

Rhythmical Variations Accompanying Gustatory Stimulation Observed by Means of Localization Phenomena

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ABSTRACT When two taste stimuli are presented, one to each side of the tongue, with a time delay of up to 1 msec., the taste sensation seems to move across the tongue. This phenomenon which is similar to directional hearing, can be used to show periodic fluctuations in sensation magnitude as well as other aspects of sensation. When the apparatus was refined to present taste stimuli, it was possible to observe rhythmic changes in the perception of taste. An analogy is demonstrated between hearing and taste sensation, even to some quantitative values.

INTRODUCTION

Our increasing knowledge of the nervous system points more and more toward a complicated network of afferent and efferent nerve fibers, which seem to form certain loops. For an electrical engineer such a feedback circuit raises the question, why does this specific circuit not begin to oscillate? Not long ago it was a difficult problem to construct an amplifier with a high gain and a wide frequency band and without unwanted oscillations. There are such oscillations in our biological systems, for instance, the heart beat. Others seem to occur under abnormal conditions, such as a ringing in the ear or the oscillating scotoma described by Fröhlich (1921). Under normal conditions they are more rarely observed. Oscillations in the visual system were described by Charpentier (1892 *a, b*) in the last century. Fröhlich (1913) made electrophysiological observations on the retina of the octopus, and Arvanitaki (1939) observed oscillation in the giant axon of the squid. But in experiments on animals it is possible that the nervous system was not observed under completely normal conditions.

In order to avoid difficulties that might arise from the question of whether conditions were normal or abnormal, the observations reported here were made psychophysically. We have tried to develop a method by which we could determine an oscillation or rhythm in the sensation magnitude. The

idea was as follows. From the localization of vibratory sensations on the skin we know (Békésy, 1959 *b*) that a random set of short clicks presented to the skin by a vibrator is localized directly under the vibrator. A second set of random clicks presented by a nearby vibrator is also located under that vibrator. But if the two sets of clicks contain two or more clicks that coincide exactly in time, as is illustrated in Fig. 1*a*, then, in addition to the two random vibrations located under the two vibrators, we localize a vibratory sensation midway between them. This phenomenon is illustrated in Fig. 1*b*. The whole sensation may last a very short time, but it can be observed. The sensation is particularly clear if it is possible to introduce at will small time delays between

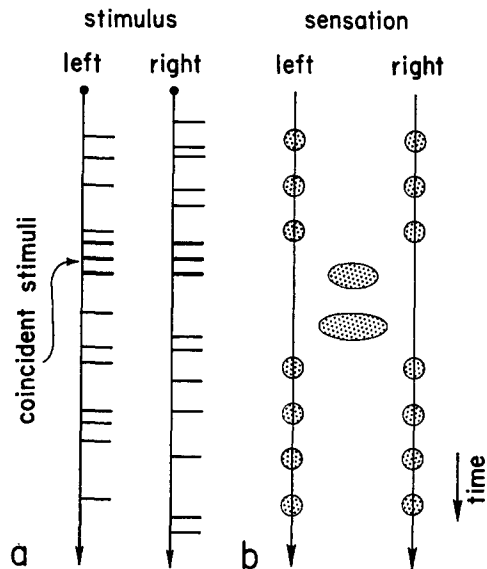


FIGURE 1. When a series of random clicks is presented to the two ears or to two vibrators on the skin, there is no interaction and they are felt separately in the two ears or on the two points of the skin under the vibrators. But if three clicks coincide in the two ears or are presented by two vibrators within 1 msec., the sensation immediately moves from the sides to a point between the two stimuli.

the coinciding clicks, so that the sensations move to the left or right in accordance with the time delays. These small lateral displacements make the vibratory sensation in the middle stand out from the constant and stationary background.

If it can be assumed that the magnitude of the taste sensation shows some fluctuations, then two equal stimuli presented symmetrically on the tongue at exactly the same moment will produce a sensation halfway between them. This is illustrated in Fig. 2*a*. When a small time delay is introduced, the locus of the sensation moves to the left or right. After the sensation is displaced to one side, a further increase in the time difference does not generally move it away from its place. But if the oscillation of the sensation magnitude shows some periodicity, then, after the time delay has reached the length of one period (Fig. 2*b*), the sensation is again localized in the middle. Naturally,

this localization is not as sharp as it was when the oscillations of the sensation magnitude coincided. If the oscillations coincide for only a few maxima, the sensation is localized on three different spots, one in the middle and one on each side under the stimulus. As a matter of fact, the lateral spread of the sensation localization may provide a measure of the number of maxima coinciding.

In order to investigate the possibility that these oscillations have a rhythm, I selected the sensation of taste, since the firing rate of this sense organ seems to be sufficiently slow for periodicity to manifest itself in some way.

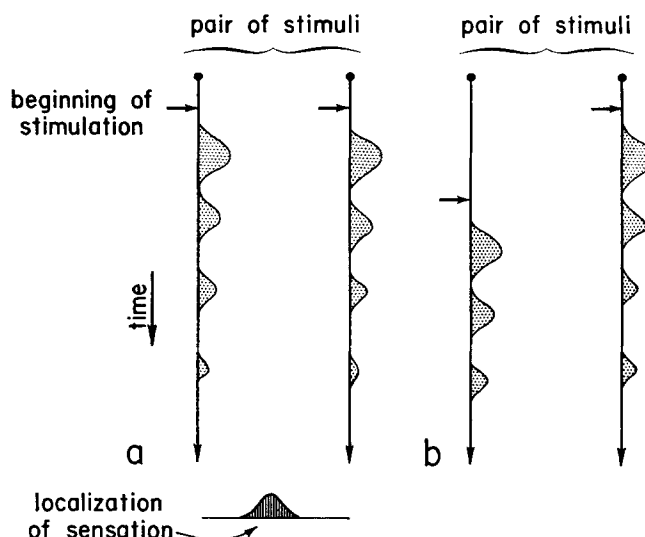


FIGURE 2. If the stimuli produce a periodic change, it is to be expected that the localization of the sensation between the two stimulators would occur not once but several times, since in periodic phenomena there should be a repetition of the situation in Fig. 1.

In recent years there has been increased interest in research on taste. Much of the research is electrophysiological in nature and is summarized in the Handbook of Neurophysiology (Pfaffmann, 1959) and in an excellent symposium on olfaction and taste (Zotterman, 1963).

The tongue is a sense organ with a large surface area. Since this is also true of the skin, the retina, and the organ of Corti, some analogies between these apparently different sense organs are to be expected. The purpose of the present paper is to show that localization of taste sensations on the surface of the tongue is very much like the localization of sound sources in directional hearing, or the localization of vibratory stimuli on the surface of the skin (Békésy, 1959 *a*). Sense organs with large surface areas seem to have something in common—independent of the specific properties of their respective end organs. These common factors are probably the nervous actions on a higher

level. We usually think of taste sensations as being very slow, and this is correct for many aspects of taste. But on the other hand, there are aspects that are sensitive to changes in time of as little as 1 msec. This is nearly the same sensitivity as in hearing. It is difficult to reconcile electrophysiological data of the auditory nerve tract with some of the phenomena of sound localization. When a tone is presented to the ear, it takes about 200 msec. for the loudness sensation to develop to its full value. But in spite of this long reaction time, a time difference of 1 msec. between the stimuli presented to the two ears is enough to move the apparent position of a sound from the midline of

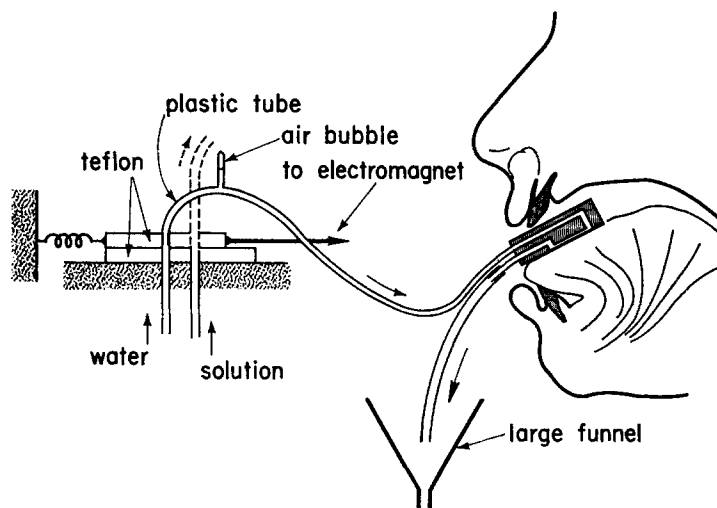


FIGURE 3. A gliding teflon sheet was displaced by means of electrodynamic driving units in order to replace the continuous flow of water by a solution for short, precisely determined times. The solution touched the surface of the tongue as it flowed through openings in a lucite block.

the head to one side. Single electrode records of auditory nerve spikes do not show such precision. Apparently in the normal ear, it is not the single nerve fiber that is of importance, but the mean value of a large group, and the mean value may show precise timing.

APPARATUS

A lucite block with a longitudinal opening made it possible to let different solutions stream along the surface of the tongue (Fig. 3). Various solutions flowed through plastic tubes to the lucite block and then drained through other tubes into a large funnel after they had been presented to the tongue. An opening in a movable teflon sheet was connected to a tube that could coincide with tubes to either the water supply or the test solution. The lateral displacements of the teflon sheet were produced by an electromagnet. Since polished teflon surfaces do not adhere to one another, the force

required to move the tube from one opening to the other is quite small. This permits a sharp and precise change from water to a solution in the tube. If the inside diameter of the openings in the lucite block is the same as the inside diameter of the tubes, a sharp cutoff line is formed between water and solution. It consists of a front eddy followed by a turbulent flow. The turbulence of flow could not be detected by the observer.

During switching there is a short time interval when the flow of the fluid is interrupted and a pressure change is produced in the tube. This change can be reduced if the switching time is made as short as possible and the tubes in the teflon switch are placed close together. The pressure produced in the switch is small at the surface of the tongue when the outlet tube between the tongue and the funnel is short. The fluid pressure is then the same on the tongue as at the end of the tube, namely, at atmospheric pressure. In Fig. 3 the same effect was achieved by increasing the diameter of the outlet tube. The pressure change can be reduced still further by placing in the inlet tube of the mouthpiece a small closed T-tube with a tiny air bubble, as indicated in Fig. 3.

At the beginning of the experiments, water was used instead of the solution to ensure that pressure changes would not interfere with the observations. The pressure sensation is so different from the taste sensations that observers can easily distinguish between them. The pressure changes occur the moment the switch operates, whereas the taste stimulus appears much later, since some time elapses before the front of the stimulating solution travels the length of the tube. All the observers had had a year of experience in vibratory localization.

The air bubble in the T-tube can be used to lengthen the build-up period of the stimulus by diminishing the sharpness of the separation between the water and the solution. The time interval between the two stimuli necessary to shift the location of the taste sensation could be prolonged to 3 to 5 msec. by attaching bottles of capacity up to 50 cc to the tubes and varying their air content. A decrease in the volume of air trapped in the top of the T-tubes resulted in an asymptotic approach to a time difference of 1 msec. The inside diameter of the tubes was 1.5 mm, and the rate of flow of the fluid was 1.5 cc/sec. The fluids were kept at room temperature.

When the mouthpiece is placed on the surface of the tongue, the ridges of the openings can be perceived. But this sensation fades out within 5 to 8 sec. if the mouthpiece is kept relatively still.

By pressing a button, the observer could present to himself the different taste stimuli for a short period, generally about 1 sec. This could be repeated at his convenience. The primary taste qualities were always recognizable as such.

Two identical sets of the equipment shown in Fig. 3 were used. The two lucite blocks could be fastened side by side, so that it was possible to present two stimuli, one to the left and one to the right side of the tongue. Since each had its own electromagnet, small time differences between the two presentations could be obtained by a mechanical or electrical timer which activated the electromagnets.

For most of the experiments it was important to adjust the sensation magnitudes of the taste on the two sides of the tongue to equality. For this purpose the concentration of the solution on one side was kept constant, and the concentration on the other side was changed easily and quickly to make the sensation magnitudes match.

The mixer used to produce these quick changes in concentration is shown in Fig. 4. It too consists of a teflon valve, driven by an electromagnet. This mixer diluted a stronger solution by combining it with water in a 1 cm spherical cavity in a lucite cube, which also served as an outlet for the diluted solution. The electromagnetic driver connected the mixing cavity alternately to the solution and the water with a period of about 1 sec. When the water flowed for the same length of time as the solution, the solution was diluted 50 per cent. By changing the time ratio between the water flow and the flow of the solution in each period, the dilution could be adjusted to any desired value, between pure water and pure solution. A mechanical timer, shown in Fig. 4, was used. It consisted of two rotating discs with contact notches and

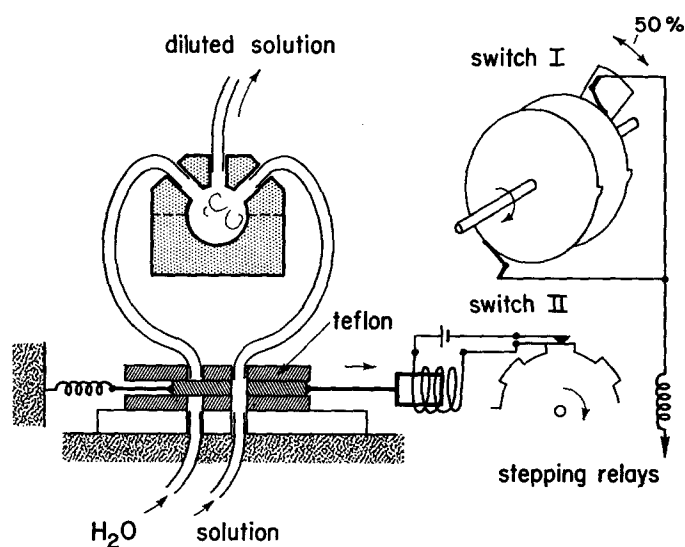


FIGURE 4. In order to change the concentration, water and a solution were permitted to flow for varying lengths of time into a mixer. The duty cycle of the teflon switch was controlled electrically and could be adjusted on a calibrated dial.

stepping relays. When switch I made a contact, and the stepping relay closed the circuit of the electromagnetic driver, the solution flowed into the mixer. But as the discs rotated further, switch II made contact and brought the stepping relay into a position that interrupted the flow of current from the electromagnet. The spring at the left of the figure pulled the teflon slide to the left and connected the water to the mixer. This process was repeated during every rotation. When switch I was opposite switch II, the dilution was 50 per cent. Changing the position of switch I caused an immediate and known change in concentration within 1 sec. The volume of the spherical mixing cavity was made as small as possible, consistent with accommodating the volume of fluid that the switch delivered in three full cycles. The switching time was 1 sec., the fluid flow 1.5 cc/sec., and the mixing cavity 4.5 cc. When colored water is used instead of the solution, the mixing occurs in the lower half of the sphere, where the eddies of the incoming fluids mix. The diluted solution of colored water did not

show ripples in color intensity along the tube and the observer did not detect fluctuations in the taste sensation.

For our experiments the solution presented to the mixer was twice as concentrated as the standard solution, so that in the 50 per cent position the solutions on both sides of the tongue had the same concentration. Since the mixer works only when the diluted solution has a chance to flow out, the dotted tube in Fig. 3 was left open when the diluted solution was used in place of a standard solution. Thus there was no delay between the adjustments of the switch position and the presentation.

The mechanical timers can be replaced by electrical timers. For the presentation of single sequences of stimuli, the start-stop mechanisms of the earlier teletype systems were useful.

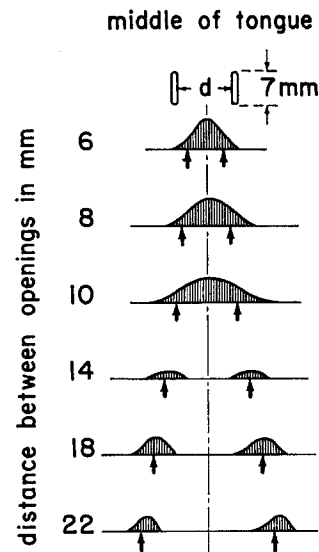


FIGURE 5. When the distance between two stimuli of equal sensation magnitude is increased, there comes a point where they inhibit each other—14 mm in the figure—and the sensation magnitude becomes smaller than when one stimulus is presented alone.

Lateral Summation and Inhibition of Taste Sensations on the Tongue

Sense organs with large surface areas have several properties in common. Perhaps the most striking ones are concerned with the localization of sensations produced by the interaction between two simultaneously presented stimuli. The analogies between auditory and vibratory localizations have been described earlier (Békésy, 1959 *a*). Examples of summation and inhibition have been found for taste on the surface of the tongue as well.

When our apparatus presents to the middle of the tongue two simultaneous stimuli which have been adjusted to equal sensation magnitude, the local distribution of the sensation magnitude is as shown in Fig. 5. The sensation magnitudes drawn in the figure are subjective estimates by the observers. First, a single stimulus was presented and the observer was asked to make a

drawing of the apparent amplitude distribution of the sensation, indicating its width. Then the two stimuli were presented simultaneously, and the observer was asked to compare the changes in lateral spread of the sensation and the sensation magnitude. Observers can be trained to make similar judgments by making drawings of the light-intensity distribution on the retina for an illuminated opening observed through an optical system more or less out of focus. Our observers had had a long training in mapping pressure-sensation distributions along the surface of the skin.

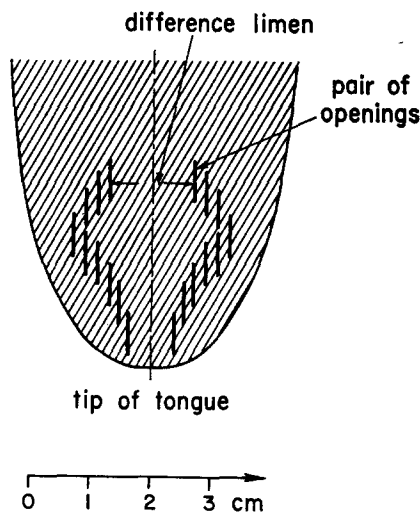


FIGURE 6. The smallest distance between a pair of stimuli that can be felt separately at different points on the tongue for sucrose solution (350 gm/liter) and a presentation time of 1 sec.

The plastic mouthpiece had a series of openings at different distances from each other which could be presented in random order. When the distance between the two openings is small, they integrate to a common sensation localized in the middle between the two openings. When the distance is increased and everything else is kept constant, the sensation shows a lateral spread as well as a loss in magnitude. This is shown in Fig. 5 for a separation of about 10 mm. A further increase in distance can, however, produce a radical change. The sensation magnitude can become extremely small—much smaller than a single stimulus would produce. At the same time the two stimuli are localized separately. An even further increase raises the magnitude of the sensation under each stimulus to the value it would have if presented alone. For increasing distances, there is summation, then inhibition, and then no interaction at all.

In this experiment, care was taken to present the stimuli simultaneously by using tubes of equal length to the openings and equal water pressures. A 1 molar NaCl solution was used at room temperature. Tap water was flowing continuously through the tubes and was replaced for 1 sec. by the salt solution only once in about 10 sec.

The difference limen for salt sensation on the tip of the tongue is about 12 mm (Fig. 5). The sensory elements of the tongue are not distributed as equally along the surface as they are, for instance, on the skin. Thus the difference limen shows considerable variation with the place of stimulation. It is smallest for salt on the tip of the tongue. Fig. 6 shows a map of the surface of the tongue with the position of the pairs of openings which could just be perceived as two separate stimuli. It illustrates how the size of the difference limen increases with the distance from the tip of the tongue to a point and then becomes

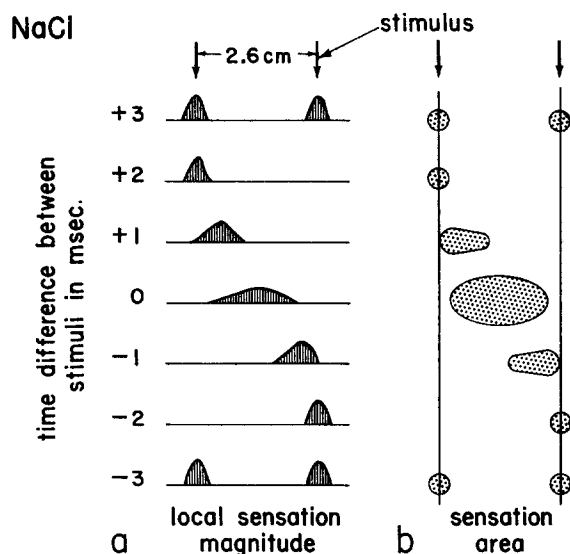


FIGURE 7. The time delay and corresponding sensation magnitudes and localizations which produce a movement of the taste sensation from one side of the tongue to the other. They are of the order of milliseconds. The relative sensation magnitude and its lateral spread and location were determined psychophysically.

smaller. In all these observations, the two openings are symmetrical on the midline of the tongue, since any lateral displacement would change the sensitivity of the tongue, and the concentrations would have to be readjusted to produce the same sensation magnitude. Similar patterns were found for acid and sugar solutions at a concentration that produced the same sensation magnitude as the salt solution.

A more interesting question is, what happens when a time difference is introduced between the two taste stimuli? When there is no time difference, the sensation is localized midway between the two stimuli (Fig. 7a). But even a time difference as small as 1 msec. is able to displace the locus of the sensation from the middle almost completely to the side that receives the stimulus first. This phenomenon is clear and easy to observe. It is similar to the change in the localization of a sound source that is produced by a time difference in

stimuli to the two ears. This is so in spite of the fact that in general the end organs of the tongue react more slowly than the ear. Thus the localizations of sound sources and tastes seem to be quite similar nervous phenomena. They probably occur on a higher level of the nervous system and are little influenced by the different reaction times of the end organs. We have in taste, therefore, a sense organ that is very slow in developing its final sensation magnitude, but in spite of this it is able to discriminate very small time differences between stimuli. The time difference necessary to move the sensation from the middle to one side depends on the sharpness with which the stimulus is presented.

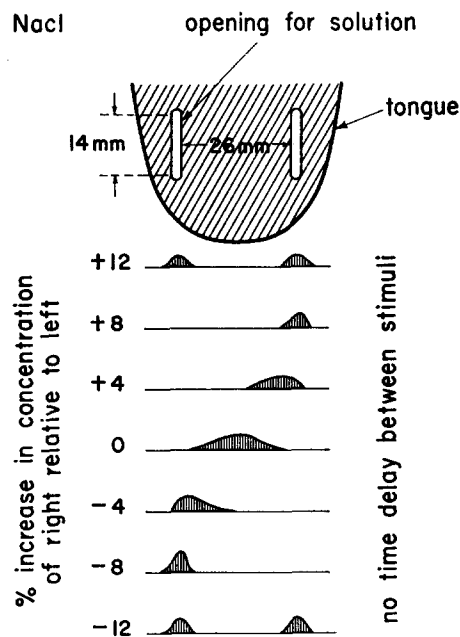


FIGURE 8. Change in the localization of the taste sensation produced by differences in the concentration of the stimulus, determined psychophysically.

The localization of the taste sensation is sharpest and the lateral spread of the sensation in the middle position is smallest when the exchange of the water with the solution occurs instantaneously. But even though the fluid exchange requires a few milliseconds, a time delay between the stimuli on the two sides of the tongue produces a well defined change in the localization, if the process of the fluid exchange is symmetrical on the two sides.

Since fluids are constantly flowing over the tongue, the time delay in the arrival of the stimulus at different sections of the tongue must play an important role in the every-day performance of the taste organs.

Figure 7*b* shows how the sensation area changes when the time difference between the two stimuli is varied. It is largest when there is no time difference, and it becomes smaller when the whole sensation is localized on one side, under one stimulus. This is exactly what we found on the skin for vibratory sensations, and for heat sensations as well.

In hearing, a displacement of the sound image is produced not only by a time difference between the sounds reaching the two ears, but also by a difference in their sensation magnitudes. We have found the same thing to be true of the taste sensation (Fig. 8). When the two stimuli are simultaneous and placed symmetrical to the middle of the tongue, and their sensation magnitudes are adjusted so as to be equal, the taste sensation is located on the midline of the tongue between the stimuli. If the concentration on one side is now decreased by as little as 8 per cent, the whole taste sensation will be located under the stronger stimulus. At the same time the sharpness of the

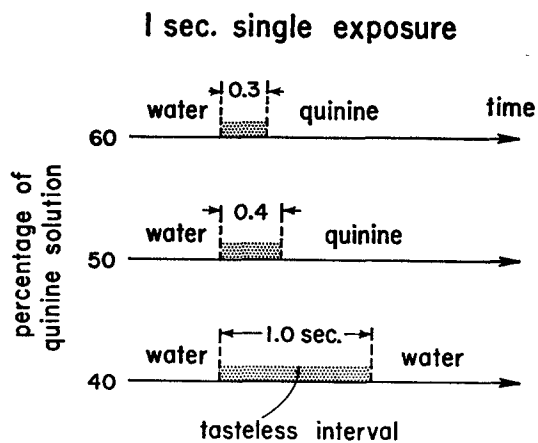


FIGURE 9. When a continuous flow of tap water is interrupted by a 1 sec. flow of quinine solution, there is an interval of inhibition producing a tasteless interval in the sequence of sensations.

sensation increases and the size of the area of localization decreases. Thus it is clear that differences in concentration at different points of the tongue can also contribute to displace the localization of taste sensations and to increase our discrimination of different tastes.

The Threshold and the Silent Interval

There seems to be a complex interaction between stimulation and inhibition even at the threshold level. With the mixing apparatus we presented a quinine sulfate solution, beginning with a concentration below threshold. As the concentration was increased very slowly, at first the only sensation was that of tap water. The sensation was localized below the opening in the lucite block. As the quinine concentration is further increased, there comes a point when the water taste fades out and there is left only a tasteless sensation. As the increase in concentration is continued, the taste of quinine appears. The concentration interval between the disappearance of the water taste and the appearance of the quinine taste I shall call the *silent interval*. It depends strongly on the temperature of the fluids as well as preliminary stimulation and adaptation. The silent interval is found for salt, sugar, and acids as well.

The silent interval can be observed in another experiment. When a quinine

solution was presented in place of the water at a concentration close to threshold for 1 sec., the build-up of the quinine sensation could be observed as a function of time. As is illustrated in Fig. 9, just before the quinine sensation appeared, there was a short time interval during which the water taste was inhibited and there was no taste at all. As is shown in the 60 per cent line of Fig. 9, this interval without taste lasted about 0.3 sec. and then the taste of quinine appeared, stayed for a while, and faded out. The duration of the tasteless interval is indicated by the length of the shaded section. When the concentration of the quinine is reduced, the tasteless interval is longer.

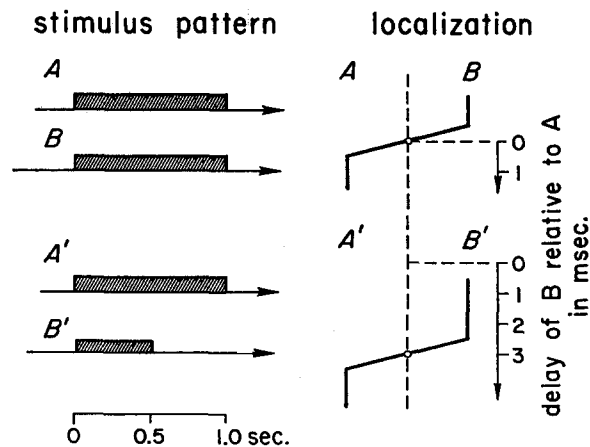


FIGURE 10. Apparently, the onset time and not the middle or end of the stimulus determines the localization of the taste sensation on the tongue.

After the tasteless interval, the quinine taste appears just above threshold. If the concentration is decreased still further, the quinine taste can no longer be observed. The concentration is below the threshold for a 1 sec. presentation. But it still has an effect on the taste organs since there is a tasteless interval during which inhibition is produced, as is shown in the drawing at the bottom of Fig. 9. Here the tap-water sensation is inhibited for a time, but after the tasteless interval the usual water taste returns. By proper adjustment of the quinine concentration, it is possible to lengthen the duration of this silent interval to a maximum of about 1 sec.

The Onset Time of the Taste Sensation

In spite of the fact that the localization of a taste sensation can be changed by a time delay of 1 msec. between two stimuli, the presentation time of a stimulus necessary to develop it to its full strength is longer than 1 sec. (Bujas, 1939). This raises the question, which section of the onset curve determines the localization? Is it the beginning of the stimulus, or some moment after the sensation magnitude has reached its full value? This can be in-

vestigated by observing the effect of the cutoff time of the stimulus on the localization. In the upper part of Fig. 10, the presentation times of the stimuli on both sides of the tongue were equal. When the stimuli start at the same time, the sensation is localized in the middle of the tongue, and small time differences between the stimuli move the sensation from one side to the other. If we now shorten the length of one stimulus from 1 sec. to 0.5 sec., the sensation can be brought back to the middle of the tongue by giving the shorter stimulus a time delay of only 3 msec. This is shown in the lower part of Fig. 10. Therefore, even a large time difference between the cutoff times of the

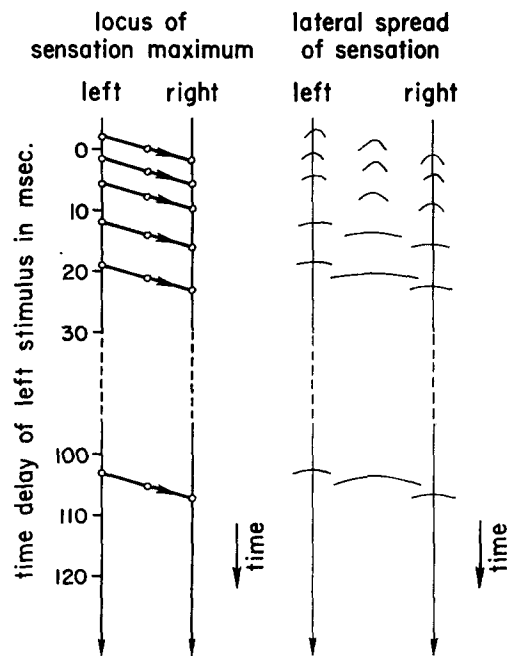


FIGURE 11. Increasing the delay time of one of the stimuli continuously from zero to 100 msec. shifts the location of the taste sensation to the middle of the tongue several times. This indicates that there is a strong periodicity in the nervous reaction of the taste produced by a stimulus of constant magnitude (see Fig. 2).

stimuli has little effect on the localization, compared with the time difference between the onsets of the stimuli. It is mainly the beginning of the sensation that determines its localization; long before the sensation magnitude has had a chance to develop to its full strength.

About the Temporal Periodicity Pattern of the Taste Sensation

Ever since the work of Adrian (1928), it has been known that a continuous stimulus on an end organ produces a series of electrical spikes in the connected nerve fibers which are transmitted to the higher nervous centers. These more or less periodic discharges may be independent in their frequency and phase for every end organ. But their common interaction on a higher level may still produce a periodic firing in a cell or cell group which is responsible for the sensation magnitude. In this case the sensation magnitude

would show some oscillation in spite of the smooth stimulus produced by the test solution. Since the localization of the taste sensations is so sensitive to small time differences, it should be possible to use this situation to test the periodicity of the oscillations of the sensation magnitude.

In this experiment we used a sucrose solution (350 gm/liter) and presented it to both sides of the tongue for 1 sec. every 10 sec. In the time between, tap water flowed through the tubes. As Fig. 11 shows, the sensation could be moved from the middle of the tongue to the sides by introducing a time difference between the stimuli. A sensation could be produced in the middle of the tongue, not only for zero time delay, but also for time delays as large as 7, 15, and 20 msec. At these larger time delays, the sensations in the middle of the tongue were not as sharp as for zero time delay, but they still moved as expected to the left and right when the time delays were shortened or lengthened by a fraction of a millisecond. The larger the time delays, the fuzzier the sensation.

This experiment suggests that there is a sort of periodicity of the sensation magnitude for the taste sensation. It is found not only for sugar but for other tastes as well. Returning to Fig. 2*b* we can see that, when the sensation magnitude shows periodic fluctuations, the time delay between the two stimuli necessary to return the sensation to the middle is equivalent to the length of a period. In our experiment the length of the period was about 7 msec., and this makes the periodicity for a convenient sensation magnitude of the order of 150 cps. This seems to correspond roughly with the number of nervous discharges observed in the taste nerves under similar conditions (Pfaffmann, 1941, 1955). The phenomenon was not difficult to observe, but it required precise apparatus for the careful presentation of the test solutions in given time patterns. The experimenter adjusted the time delays in random order, and the observer stated the locus of his taste sensation relative to the stimuli. The observations were recorded by the experimenter on graph paper, and the mosaic of dots was connected into curves. For localizations produced by time delays, it is necessary to keep the sensation magnitudes for the stimuli on the two sides of the tongue equal.

The periodicity pattern of Fig. 11 does not change with an increase in the surface of the stimulated area. It hardly changes when the concentration of an NaCl solution is increased in the ratio 1:50. It is about the same for salt, sugar, acid, and cold and warm water stimuli. Furthermore, it is possible to show that when the time delay between the left and right stimuli is adjusted from zero to the various values in Fig. 11 which produce a sensation localization in the midline, they are all displaced in the same way by a small change in the magnitude of one stimulus.

Thus the periodicity pattern obtained from localization experiments is not directly connected with the periodicity pattern observed electrophysio-

logically in the taste fibers. Their frequencies are far more dependent on the magnitude of the stimulus, adaptation time, and so forth. The periodicity pattern obtained from localization observations probably stems from the activity of a higher nerve center.

From a theoretical point of view, it may be of interest to know whether there is a difference in the periodicity patterns produced by a taste stimulus and by electrical stimulation. For this purpose two concentric electrodes were placed on the tongue, as indicated in Fig. 12. They were imbedded flush with the surface of a 1 cm thick lucite plate. Between the center and ring electrodes,

duration of electrical stimulus : 10 msec.

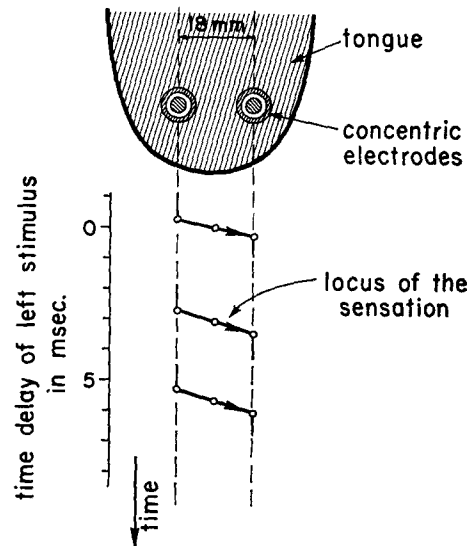


FIGURE 12. For electrical stimulation of the tongue as well, there is a periodicity of the sensation similar to that found for ordinary taste stimuli.

there was an air space that did not fill with saliva. As can be seen from Fig. 12, the periodicity pattern is about the same for electrical stimulation. Certainly the time delay necessary to shift the position of the somewhat acid taste from one side to the other is about 0.5 msec., which is a little smaller than for a taste sensation produced by a solution. The spread of the sensation-magnitude distribution is as usual larger in the middle position than on the sides. A 10 per cent increase or decrease in the stimulating current moves the locus of the sensation from the middle to one or the other side. This seems to indicate that, in this situation, electrical current, like a taste solution, stimulates primarily the end organs, since with both kinds of stimuli the receptors showed the same sensitivity. All the observations with electrical stimulation were made just a little above threshold for a pure taste sensation.

Periodicity Pattern in Hearing

When each ear was presented with a sharp click 0.5 msec. in duration, the sound image was localized in the midplane of the head if there was no time delay between the two clicks. A time delay produced the expected displacements to the left and right. As little as 1 msec. was enough to displace the sound image to one side. But though the time difference was increased slowly from 1 msec. to larger values, we were unable to find a second time difference for which the sound image returned to the middle position.

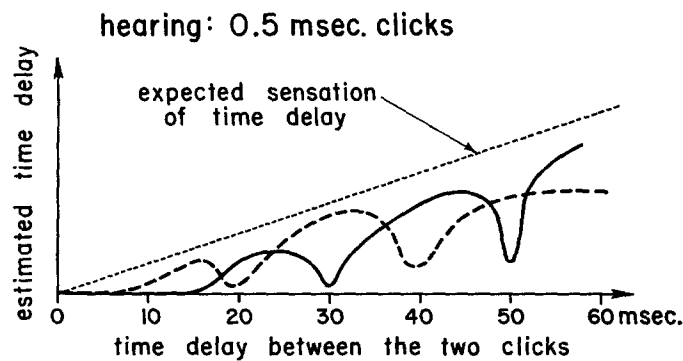


FIGURE 13. In hearing, the only periodicity observed had much longer periods which were irregular and changing. It concerned the sensation of time differences between the two ears, relative to the physical time differences of the stimuli.

A trace of a weaker and probably a different sort of periodicity was found in hearing when the observers were asked to describe the time difference between the clicks. When the delay between the clicks in the two ears is between 2 and 5 msec., the clicks seem to occur simultaneously. When the delay is increased, there comes a point when a distinct time difference between the clicks is observed on one side. A further continuous increase in the delay does not seem to increase the sensation of time difference proportionally, but there is a time delay for which the difference seems very small. As is illustrated in Fig. 13 for two different observers, the time difference sensation can go through several minima. But this periodicity is unstable, is different for different observers, and is not the same as we found for taste.

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