ear.

3. Regular discharge units were classified into three types on the basis of their spontaneous activity patterns. Discharge of most of the units could be affected by static dislocations of tissues of the soft palate and pharynx. Discharge patterns, evoked and spontaneous, tended to be extremely regular.

4. Tongue units seemed to constitute an extremely diverse population. Wide variability was shown on every measure taken of tongue unit activity. Spontaneous activity patterns varied markedly from unit to unit, with bursting discharge common. Most units could be discharged by electrical stimulation of papillae of the tongue, although the number of stimulatable papillae varied from unit to unit as did latency measures. Some tongue units were discharged by mechanical stimulation of the tongue, most by chemical stimulation of the tongue (with salt, acid, quinine and common cat foods), and some by both.

Key Words: Geniculate ganglion — Facial nerve — Cat sensory systems — Taste — Tongue chemoreceptors — Fungiform papillae — Cat tongue

Introduction

The cat geniculate ganglion (Fig. 1) is situated deep in the petrous portion of the temporal bone at the junction of the facial nerve, nervus intermedius and greater superior petrosal nerve. The wedge-shaped ganglion is about 1.25 mm across at the base and 1.75 mm from base to apex (Bruesch, 1944). There are

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approximately 1800 cells in the cat geniculate ganglion (Bruesch, 1944; Buskirk, 1945; Foley and DuBois, 1945; Foley *et al.*, 1946). All of the cells are apparently of the sensory pseudo unipolar type (Ramon y Cajal, 1909), although differences in cell size and staining characteristics are detectable (Gaetani, 1906; Kuré and Sano, 1935). The peripheral processes of geniculate ganglion cells leave the ganglion with the facial nerve or the greater superior petrosal nerve. The central processes of the cells form the bulk of the fibers within the nervus intermedius.

The cells of the geniculate ganglion subserve more than one sensory system. It is known that the cells supply the innervation via the chorda tympani for the front part of the tongue (Gaetani, 1906; Rhinehart, 1918; Weigner, 1905). Hunt demonstrated with clinical cases that the geniculate ganglion supplies innervation to the skin of the inner surface of the human ear (Hunt, 1907, 1910, 1915, 1937). Later anatomical studies traced fibers from the cells of the geniculate ganglion via the posterior auricular nerve to the outer dermal layers of the skin of the ear (Rhinehart, 1918). Anatomical studies (Larsell and Fenton, 1928; Rhinehart, 1918), also demonstrated that fibers having their origin in the geniculate ganglion innervate the soft palate and deep nasal areas.

In this study we present some electrical measures of single unit activity recorded within the cat geniculate ganglion. To our knowledge this study represents the first attempt to record from units in the geniculate ganglion.

Techniques

The Preparation[3]

The cat was anesthetized with an intraperitoneal injection of sodium pentobarbital (60 mg/kg) and, following a tracheotomy, secured in a stereotaxic headholder. The skin and muscles were cleared from the occipital portion of the skull, a portion of the cranium was removed and a partial cerebectomy of the neural matter overhanging the superior aspect of the petrous portion of the temporal bone was performed. The petrous bone overlying the ganglion was planed away with a carbide dental burr until the geniculate ganglion (and portions of the facial and greater superior petrosal nerves) was exposed. Care was taken to preserve the blood supply to the ganglion. Difficulty was encountered in penetrating the connective tissues covering the ganglion and slitting this covering with a fine razor blade knife was often unsuccessful or damaged the ganglion. Accordingly, the outer sheaths were partially dissolved with a saturated solution of alpha chymotrypsin and trypsin. This solution was applied topically and left on from 5—20 min until the sheaths fragmented sufficiently to permit the entry of the microelectrode. Even with the use of the enzymes penetration into the ganglion was difficult.

Recording Conditions

Both tungsten and gold-plated stainless steel (Boudreau *et al.*, 1968) microelectrodes were used for recording. The tungsten electrodes seemed to record sharper spikes with lower noise levels than the stainless steel, but this may have occurred because the insulation on the tungsten electrodes tends to be pushed back resulting in large tip exposures (often many tens of microns). Apparently small tip size is not necessary to isolate geniculate ganglion cells electrically though they themselves are small. Although multiunit recordings were common, the spikes

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[3] This exposure of the geniculate ganglion was described to us by Dr. Bennett M. Stein.

Fig. 1. *Sagittal section through the geniculate ganglion showing the relationship of the ganglion to the facial nerve (7th) and greater superior petrosal nerve (gr. sup. pet.).* The nose of the cat is to the right of the figure, the ear out toward the reader and the brain in toward the back of the journal. The nervus intermedius exits from the left proximal portion of the ganglion

from one unit were either much larger than the others or could be made so by advancing the electrode. Units could frequently be held for long traverses of the electrode and movements

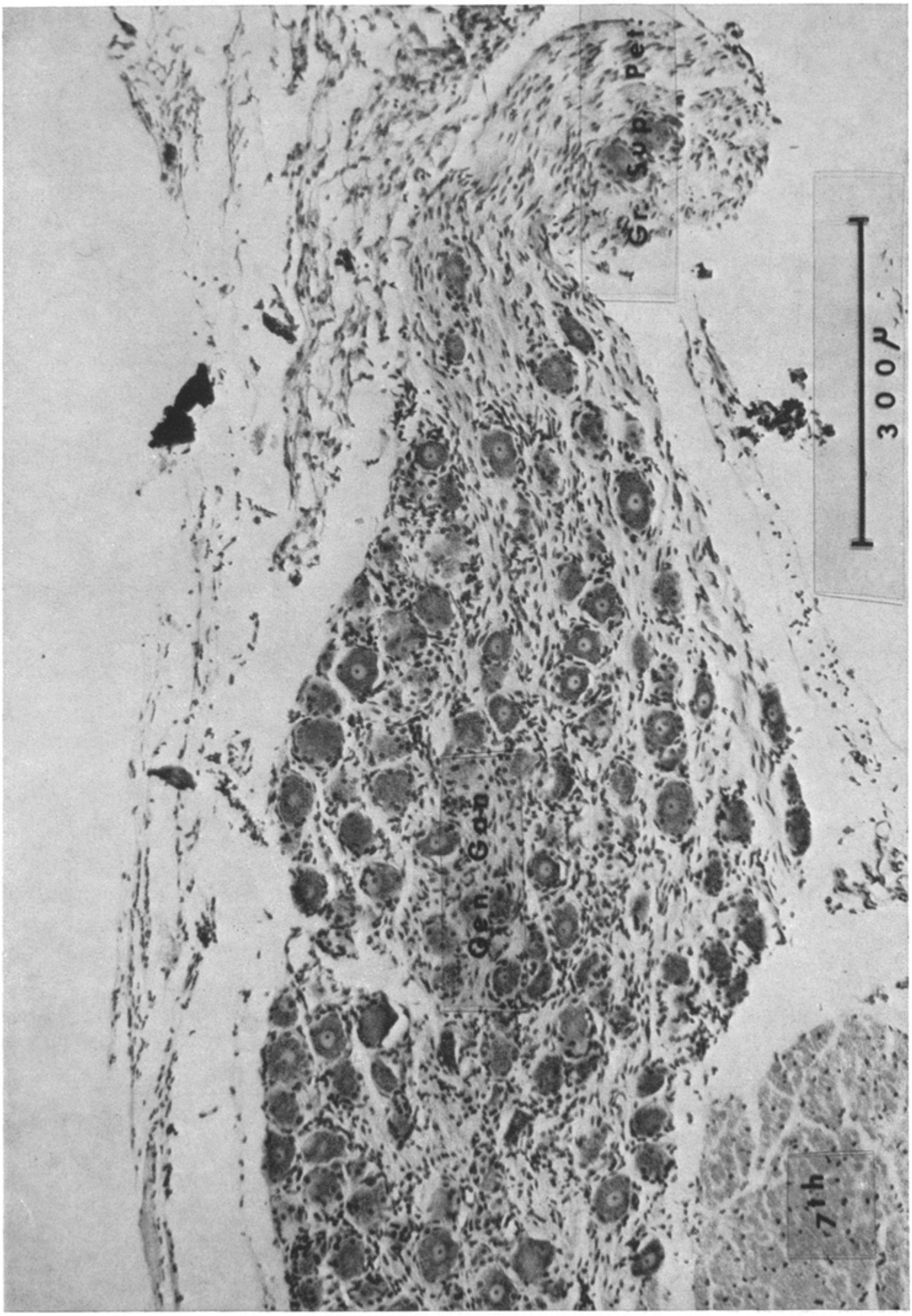

Fig. 1

of the preparation or tapping on the headholder did not usually result in loss of unit potentials. It seems that despite high cell density throughout most of the ganglion (see Fig. 1), only a few units can be recorded from during any penetration and that these units produce large extracellular potential fields.

The microelectrode was advanced into the ganglion with a hydraulic microdrive. Selection of signal/noise cutoff levels was facilitated with a differential amplitude discriminator (Spalla and Boudreau, 1967). Samples of spontaneous activity or discharges to stimulation were tape recorded for further study. Spike potentials were processed with a CAT computer or counted on a counter. The CAT digital output was fed into a LINC-8 computer for computation and graphing.

The spike potentials recorded were either initially negative or initially positive. Initially positive potentials constituted about 30% of the population, a percentage found for all three major response types: 35 of 113 tongue units, 7 of 27 ear units and 11 of 38 regular discharge units were positive units. Polarities did not reverse during advances of the electrode but remained at their initial polarity. Although it was frequently possible to advance the electrode and hold units with both types of polarity and even increase their amplitudes, moving the animal (e.g. pulling the tongue out) was more likely to result in the loss of contact with positive units than negative units. Occasionally a notched peak was observed on the initial spike potential; notched peaks were seen on potentials recorded from tongue units, ear units and regular discharge units.

Injury, as defined by changes in discharge pattern with electrode advance, was definitely observed to occur only with regular discharging units (Fig. 2). No interval measures were taken from units observed to produce injury discharges.

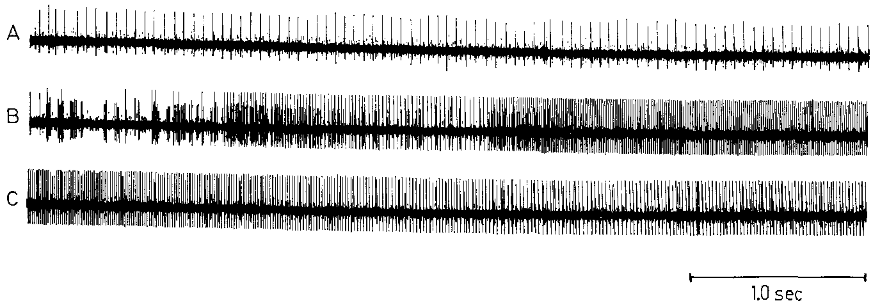

Fig. 2. *Changes in spontaneous activity from a regular discharge unit resulting from movements of the electrode.* Top line: Spontaneous activity before electrode movement. Middle and bottom lines: Spontaneous activity during electrode movement. All records continuous in time

Stimulation of the Tongue

The method employed to stimulate the tongue electrically was similar to that described by Békésy (1964). Papillae were electrically stimulated with small metal probes (in our case, tungsten wires) with a large indifferent electrode clamped to the opposite side of the tongue. A constant current stimulator was used to deliver 0.1 msec pulses at a rate of 10/sec. The tungsten probe was positive and the indifferent electrode was negative. Thresholds were measured in milliamps. Spike latencies were measured from the oscilloscope face and are probably accurate only to within 10%.

In the text there is the occasional remark that the tongue has not been stimulated. This remark means that there has been no electrical or chemical stimulation of the tongue other than a rinse or two with saline or distilled water to avoid dryness.

We examined the response of tongue units to three standard chemical solutions and to various foods that cats eat. The three standard solutions were 1.0 M NaCl, 0.01 M quinine hydrochloride and 0.1 M citric acid. The foodstuffs used were pork liver, pork kidney, chicken breast, beef, beef heart, canned tuna (Purina tuna for cats) and frozen cod fillets. With the exception of the tuna and the cod, these foods were acquired fresh and unadulterated. The foods were divided into 5 gm portions and frozen. Hours prior to the recording, the foods were chopped and each placed in 10 cc of distilled water. In addition to these foods, egg white, egg yolk (each in 10 cc of distilled water) and sucrose (1.7 M solution) were occasionally used.

Chemical substances at room temperature (21—23° C) were applied to the tongue with eye droppers into the area known to be innervated by a tongue unit. Such an application flooded a large area of the tongue. The change in discharge for a ten second period following stimulation was compared to the spontaneous activity level in one or more 10 sec periods prior to stimulation. Since many chemoreceptive tongue units exhibited high levels of spontaneous activity, the response to chemical stimulation was expressed as the number of spikes during 10 sec of stimulation minus the spontaneous activity level.

Results

Almost all units encountered in the geniculate ganglion could be divided into three groups: ear units, regular discharge units and tongue units. The majority of the regular discharge units could be affected by movement of tissues of the soft palate and pharynx. Thus the units in these three groups were affected by stimulation of different areas of the head. In addition, the units in these three groups tended to be encountered in different areas of the geniculate ganglion. The ear units were located in the dorsal layers of the ganglion adjacent to the seventh nerve; the tongue units were usually underneath them in the ventral layers of the ganglion; and the regular discharge units were usually located in the region where the greater superior petrosal originates (Fig. 1), although they were often spread throughout the ventral layers of the ganglion. These locations are based upon observations during penetrations into different parts of the exposed ganglion.

Ear Units

The geniculate ganglion units classified as ear units seemed to constitute a homogeneous population. These units exhibited little or no spontaneous activity. They were excited into discharge by moving the hairs projecting from the inner surface of the pinna. The hair cover on the inner surface of the cat's ear, like that of the dorsal surface of the ear, is distinct from the fur covering most of his body. Rather than being composed of mixed fine and coarse hairs, the hairs in the ear are arranged with long hairs near the outer and anterior portions of the pinna and short bristly hairs extending down into the auditory canal. The hairs on the dorsal surface of the ear are also different from the body hairs, although analogs of guard and down hairs are distinguished (Brown *et al.*, 1967).

Ear units all seemed to be the same, except for the area innervated. When an ear unit was isolated, the location of its receptive field was determined by moving hairs in and around the ear. In all cases units were discharged only by moving hairs on the inner surface of the pinna. This stimulation area is shown in Fig. 3. Because of the headholder ear bars, we were not able to investigate hairs on the anterior part of the inner surface of the pinna nor areas deep within the auditory canal. We have no doubt, however, that the entire inner surface of the pinna with its distinctive hair system is innervated by the geniculate ganglion, since we encountered many units we could discharge by moving anterior portions of the pinna; undoubtedly their discharge was a result of the rubbing against the ear bar of hairs from areas inaccessible to us.

An example of a receptive field of an ear unit can be seen in Fig. 3. All geniculate ganglion ear unit receptive fields were small, of several square millimeters in

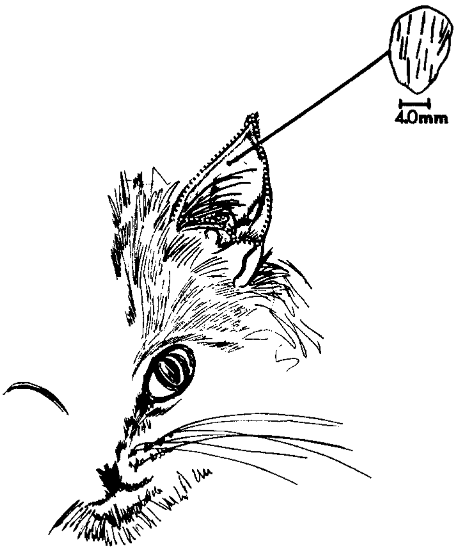

Fig. 3. *Geniculate ganglion ear units could be discharged by moving hairs on the inner surface of the pinna.* The area within which hair movements were effective is outlined with a dotted line. Geniculate ganglion ear units had small receptive fields, an example of which is shown in this figure (inset)

extent. The number of hairs within a unit's receptive field varied from as few as six to more than 15. Fewer hairs were seen in the receptive fields deep within the ear. The receptive fields with the largest number of hairs were located near the outer regions of the pinna where the hairs are the most dense.

An ear unit could be excited into discharge by extremely small movements of a single hair within the unit's receptive field. Discharge occurred only during movement, was maintained throughout the period of movement, and seemed proportional to rate of movement. The direction of hair movement did not seem to matter. Discharge of a unit could be augmented by simultaneously moving more than one hair.

Spontaneous discharges from ear units were occasionally seen. This spontaneous activity usually consisted of a low fairly regular discharge. In one case, spontaneous activity was accidentally produced in an ear unit when the skin in its receptive field was scratched in an attempt to scrape off ear wax. The induced spontaneous activity from this unit was eliminated by infiltrating procaine into the skin of the unit's receptive field. It is possible that the spontaneous activity observed for other ear units was produced by skin abrasions resulting from the process of fitting the cat to the stereotaxic instrument.

Regular Discharge Units

Three types of units were classified as regular discharge units: (1) units that spontaneously emitted at a high rate a continuous train of spikes separated by extremely regular intervals (25 units); (2) units that emitted long trains of regularly spaced spikes at irregular intervals, the spike trains being frequently separated by several seconds of silence (seven units); (3) units with no spontane-

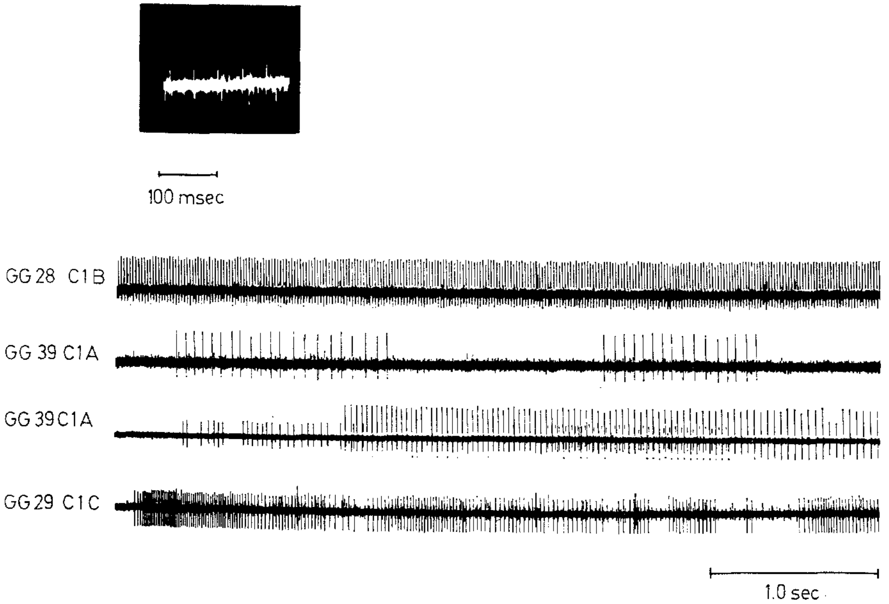

Fig. 4. *Regular Discharge Units.* First line: Spontaneous activity of continuously discharging unit. Inset: Two of these units firing in near synchrony. Second line: Spontaneous activity of periodically discharging unit. Third line: Response of periodically discharging unit to pressure on soft palate. Fourth line: Response of unit with no spontaneous activity to pressure on soft palate

ous activity, which responded to stimulation with a fairly regular train of spikes (five units). Examples of all three types of units can be seen in Fig. 4. It was possible to affect the discharge of most of the regular discharge units by one or more of the following procedures: pressure on the soft palate, pulling out the tongue or pushing in the eyeball. These manipulative procedures produced static dislocations of tissues of the soft palate, pharynx and, to some extent, deep nasal areas. Examples of unit discharge to pressure on the soft palate can be seen in Fig. 4. The discharge of six of the regular discharge units with continuous spontaneous activity could not be affected by these manipulative procedures.

Regular discharge units with continuous activity were the most common type encountered. With multiunit recordings it was sometimes observed that two or more units tended to fire in near synchrony (Fig. 4). Interspike interval measurements (Rodieck *et al.*, 1962) of the spontaneous and evoked activity of these units illustrate the fixed frequency of discharge (Fig. 5). A plot of the mean intervals observed for units with continuous regular spontaneous activity is presented in Fig. 6. The different symbols in this figure represent the type of stimulation observed to be effective for the unit. With stimulation the discharge of these units could be increased or decreased. The mean rates of spontaneous activity for the six cells that we could not stimulate are also presented in Fig. 6.

Tongue Units

Although the most inaccessible, tongue units were the most intensively investigated and were the original object of the quest. Measures were taken of

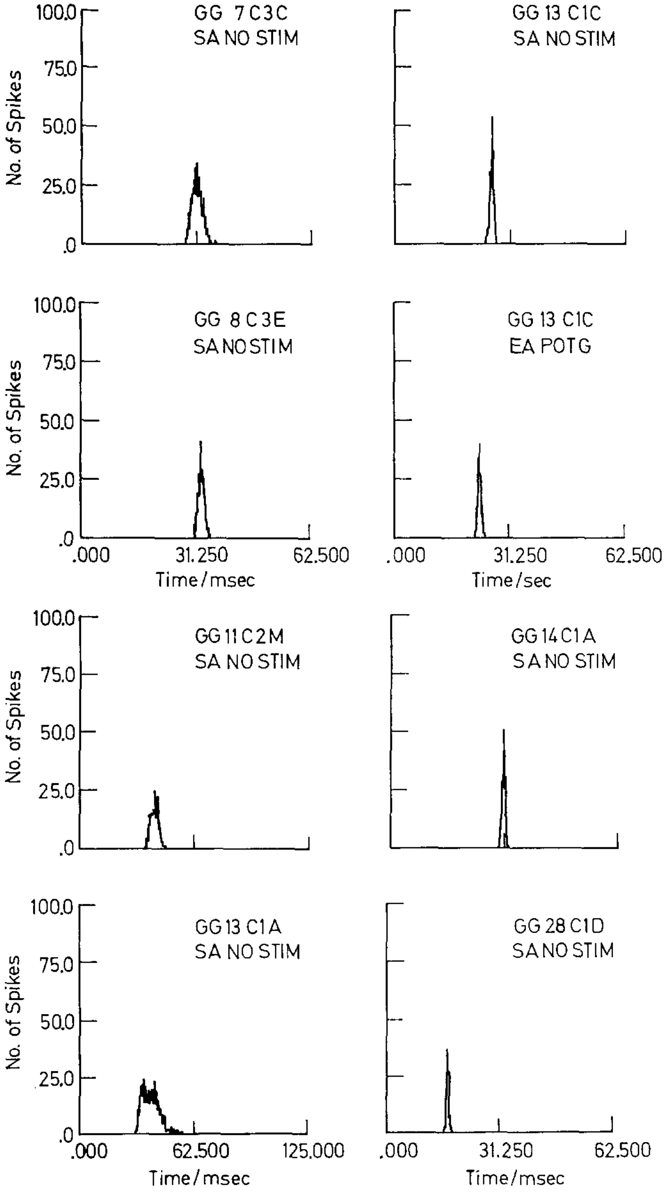

Fig. 5. *Interspike interval (ISI) histograms of the spontaneous and evoked activity of eight different regular discharge units.* Ordinate scaled in terms of No. of spikes (i.e. no. of intervals) and abscissa in terms of time between spikes (i.e. length of intervals). All units except GG13C1A and GG8C3E were continuously discharging units. Unit GG13C1A was a periodically discharging unit (similar to GG39C1A in Fig. 4). The ISI histogram for unit GG13C1C labeled POTG is the only histogram of evoked activity; in this case the spike train was elicited by pulling the tongue out. The other histogram of GG13C1C is of spontaneous activity from the same unit with the tongue in

the spontaneous activity of tongue units and their responsiveness to electrical, mechanical and chemical stimulation of the tongue. Tongue units varied widely

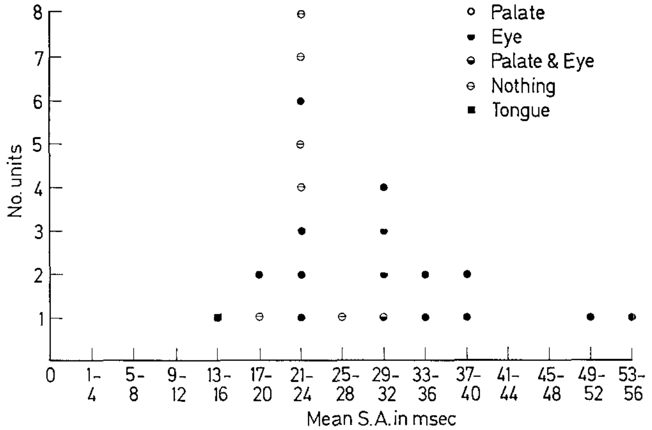

Fig. 6. *Histogram of the mean rate of spontaneous activity of 22 continuously discharging regular discharge units.* Mean rates calculated from ISI histograms such as those in Fig. 5. The symbol indicates the locus of the effective pressure stimulus for affecting the spontaneous discharge. Many of the units were affected by pressure on more than one locus. The spontaneous activity of six units could not be altered by any stimulus

with respect to any measurement parameter. In this section we present some of the differences and similarities displayed by tongue units with respect to our measurements.

I. Spontaneous Activity

Most of the tongue units encountered displayed some degree of spontaneous activity. To an extent, this statement is qualified by the fact that we detected units on the basis of the spontaneous emission of spikes. Many of our recordings were multiunit recordings since we had large tipped electrodes and we occasionally excited an inactive unit while stimulating one with spontaneous activity. It was in this manner that the units with no spontaneous activity were observed. Examples of spontaneous activity patterns emitted by geniculate ganglion tongue units are presented in Fig. 7. These spontaneous discharge patterns vary markedly from unit to unit both in the number of spikes emitted and the order in which they occur. One characteristic feature of tongue unit spontaneous activity is the frequent occurrence of bursts of two or more spikes. The tendency for bursting varied widely from unit to unit, with some units emitting a majority of their spike activity in bursts and others exhibiting little or no bursting. The number of spikes in a burst also displayed great variability from unit to unit.

The average rate of discharge for 77 units is presented in Fig. 8. These crude rate measures (spikes/10 sec) indicate wide variation in spontaneous activity rates among tongue units. The modal value of the distribution in Fig. 8 is centered at about 12 spikes/10 sec. Many units, however, exhibited rates far above this value, with three units emitting spikes at a spontaneous rate of about 100 spikes/10 seconds.

The spontaneous discharges were studied with interspike interval distributions, examples of which are presented in Fig. 9. As would be expected from the spike trains illustrated in Fig. 7, a variety of interspike interval (ISI) distribu-

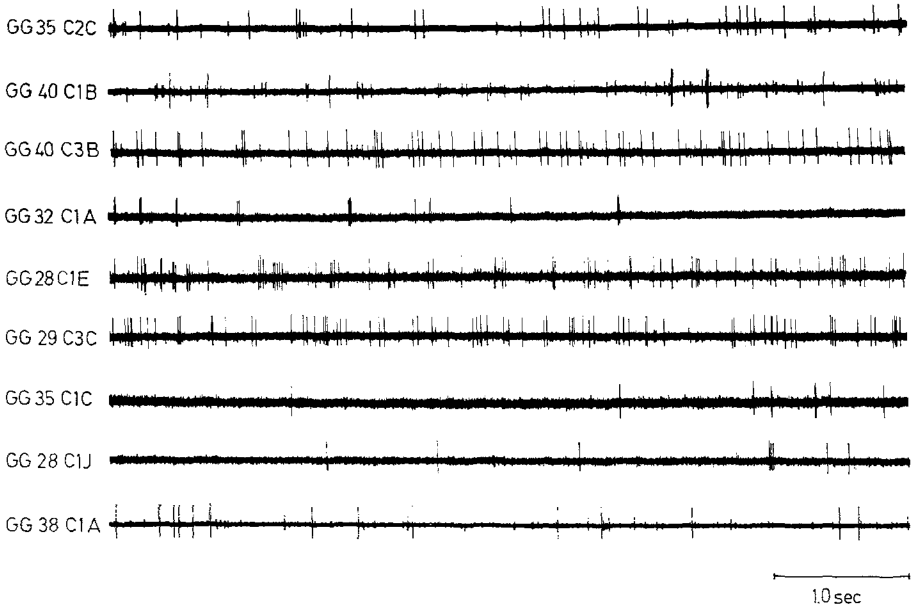

Fig. 7. *Examples of the spontaneous activity patterns* recorded from nine geniculate ganglion tongue units

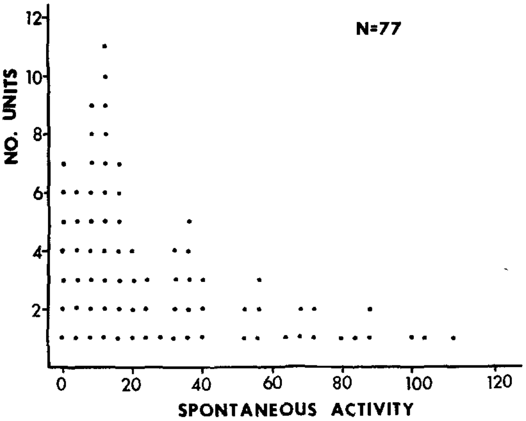

Fig. 8. *Mean rates of spontaneous discharge for 77 geniculate ganglion tongue units.* Rates were calculated by averaging the total spike discharge occurring during several 10 sec periods. Rate of spontaneous activity is in terms of No. spikes/10 sec

tions are formed from measures of spontaneous activity. The simplest type of ISI distribution is that seen for high discharge rate units with little or no bursting activity. These distributions are skewed toward long interval lengths with modal values around 40—70 msec. Two examples (GG17C4C and GG43C1D) of this type of ISI distribution can be seen in Fig. 9. ISI distributions calculated from units which emitted spikes primarily in bursts were more markedly skewed with modal values of around 10 msec (Fig. 9). The ISI distributions of the majority

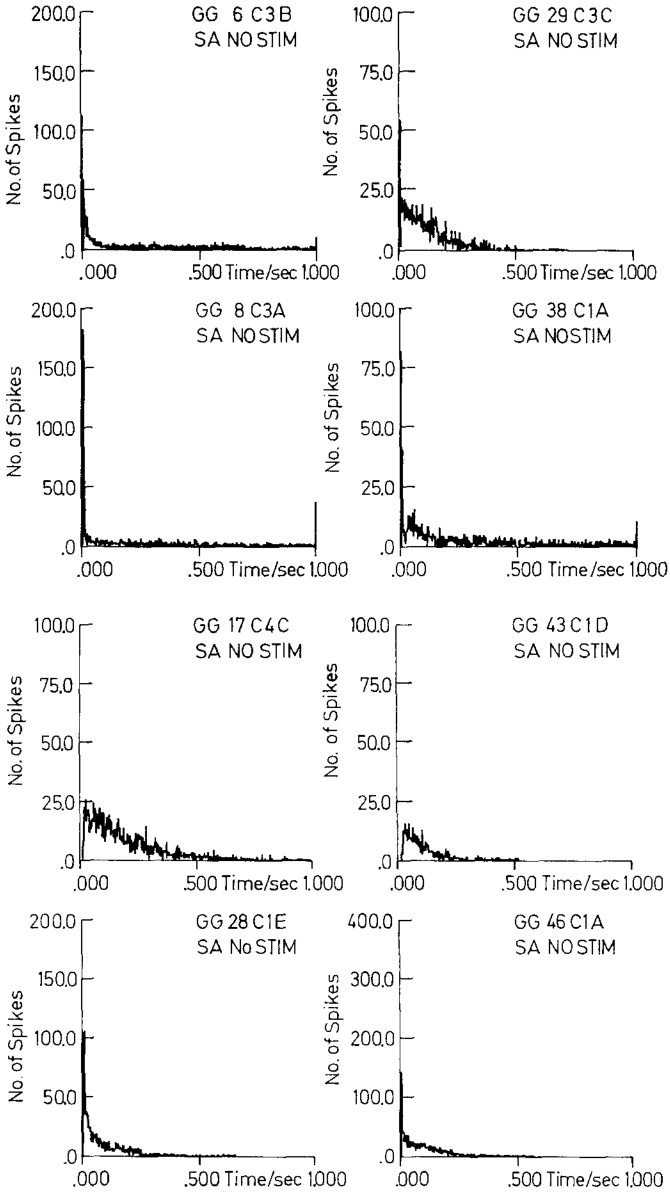

Fig. 9. *Interspike interval (ISI) histograms* of the spontaneous activity of eight geniculate ganglion tongue units. The last bin is an overflow bin for intervals longer than 1.0 sec

of units tended to fall somewhere in between these two extremes and were often multimodal.

The short interval peak in the ISI histograms shown in Fig. 9 is the result of the bursts of spikes separated by short intervals. If only the initial 62.5 msec of the ISI distribution is examined, it is observed that the distribution of short intervals rises precipitously from a minimum interval value (Fig. 10). This part

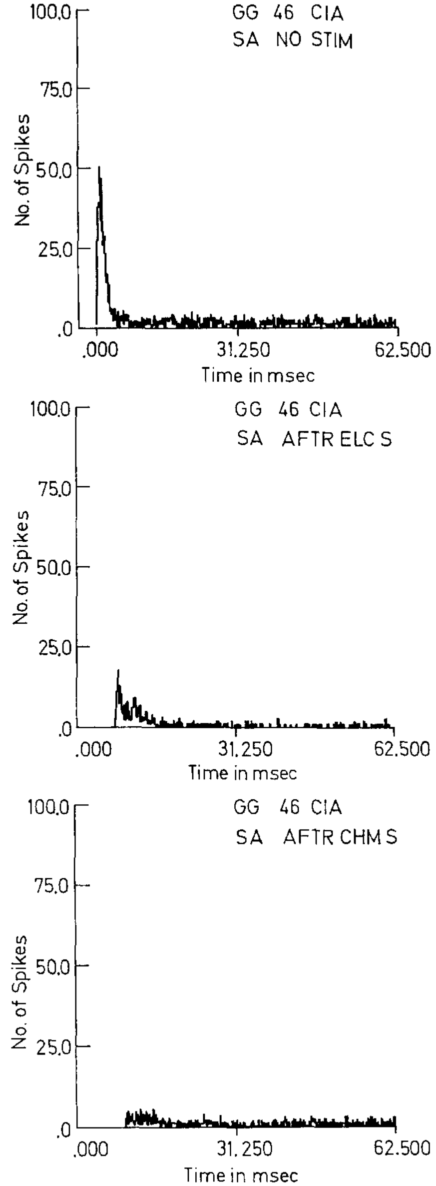

Fig. 10. *The initial 62,5 msec of the interspike interval distribution of the spontaneous activity of a tongue unit.* The spontaneous activity of this unit was characterized by much short-interval bursting activity, which is responsible for the peak at the extreme left of the distribution. First line: ISI histogram of spontaneous activity from unit with tongue unstimulated. Second line: ISI histogram of spontaneous activity of same unit after electrical stimulation of one of the three papillae in its papilla system. Third line: ISI histogram of spontaneous activity of same unit after chemical stimulation of the tongue. The cut-off values in Table I were defined from these histograms as the first bin within which the spike count was greater than two

of the ISI distribution is a result of spikes appearing in nearly fixed interval bursts. We denote the minimum interval value in distributions such as those in Fig. 10 as the "cut-off" value (defined as that of the first bin within which the spike count is greater than two). Cut-off values of unstimulated units were 4 to 6 msec in most cases. After chemical or electrical stimulation of the papilla systems, these cut-off values increased. The 62.5 msec ISI distributions of a unit before stimulation, after electrical stimulation of one of its three papillae, and after chemical stimulation of the tongue are shown in Fig. 10. Some cut-off values obtained for units before and after stimulation of the tongue are presented in Table 1. These cut-off value changes indicate that the intervals between spikes in bursts increase with stimulation of the tongue.

Table 1. *Cut-off values in msec calculated from ISI distributions of spontaneous activity measured from geniculate ganglion tongue units*

Unit		Tongue	Tongue
GGNo.	CNo.	Unstimulated	Stimulated
14	1M		6.88
17	4C		15.0
17	2D		6.25
19	1A		8.75
22	1F		12.50
35	1B	3.59	
39	1B	4.22	
40	1A	4.69	
40	1B		7.34
40	3B		10.31
42	1A	8.44	19.06
43	1A	5.0	
43	1B		6.88
44	1C	5.94	
45	1B	5.16	9.84
46	1A	3.75	10.0
47	1A	4.22	

II. Electrical Stimulation

The surface of the cat tongue is covered with various protuberances known as papillae. Most of the anterior central portion of the tongue is covered with filiform papillae, papillae with sharp hooks on the top. Circumvallate papillae are large specialized chemoreceptive systems located at the back of the tongue. The cat has a very small structure which may be identified as a foliate papilla (Gmelin, 1892) which may however be absent from one or both sides (Becker, 1908). These papillae are known to contain large numbers of taste buds innervated by neurons located in the petrosal ganglion of the glossopharyngeal nerve. On the back sides of the tongue are located rows of large floppy papillae known as papillae clavatae (Sonntag, 1923). No function is known for these papillae. The anterior parts of the tongue are dotted with fungiform papillae. Fungiform papillae vary widely in shape depending upon their location on the tongue; those in the back of the tongue are usually large (about 3/4 mm in diameter) and on stalks; some in the front on the upper surface and sides are about a quarter of a millimeter in diameter and are almost flush with the surface of the tongue.

It was possible to excite most tongue units by electrical stimulation of the surface of the tongue. Although occasionally one encountered a unit in which the response to electrical stimulation was labile and of extremely high threshold, in most cases thresholds were less than 1.5 mA and a spike discharge could be consistently elicited. Spike discharges were observed to be elicitable by electrical stimulation of fungiform papillae, filiform papillae and, in one case, a clavate papilla (Fig. 13). To excite with threshold currents the stimulating electrode had to be in contact with the stimulatable papilla.

We shall designate the papilla or papillae that excite a unit when electrically stimulated as the "papilla system" of that unit. Papilla systems may be composed entirely of fungiform papillae, entirely of filiform papillae, or of an admixture of the two. In one case a clavate-fungiform papilla system was observed.

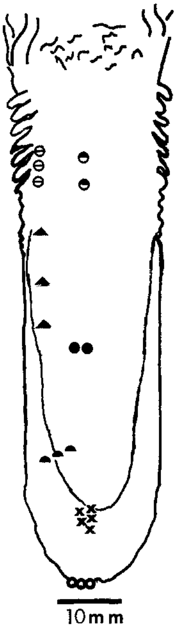

Fig. 11

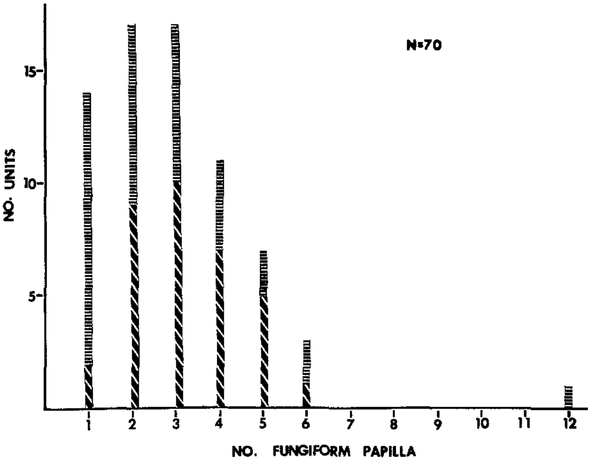

Fig. 12. *Histogram of the number of fungiform papillae in the fungiform papilla systems of 70 geniculate ganglion tongue units.* The tops of the cross-hatched bars indicate the distribution found for all 70 units. The tops of the diagonally-hatched bars indicate the distribution found for the last 35 units investigated

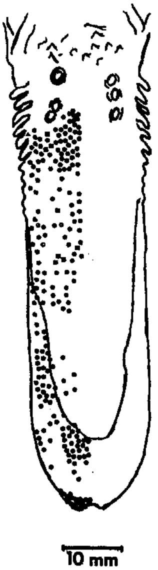

Fig. 13

Fig. 11. *Examples of the multiple fungiform papilla systems* of seven geniculate ganglion tongue units determined by electrical stimulation. The separate symbols denote the fungiform papillae which when electrically stimulated excite a unit

Fig. 13. *Location of all the papillae found to excite geniculate ganglion tongue units when electrically stimulated.* Schematic tongue drawn to scale. Border of main filiform papilla region indicated with line. All unit recordings were taken from the right geniculate ganglion
● Fungiform — ■ Filiform — ▲ Clavate

The papilla systems of most units consisted entirely of fungiform papillae and were composed of one or more papillae. As has been observed in the frog (Rapuzzi and Casilla, 1965), most fungiform papilla systems observed were composed of multiple papillae (Fig. 11), and as we became more skilful in locating fungiform papillae, single papilla systems became rarer and rarer. Twelve of the first 35 papilla systems investigated were single papilla systems but only two of the last 35 papilla systems measured were single (Fig. 12).

Fungiform papilla systems can be roughly classified as two types — "compact" and "distributed", although variants occur (Fig. 11). "Compact" papilla systems were composed of a cluster of funigform papillae within a few millimeters of one another. The papillae were rarely more than two or three millimeters apart and frequently were in a line or small group. There were usually no electrically inexcitable fungiform papillae interspersed between the fungiform members of a compact papilla system. "Distributed" papilla systems were composed of large fungiform papillae scattered several millimeters apart (Fig. 11). These distributed papilla systems were only found in the back of the tongue. In some cases electrically inexcitable papillae were interposed between members of a distributed papilla system. It is likely that some of the single papilla systems observed were

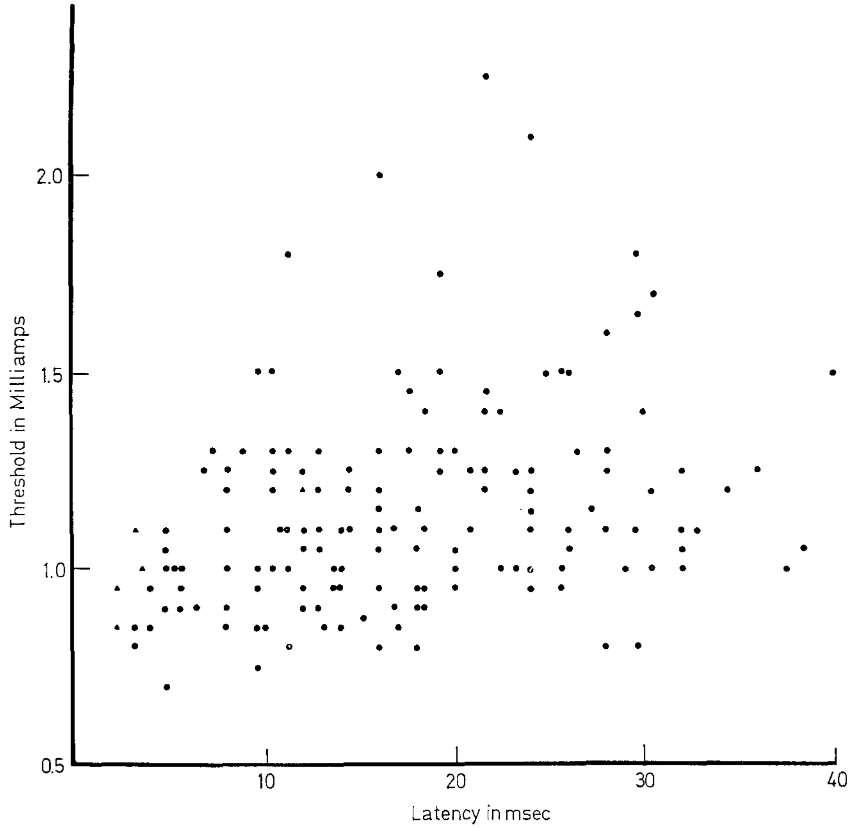

Fig. 14. *Latency of tongue unit spike* elicited by electrical stimulation of the tongue plotted against the threshold intensity in milliamps. Measures from all papillae electrically stimulated are included in this figure
○ Clavate Pap. — ▲ Filiform Pap. — ● Fungiform Pap.

actually part of a distributed papilla system, since the farther apart papillae were, the more difficult they were to detect.

Electrical stimulation of a member of a unit's papilla system elicited one or more spikes from the unit. In almost all cases a threshold in milliamps was determined and latency for the first spike was measured. A compilation of these measurements discloses tremendous variability among papillae (Fig. 14). There are several sources for this variability. In the first place latency may vary with the intensity of the electrical stimulation. Frequently latency shifts occurred as the current was increased. The longer the initial latency at threshold, the more likely would be a sharp decrease in latency as current increased (Fig. 15). These latency shifts were usually abrupt and not progressive. Not all units showed latency shifts with intensity changes, however.

Electrical stimulation of the papillae within a unit's papilla system may elicit spikes of similar latency or dissimilar latency. For instance, electrical stimulation of the three papillae of the papilla system of cell GG42C1C elicited spikes with latencies of 12.0, 13.5 and 18 msec with little change to 3.0 mA.

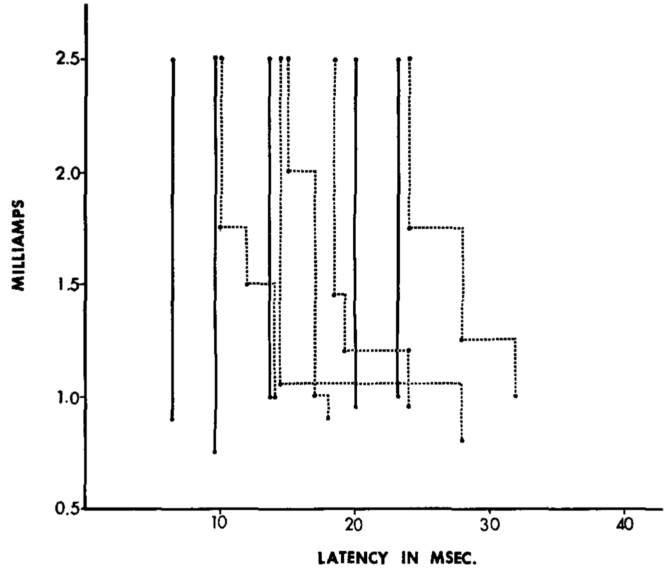

Fig. 15. *Latency of discharge of ten tongue units to electrical stimulation of a single papilla of each unit's papilla system.* Different intensities of electrical stimulation were used. Latencies of discharge for many units showed abrupt shifts as indicated here. More and greater latency shifts were found when the latency at threshold was greater than 20 msec. Electrical stimulation of different papillae within the same papilla system often elicited widely different initial latencies as well as different shifts with different stimulus intensities

Other, much more complicated, latency patterns for papilla systems were observed.

We also found that the latencies measured for some units are subject to change after chemical stimulation. In the few cases observed, these shifts were toward shorter latencies. For example, the latencies at 1.5 mA of the four fungiform papillae of unit GG44C1C were 20, 23.5, 37.5 and 14 msec before chemical stimulation. After chemical stimulation the latencies were 10, 12, 15 and 13 msec.

In four cases we observed that two different tongue units could be excited by the electrical stimulation of the same fungiform papilla, that is their papilla systems included shared fungiform papillae. In all cases the latencies of the spikes elicited from the two units by electrical stimulation of the common papillae varied markedly. For instance, unit GG9C4A exhibited threshold latencies of 3.8 msec to electrical stimulation of six fungiform papillae, electrical stimulation of two of these papillae elicited spikes from unit GG9C3A with latencies of 13.5 and 13 msec. Units GG40C3B and GG40C4B each had fungiform papilla systems composed of three papillae, two of which were shared. Electrical stimulation of the shared papillae elicited spikes from GG40C3B with threshold latencies of around 16 msec and spikes from GG40C4B at 24 and 30 msec.

III. Mechanical Stimulation

Gentle mechanical stimulation of the surface of the tongue with a blunt wood or glass instrument will elicit discharge from some geniculate ganglion tongue

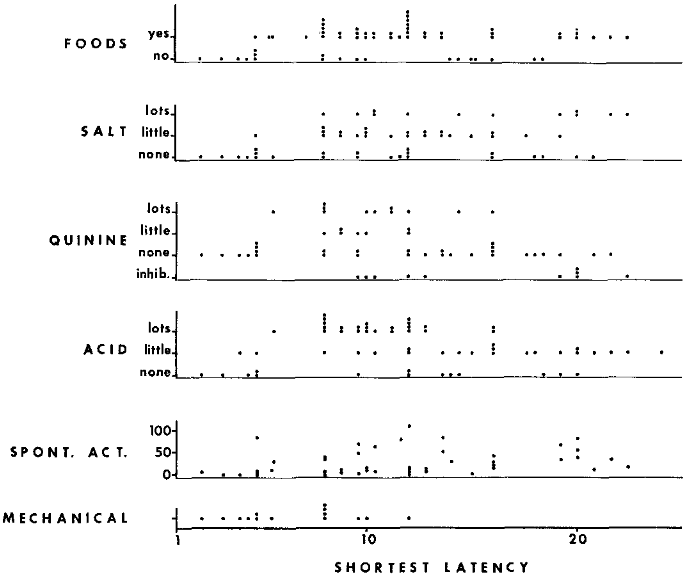

Fig. 16. *Summarizing diagram for the response measures from geniculate ganglion tongue units.* Each unit is represented in terms of the shortest latency of discharge to electrical stimulation of any papilla within its papilla system. Response to mechanical stimulus defined by discharge elicited by rubbing tongue with blunt instrument. Spontaneous activity measured in terms of spikes/10 sec. Chemical stimuli are the same as those described in Fig. 17. A food response was defined as a noticeable increase in discharge to one of the food substances. The terms "little" and "lots" correspond respectively to a near threshold response and a sustained discharge. Only inhibition to quinine is indicated here although inhibition with acid and kidney were also seen

units. All mechanically sensitive units were of the phasic type; i.e. they only discharged during movement. They were discharged by movement of filiform or fungiform papillae, sometimes both. No tonic discharges in mechanically sensitive units like those described by Iggo and Leek (1967) were seen. The papilla systems of most mechanically sensitive units were comprised of multiple papillae. Whether or not a unit responded to mechanical stimulation was to a great extent predictable from knowledge of the unit's latency to electrical stimulation. Mechanically sensitive units tended to exhibit short stable latencies to electrical stimulation. In order to compare the latencies of mechanically sensitive units to those of the rest of the tongue cell population, the graph in Fig. 16 was prepared. In this graph each cell is plotted in terms of the shortest latency elicited by stimulation of any papilla at any stimulus intensity. In most cases each papilla of the papilla systems of the units in Fig. 16 was studied with electrical intensities from threshold to 2.5 mA. Measurements from one cell are omitted from this graph. Only a single latency measurement at a single intensity (36 msec at 1.5 mA.) was available for this cell. Despite the great variability inherent in latency measurements (see the preceding section) mechanically sensitive cells separate out from the rest of the population: all but one of 15 mechanically sensitive cells possess latencies of 10 msec or less. Sensitivity of units to mechanical stimulation was not routinely tested until late in this study and therefore some mechanically sensitive units

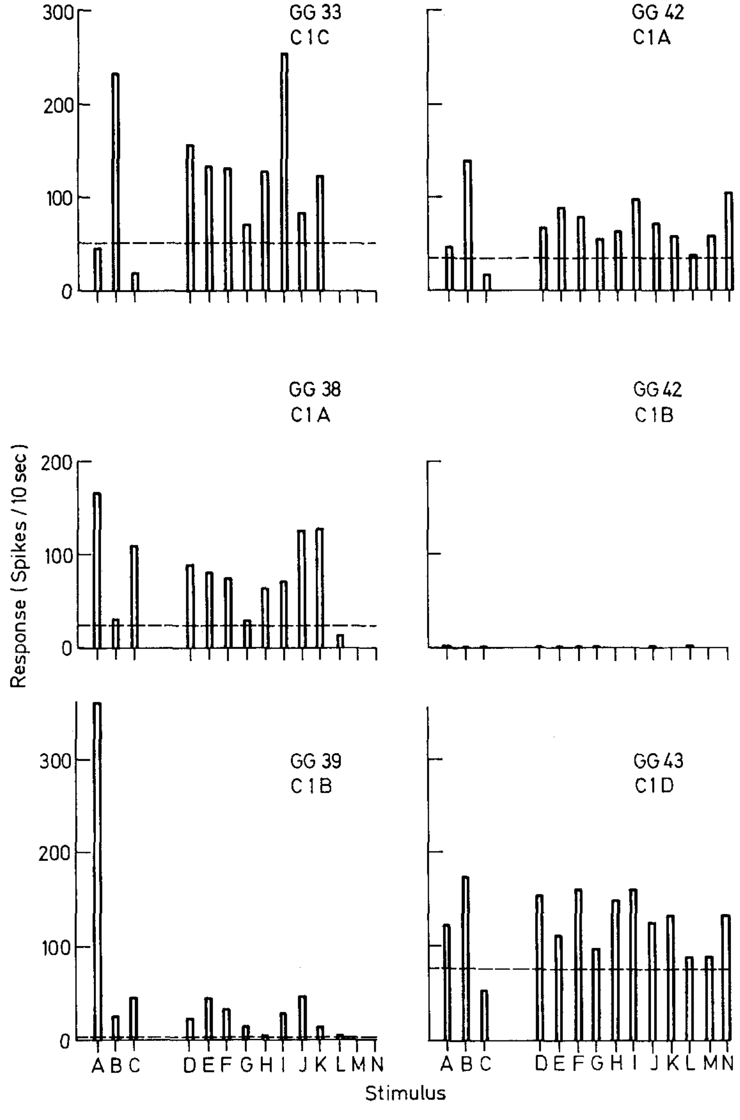

Fig. 17. *Response profiles of six geniculate ganglion tongue units to stimulation with different chemical stimuli.* The response was the spikes occurring during the 10 sec following tongue application of the stimulus. The spontaneous activity level of each unit is indicated with a dotted line parallel to the abscissa. The following standard stimulus solutions were used: A. 0.1 M citric acid, B. 1.0 M NaCl, C. 0.01 M quinine hydrochloride. The following foods were applied in distilled water solutions: D. pork liver, E. chicken, F. tuna, G. cod, H. milk, I. pork kidney, J. beef heart, L. sucrose, M. egg white, N. egg yolk

were probably missed. The sensitivity to chemical stimulation is also markedly different for the units; units with latencies below 8.0 msec are usually insensitive to the chemicals used, whereas units with latencies greater than 8.0 msec are excited by many substances (Fig. 16).

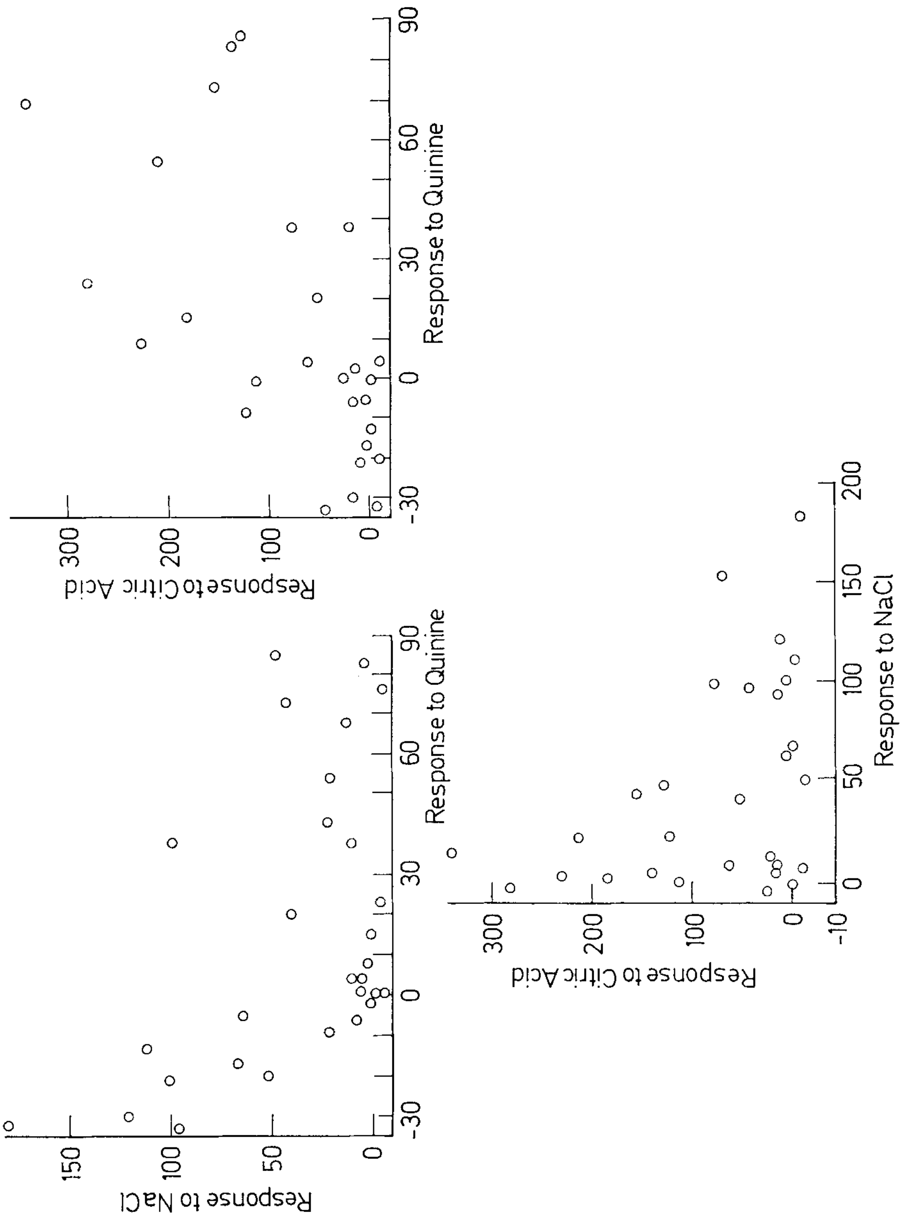

Fig. 18. *Relationship between the number of spikes elicited by the standard solutions from different tongue units.* Each dot in a graph indicates the response of a different unit. The response was obtained by subtracting the number of spikes occurring during the 10 sec period following stimulation from the spontaneous level of discharge present in one or more 10 sec intervals prior to stimulation

IV. Chemical Stimulation

Units varied widely in their responsiveness to the standard chemicals and to foods. Some units were completely unresponsive to all stimuli applied; others

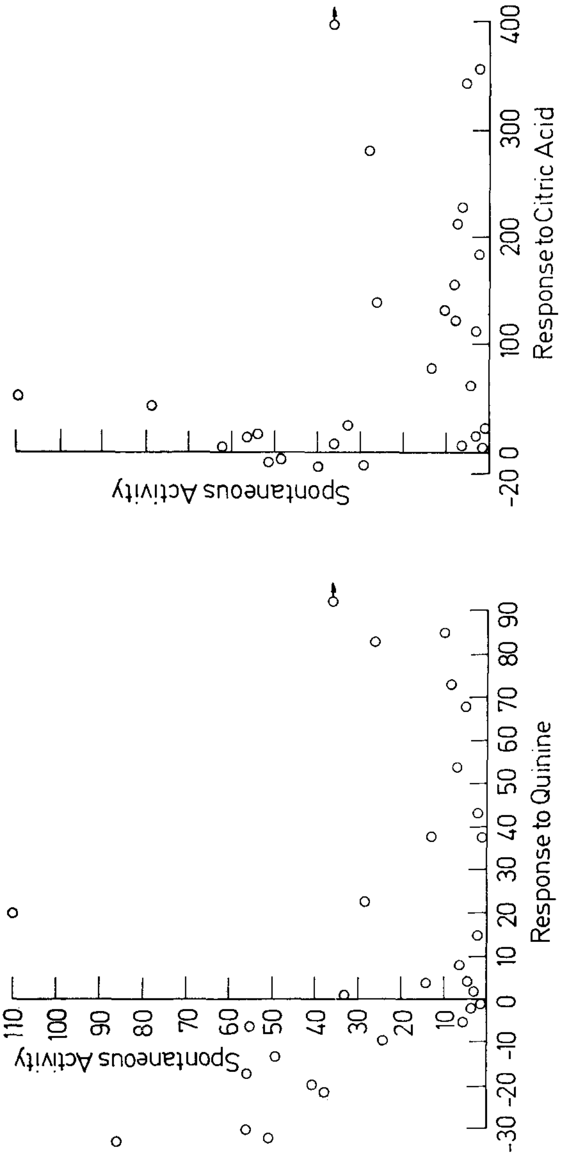

Fig. 19. *Relationship between the rate of spontaneous activity (spikes/10 sec) of 28 geniculate ganglion tongue units and their discharge to citric acid and quinine*

were responsive to almost all the stimuli. Although most stimuli, if they were effective at all, increased discharge above the resting level, quinine sometimes lowered the discharge rate below the resting level. Kidney solution twice was observed to excite initially and then profoundly depress the spontaneous activity for as long as a minute following application. Response profiles of individual units to the chemical stimuli used are presented in Fig. 17. As can be observed, cells tended to be selectively responsive to both the standard chemicals and the food substances.

The responsiveness of the population of geniculate ganglion tongue units to the different chemical stimuli can be visualized in Fig. 16, wherein the units are arranged according to their shortest latency. As can be seen, units with extremely short latencies (usually mechanically sensitive units) are in general insensitive to the chemical substances used. Units responsive to acid and salt are most widespread although units with shortest latencies of about 20 msec or greater are relatively insensitive to acid and inhibited by quinine. Food sensitivity is as widespread as sensitivity to any standard chemical solution.

The relationships between the responsiveness of geniculate ganglion tongue units to the three standard chemical solutions used are presented in three graphs in Fig. 18. In these graphs the response of the 28 units to one standard solution is graphed against the response to another standard solution. The selectivity of responsiveness of the cells to the different standard chemical solutions is demonstrated in these graphs. For the 28 units studied in this manner high responsiveness to citric acid is associated with low responsiveness to salt and vice versa. Inhibition by quinine is associated with low response to citric acid and high response to NaCl.

Discharge of units to quinine or citric acid seemed to be related to the spontaneous activity levels measured from the cells. Units with high levels of spontaneous activity tended to be unresponsive to citric acid (Fig. 19) and, in some cases, inhibited by quinine (Fig. 19). Units with low levels of spontaneous activity were found to be highly responsive to citric acid, if they fired to anything.

Many of the units responsive to the three standard chemical solutions were also responsive to food substances (Fig. 17). For two units the largest response to food was larger than the unit's responses to any of the three standards. In most cases if a unit responded well to one food, it also responded well, though not always equally well, to other foods (Fig. 17). The response of the 28 units to food is shown in Fig. 20. The bottom graph in this figure illustrates the magnitude of the discharge elicited by the different foods; the top graph shows the stimulation effectiveness of the various foods as determined by the rankings of individual unit discharges. The most effective food stimuli are seen to be liver, kidney, tuna and chicken; the least effective stimuli were egg white and sucrose, although these foods were not tested on all units, and thus were not included in the effectiveness measures.

The responsiveness of a unit to food substances seems to be related to the response of a unit to the standard quinine solution used. Units excited or inhibited by quinine tend to be highly responsive to foods.

Units Not Responsive to Stimulation

In the preceding pages we have discussed the three major types of units encountered in the geniculate ganglion, and some of their characteristics. There were a number of units that were categorized as tongue units (13 units) on the basis of their spontaneous activity, but electrical contact with them was lost before their stimulus-response properties could be investigated. In addition, six units were classified as regular discharge units even though they did not respond to any of the stimuli effective upon other regular discharge units. The characteristics of these units are treated in the section on "Regular Discharge Units."

There remained a small group of units (six) which we were able to hold for a while, but were not able to discharge by stimulation of the ear, tongue and palate

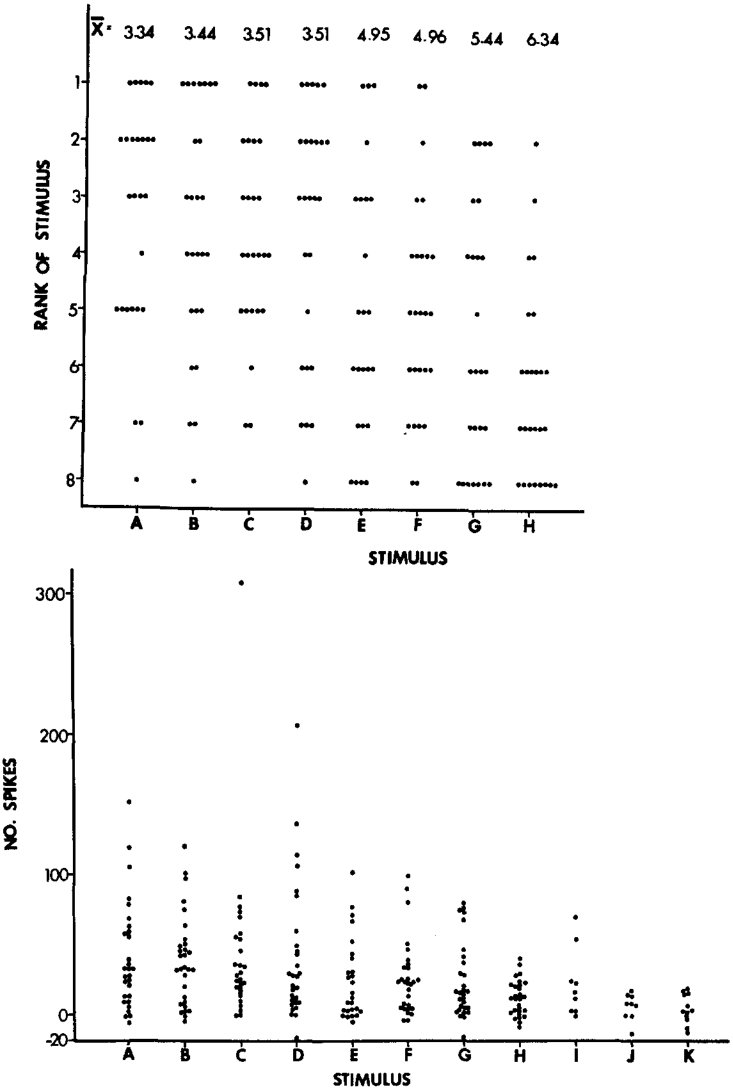

Fig. 20. *Response of 28 geniculate ganglion tongue units to solutions of foodstuffs.* Reading from A to K the foodstuffs are pork liver, tuna, chicken, pork kidney, beef heart, cod, milk, egg yolk, egg white and sugar. In the bottom graph the number of spikes occurring during a 10 sec stimulation period (corrected for spontaneous activity level) is shown for each food stimulus. In the top graph are shown the food preferences as determined by the rankings of the individual unit discharges. The mean rank for each food is also shown

with normally effective stimuli. It is probable that most of these units would be categorizable into one of the three major geniculate ganglion classifications, provided that the appropriate stimulus had been applied. For example, many tongue units were unresponsive to many chemical stimuli but could usually be discharged with electrical or mechanical stimulation of the tongue. A few tongue units displayed high thresholds to electrical stimulation, and their papilla systems were frequently difficult to locate. Since high intensity electrical stimulation of the tongue was believed to affect the response properties of tongue units, occasionally the search was curtailed. There remains the possibility that some of these units are members of entirely different neural populations in the geniculate ganglion.

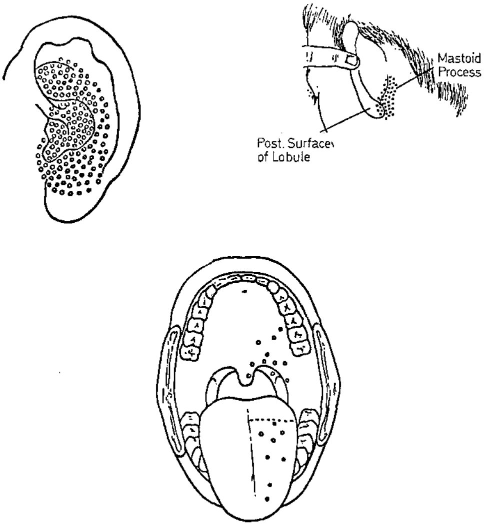

Fig. 21. *Projection zones of the human geniculate ganglion* as determined by Hunt on the basis of herpes zoster distributions. Figures reproduced from Hunt (1937)

Discussion

Early anatomical studies established that the cells of the geniculate ganglion were of the pseudounipolar type classified as sensory (Lenhossék, 1894; Ramon y Cajal, 1909). That the ganglion is involved in the tongue senses via the chorda tympani was known from early fiber tracing studies and chromatolytic degeneration studies (Amabilino, 1898; Gaetani, 1906; Weigner, 1905). In 1907, Hunt observed that herpes zoster of the inner surface of the ear often accompanied neurological involvements of the seventh and eighth nerves. Reasoning that the herpes zoster distributions were defining the projective field of a sensory nerve, Hunt, on the basis of clinical signs and a judicious process of elimination, concluded that the seventh nerve (or geniculate ganglion) possessed a hitherto unrecognized cutaneous sensory function. Later anatomical studies (Rhinehart, 1918) demonstrated that the geniculate ganglion did indeed send fibers to the skin of the ear. Other anatomical and clinical studies demonstrated a geniculate ganglion projection to the soft palate and nasal areas (Hunt, 1937; Kuré and Sano, 1935; Larsell and Fenton, 1928; Rhinehart, 1918). By 1937, Hunt was able to present a fairly complete description of the sensory composition of the seventh nerve. His description of the sensory projections of the geniculate ganglion in terms of herpes zoster distribution can be seen in Fig. 21. These projections in the human are apparently the same as those seen by us in the cat, except for the area behind the ear.

Ear Units

As described by Rhinehart (1918) in the mouse, fibers from the geniculate ganglion course along with the bulk of the fibers in the facial nerve and emerge, along with fibers of the vagus, in branches of posterior auricular nerve. Fibers of the posterior auricular nerve were observed to "end in a plexiform manner immediately under the epithelium or around the hair follicles" (Rhinehart, p. 119). The innervation of the rabbit's ear has been studied in some detail by Weddell and his associates (Weddel and Pallie, 1955; Weddel *et al.*, 1955a, 1955b). In addition to being innervated by various cranial nerves (vagus, facial and trigeminal), the ear is innervated by the second and third cervical cranial roots. As we have seen, the units in the geniculate ganglion that innervate the ear in the cat can all be discharged by moving the hairs on the inner surface of the pinna (Fig. 4). Brown *et al.* (1967) have recorded from fibers innervating hairs on the dorsal and ventral (inner) surface of the rabbit's ear. We do not know if the fibers innervating the inner surface of the rabbit's ear correspond to the geniculate ganglion ear units, since neither we nor they studied these units in any detail. Units innervating hairs on the dorsal surface of the rabbit's ear were divided into two types on the basis of conduction velocity (Brown *et al.*, 1967). We did not measure conduction velocities for geniculate ganglion units. According to anatomical studies, the geniculate ganglion fibers that innervate the ear are small, myelinated fibers averaging about three microns in diameter (Bruesch, 1944). Such a small size would indicate low conduction velocity. Fibers responsive to movement of body hairs in the cat have been found to be of various diameters and conduction velocities. The fibers most sensitive to body hair movement were the type D fibers which innervate down hairs and have small myelinated fibers conducting at less than 24 m/sec (Burgess *et al.*, 1968; Iggo, 1968).

Movement of the pinna hairs innervated by the geniculate ganglion produces an immediate aversive behavioral response in the unanesthetized cat: the ear is flicked rapidly in response to gentle hair bending. If one continues to move these hairs the cat gives every indication of extreme annoyance and will move away if the disturbance is continued. The only time a cat will countenance movement of these hairs is in the throes of petting, when intra-aural rubbing seems to produce an intense sensation.

Inspection of the inner surface of the human ear reveals many small hairs as in the cat. The main difference, other than length of hairs, is that the density of pilation is much less outside the auditory canal and the regions immediately surrounding it. Movement of the hairs in the human auditory canal seems to produce a sensation distinct from touch, with "tickle" being commonly reported.

Regular Discharge Units

The geniculate ganglion contributes fibers to the greater superior petrosal nerve (Kuré and Sano, 1935; Larsell and Fenton, 1928). which also contains nonsensory fibers of central origin. Originating at the anterior pole of the geniculate ganglion the greater superior petrosal nerve exits via the hiatus of Fallope; traverses the middle fossa of the skull to the anterior lacerated foramen, at which point it joins the deep petrosal nerve and continues, as the vidian nerve. The vidian nerve courses through the vidian canal to the sphenopalatine (Meckel's) ganglion. Anatomists (Larsell and Fenton, 1928; Rhinehart, 1918) have demonstrated that the fibers of geniculate ganglion origin pass through the ganglion without interruption and join the posterior nasal and palatal branches of the nerves from the sphenopalatine ganglion. These nerves are distributed to the posterior palatal and posterior nasal regions. The mode of termination of these fibers in the palatal and nasal regions has not been described.

The nature of the type of sensory information transmitted over the greater superior petrosal nerve cannot be ascertained from anatomical studies or from this study which only demonstrates that the receptors in the palatal areas are sensitive to static displacements of tissue.

Tongue Units

The largest peripheral outflow of geniculate ganglion fibers is contained in the chorda tympani which merges into the lingual nerve to innervate the tongue and salivary glands. The chorda tympani is a mixed nerve containing both sensory and efferent fibers (Foley, 1945; Kitchell, 1963). Estimates of the geniculate ganglion contribution to the chorda tympani range from 800 to about 1,000 fibers (Bruesch, 1944; Buskirk, 1945; Foley *et al.*, 1946). In addition, the chorda tympani contains about 800 efferent fibers and a small contribution from the auricular branch of the vagus (Bruesch, 1944).

In 1935, Zotterman demonstrated that fibers in the cat chorda tympani were responsive to solutions of quinine sulphate, sodium chloride and acetic acid applied to the tongue. Only one fiber was observed to respond to sugar solutions. Chorda tympani fibers were observed to respond to tongue applications of warm and cold tap water. Units responsive to mechanical stimulation of the tongue were also observed by Zotterman. Later Pfaffmann (1941, 1955) demonstrated that chorda tympani fibers can be excited by electrical stimulation of the tongue and that chemoreceptive fibers can be discharged by mechanical stimulation. Pfaffmann examined the responsiveness of chorda tympani fibers to tongue application of sugar, quinine, NaCl and HCl solutions in some detail, finding most fibers sensitive to HCl and many fibers sensitive to more than one solution. Sugar response was rarely observed. Nagaki, Yamashita and Sato (1964) have provided quantitative measurements on the discharge elicitable in the cat chorda tympani fibers with chemical, thermal and mechanical stimulation of the tongue. Of 38 chorda tympani fibers, 10 responded to mechanical stimulation, 26 to thermal stimulation (23 of these to chemical stimulation also) and two to chemical stimulation only.

Attempts have been made to classify cat chorda tympani fibers on the basis of various measurements. In all cases the primary measurement was the fiber discharge to a single solution of one of the so-called four basics (acid, quinine, salt and sugar). Classification of units in terms of their response to a select group of chemicals is fraught with difficulties, since units may differ widely in their thresholds and in the magnitude of discharge to any chemical. Few studies have been undertaken to determine what relationship exists between discharge rate and chemical concentration, and one of these studies indicates that the discharge rate may in some cases be a nonmonotonic function of concentration (Nagaki *et al.*, 1964). We also have observed some units to lose sensitivity upon continued stimulation, either to all chemicals or, in some cases, to selected chemicals. The possibility also exists that two units may respond to different chemical properties of the same solution.

In our study, the responses of geniculate ganglion tongue units to acid, salt and quinine did not clearly differentiate between units. The most useful measures for discriminating among units were spontaneous activity level, sensitivity to mechanical stimulation, and, for all its imperfections, latency of discharge to electrical stimulation.

The latency measurements presented in this paper showed great variability. Some of the sources of this variability have been identified; e.g. the intensity of electrical stimulation and the influence of prior chemical stimulation. Iriuchijima and Zotterman (1961) performed similar experiments on the dog where they used the latencies to electrical stimulation to estimate conduction velocities of the fibers involved. Should the dog be similar to the cat, however, latency measurements to electrical stimulation of the end organs are not equivalent to stimulation of the nerve and cannot be used to estimate conduction velocity. Iggo and Leek (1967) have estimated conduction velocities of tongue chemoresponsive fibers in the sheep where they directly stimulated the fibers electrically. They provide evidence that there exist separate chemoreceptive systems with different fiber diameters. Cohen *et al.* (1955) found a correlation between spontaneous activity rates for cat chorda tympani fibers and sensitivity to different chemical stimuli. Spontaneous activity rates have also been found to be useful for differentiating among rat and hamster chorda tympani fibers (Sato *et al.*, 1969).

The studies on cat chorda tympani fibers and the measurements presented in this report indicate that the tongue sensory system contained in the geniculate ganglion and chorda tympani is composed of a heterogeneous population of neural elements. A more comprehensive understanding of the variables influencing discharge is required to uncover even the skeletal outlines of the functional organization of the geniculate ganglion tongue units.

Other Possible Senses

There is some evidence that the geniculate ganglion may innervate areas other than those described above.

There may be a small contribution from the ganglion to the stapedius nerve (Bruesch, 1944; Weigner, 1905). Both clinical (Davis, 1923) and anatomical (Bruesch, 1944) studies indicate that the geniculate ganglion may be involved in sensibility of the muscles of the face. We have frequently rubbed muscles of the cat's face, but we have never elicited a discharge in the geniculate ganglion, although it is possible that either our electrodes were in the wrong parts of the ganglion or the stimulus was inadequate.

There is a degree of uncertainty in all the studies tracing anatomical connections of the geniculate ganglion. Weigner (1905), who studied ground squirrel and human preparations, stresses the fact that the geniculate ganglion is not the sole source of sensory fibers in the seventh nerve complex. He observed scattered sensory cells in the nervus intermedius, greater superior petrosal nerve, and peripheral facial nerve. Small ganglia were observed at points where the stapedius nerve and chorda tympani depart from the facial nerve. Fiber counts disclose that although the number of fibers in the de-efferented nervus intermedius is about equal to the number of cells in the geniculate ganglion, the number of fibers distal to the ganglion is frequently greater than the number of geniculate ganglion cells (Bruesch, 1944; Foley *et al.*, 1946). Many anatomists have reported that there are fibers, bypassing the ganglion, which connect the greater superior petrosal nerve with the peripheral portion of the seventh (Buskirk, 1945; Gaetani, 1906; Lenhossék, 1894; Weigner, 1905). The number, origin and peripheral distribution of these fibers is not known.

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