J. Physiol. (1978), **285**, *pp.* 35–47
With 7 text-figures
Printed in Great Britain

STUDIES ON NEURAL MECHANISMS OF THE GUSTATORY-SALIVARY REFLEX IN RABBITS

BY YOJIRO KAWAMURA AND TAKASHI YAMAMOTO

From the Department of Oral Physiology, Dental School, Osaka University, 4-3-48 Nakanoshima, Kitaku, Osaka 530, Japan

(*Received 13 March 1978*)

SUMMARY

1. Submandibular salivary secretion and the electrical activity of the parasympathetic preganglionic fibres innervating the submandibular gland were recorded in decerebrated rabbits in response to taste stimulation of the tongue. The electrical activity of a taste nerve (chorda tympani) responding to varying taste stimuli was also recorded in the deeply anaesthetized rabbits. These data representing input and output information were compared with each other.

2. Sucrose, quinine, tartaric acid, NH_4Cl and KCl which induced a long-lasting response in the taste nerve evoked a continuous salivary secretion, and those chemicals such as NaCl, $CaCl_2$ and $MgCl_2$ which induced a transient activity of the nerve evoked a transient salivary secretion.

3. The magnitude of responses of the whole taste nerve to moderate concentrations of chemical stimuli applied to the anterior part of the tongue was statistically significantly correlated with the volume of reflex submandibular salivation.

4. Parasympathetic preganglionic fibres to the salivary gland were classified into two types according to their responsiveness to taste stimuli; taste-sensitive and taste-insensitive fibres. The magnitude of electrical activity of the taste nerve fibres was significantly correlated with that of the taste-sensitive preganglionic fibres to stimulation of the tongue with varying taste stimuli.

5. By calculating correlations between responses of the taste fibres to each of the four basic taste stimuli and all the stimuli tested, it was concluded that afferent inputs from the taste of sucrose and NaCl were different, while those of HCl and quinine were similar. On the other hand, it was found by the same procedure for the preganglionic fibres that sucrose and NaCl, and HCl and quinine produced a similar response profile, respectively. This result means that the afferent taste inputs are processed into appropriate outputs (perhaps on a hedonic basis) in the lower brain stem without involvement of higher central nervous mechanisms.

INTRODUCTION

The volume and the chemical composition of saliva induced reflexly by taste stimulation are markedly different depending upon the quality of the stimulus (Baxter, 1933; Gantt, 1937; Kerr, 1961; Newbrun, 1962; Funakoshi & Kawamura, 1967; Suhara, Takashita & Yazaki, 1967; Miyake, 1969; Ericson, 1971). In this regard Babkin (1950) has already mentioned that 'qualitatively different impulses

may be conveyed to the salivary glands along one and the same secretory fibre of the chorda tympani...', the parasympathetic and sympathetic nerve fibres innervating the salivary glands may be differently activated according to the nature of taste stimuli. However, the neurophysiological mechanisms of interrelations between the input taste information and the characteristics of secretory nerve responses still remain obscure.

In animal experiments the salivary secretion has generally been induced by application of a taste solution or food into the mouth of a conscious animal. Under such experimental conditions, however, not only the gustatory afferents but also various other oral and perioral afferents will be concerned with the reflex salivation. In addition, the application of a taste solution to the oral cavity may stimulate taste receptors situated over a wide area in the mouth, and an activation of higher central nervous system as well as a simple bulbar reflex arc may be involved in the salivation in a conscious animal.

The purpose of the present study is to analyse the relationship between a part of the afferent taste information and the efferent activity in one secretory nervous pathway to the salivary gland in terms of a bulbar reflex arc. To avoid the above mentioned complicated factors the animals were decerebrated, the sympathetic nerve was sectioned, and the taste solutions were applied exclusively to the anterior part of the tongue. Relationships between the magnitude of electrical activity of the chorda tympani taste nerve and the volume of reflexly induced submandibular saliva were first examined. In addition, single fibre analyses were performed on both the taste nerve and the parasympathetic nerve to reveal the mode of transmission of taste information through the bulbar salivatory nucleus.

METHODS

Forty-one rabbits of either sex and weighing between 1·7 and 2·5 kg were used.

Anaesthesia was induced by a mixture of α-chloralose (0·16 m-mole/kg) and urethane (5·6 m-mole/kg) given via the marginal ear vein and additional urethane only was supplied, if required, via a cannula placed in the femoral vein. Each animal was decerebrated at the pre-collicular level of the mid-brain and both sides of the sympathetic nerve trunk were cut at the neck except in the case where the activity of taste nerve fibres and of preganglionic fibres was recorded.

Salivation. A fine polyethylene tubing of 0·3 mm internal bore and 0·5 mm external bore was inserted into the oral opening of the submandibular duct. The other end of the tubing was connected to a small bottle with a clamp, then to a pressure-sensitive transducer (Nihonkoden Co. type LPU-0·1). The flow of saliva was measured in a closed system and the effect of the increase of air pressure in the bottle on the transducer was recorded on a pen-recorder. After recording for a desired period (usually 1 min), the clamp was opened to release the pressure. The clamp was closed again before the next recording. Increase of the pressure was read as a flow of saliva (μl.). Calibration was made by measuring the deflexion of the pen induced by injection of a set amount of saline into the bottle. 0·1 μl. saliva could be detected by this method.

Recording of taste nerve discharges. After anaesthesia, the trachea was cannulated and the head clamped. The hypoglossal nerves were cut bilaterally to avoid tongue movements. The masseter muscle and the mandibular ramus were partially removed and the chorda tympani, which innervates the taste buds on the anterior part of the tongue, was exposed under a stereoscopic dissecting microscope. The nerve was carefully separated from the surrounding connective tissues. A monopolar platinum wire electrode (100 μm in diameter) was used for recording nerve discharges of the whole bundle of the chorda tympani, and of single or a few fibres of the nerve. A small silver plate was fixed to surrounding tissues as an indifferent electrode. The electrical activity was recorded with conventional electrophysiological equipment consisting

of a differential a.c. preamplifier, oscilloscope and kymographic camera. The activity of the whole nerve bundle was shown as a conventional mean summated response or as a cumulatively integrated response (successive summation of the nerve discharges). In some animals, salivary secretion from one side of the submandibular gland and nerve discharges of the whole chorda tympani of the other side were recorded simultaneously in response to gustatory stimulation.

Recording of preganglionic secretory nerve discharges. The chorda-lingual nerve on its peripheral course gives off branches to the submandibular gland, and histological examination revealed that ganglion cells were scattered on the surface of the duct of the submandibular gland. The activity of fine strands of preganglionic efferent fibres from these branches was recorded at a point before contact with the duct. Recording electrodes and recording equipment were the same as those described above. As rabbits lack the major sublingual glands, these efferent fibres exclusively innervate the submandibular gland. Before application of taste stimuli onto the tongue, fibres were checked to be efferents by recording a reflex discharge induced by electrical stimulation of the ipsilateral upper or lower lips. Some animals were immobilized by intravenous injection of gallamine triethiodide (Flaxedil, 0·03 m-mole/kg) and artificially respirated, when the electrical stimulation induced a local muscular twitch which might interfere the precise measurement of the onset latency of the reflex discharge in the efferent fibres.

Gustatory stimulation. The anterior part of the tongue was covered with a flow-chamber made of glass with an inlet and outlet. The inlet was connected with a rubber tube to a funnel fixed about 10 cm above the flow-chamber. Taste solutions and rinsing water were applied to this funnel. Reagent grade of chemicals were dissolved in distilled water. Taste solutions were 0·5 and 1 M-sucrose, 0·5, 1 and 2 M-NaCl, 0·01 M-HCl, 0·1, 0·25 and 0·5 M-tartaric acid, 0·02 and 0·05 M-quinine-HCl, 0·5 M-DL-alanine, 0·5 M-KCl, 0·5 M-$CaCl_2$, 0·5 M-$MgCl_2$, 0·5 M-NH_4Cl and 0·3 M-Na-saccharin. These strong solutions were necessary to obtain sufficient salivary secretion and efferent nerve discharges in the anaesthetized animals. About 25 ml. of a test solution was passed by gravity flow, followed after each stimulation by tap water. A fine wire was inserted into the flow-chamber and attached to the tongue surface, and this wire was connected to another channel of the pen-recorder or the oscilloscope. Thus, the application of the stimulus was indicated by an artificial deflexion of the pen or the beam. The taste solutions and rinsing water were kept at 36–37 °C.

RESULTS

Relationship between taste nerve responses and salivary flow

Taste nerve responses induced by chemical stimulation of the tongue were roughly classified into two types depending upon the chemicals applied. One is a long-lasting response which showed an initial burst of activity followed by a steady response that continued during the course of gustatory stimulation. An example of this type is shown in Fig. 1*Aa* and *b*. Mean summated response of the whole chorda tympani to 0·5 M-NH_4Cl is shown in Fig. 1*Aa*. When the nerve impulses were integrated (or cumulatively summated), the nerve responses to 0·5 M-NH_4Cl show a continuously increasing curve (Fig. 1*Ab*). Sucrose, alanine, HCl, tartaric acid, NH_4Cl, KCl and quinine-HCl induced this long-lasting response. The other is a transient response which showed a sharp initial burst activity with little steady response. A sample record of this type in response to 0·5 M-$MgCl_2$ is shown in Fig. 1*Ba* and *b*. Mean summated response of the whole taste nerve shows initially a large transient response followed by a small steady response and finally an off-response at the moment of onset of rinsing (Fig. 1*Ba*). The integrated response shows a sharply increasing curve followed by a gradually increasing curve (Fig. 1*Bb*). NaCl, $CaCl_2$ and $MgCl_2$ belonged to this transient response type.

The salivary outflow was also classified into two types. The chemicals which induced a long-lasting response of the taste nerve induced steadily increasing salivation during the course of chemical stimulation (Fig. 1*Ac*), and those which induced a

transient response provoked an initial rapid secretion (Fig. 1*Bc*). All the records in Fig. 1 were taken from different animals.

The volume of salivary secretion induced by different stimuli is rank-ordered in Fig. 2. Each value represents the mean ± S.D. (n = 4) for 1 min of recording. The moderate concentration of chemical stimuli evoked relatively slight salivation ranging from 2·5 μl./min to 6·5 μl./min, while the high concentration of chemicals such as 2M-NaCl, 0·25 and 0·5M-tartaric acid induced a copious salivation. 0·5M-tartaric acid which may interfere with the normal physiological functions of taste receptor cells induced a particularly copious salivation (29·1 μl./min).

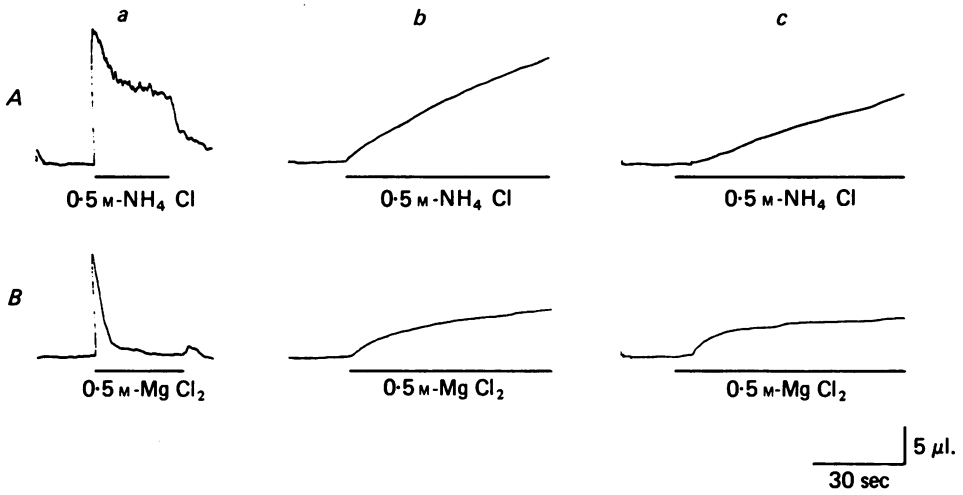

Fig. 1. Responses of the afferent chorda tympani nerve fibres and the submandibular salivary secretion in response to chemical stimulation of the tongue. Taste responses of the whole chorda tympani and reflex salivation are classified into a long-lasting type (*A*) and a transient type (*B*) according to the quality of stimulation. NH_4Cl induced a long-lasting response as seen by summated response of the chorda tympani (*Aa*) and by integrated (cumulatively summated) response (*Ab*). Correspondingly reflex salivary secretion was induced continuously during the course of NH_4Cl stimulation (*Ac*). $MgCl_2$ induced a transient response with little steady response as seen by summated (*Ba*) and integrated (*Bb*) responses. Transient salivation was induced by $MgCl_2$ stimulation (*Bc*). Bar shows the period of taste stimulation.

The relationship between the volume of salivary flow and the magnitude of chorda tympani responses to varying chemical stimuli is shown in Fig. 3. The abscissa shows the mean volume of salivary flow for the 1 min duration immediately after applying the solution, where the volume of salivary flow to 0·5M-NH_4Cl is taken as the standard (10). The ordinate shows the magnitude of the peak of the initial phasic response to the summated response (Fig. 3*A*) and the magnitude of the integrated response during the first 1 min of recording (Fig. 3*B*). The magnitude of chorda tympani responses represents the relative value (mean value, n = 4) when the magnitude of the chorda tympani response to 0·5 M-NH_4Cl is taken as the standard (100). These graphs show that the volume of salivary flow was fairly proportional to the magnitude of taste nerve responses. The correlation coefficient between the volume of salivary flow and the magnitude of peak summated response to all the

twelve taste stimuli tested was 0·56 ($P > 0·05$, t test), and that to the taste stimuli ($n = 11$) except 0·5 M-tartaric acid was 0·82 ($P < 0·01$), and that to the stimuli ($n = 9$) except 2 M-NaCl and 0·25 and 0·5 M-tartaric acid was 0·92 ($P < 0·01$). On the other hand, the correlation coefficient between the volume of salivary flow and the magnitude of the integrated response for 1 min recording to all the twelve taste

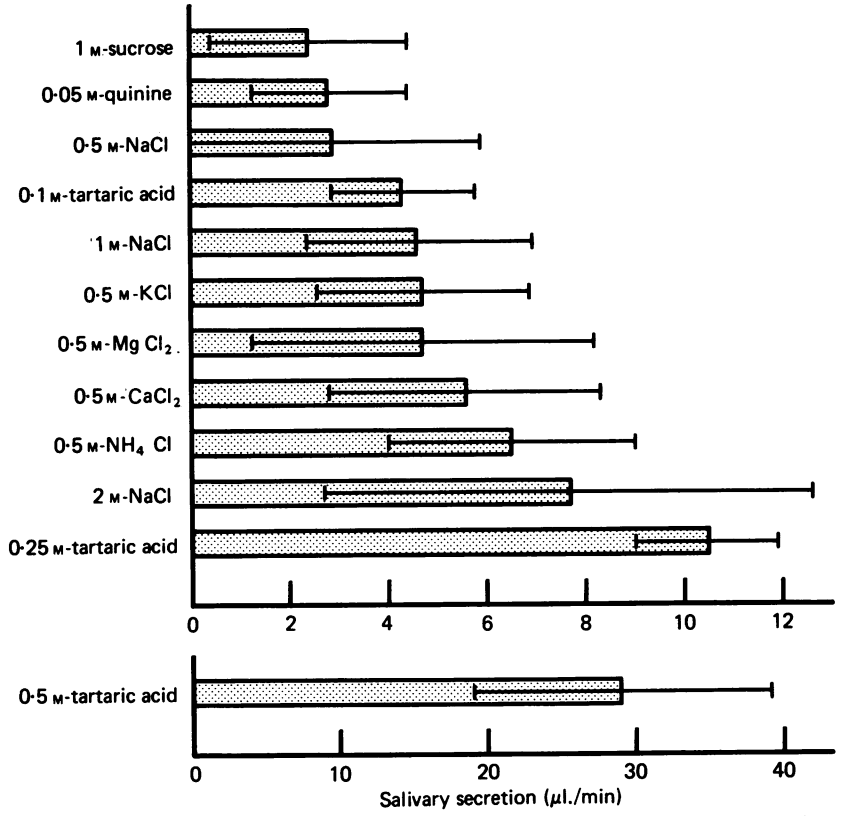

Fig. 2. Salivary secretion reflexly induced by different chemical stimuli applied to the anterior region of the tongue. Bars are mean ± S.D. values for 1 min recording obtained from four different animals. Note that 0·5 M-tartaric acid induced a particularly copious salivation.

stimuli was 0·76 ($P < 0·01$), and that to the eleven stimuli was 0·67 ($0·01 < P < 0·05$), and that to the nine stimuli was 0·70 ($0·01 < P < 0·05$). From these values it may be concluded that the volume of salivation was proportional to the peak summated response of the taste nerve when the moderate concentrations of taste solutions were applied, while the volume of salivation was proportional to the integrated response for the high concentrations of taste solutions.

Activities of the parasympathetic preganglionic fibres

Electrical activity of functionally single fibres and/or few fibre strands of the preganglionic fibres was recorded and a total of sixty-four unitary activities were sampled. They were roughly classified into two types according to the responsiveness

to taste stimuli. One group consisted of twenty-one fibres in which their firing rates were increased by taste stimuli. These fibres showed spontaneous firing of $1{\cdot}6 \pm 1{\cdot}8$ impulses/sec (mean $\pm$ S.D., $n = 21$), and they responded to electrical stimulation applied to the ipsilateral lower gingiva with a latency of $58{\cdot}3 \pm 39{\cdot}8$ msec ($n = 6$). A sample record of this type is shown in Fig. 4*A*. The other group consisted of forty-three fibres which did not respond to taste stimuli, but some of them increased their firing rates in response to pinching or electrical stimulation of the perioral tissues. These fibres showed spontaneous firing of $4{\cdot}3 \pm 3{\cdot}8$ impulses/sec ($n = 11$), and they responded to electrical stimulation of the ipsilateral lower gingiva with a latency of $9{\cdot}7 \pm 2{\cdot}8$ msec ($n = 11$). A sample record of this type is shown in Fig. 4*B*.

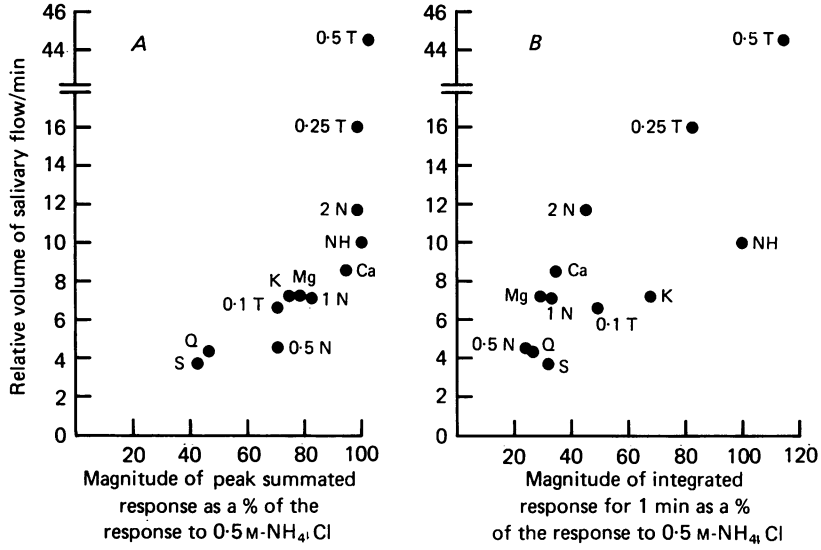

Fig. 3. Relationship between the mean volume of salivary flow and the mean magnitude of taste nerve responses in the chorda tympani to twelve different chemical stimuli. Responses of the taste fibres were expressed as the peak summated response (*A*) and the integrated response (*B*). The salivation and the integrated response were measured for 1 min after onset of chemical stimulation. The value for 0·5 M-NH_4Cl was taken as the standard. The volume of salivation correlated better with the integrated responses than the peak summated response for the twelve chemicals tested, but the reverse was true for all stimulants except 2 M-NaCl and 0·25 and 0·5 M-tartaric acid. Test chemicals were 1 M-sucrose (S), 0·05 M-quinine-HCl (Q), 0·5 M-NaCl (0·5 N), 0·1 M-tartaric acid (0·1 T), 1 M-NaCl (1 N), 0·5 M-KCl (K), 0·5 M-$MgCl_2$ (Mg), 0·5 M-$CaCl_2$ (Ca), 0·5 M-NH_4Cl (NH), 2 M-NaCl (2 N), 0·25 M-tartaric acid (0·25 T) and 0·5 M-tartaric acid (0·5 T).

Taste-sensitive preganglionic fibres generally showed a non-specific response to varying chemicals applied to the tongue surface, although the magnitude of discharges was different for each chemical stimulation. In the next step, discharges of the afferent taste fibres and those of the efferent preganglionic fibres in response to varying chemical stimuli were compared with each other. In Fig. 5, the mean number of impulses/5 sec in the taste nerve fibres are plotted against the mean number of impulses/5 sec in the taste-sensitive preganglionic fibres. The magnitude of responses

of the preganglionic fibres is statistically significantly correlated ($r = 0{\cdot}73, P < 0{\cdot}01$, t test) with the afferent responses. It was also found from this graphical analysis that the magnitude of preganglionic responses was deamplified by a factor of about 5·2.

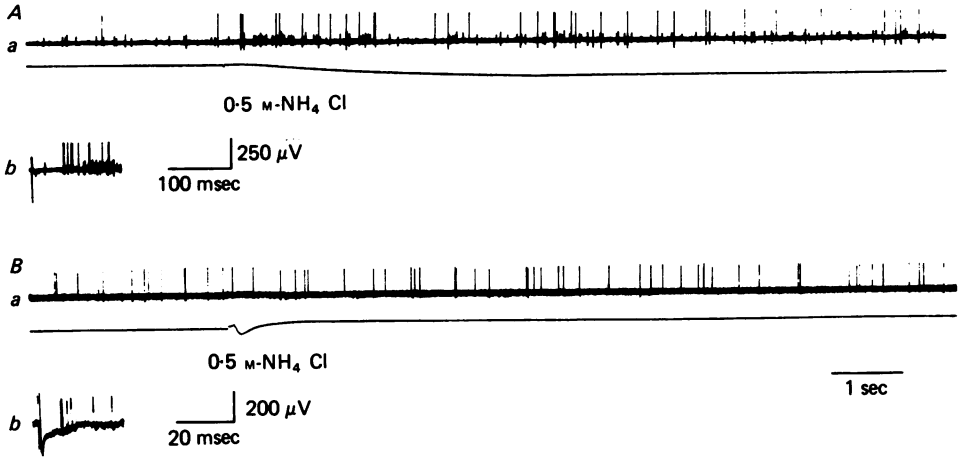

Fig. 4. Examples of taste-sensitive (*A*) and taste-insensitive (*B*) fibres in the parasympathetic preganglionic fibres innervating the submandibular gland. Line under the actual recordings (*Aa*, *Ba*) shows an artificial deflexion which indicates the moment of stimulus onset. *Ab* and *Bb* show how suprathreshold electrical stimulation to the ipsilateral lower gingiva evoked unitary discharges (five superimposed tracings). Note the difference in the rate of spontaneous firing and in the latency to the electrical stimulation in the taste-sensitive and taste-insensitive fibres. The records were retouched.

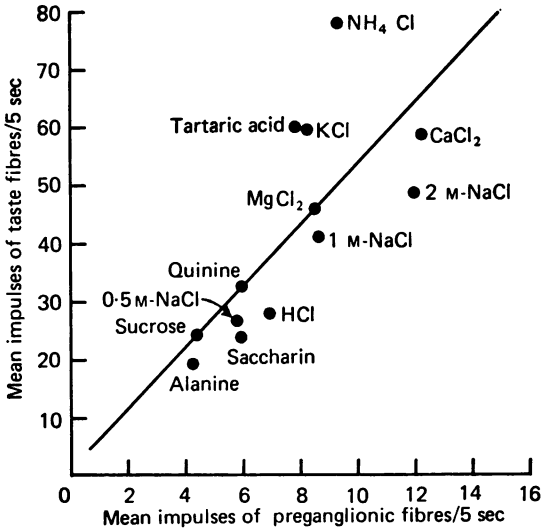

Fig. 5. Relationship between the mean number of impulses/5 sec in 'single taste fibres' of the chorda tympani and that in 'single preganglionic fibres' in response to twelve different chemical stimuli. The concentration of chemicals which is not indicated in the Figure is the same as that described in the legend for Fig. 6.

Interstimulus correlation coefficient among the taste nerve fibres and the preganglionic fibres

Correlation coefficients were calculated between the number of impulses for the first 5 sec after onset of stimulation produced by a pair of stimuli in twenty-eight taste fibres of the chorda tympani and in twenty-one preganglionic fibres. Correlations between responses of the taste fibres to each of the four basic taste stimuli (0·5 M-sucrose, 0·5 M-NaCl, 0·01 M-HCl and 0·02 M-quinine-HCl) and all the thirteen

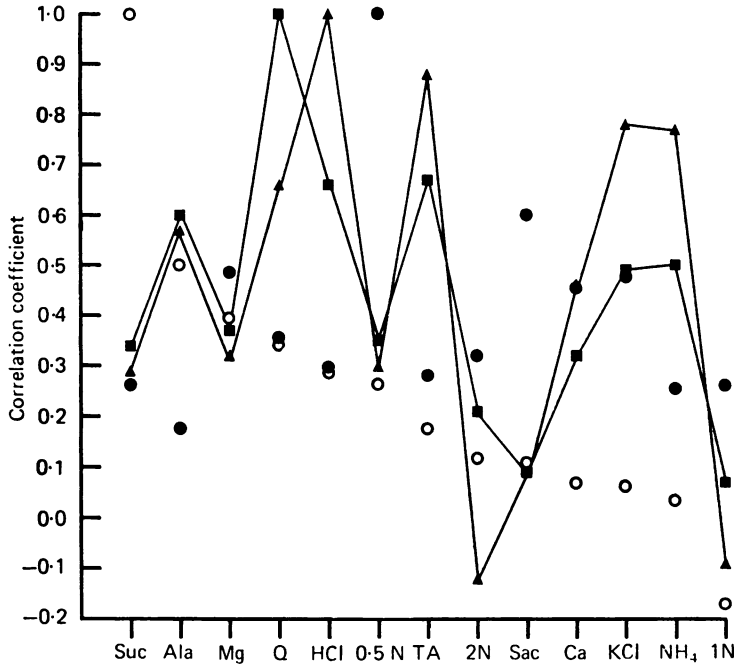

Fig. 6. Correlations between responses of the taste fibres of the chorda tympani to each of the four basic taste stimuli (sucrose, NaCl, HCl and quinine-HCl) and all the test stimuli. The chemicals shown in abscissa are arranged arbitrarily according to the magnitude of correlation coefficients between responses to sucrose and all the test stimuli (○). Correlation coefficients for HCl pairs (▲——▲) are similar to those for quinine pairs (■——■), while those for NaCl pairs (●) are different from those for any other basic taste stimulus pairs. Calculation was based on the number of impulses/5 sec after onset of stimulation. Test chemicals are 0·5 M-sucrose (Suc), 0·5 M-DL-alanine (Ala), 0·5 M-$MgCl_2$ (Mg), 0·02 M-quinine-HCl (Q), 0·01 M-HCl (HCl), 0·5 M-NaCl (0·5 N), 0·1 M-tartaric acid (TA), 2 M-NaCl (2 N), 0·3 M-Na-saccharin (Sac), 0·5 M-$CaCl_2$ (Ca), 0·5 M-KCl (KCl), 0·5 M-NH_4Cl (NH_4) and 1 M-NaCl (1 N).

different taste stimuli are shown in Fig. 6. The chemicals shown in abscissa are arranged according to the magnitude of correlations between responses to sucrose and all the stimuli. It is shown in this Figure that correlation coefficients for HCl pairs are similar to those for quinine pairs. The correlation (r) between the correlation coefficients for HCl pairs and quinine pairs is statistically significant ($r = 0{\cdot}79$, $P < 0{\cdot}01$, t test). The correlations between the correlation coefficients for any other basic taste stimulus pairs were not significant, for example, $r = -0{\cdot}12$ ($P > 0{\cdot}10$) for

sucrose pairs and NaCl pairs, and $r = -0{\cdot}25$ ($P > 0{\cdot}10$) for NaCl pairs and quinine pairs.

Correlations between responses of the preganglionic fibres to each of the four basic taste stimuli and all the thirteen different taste stimuli are shown in Fig. 7. The chemicals shown in abscissa are arranged according to the magnitude of correlations between responses to sucrose and all the stimuli. It is shown in this Figure that correlation coefficients for sucrose pairs are very similar ($r = 0{\cdot}96$, $P < 0{\cdot}01$, t test)

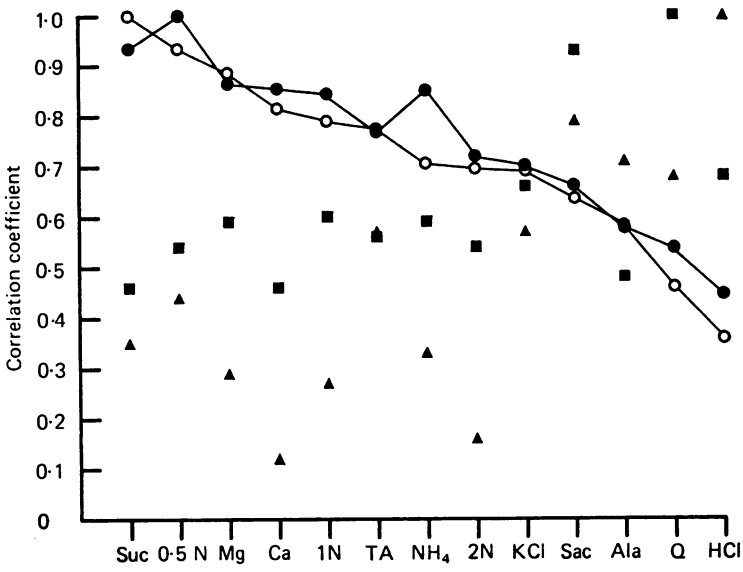

Fig. 7. Correlations between responses of the preganglionic taste-sensitive fibres to each of the four basic taste stimuli and all the test stimuli. The chemicals shown in abscissa are arranged arbitrarily according to the magnitude of correlation coefficients between responses to sucrose and all the test stimuli. Correlation coefficients for sucrose pairs (○——○) are very similar to those for NaCl pairs (●——●), and those for HCl pairs (▲) are similar to those for quinine pairs (■). Other details are as for Fig. 6.

to those for NaCl pairs, and those for HCl pairs are also similar ($r = 0{\cdot}55$, $0{\cdot}01 < P < 0{\cdot}05$) to those for quinine pairs. Another finding is that correlation coefficients for sucrose pairs and/or NaCl pairs are reversely correlated with those for HCl pairs and/or quinine pairs. For example, the correlation between the correlation coefficients for sucrose pairs and quinine pairs was $-0{\cdot}58$ ($0{\cdot}01 < P < 0{\cdot}05$) and the correlation for NaCl pairs and HCl pairs was $-0{\cdot}75$ ($P < 0{\cdot}01$).

DISCUSSION

The volume of salivary secretion induced by taste stimulation was fairly small in anaesthetized, decerebrated and sympathectomized rabbits; the slightest amount was 2·4 μl./min (mean value, $n = 4$) for 1 M-sucrose, and the largest amount was 29·1 μl./min of salivation which was produced by 0·5 M-tartaric acid. However, this concentration of tartaric acid is nearly a noxious stimulant to the taste receptors.

Noxious stimuli applied to the intra- and peri-oral region generally induce a very copious salivation in rabbits (Kawamura & Yamamoto, 1977). In normal conscious rabbits, more copious reflex salivation will be obtained in response to taste stimuli because salivary secretion is very susceptible to systemic anaesthesia (Robbins, 1935) and cortical ablation markedly decreases salivary secretion to taste stimulation (Funakoshi, Kasahara, Yamamoto & Kawamura, 1972). In the rabbit submandibular gland, Smaje (1973) reported that the rate of spontaneous salivation was $0{\cdot}25 \pm 0{\cdot}01$ μl./min (mean $\pm$ S.E., $n = 11$). Therefore, although the volume of salivation to taste stimulation was small, it is obvious that this secretion was induced reflexly by activation of the taste receptors of the tongue and was not due to spontaneous salivation.

It is known that the volume of saliva produced by taste stimuli is markedly different depending upon different qualities of taste sensation. Funakoshi & Kawamura (1967) calculated the ratios between volumes of saliva and taste nerve activity in the dog. They found that quinine induced the most copious parotid secretion, tartaric acid was the next, followed by NaCl and sucrose. They concluded that the volume of saliva induced by four basic taste stimuli was not proportional to the electrical activity of the taste nerve. On the other hand, we reached the opposite conclusion in the present study, that is, the volume of submandibular salivary secretion was proportional to the magnitude of taste nerve activities. Our conclusion was derived from the following observations. First, chemicals which induced a long-lasting response in the taste nerve evoked a continuous salivary secretion and those inducing a transient activity evoked a transient salivary secretion. Secondly, the magnitude of taste nerve responses to moderate concentrations of chemical stimuli was statistically significantly correlated with the volume of salivation. Copious salivation induced by very strong chemical stimuli may be attributed in part to the activation of other sensory receptors than taste receptors, because such strong chemicals applied to the tongue are known to induce responses in the lingual branch of the trigeminal nerve which does not contain taste-sensitive fibres (Kawamura, Okamoto & Funakoshi, 1968). Thirdly, single fibre analyses showed that the number of impulses induced by taste stimuli in the taste nerve fibres were statistically significantly correlated with those in the preganglionic taste-sensitive fibres.

There are some differences in experimental procedures which may explain the discrepancy between the result obtained in this study and that in the study of Funakoshi & Kawamura. They used unanaesthetized conscious dogs, while we used anaesthetized decerebrated rabbits. In conscious animals, not only a simple bulbar reflex arc but also more complex networks involving hypothalamic, limbic and cortical systems are most likely involved in salivation to taste stimuli. Qualitative and quantitative differences in evoked saliva depending upon the nature of taste stimuli may be attributed to the information processing, particularly within these complex networks involving the higher central nervous system. Further, since a conscious animal moves his mouth and tongue more vigorously by application of rejective substances such as acids or bitters than by palatable NaCl or sucrose, the difference of magnitude of afferent inputs from the mechanoreceptors as well as the taste receptors may also contribute to the different volume of reflex salivation.

Another difference is that they collected parotid saliva induced by application of a taste solution to the entire mouth, while we collected submandibular saliva induced by application of a taste solution to the anterior part of the tongue. Miller (1913) and Miyake (1969) have suggested that gustatory information via the glossopharyngeal nerve plays a more important role in the reflex parotid secretion than that via the chorda tympani in cat and dog. As noted by Nowlis & Kessen (1976), if gustatory information via the glossopharyngeal nerve may play an important role in rejection behaviour, then glossopharyngeal taste input may connect more closely with cells in the salivatory nucleus in the medulla to wash away or dilute the unpalatable substances.

In the present study, preganglionic fibres were classified into two groups according to their responsiveness to taste stimuli, one is taste-sensitive and the other taste-insensitive. It was also noted that the rate of spontaneous firing was higher in the taste-insensitive fibres than in the taste-sensitive fibres and the latency of the response to electrical stimulation of the lower gingiva was shorter in the taste-insensitive fibres than in the taste-sensitive fibres. In our previous study (Yamamoto & Kawamura, 1977), we mentioned that the magnitude of discharges of taste-sensitive preganglionic fibres was statistically significantly correlated with the volume of salivary secretion in the rabbit, and we suggested that the efferent fibres to the gland which respond to taste stimuli are secretory fibres. The role of the taste-insensitive fibres is not clear. Since the electrical stimulation of the lower gingiva evoked reflex discharges in these fibres, these fibres may be activated by other different sensory input than taste. Alternatively, these fibres may have a different function such as maintenance of the enzyme activity in the salivary gland (Ekström, 1977) or perhaps vasodilatation.

Since most of the taste fibres (afferent fibres) respond to more than one kind of taste stimulus (Pfaffmann, 1955), it has been proposed that the qualities of stimuli are coded by the response pattern across many neurones. Erickson (1963) has suggested that any pairs of stimuli which show similar response profiles across many neurones produce a similar taste, and those which give different profiles induce a different taste. A measure of the similarity of these patterns is given by the correlation between the magnitude of the responses produced by these stimuli in many fibres. Correlations between responses of the chorda tympani to the four basic taste stimuli and all other stimuli (Fig. 6) suggest that the rabbits can discriminate the taste of sucrose and NaCl, while they can hardly discriminate the taste of HCl and quinine. This result corresponds with that obtained in the rat and hamster (Ogawa, Sato & Yamashita, 1968). On the other hand, at the preganglionic fibre level, the magnitude of responses to sucrose and NaCl is significantly correlated, and responses to HCl and quinine are also significantly correlated in their magnitude. This means that after traversing synapses taste input is transformed to a sucrose-NaCl group and a HCl-quinine group to activate the salivatory nuclear cells. In the hedonic features of taste sensation in man, Pfaffmann (1960) showed that sucrose and NaCl were acceptable and HCl and quinine were rejective, and Carpenter (1956) showed in the two-bottle preference test that sucrose and NaCl were preferred while quinine was rejected by the rabbit. It is of great interest that in the gustatory-salivary reflex the basic acceptance-rejection dimension is already determined in

the brainstem without involving the higher central nervous system. The finding that the acceptance-rejection behaviour induced by taste stimuli is accomplished in the lower brainstem has also been reported in the rat (Pfaffmann, Norgren & Grill, 1977), and Steiner (1973) also reported that anencephalic and hydroanencephalic neonates expressed their facial reactions as displeasure (rejection) or pleasure (acceptance) depending upon the quality of taste stimulation.

This study was supported by a scientific grant from the Ministry of Education of Japan (no. 144068).

REFERENCES

BABKIN, B. P. (1950). *Secretory Mechanism of Digestive Glands*, 2nd edn. New York: Hoeber.

BAXTER, H. (1933). Variations in the inorganic constituents of mixed and parotid gland saliva activated by reflex stimulation in the dog. *J. biol. Chem.* **102**, 203–217.

CARPENTER, J. A. (1956). Species differences in taste preferences. *J. comp. physiol. Psychol.* **49**, 139–144.

EKSTRÖM, J. (1977). The effect of teeth amputations on the choline acetyltransferase activity of rat submaxillary glands. *Acta physiol. scand.* **99**, 48–52.

ERICSON, S. (1971). The variability of the human parotid flow rate on stimulation with citric acid, with special reference to taste. *Archs oral Biol.* **16**, 9–19.

ERICKSON, R. P. (1963). Sensory neural patterns and gustation. In *Olfaction and Taste*, vol. 1, ed. ZOTTERMAN, Y., pp. 205–213. New York: Pergamon.

FUNAKOSHI, M., KASAHARA, Y., YAMAMOTO, T. & KAWAMURA, Y. (1972). Taste coding and central perception. In *Olfaction and Taste*, vol. 4, ed. SCHNEIDER, D., pp. 336–342. Stuttgart: Wissenschaftliche Verlagsgesellschaft MBH.

FUNAKOSHI, M. & KAWAMURA, Y. (1967). Relations between taste qualities and parotid gland secretion rate. In *Olfaction and Taste*, vol. 2, ed. HAYASHI, T., pp. 281–287. Oxford: Pergamon.

GANTT, W. H. (1937). The nervous secretion of saliva: quantitative studies in the natural unconditioned reflex secretion of parotid saliva. *Am. J. Physiol.* **119**, 493–507.

KAWAMURA, Y., OKAMOTO, J. & FUNAKOSHI, M. (1968). A role of oral afferents in aversion to taste solutions. *Physiol. & Behav.* **3**, 537–542.

KAWAMURA, Y. & YAMAMOTO, T. (1977). Salivary secretion to noxious stimulation of the trigeminal area. In *Pain in the Trigeminal Region*, ed. ANDERSON, D. J. & MATTHEWS, B., pp. 395–404. Amsterdam: Elsevier/North-Holland Biomedical.

KERR, A. C. (1961). *The Physiological Regulation of Salivary Secretions in Man*. New York: Pergamon.

MILLER, F. R. (1913). On the reactions of the salivary centres. *Q. Jl exp. Physiol.* **6**, 57–72.

MIYAKE, Y. (1969). Chorda versus glossopharyngeal nerve in the reflex parotid secretion. *J. physiol. soc. Jap.* **31**, 268–276 (in Japanese).

NEWBRUN, E. (1962). Observations on the amylase content and flow rate of human saliva following gustatory stimulation. *J. dent. Res.* **41**, 459–465.

NOWLIS, G. H. & KESSEN, W. (1976). Human newborns differentiate differing concentrations of sucrose and glucose. *Science, N.Y.* **191**, 865–866.

OGAWA, H., SATO, M. & YAMASHITA, S. (1968). Multiple sensitivity of chorda tympani fibres of the rat and hamsters to gustatory and thermal stimuli. *J. Physiol.* **199**, 223–240.

PFAFFMANN, C. (1955). Gustatory nerve responses in rat, cat and rabbit. *J. Neurophysiol.* **18**, 429–440.

PFAFFMANN, C. (1960). The pleasures of sensation. *Psychol. Rev.* **67**, 253–268.

PFAFFMANN, C., NORGREN, R. & GRILL, H. J. (1977). Sensory affect and motivation. *Bull. N.Y. Acad. Sci.* **290**, 18–34.

ROBBINS, B. H. (1935). Effect of various anesthetics on salivary secretion. *J. Pharmac. exp. Ther.* **54**, 426–432.

SMAJE, L. H. (1973). Spontaneous salivation in the rabbit submandibular gland. *J. Physiol.* **231**, 179–193.

STEINER, J. E. (1973). The gustofacial response: observation on normal and anencephalic newborn infants. In *Fourth Symposium on Oral Sensation and Perception*, ed. BOSMA, J. F., pp. 254–278. Washington, D.C.: U.S. Government Printing Office.

SUHARA, R., TAKASHITA, H. & YAZAKI, S. (1967). Study on the parotid salivary secretion due to taste stimuli in rabbits. In *Olfaction and Taste*, vol. 2, ed. HAYASHI, T., pp. 337–342. Oxford: Pergamon Press.

YAMAMOTO, T. & KAWAMURA, Y. (1977). Responses of the submandibular secretory nerve to taste stimuli. *Brain Res.* **130**, 152–155.