THE EFFECT OF TEMPERATURE ON NEURAL TASTE RESPONSE OF CATS

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In the preceding paper NAGAKI, YAMASHITA and SATO⁷⁾ have shown that the magnitude of response of the chorda tympani nerve of cats to taste stimuli was, in most cases, greatest when the temperature of taste solutions was at about 30°C or at the temperature of the tongue. In this study, however, the temperature of the tongue was not controlled accurately, but only the temperature of solutions was changed. Consequently, both thermal and taste responses were included in the chorda tympani response, and the magnitude of taste response at various temperatures had to be estimated by subtracting the thermal response from the whole chorda tympani response to a taste solution at any temperature.

In the present study the tongue had been adapted to a certain temperature before taste stimulations were performed in order to eliminate the thermal response and to measure only the magnitude of taste response. This method of preadapting the tongue to a temperature similar to that of stimulating solution, adopted previously by ABBOTT¹⁾ on rats, has enabled us to work out the relationship between the taste response of the chorda tympani and temperature more accurately than did the previous experiment. The results of the present experiment confirm those of the previous study, showing that the greatest taste response is obtained at about 30°C for four kinds of taste solutions.

METHODS

Twelve adult cats were used in this experiment. The experimental methods were almost the same as those described in the preceding paper⁷⁾ except for that of the stimulation of the tongue. Temperature of the surface of the tongue, measured with a thermistor, ranged from 29.2° to 33.4°C (mean of twelve cats; 30.8°C).

The magnitude of the integrated response immediately and 10 sec after the stimulation was measured and taken as representing the magnitude of initial and steady

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responses, respectively.

Method of stimulation. First, Ringer's solution of a certain temperature was passed into a flow chamber, in which the tongue had been placed. One minute after the onset of the flow of Ringer's solution, during which the thermal response of the chorda tympani nearly subsided and temperature of the tongue attained almost a steady level (FIG. 1), the first stimulus was applied to the tongue through a flow chamber. The stimulation lasted for 15 sec and this was followed by a flow of Ringer's solution. Thirty seconds after the end of the first stimulus the next stimulus was applied for 15 sec, followed by a flow of Ringer's solution for 30 sec and finally the third stimulus was given to the tongue. In this way three successive stimulations were made, each being interposed by a flow of Ringer's solution for 30 sec. Each stimulus had the same temperature as that of the preadapting Ringer's solution, so that the thermal response could be avoided. When the three successive stimuli were identical, the successive chorda tympani responses showed almost equal magnitude, as shown in FIG. 1. This ensures that the preceding stimulus does not affect the subsequent response.

FIG. 1. Integrated response of the chorda tympani of a cat to three successive stimulations of the tongue by 0.5 M NaCl of 20°C, preceded by a flow of Ringer's solution at the same temperature (upper trace), and temperature change of the surface of the tongue (lower trace).

Experiments on the lingual nerve. Three cats out of the 12, used in this experiment, were employed for investigating the response of the lingual nerve to thermal stimulation of the tongue. For the stimuli Ringer's solution of varying temperatures was applied through a flow chamber to the tongue for more than 1 min.

Solutions. As test stimuli 0.25, 0.5 and 1 M NaCl, 0.5 M KCl, 0.005 M quinine hydrochloride and 0.005 M HCl were employed, NaCl and KCl being dissolved in deionized water and quinine and HCl in Ringer's solution (NaCl 154 mM, KCl 5.6 mM, CaCl_2 2.16 mM).

RESULTS

Response to NaCl. Three experiments using 0.25, 0.5 and 1 M NaCl as test stimuli were carried out. The results are summarized in FIG. 2, in which each point indicates average of three experimental results. FIG. 2 indicates

FIG. 2. Relationship between the magnitude of response to 1 M ($\times$), 0.5 M ($\circ$) and 0.25 M ($+$) NaCl and temperature. The magnitude of the initial response is shown in the left and that of the steady response (10 sec after the stimulation) in the right. Each point represents the average value of three experiments, expressed relative to the magnitude of response to 1 M NaCl at 30°C.

that the magnitude of response immediately and 10 sec after the stimulation shows a maximum value at 30°C for all concentrations except the initial value for 0.25 M. The response to 0.25 M NaCl in FIG. 2 is greatest at 40°C. However, this does not seem to be significant, because in one experiment the greatest response magnitude was obtained at 30°C, and in another experiment at both 30° and 40°C while in the remaining experiment the value at 40°C was exceptionally greater than those at other temperatures. From this one may probably be safe to assume that the magnitude of response to 0.25 M NaCl shows a maximum value at 30°C.

Response to HCl, KCl and quinine. Two experiments were carried out using 5 mM HCl, 5 mM quinine and 0.5 M NaCl as test stimuli and four experiments using 5 mM HCl, 5 mM quinine and 0.5 M KCl. An example of the latter experiments is shown in FIG. 3, and all the results of 6 experiments are summarized in FIG. 4, in which the magnitude of responses to NaCl, KCl and quinine relative to that for HCl at 30°C is shown as function of temperature. FIG. 4 indicates that 0.5 M NaCl, 5 mM HCl and 5 mM quinine produce a maximum response at 30°C while the greatest response for KCl lies at 35°C. The magnitude of response 10 sec after the stimulation shows a maximum at

FIG. 3. Integrated response of the chorda tympani to three successive stimulations of the tongue by 0.5 M KCl, 5 mM quinine and 5 mM HCl, preceded by a flow of Ringer's solution at varying temperatures (upper trace), and temperature change in the tongue (lower trace). In the experiment at 50°C only Ringer's solution was applied to the tongue.

30°C not only for NaCl, HCl and quinine but also for KCl (FIG. 4, right). The magnitude of the initial response to KCl was greatest at 30°C in one experiment, at 40°C in another and at 35°C in the remaining two experiments. Therefore it is rather likely that the magnitude of initial response to KCl shows a higher optimal temperature than that to other kinds of stimuli.

The relative magnitude of response to 0.5 M NaCl, 0.5 M KCl, 5 mM HCl and 5 mM quinine, calculated from the initial response magnitude, is NaCl: KCl: HCl: quinine=0.36: 1.00: 1.72: 1.50 at 30°C, but it becomes 0.28: 1.00: 1.17: 1.15 at 10°C and 0.25: 1.00: 0.75: 0.48 at 45°C, while the response ratio for the steady response magnitude is 0.51: 1.00: 2.14: 1.32 at 30°C, 0.13: 1.00: 1.06: 0.74 at 10°C and 0.77: 1.00: 0.91: 0.40 at 45°C. Although these ratios

FIG. 4. Relationship between the magnitude of response to 0.5 M NaCl (○), 0.5 M KCl (●), 5 mM quinine (+) and 5 mM HCl (x) and temperature. The magnitude of the initial response is shown in the left and that obtained 10 sec after the stimulation in the right. Each point represents the average value of two experiments for NaCl, four experiments for KCl and six experiments for quinine and HCl, and is expressed relative to the magnitude of response to HCl at 30°C.

are very approximate, it may be concluded that the relative magnitude of response to acid and quinine decreases markedly at very cold or warm temperatures.

Temperature coefficients of taste response. From the results of 9 experiments the temperature coefficient (Q_{10}) for the magnitude of response to four

TABLE 1
Temperature coefficients (Q_{10}) for the chorda tympani response to NaCl, KCl, HCl and quinine at respective temperature range.

Stimulating solutions	Number of experiments	10°-20°C	15°-25°C	35°-45°C
0.5 M NaCl	5	1.54	1.38	-1.70
0.5 M KCl	4	1.92(2.16)	1.43(1.83)	-1.31(-1.14)
5 mM HCl	6	3.46(4.33)	1.76(1.99)	-2.38(-2.50)
5 mM Quinine	6	2.34(3.50)	1.93(2.53)	-3.60(-3.64)

Numerals in the parentheses indicate the Q_{10} for the steady response magnitude and those outside that for the initial response magnitude.

kinds of taste stimuli is calculated and is shown in TABLE 1. As can be seen in this table, Q_{10} for the response to NaCl and KCl is about 2 between 10° and 30°C and less than -2 between 35° and 45°C, while Q_{10} for the quinine and HCl response is much greater than the former. Such distinct differences in the Q_{10} values between the responses to salts and those to acid and quinine suggest that the reaction between taste receptors and stimulating substances are not the same in these two groups of stimulations, and a relatively small Q_{10} value for the salt response indicates that the reaction is physical or physicochemical rather than enzymatic.

Response of the chorda tympani and the lingual nerve to temperature change of the tongue. At the onset of a flow of Ringer's solution of varying temperatures over the tongue thermal responses appeared in the chorda tympani (FIGS. 1 and 3). The response attained a maximum magnitude immediately after the onset of the flow and ceased approximately during the next minute. The magnitude of response, measured immediately after the flow, was increased as the temperature was lowered or raised from 30°C, where little response was seen; this confirmed the results by NAGAKI *et al.*⁽⁷⁾. In addition, when the temperature was raised to as high as 50°C, a massive and persistent discharge appeared following the initial thermal response (FIG. 3, bottom record). This response is different in its time of occurrence and pattern from the thermal response and may be considered as a pain discharge.

The lingual nerve response to thermal change of the tongue differed from the chorda tympani response, as shown by NAGAKI *et al.*⁽⁷⁾. An example of the integrated response of the lingual nerve is shown in FIG. 5. As seen in this figures, there is a transient and big response to the lowering of temperature, but on raising the temperature the level of the integrator output was lowered and a further rise in temperature resulted in a delayed but massive

FIG. 5. Integrated response of the lingual nerve to thermal stimulation of the tongue (upper trace) and change in temperature of the tongue (lower trace).

FIG. 6. Relationship between the magnitude of the lingual nerve response to thermal change of the tongue and temperature. ○; the magnitude of response immediately after stimulation, and ●; the magnitude of response 1 min after stimulation.

discharge (record at 50°C in FIG. 5). The delayed discharge at 50°C is the same in its pattern as that in the chorda tympani, and is also considered as a pain discharge. The relationship between the magnitude of thermal response immediately and 1 min after the stimulation and the temperature is shown in FIG. 6. The initial response tends to become smaller in magnitude as the temperature gets higher, while the magnitude of the steady response shows a maximum at 25°C.

DISCUSSION

NAGAKI *et al.*⁷⁾ have shown that the greatest taste response of the chorda tympani of cats to stimulation of the tongue by NaCl, quinine and HCl is obtained when the temperature of taste solutions is at about 30°C or at the temperature of the tongue. In their experiment taste receptors were stimulated by solutions of varying temperatures, and consequently the magnitude of taste response was estimated by subtracting the thermal response from the whole response of the chorda tympani at each temperature. However, the present experiment, in which the thermal response was eliminated by

preadapting the tongue to the temperature for stimulation, yielded the results similar to those by NAGAKI *et al.*⁷⁾. Although in the paper by NAGAKI *et al.*⁷⁾ the optimal temperature for NaCl has been shown to vary as the concentration changes, this has not been confirmed in the present experiment.

Temperature characteristic of the taste response such as showing an optimal temperature at 30°-35°C appears to be a common attribute of all mammals, since similar observations to those on cats have been shown on rats by SATO and YAMASHITA⁸⁾. However, taste receptors of insects and amphibians behave differently from those of mammals with respect to temperature change. The former is not influenced significantly by changes in temperature at which stimulations are carried out^{2,5)}, and the latter shows the optimal temperature close to the environmental temperature where animals live but differing to some extent according to the quality of taste stimuli^{6,9)}.

The temperature coefficient for the magnitude of response to various kinds of stimuli has been calculated. The Q_{10} values for NaCl and KCl are small compared with those for HCl and quinine; such small Q_{10} values for the former as shown in the table probably indicate that the reaction between these ions and taste receptors is of physical or physicochemical nature and the marked difference between the Q_{10} values for salts and those for HCl and quinine suggests that the reaction involved in these two cases of stimulation is of different one. Similar results were obtained on frogs by YAMASHITA⁹⁾ and on rats by SATO and YAMASHITA⁸⁾.

In the above discussion it has been assumed that the neural response reflects the magnitude and the time course of the receptor process in taste cells which ultimately leads to repetitive initiation of impulses at the nerve terminal and that temperature change affects the receptor process exclusively. However, it may be possible that temperature change itself affects the electrical properties, such as the threshold, recovery period and accommodation, of nerve terminals innervating taste cells, thereby modifying the chorda tympani nerve response to taste stimulation. But it is difficult to assess how much this contributes to the results obtained in the present experiment. On the contrary, since there is evidence that almost all taste units in the chorda tympani of cats respond to temperature change as well⁷⁾, indicating that temperature change can modify properties of taste cells, the present authors are inclined to consider that changes in the neural response reflect, to a great extent, variations in the receptor process.

In the results behaviours of the chorda tympani nerve and of the glosso-pharyngeal nerve to thermal stimuli of the tongue were described. The chorda tympani shows an increasing magnitude of response with increasing difference in temperature between the flowing solutions and the tongue, while the lingual nerve indicates a decreasing magnitude of response with increasing temperature of solutions. Such results are in good agreement with those

by NAGAKI *et al.*⁷⁾. When the magnitude of response 1 min after the stimulation is measured, the lingual nerve response shows a maximum at 25°C. This is consistent with the finding by HENSEL and ZOTTERMAN⁴⁾ on single *cold fibres* in cats; they showed that discharge frequency in single *cold fibres* increases with temperature rise between 15°C and 25°C, decreases to zero from 25°C to 35°C and rises further from about 47°C. The discharge at about 50°C was called the *paradoxical discharge* by these authors. But the discharge observed in the lingual nerve at 50°C in the present experiment may not be the same as the *paradoxical discharge*, although the former includes the latter. The discharge in the lingual nerve at 50°C appears to result mostly from pain fibres, since i) the discharge pattern at 50°C is quite different from that at the temperature below 40°C, ii) similar discharges were observed in the chorda tympani and iii) recordings of impulses in the present experiment were made from the whole nerve. The magnitude of steady thermal discharge in the chorda tympani declined as the temperature was raised up to 45°C. This is probably because the nerve contains both *cold* and *warm fibres*⁷⁾, the latter of which, according to the experimental results by DODT and ZOTTERMAN³⁾, should show a maximum frequency of impulses at steady temperature of about 40°C.

SUMMARY

1. The effect of temperature change on the chorda tympani response of the cat has been investigated, by carrying out the stimulation of the tongue by NaCl, KCl, HCl and quinine at varying temperatures.
2. The greatest response magnitude was obtained at 30°C for NaCl, HCl and quinine, while the response to KCl showed a maximum magnitude at 35°C.
3. The Q_{10} values for NaCl and KCl stimulation were small compared with those for HCl and quinine. A possible significance of this result for the mechanism in receptor-substance reaction was discussed.
4. The thermal responses in both the chorda tympani and the lingual nerve to temperature change of the tongue were described.

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