Temperature Coefficients of the Electrical Thresholds of Taste Sensations

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ABSTRACT Each papilla in an enlarged photograph of the tip of the tongue was identified electrically as belonging to one of the four basic taste sensations. The temperature coefficient of the threshold for electrical stimulation was observed for single papillae. The results seem to divide the four basic taste sensations into two different groups: sour-salty and sweet-bitter. This is the same division that has been reported with other methods.

METHODS OF DETERMINING THE TASTE THRESHOLD

Investigating the threshold for chemical stimulation of the tongue, we found that threshold observation for chemical taste sensations is more difficult than analogous measurements for hearing and the vibratory senses. The main difficulty is the adaptation of taste sensations. The smallest chemical stimulus presented to the tongue immediately raises the threshold (Békésy, 1965), and it is difficult to follow this rise. Adaptation depends on concentration, presentation time, temperature, etc. The threshold observations become unreliable, mainly because of the difficulty of making sure that it is always exactly the same group of papillae that is being stimulated. If, during the presentation time of the stimulus, new papillae come to be involved, their threshold is unadapted and very different from the adapted one. This will ruin the whole observation. The leakage of the solution from the test area to surrounding papillae produces a large spread in threshold values.

There are two ways to minimize the effect of adaptation on threshold observations: (a) The test solution is presented for only a short time between long intervals. Since 1 second is about enough to produce a well defined sensation, this was used as the presentation time. The interval between these short stimuli had to be as long as 10 to 20 seconds to reduce the threshold drift. (b) The second method is to use a semi-automatic gustometer which permits one to follow the threshold shift. The subject recorded, by pressing and releasing a button, the concentrations of the test solution for which alternately the sensation was present or just disappeared. Such a record is presented in Fig. 1. The ordinate represents the concentration of the test solution necessary to follow the continuous shift in the threshold from the time when the observations were started. The stimulus was always near the threshold, but even so the shift is considerable. To determine the threshold, the midpoints between “sensa-
tion" and "no sensation" corners were taken (the black dots in the figure) and these were extrapolated to the concentration value which lay between the maxima and minima of the beginning of the trace. This extrapolated threshold value is represented by a circle in Fig. 1. There is no difficulty in extrapolating, since the midpoints are generally in a straight line. If, however, during the observations the tongue moved only slightly in relation to the opening where the taste solutions were presented, unadapted papillae would come into action, and the threshold would suddenly drop. The midpoints would then come down to values corresponding to the beginning observations. Since extrapolation is difficult for a curved line, these observations were discarded.

A possible third method is to combine the first two. When the stimulus is not presented continuously, but is presented only every 20 seconds for 1 second, then the maxima and minima in Fig. 1 lose their regularity. But the line of the midpoints becomes almost horizontal, since the threshold shift through adaptation is reduced. This improves the extrapolated threshold.

All three methods were tried, but there were no important differences among them relative to the stability of the threshold values. The method of the short presentation time is best when the observers can hold their tongues in the same position for more than 3 minutes, since even with the long intervals there is a little adaptation. If there were no adaptation, a movement of the tongue would hardly affect the threshold values if the stimulating area were large enough.

Besides the difficulty with adaptation there are the large variations for different
observers. We found girls 18 to 28 years of age very suitable for the observations. The changes of taste in later years seem to be considerable, but they were not investigated. Smoking and drugs like sleeping pills seem to attack the sweet papillae first. We had some subjects who seem to live with only 3 to 5 sweet papillae, as found by electrical and chemical stimulation of small test areas.

Under these circumstances it is not surprising that the effect of temperature on chemical taste thresholds led to such different results. The effects of temperature have been observed by means of threshold shifts (Chinaglia, 1915; Hahn, 1949, Fig. 21, p. 147; Pfaffmann, 1959, pp. 523–533, including Fig. 14; Sato, 1963; and Komuro, 1921) and by electrophysiological methods (Beidler, 1954).

Study of a large set of our observations of thresholds for chemical stimuli as a function of temperature indicated that the variability in the results was due to two factors: (a) Sensitivity, rate of adaptation, etc., may change considerably along the surface of the tongue. Therefore, reproducible results can be expected only when it is possible to stimulate exactly the same spot on the tongue repeatedly. This led to our interest in the possibility of identifying single papillae and plotting them on a map in order to be able to stimulate them over and over again. Electrical stimulation of single papillae (Békésy, 1964) proved to be successful on several subjects although some had more difficulty than others. Papillae on the tongue are as different as the faces of people. (b) The second factor was the problem of obtaining a well defined temperature change.

Methods for Changing the Temperature of the Taste Papillae

It was found that a tenfold increase in the surface area heated would stabilize the temperature coefficient of the threshold for chemical stimuli. Anatomically this seems to be quite possible, since the taste buds lie in folds below the apparent surface of the tongue. If the tongue does not move, there is little chance for the warmed fluid to penetrate into the folds and change the temperature of the buds. From this it was concluded that, besides adaptation, the heat conductivity from the surface of the tongue to the taste buds themselves may be also responsible for the different results.

For electrical stimulation of the papillae, the main requirement is that, during warming or cooling, the moistness of the surface of the papillae is not changed, since this, too, can produce a change in sensitivity. At the same time, the temperature change should penetrate to a certain depth below the surface of the tongue. We tried to fulfill these requirements by lightly pressing with a pencil-like holder a silver tube of about 1 mm inside diameter against the surface of the tongue. The warming and cooling fluids passed through the tube. Its heat conductivity was reduced only a little by gold plating. The gold plating seems to eliminate any taste sensations which might interfere with the measurements. The loop is shown in Fig. 2A, with the placement of the electrode tip in its center. In this situation the papilla is warmed from inside. Since the heat loss to the air on the surface of the tongue must be relatively small, the whole papilla is eventually warmed up. This deep warming changes the metabolism, since a change in the blood supply in the capillaries can often be observed. But simply touching a papilla can produce an even greater change in the capillaries.

The temperature change of the fluid in the loops for electrical stimulation was
controlled by an electrodynamically driven switching system (Fig. 2B). We started with a fluid of 25°C, which could be used for cooling the tongue by letting it flow straight through the loop. Beside the upper tube there was a parallel second tube made from very thin silver. It was surrounded by a second, larger tube filled with the warming fluid of 38°C. Through both tubes the fluid streamed constantly with the same speed, since all the tubes had their plastic sections adjusted so that they had the same streaming resistance independent of whether the fluid went through the loop or into the outlet. The electrodynamical switch was made from teflon sheets. In the position drawn in Fig. 2B, warm water is flowing into the loop. When the switch is moved, the cold water will flow through the loop, and the warm water will flow into the outlet tube. Its speed stays the same, so the temperature exchange is the same. A reversal of the switch will produce an instantaneous temperature change.

The temperature sensation produced by the loop seems to adapt just as rapidly as taste sensations and quickly fades out, so it does not distract from the observation of the taste sensations.

THE TEMPERATURE COEFFICIENT OF THE TASTE THRESHOLD FOR ELECTRICAL STIMULATION

It was indicated in an earlier paper (Békésy, 1964) that each of the basic chemical stimuli has side components also stimulating all the other taste re-
ceptors to some degree. Since the temperature coefficient can be positive or negative for the side components, the over-all picture can be dependent on the types of receptors in the chemically stimulated area. This is different, however, for electrical stimulation. Here we found that it is possible to stimulate a single taste papilla with a point electrode and short electrical pulses if the electrode is placed on the middle of the top of the papilla. It is therefore possible to produce the four basic taste sensations, sour, salty, bitter, and sweet, much more precisely than with chemical stimulation.

We found that in most cases a single papilla produces the same taste quality on all of its areas, when stimulated electrically. This seems to indicate that all taste buds within a single papilla are of the same quality. There are a few taste papillae which look like two ordinary papillae combined, and these may show two different taste qualities. But they are generally larger. They are quite rare on the upper part of the tip of the tongue but occur on the edge. Most of the papillae on the palate and the throat are also combined and large. The lower surface rarely has papillae.

The observations were made on the tip of the tongue. To start, a cover glass was placed on the surface and, with an electronic flash, microphotographs were taken of adjacent sections. They show the papillae clearly and the blood supply fairly well. Comparing the photographs with the actual view of the same spot under a stereoscopic microscope (40 X magnification) it was possible to paste the different sections together into a large picture, so that at any time a papilla seen in the microscope could be identified on the map of the taste papillae. Fig. 3 represents the tip of the tongue of Mrs. Patricia Lemon, 25. The photograph looks a little different from what we would expect from the known anatomical illustrations. The reason for this is that most of the anatomical drawings show more or less shrunken preparations.

After that, in about 2 days' work, every single papilla is electrically stimulated and its reported taste quality recorded on the photograph by squares and circles. There were only five different situations reported. Each papilla tasted either sour or salty, or bitter or sweet. No other taste sensations were reported at all, so they represent the four basic taste sensations. The fifth possibility was that the papilla was insensitive to electrical stimulation. The map shown in Fig. 3 was in almost continuous use for 9 months, and no changes seemed to be necessary. There was no difficulty at any time in picking out a papilla with a specific basic taste sensation for further investigation. Other subjects have similar maps, often with fewer sweet papillae.

One difficulty during some of the observations in heated rooms was that sticking out the tip of the tongue for two or three minutes was enough to dry out the tip and reduce the sensitivity. To avoid that, an airstream with 100 per cent humidity was blown against the tip of the tongue (Fig. 4). Care had to be taken that the tube with the humid air was always directed upwards, so that any water condensed in the tube could properly flow back into the
Every papilla was tested electrically to determine its taste sensation. They all belonged to one of the four basic tastes. No fifth basic taste was found. Some of the papillae were insensitive to electrical taste stimulation. The map was used to pick out a particular papilla for experiments. Magnification 9.

After a certain papilla was selected and mapped, the loop of Fig. 2 was placed around the papilla and the gold-plated electrode placed in the middle.
of the top of the papilla. The stimulating voltage consisted of a series of square pulses of 0.1 millisecond, and the pulse rate was selected to an optimum according to earlier observations (Békésy, 1964, Fig. 7). To avoid adaptation the pulse series was presented for 0.2 second every 2 seconds. The voltage of the threshold was adjusted by the subject himself. This usually took about 6 seconds. The whole procedure often took no more than 1 minute. When the observations were done with a semiautomatic device, a quarter of the session took 2 minutes.

Since there was no difficulty in coming back to the same papilla and stimulating only that particular one, the measurements permitted short rests after every automatic record. Thus they were done in four repeated placements of the electrode, with the temperatures of the loop surrounding the electrode alternated. Representative records of the four taste qualities with the same subject are shown in Figs. 5 and 6. The ordinate in the figures represents a potentiometer setting and not the voltage on the papilla; it is only a relative measure. The heavy lines are for the 25°C and the thin lines for the 38°C loop temperature.

As can be seen from Fig. 5 and other observations, there was no pronounced change in the sensitivity for acid and salt in the given temperature range. The mean value of the changes produced by the temperature changes was almost zero. For sweet and bitter taste sensations, however, the electrical voltage at threshold was definitely smaller at higher temperatures. This can also be observed in Fig. 6. The same observations were repeated for 3 months on four
subjects, and the recordings obtained were very similar in every respect. The observations are very tiring, since the electrode has to be held carefully on the same papilla. It is necessary to have special headrests and hand supports to be able to do so. They will be described on another occasion.

As far as can be seen, therefore, the temperature coefficient observations for the electrical thresholds do seem to group the four taste qualities in two groups—sour-salty and sweet-bitter—as other observations had done earlier (Shore, 1892; Békesy, 1964).

![Graph](image)

**Figure 6.** The same as Fig. 5 but for a single sweet and a single bitter type papilla. These papillae show an increase in sensitivity when the temperature is increased. Figs. 5 and 6 together indicate that there is a grouping of the four taste qualities in two groups: sour-salty and sweet-bitter.

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**REFERENCES**


Hahn, H., 1949, Beiträge zur Reizphysiologie, Heidelberg, Scherer Verlag.

Komuro, K., 1921, Le sens du goût a-t-il un coefficient de température? *Arch. néerl. physiol.*, **5**, 572.

Pfaffmann, C., 1959, The sense of taste, in Handbook of Physiology, Section 1,

Shore, L. E., 1892, A contribution to our knowledge of taste sensations, J. Physiol., 13, 191.
