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THE CHARACTERISTICS AND REGIONAL DISTRIBUTION OF AFFERENT FIBRES IN THE CHORDA TYMPANI OF THE CAT

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SUMMARY

1. Experiments were carried out on the cat's tongue to investigate regional variations in sensitivity to gustatory and thermal stimuli and to determine whether taste buds responding to particular stimuli are unique to specific areas.

2. In ten cats, integrated whole-nerve activity was recorded from the left chorda tympani during stimulation of the anterior, middle or posterior segments of the tongue. The level of activity produced by gustatory or thermal stimuli increased towards the posterior segment of the tongue but the relative activity evoked by each stimulus was similar for each segment.

3. Recordings were made from 108 single units dissected from the chorda tympani; fifty-five responded principally to gustatory stimuli, twenty were principally thermosensitive and thirty-three were purely mechanosensitive.

4. The gustatory units could be subdivided according to the stimuli which evoked the most vigorous discharge; there were sixteen salt units, eighteen acid units, nineteen salt–acid units and two quinine units. The salt units had a higher level of spontaneous activity than the other groups and the acid units supplied more fungiform papillae with a greater separation between them.

5. The two quinine units were both located near to the mid-line posteriorly but all other groups of gustatory, thermosensitive and mechanosensitive units were distributed over all regions of the dorsal surface of the tongue and did not have higher discharge rates in specific areas.

6. Individual stimulation of the fungiform papillae supplied by a single unit revealed that similar responses were evoked from each papilla but stimulation of a single papilla supplied by two or more units could evoke a different response in each unit.

7. This study revealed that the relative sensitivity to gustatory and thermal stimuli was similar in each region of the tongue and that taste buds responding to particular stimuli are not confined to specific areas.

INTRODUCTION

Psychophysical tests carried out in man have suggested that the tongue is not uniformly sensitive to gustatory stimuli (Hanig, 1901; Dastur, 1961; Collings, 1974). Hanig (1901) found the lowest threshold for bitter taste to be at the back of the tongue, for sour on the sides posteriorly, for sweet on the sides anteriorly and for salt at the front. Collings (1974) reported similar regional variations except that she found the lowest threshold for bitter sensation to be at the front of the tongue. The basis for this regional variation is not clear but must presumably result from taste buds principally responsive to a particular stimulus being either unique to certain areas, or present in a greater density. Pfaffman (1941) recorded whole-nerve activity from the chorda tympani in the cat and reported a similar regional variation in sensitivity to that found in man; bitter sensitivity was located at the back of the tongue, sour at the sides and back, salt near the front and occasional responses to sweet stimuli were seen with stimulation of the lateral margins. In the present study, recordings have been made from single chorda tympani fibres in the cat to re-examine the extent of this regional variation and to investigate its basis.

The chorda tympani contains gustatory afferent fibres from fungiform papillae on the dorsal surface of the tongue, mechanosensitive fibres (Biedenbach & Chan, 1971), preganglionic parasympathetic secretomotor fibres to the submandibular and sublingual salivary glands and efferent vasodilator fibres to the tongue (Erici & Uvnas, 1952). Previous studies on the gustatory fibres in the cat (Pfaffman, 1941, 1955; Cohen, Hagiwara & Zotterman, 1955; Nagaki, Yamashita & Sato, 1964; Ishiko & Sato, 1973) have revealed a range of fibres with different response properties but the majority of them respond to more than one type of gustatory stimulus. Attempts to classify these units have been carried out using taste response profiles (Pfaffman, 1941; Cohen *et al.* 1955), responses to temperature change (Nagaki *et al.* 1964) or based on their levels of spontaneous activity and conduction velocity (Boudreau & Alev, 1973). The number of units examined in these studies has usually been small, however, and with the exception of the experiments of Oakley (1975) the precise location of the receptive fields of the units has not been reported. In the present study, afferent chorda tympani fibres have been characterized by determining their responses to gustatory and thermal stimuli, as well as their conduction velocities and levels of spontaneous activity. The receptive field of each unit has been precisely determined and any possible relationships between location and properties have been investigated.

Preliminary reports of these findings have been published (Robinson, 1988).

METHODS

Ten adult cats (1·75–4·5 kg) anaesthetized with sodium pentobarbitone (induction 42 mg/kg I.P., maintenance: 3 mg/kg I.V.) were used in the experiments. The trachea was cannulated and body temperature was maintained with an electric blanket thermostatically controlled from a rectal thermistor.

Whole-nerve recording

The left chorda tympani nerve was exposed central to its junction with the lingual nerve by excising the masseter muscle and ramus of the mandible, to uncover the nerve as it passed beneath. The nerve was freed of its investing connective tissue and placed on a pair of platinum wire electrodes (0·15 mm diameter) in a pool of warm liquid paraffin. Activity in the nerve was full-wave rectified and integrated (time constant, 500 ms) and the maximum amplitude was recorded while passing solutions over sections of the dorsal surface of the tongue (Biedler, 1953; Diamant, Oakley, Strom, Wells & Zotterman, 1965). The tongue was sutured into a Perspex chamber (5 × 2·2 cm) with the back of the chamber positioned just anterior to the circumvallate papillae. The lid of the chamber incorporated transverse strips of Perspex (2 mm wide) which were coated with a dental impression material (Permadyne, Espe, F.R.G.) and divided the chamber into three sealed segments (anterior, middle and posterior). Solutions were maintained at constant temperatures, and passage over the surface of the tongue was controlled, using a valve system similar to that described by Kollman & Matthews (1982). This system permitted the maintenance of the temperature of solutions during their passage from a reservoir to the valve which was placed within a few centimetres of the tongue surface. The following gustatory stimuli were used; 0·5 M-ammonium chloride, 0·2 M-acetic acid, 0·5 M-sucrose, 5 mM-quinine hydrochloride and distilled water. The concentrations of these solutions were chosen as sufficient to stimulate but weak enough to cause no irreversible effects (Oakley, 1975) and the temperature of the solutions was maintained at 30 °C (Nagaki *et al.* 1964). Thermal stimuli were applied using Ringer solution at 45 and 15 °C. Between stimuli the tongue was kept moist with Ringer solution as this evokes the lowest level of spontaneous activity on the cat (Cohen *et al.* 1955). Each of the stimuli was applied for a 5 s period and this was immediately preceded and followed by passing Ringer solution at 30 °C over the tongue surface. Solutions were applied at a constant rate of approximately 1·2 ml/s. The change of solution caused minimal disruption of flow and thus avoided any discharge due to mechanical displacement of the tongue.

Single-unit recordings

The top of the chamber was removed to expose the dorsal surface of the tongue and recordings were made from single units in fine filaments dissected from the chorda tympani. The criteria for accepting a single unit were constancy of the size and shape of action potentials. The receptive fields of the units were identified by (a) mechanical stimulation of fungiform and filiform papillae with a glass probe or cotton bud, (b) local application of a taste mixture consisting of equal volumes of the four taste solutions using a fine camel hair brush, and (c) electrical stimulation of papillae using a concentric electrode (outside diameter 1·5 mm) and constant-current stimuli of 0·1 ms in duration and up to 5·0 mA in intensity. For each unit, the location of its receptive field was measured and, if fungiform papillae were innervated, their number was recorded as well as their greatest distance apart as an indication of receptive field size. The level of spontaneous activity was determined by recording the mean discharge over a 30 s period. Conduction velocity was measured using electrical stimulation at the maximum intensity of 5·0 mA, 0·1 ms in an attempt to avoid long-latency coupled responses (Lisney, 1981). Thermal and gustatory stimuli were passed over the receptive field, as described for the whole-nerve recordings, and the neural discharge was recorded on disc, using a threshold discriminator as necessary. Data storage and spike analysis was carried out using a BBC microcomputer with SPI2 interface and software (Grafitek Electronics Ltd, U.K.). Each stimulus was applied three times with a 10 s interval and the mean number of impulses occurring during the 5 s period of stimulation was counted and the level of spontaneous activity recorded over a similar period was subtracted. Peri-stimulus time histograms were obtained for all stimulus trials and these were used to determine the presence or absence of a response. The maximum frequency of discharge (based on the number of action potentials in a 100 ms period) was also determined.

For some units, responses were recorded during stimulation of individual fungiform papillae. This allowed a comparison of the discharge evoked by stimulating taste buds innervated by the same fibre but located on different papillae. It was carried out using a device based on that described by Oakley (1975). This consisted of two coaxial tubes, the outer having an internal diameter of approximately 1 mm. Solutions were passed down the inner tube and were drawn up the outer tube by suction. The suction also sealed the outer tube against the tongue surface, thus preventing any leakage of solutions onto the adjacent papillae.

Data were analysed using the Student's t test or χ^2 test with Yates correction for small numbers, where appropriate.

RESULTS

Whole-nerve recording

The level of integrated whole-nerve activity produced by each stimulus varied in different animals, but when each response was expressed as a percentage of the maximum response and the data combined from all ten animals, a clear pattern emerged. For all three segments of the chamber, 0·5 M-ammonium chloride evoked the greatest discharge, followed by 0·2 M-acetic acid, Ringer solution at 45 °C, Ringer solution at 15 °C, 5 mM-quinine hydrochloride, 0·5 M-sucrose and distilled water (Fig. 1). The level of activity evoked by each stimulus increased towards the posterior segment. The amplitude from the anterior segment was, on average, 79% of that from the middle segment and 48% of that from the posterior segment (Fig. 1).

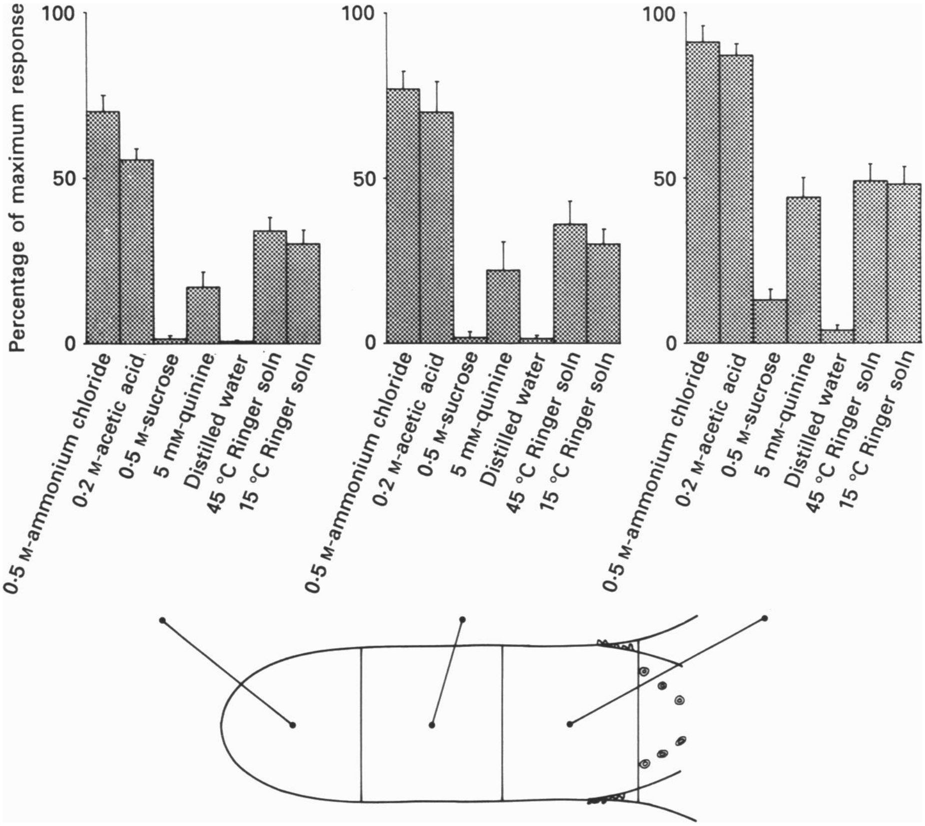

Fig. 1. The level of integrated activity recorded from the left chorda tympani during stimulation of each segment of the chamber. For each animal the amplitude is recorded as a percentage of the maximum response and the data shown are the means from all ten animals. The standard errors of the mean are indicated.

Single-unit recordings

A total of 108 single units were isolated from the chorda tympani and these could be divided into groups according to the type of stimulus which evoked the greatest number of impulses over the 5 s period of stimulation. There were fifty-five units which responded principally to gustatory stimuli, twenty units which were principally thermosensitive and thirty-three units responded only to mechanical and electrical stimulation of papillae. The distribution of the receptive fields of the units over the surface of the tongue is shown in Fig. 2.

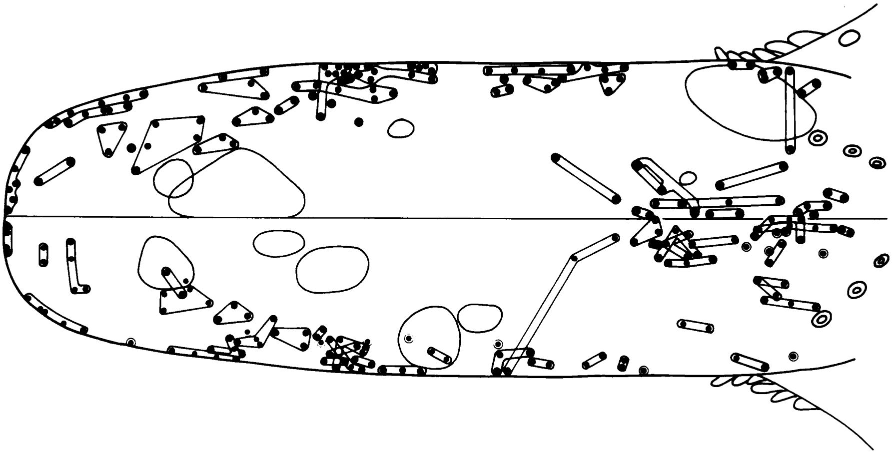

Fig. 2. The receptive fields of 108 single chorda tympani units from ten cats. Each black dot represents a fungiform papilla and the papillae supplied by a single unit are enclosed by a line. All units were recorded from the left chorda tympani and did not extend beyond the mid-line but for clarity, half of the units have been transposed to the right side.

Gustatory units. All fifty-five of these units innervated fungiform papillae, with a mean of 2·6 papillae per unit (range 1–7) and a maximum separation of up to 7 mm (mean, 2·2 ± 0·2 mm, S.E.M.). Fifty-four of the units were spontaneously active with a firing rate of up to 12·3 impulses/s (mean 2·6 ± 0·4 impulses/s). There was no apparent correlation between the level of spontaneous activity and the number of fungiform papillae supplied. Forty-five of the units responded to mechanical stimulation of the papillae with a glass probe or Von Frey hair but these responses were inconsistent and invariably rapidly adapting. The mean peak to peak amplitude of the units was 114 ± 13 μV and their conduction velocity was 9·5 ± 0·6 m/s (range 3–23·2 m/s, Fig. 3). The maximum frequency of discharge for each unit was 84 ± 4 impulses/s and the maximum number of impulses evoked by any of the stimuli over the 5 s period of stimulation was 97 ± 8.

When further subdivided according to the type of gustatory stimulus which produced the greatest discharge over the period of stimulation, there were sixteen salt units, eighteen acid units, nineteen salt–acid units (impulse counts resulting from salt and acid stimulation within 30 % of each other) and two quinine units. The responses of a salt–acid unit are shown in Fig. 4. The characteristics of each of these subgroups are summarized in Table 1 and their distribution on the tongue surface

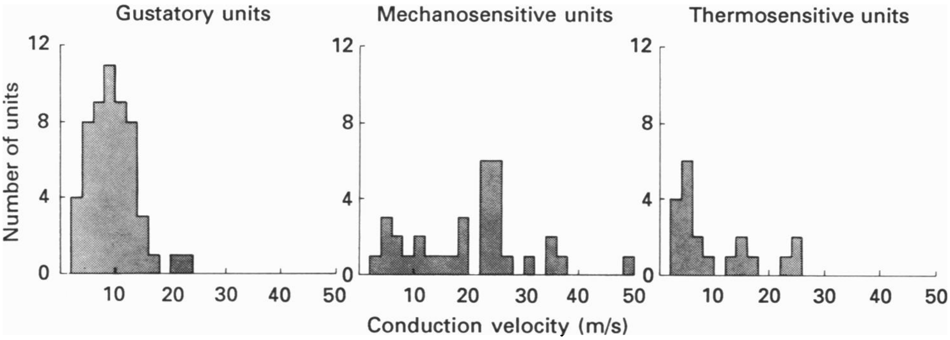

Fig. 3. Histograms indicating the conduction velocity of the gustatory, thermosensitive and mechanosensitive units (bin width, 2 m/s).

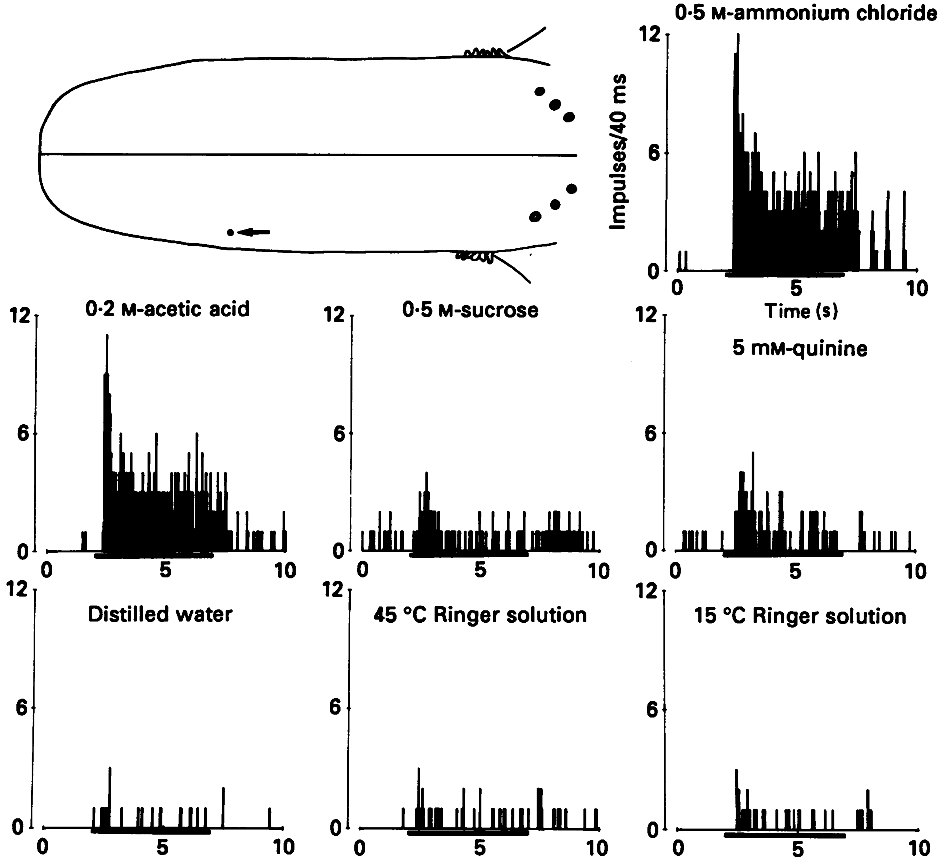

Fig. 4. Peri-stimulus time histograms (bin width, 40 ms) evoked by gustatory and thermal stimuli applied to a salt–acid unit. This unit supplied only one fungiform papilla, and its location is indicated by the arrow in the diagram at the top. The line beneath each histogram indicates the period of stimulus application.

is shown in Fig. 5. There was no evidence to suggest that for any group of units the discharge evoked was greater for units located in particular areas of the tongue. The level of spontaneous activity of the salt units (5·0 ± 1·2 impulses/s) was significantly greater than for the acid ($P < 0{\cdot}01$), salt–acid ($P < 0{\cdot}05$) and quinine ($P < 0{\cdot}02$) units. The number of fungiform papillae supplied by the acid units (3·5 ± 0·3) was significantly greater than for the salt ($P < 0{\cdot}01$) and salt–acid ($P < 0{\cdot}01$) units, and the maximum separation of these papillae (3·4 ± 0·4 mm) was also greater than for the salt ($P < 0{\cdot}001$), salt–acid ($P < 0{\cdot}01$) and quinine ($P < 0{\cdot}01$) units. The impulse count over the 5 s period of stimulation was significantly smaller for the two quinine units than for each of the other groups ($P < 0{\cdot}001$) and the maximum firing rate was also smaller than for the acid ($P < 0{\cdot}05$) and salt–acid ($P < 0{\cdot}01$) units.

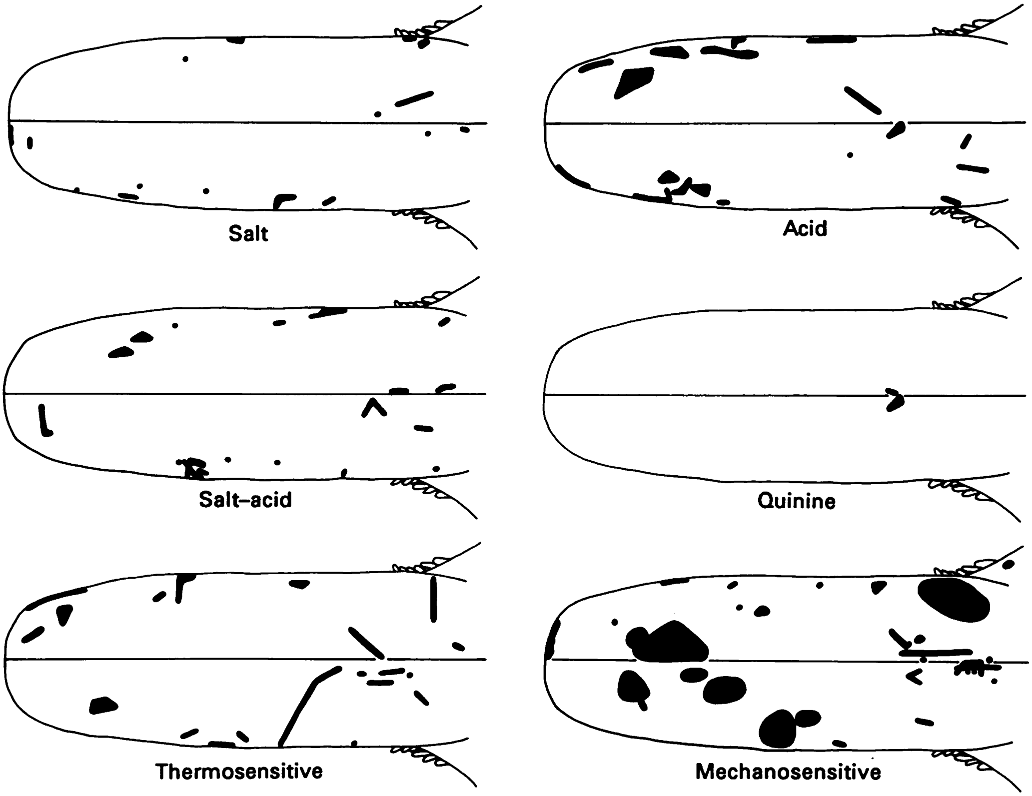

Fig. 5. The receptive fields of single units classified according to the stimulus which evokes the most vigorous discharge. Gustatory and thermosensitive units did not have receptive fields in the mid-region of the tongue which is devoid of fungiform papillae.

Many gustatory units responded to multiple stimuli and the number of each type of unit which also responded (but less vigorously) to other stimuli is indicated in Table 2.

Thermosensitive units. This group of twenty units innervated fungiform papillae and responded most vigorously to thermal stimuli. Their other characteristics (Table 1) were not significantly different from those of the gustatory units with the

TABLE 1. Characteristics of the 108 single units examined. Standard error of the mean is indicated

	All gustatory units	Salt units	Acid units	Salt–acid units	Quinine units	Thermo-sensitive units	Mechano-sensitive units
Number of units	55	16	18	19	2	20	33
Number of fungiform papillae supplied	2·6±0·2	2·0±0·2	3·5±0·3	2·3±0·3	2·5±0·5	2·8±0·3	—
Maximum separation of fungiform papillae (mm)	2·2±0·2	1·2±0·3	3·4±0·4	1·8±0·3	2	3·1±0·6	—
Proportion responding to mechanical stimulus (%)	82	75	89	79	100	85	100
Proportion of units spontaneously active (%)	98	100	94	100	100	90	6
Spontaneous activity (impulses/s)	2·6±0·4	5·0±1·2	1·2±0·2	2·0±0·6	1·1±0·9	1·3±0·4	2·5±1·4
Peak to peak amplitude of unit (μV)	114±13	104±16	156±32	89±17	62·5±13	86±15	188±31
Conduction velocity (m/s)	9·5±0·6	6·9±0·8	10·8±1·0	10·7±1·0	6·5±0·9	9·9±1·7	20±1·9
Mean impulse count during 5 s stimulation with the most effective stimulus, minus the spontaneous discharge	97±8	88±14	100±16	111±10	9±6	23±6	—
Maximum firing rate (impulses/s)	84±4	79±8	79±6	95±6	45±15	47±7	—

TABLE 2. The number of gustatory units of each type which also responded (but less vigorously) to the other stimuli

	0·5 M-NH_4Cl	0·2 M-acetic acid	0·2 M-sucrose	5 mM-quinine	Distilled water	45 °C Ringer soln	15 °C Ringer soln
Salt units (16)	—	11	4	4	4	9	14
Acid units (18)	16	—	9	9	5	12	16
Salt–acid units (19)	—	—	10	8	8	12	18
Quinine units (2)	0	0	0	—	0	1	0
Thermosensitive units (20)	10	8	3	4	2	—	—

exception that the maximum firing rate (47 ± 7 impulses/s) was lower ($P < 0{\cdot}001$). Most of these units also responded to gustatory stimuli (Table 2) and the responses of one unit are shown in Fig. 6. The conduction velocities of the thermosensitive units are shown in Fig. 3 and their locations are shown in Fig. 5.

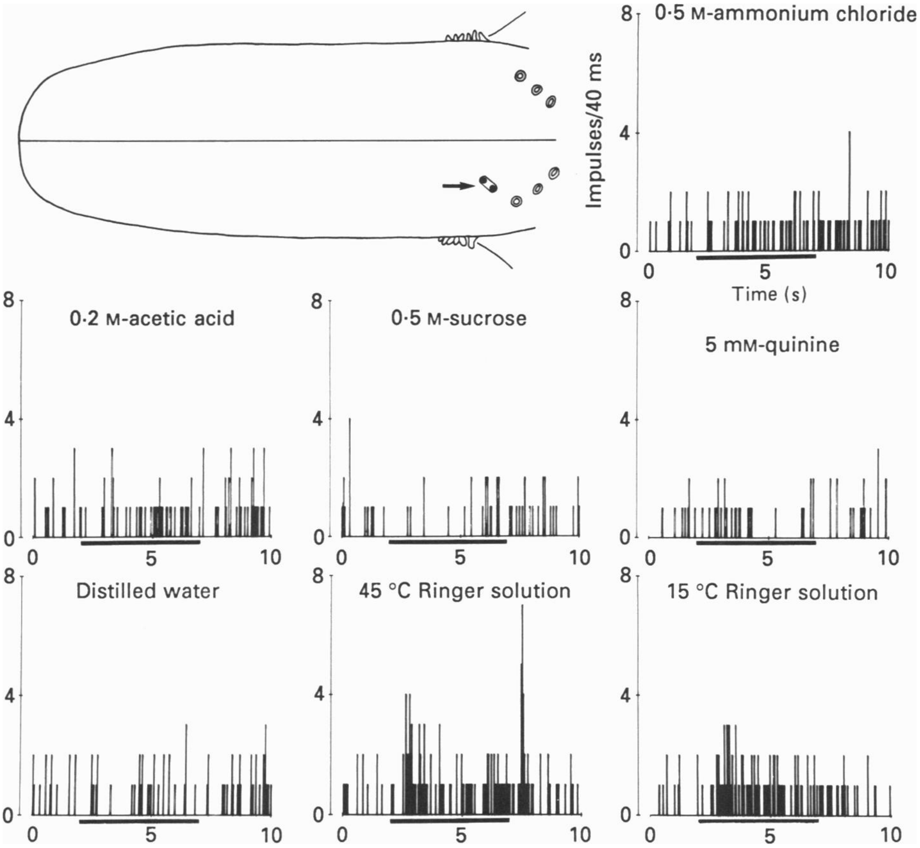

Fig. 6. Peri-stimulus time histograms (bin width, 40 ms) evoked by gustatory and thermal stimuli applied to a thermosensitive unit. This unit supplied two fungiform papillae and their location is indicated by the arrow in the diagram. The line beneath each histogram indicates the period of stimulus application.

Mechanosensitive units. This group of units did not respond to any of the gustatory or thermal stimuli, but responded purely to mechanical and electrical stimulation. Of the thirty-three units, eighteen innervated groups of fungiform papillae, fourteen innervated areas of filiform papillae which sometimes included one or two fungiform papillae, and one unit innervated a small area of mucosa on the fauces. Some units were more sensitive to stimulation of a broad area with a cotton bud than to stimulation with a glass probe. The distribution of the units is shown in Fig. 5. Only two of the units were spontaneously active (Table 1), their peak to peak amplitudes were significantly greater than for the gustatory ($P < 0{\cdot}05$) or thermosensitive ($P < 0{\cdot}01$) units and the mean conduction velocity was also greater than for the gustatory ($P < 0{\cdot}001$) or thermosensitive ($P < 0{\cdot}001$) units (Fig. 3).

Stimulation of individual fungiform papillae

The responses of six units were examined during stimulation of individual fungiform papillae. Results were obtained from two or three papillae for each unit. Four of the units responded principally to acid stimulation and for three of these, similar responses were obtained for stimulation of each papilla. In the other, one of the papillae responded only to mechanical stimulation. Two units responded principally to thermal stimuli and one gave similar responses to stimulation of each papilla. Of the three papillae innervated by the other unit, two papillae were principally thermosensitive and the other responded only to quinine.

By chance, ten fungiform papillae were encountered which were innervated by two units and one papilla was innervated by three units. A comparison of the properties of units sharing the same papilla would indicate whether a fungiform papilla carries taste buds of only one type. Of the twenty-three units involved, six were acid units, five salt–acid, one quinine, four thermosensitive and seven mechanosensitive. Stimulation of only four of the fungiform papillae evoked similar responses in each unit and for the remaining seven papillae, different responses were evoked in each unit.

DISCUSSION

The results of this study did not confirm the regional variation in taste sensitivity over the surface of the cat's tongue as described by Pfaffman (1941). The relative integrated whole-nerve activity evoked by the gustatory and thermal stimuli was similar for each segment of the chamber although there was an increase in sensitivity towards the back of the tongue. Although there are fewer fungiform papillae posteriorly than at the tip of the tongue, each papilla is larger and has a greater number of taste buds on its surface (P. P. Robinson, unpublished observations). Ishiko (1974) investigated regional differences in sensitivity of the cat's tongue by recording from the three terminal branches of the lingual nerve, supplying anterior, middle and posterior segments of the tongue. He recorded the smallest responses from the branch supplying the anterior part, consistent with the present study, but also found that the middle section of the tongue was most sensitive to NaCl and the posterior section to HCl. This apparent discrepancy with the present results may have arisen because of the different gustatory stimuli employed. The single-unit recordings made in the present study also failed to reveal any specific regional distribution; units responding principally to salt, acid, salt–acid and thermal stimuli were located in all regions which have fungiform papillae and they did not appear to have higher discharge rates in specific areas (cf. Oakley, 1975). The two units which responded principally to quinine stimulation were both located posteriorly but no judgement regarding general distribution can be made about units which occur so infrequently. It seems that the regional variation in sensitivity which exists in man (Hanig, 1901; Dastur, 1961; Collings, 1974) is very different to that found in the cat and the neurophysiological basis for it cannot be investigated using the cat as an animal model.

Development and acceptance of a universal classification for gustatory units has proved difficult as the majority of units respond to two or more different stimuli and most studies have used slightly different methodology (Pfaffman, 1941; Cohen *et al.* 1955; Ishiko & Sato, 1973; Boudreau & Alev, 1973). In the present study, attempts have been made to ensure that all gustatory stimuli were applied for exactly the same period, at the same temperature and at a constant flow rate with no mechanical disturbance of the tongue surface. The spike counts generated by each stimulus can therefore be compared directly and the units categorized. The simplest and most useful classification appears to be that based on the type of stimulus which evokes the most vigorous discharge, as used by Pfaffman (1941) and Cohen *et al.* (1955). In the present study, units have been divided into salt, acid, salt–acid, quinine, thermosensitive and purely mechanosensitive. The acid units supplied more fungiform papillae than the other groups and the papillae were more widely separated. There appears to have been no previous report of receptive field size being related to gustatory function. The salt units had the highest levels of spontaneous activity, as reported by Cohen *et al.* (1955). Quinine units were found infrequently and produced a less-vigorous discharge than the other types of unit. No units could be categorized as 'water fibres' although such units have previously been described (Cohen *et al.* 1955; Liljestrand & Zotterman, 1956; Iskiko & Sato, 1973). Whilst nineteen units responded to the application of distilled water (Table 2), this was never the stimulus which evoked the most vigorous discharge. Although responses to water appear to be dependent upon the solution previously present on the tongue (Bartoshuk, Harned & Parks, 1971), the use of Ringer solution to keep the tongue moist has been used by others who have described water fibres (Cohen *et al.* 1955). Cohen *et al.* (1955) reported that water fibre responses may be depressed when stimulating the tongue with acids of pH less than 2·5 but the acetic acid used in the present experiments was pH 2·8. A reciprocal responsiveness between salt and water stimulation (Cohen *et al.* 1955; Ishiko & Sato, 1973) was not apparent in the present study and may be attributed to the use of NH_4Cl instead of NaCl for the salt stimulus.

The gustatory units supplied an average of 2·6 fungiform papillae, similar to previously reported values (Boudreau, Bradley, Bierer, Kruger & Tsuchitani, 1971; Oakley, 1975). In agreement with Oakley (1975), two sets of taste receptors innervated by a single fibre had similar relative chemical sensitivity although some papillae appeared insensitive and there was some variation in the response to thermal stimuli. This result indicates that the branches of a taste fibre are not connected at random to the various kinds of taste receptor cells (Oakley, 1975). In the present study, ten fungiform papillae were found which were innervated by two or more of the units examined. A comparison of the properties of these units revealed that an individual fungiform papilla may carry taste buds with different response characteristics. If the matching of fibres and appropriate receptor cells involves diffusible neurotrophic factors (Sloan, Hughes & Oakley, 1983), several such agents must be present in each fungiform papilla.

The twenty units which responded principally to thermal stimuli all supplied fungiform papillae and twelve of them also responded less vigorously to stimulation with one or more of the gustatory stimuli (see also Nagaki *et al.* 1964). Their properties were very similar to those of the gustatory units (Table 1) and these units may represent a subgroup of gustatory units for which either the appropriate stimulus was not applied, or which were relatively insensitive during a period of remodelling of taste-cell contacts (Biedler & Smallman, 1965).

The units which were purely mechanosensitive appear to represent a distinct group with larger amplitudes, faster conduction velocities and rarely any spontaneous activity. Approximately half of the units in this group innervated areas of filiform papillae, the remainder innervating groups of fungiform papillae. Once again, it is possible that some of the latter fibres were gustatory units which were either temporarily or permanently insensitive to the stimuli applied. The functional significance of mechanosensory information being carried in both the lingual and chorda tympani nerves is not clear but it is possible that fibres in the chorda tympani may be involved specifically in the localization of gustatory stimuli.

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