Electrogustometry III

Adaptation in electrical taste

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Introduction

When a sense organ is subjected to a maintained stimulus, the frequency of the afferent neural discharge shows an initial decrement followed by a constant level of activity. This decline in frequency is what the electrophysiologist understands by adaptation. When sensory perception is studied in psychophysical experiments, a similar adaptation of sensation can be demonstrated. Peripheral phenomena seem to be a major cause of this (Sinclair, 1967), but central factors may also be active. Filtering mechanisms involving facilitation/inhibition and descending impulses in the central nervous system are known to modify the peripheral sensory message before it produces a sensation.

Adaptation was originally considered a mere loss of sensory information, a fading out of excitability of the sense organ, not much different from fatigue. Increasing experimental evidence (Keidel *et al.*, 1959) has placed adaptation as a very basic principle within the total system of sensory communication. This view is supported by the fact that adaptation is not equally pronounced in all sense organs. Interoceptors, touch and taste adapt very rapidly, exteroceptors such as vision and hearing more slowly and proprioceptors slowest of all. A rapidly adapting sense organ reacts to an environmental change with a transient increase in firing rate which is very similar to 'overshoot' in electronics. The change is perceived, whereupon the slate is wiped clean by adaptation and is ready to receive new impressions.

In audiology adaptation is often studied by means of the so-called Békésy technique (Békésy, 1947). It is a semi-automatic method which permits the subject to trace his own threshold. The attenuator of the audiometer is connected with a reversible electric engine operated by a press button. A continuous or interrupted tone is presented to the subject who is instructed to control the sound pressure. When he hears the tone, he presses the button, and the sound pressure begins to fall continuously. If he then finds that the tone is not heard, he releases the button, whereupon the sound pressure rises. Graphic registration of the ups and downs of sound pressure gives a characteristic saw-tooth shaped curve, the spike height depending on the accuracy of the threshold tracing. In this Békésy audiogram adaptation may be demonstrated in two different

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ways (Jerger, 1960). The threshold tracing for the continuous tone may drop progressively over time, or a substantial difference between thresholds for continuous and interrupted tones may be found. Normally, acoustic stimulation at threshold intensities causes very little adaptation. In patients with disorders of the VIIIth cranial nerve, however, a pronounced degree of adaptation leads to the type of Békésy audiogram described above.

Although primarily working with audition, Békésy has also applied his audiometric principle on the sense of taste (Békésy, 1965). By means of a semi-automatic gustometer similar to the Békésy audiometer he investigated adaptation in chemical taste. The continuous changes of the concentration of the taste solution were obtained by mixing water and a strong standard solution in a differential pump from which the mixed fluid was led to a plastic chamber placed on the tongue surface. The resulting threshold tracing showed a progressive increase of the threshold concentration to 3–4 times the initial value over a test period of 2–4 minutes. There were moderate individual differences but none of the subjects reached a constant threshold level. This is a striking contrast to auditory threshold tracings which in normal subjects reach a constant sound pressure level very near the ordinary audiometric threshold.

Békésy's experiments with the semi-automatic gustometer prove that the refinement of chemical stimulation can be carried very far. Compared with acoustic stimulation, however, it is still rather primitive due to problems which sometimes seem insurmountable. As the afferent tube and the fluid chamber on the tongue cannot be washed out instantaneously, the onset and interruption of the chemical stimulus can only be gradual and a change of the concentration of a continuous chemical stimulus will reach the tongue surface with a certain delay. In pure-tone audiometry the accurate frequency control ensures stimulation of a well-defined part of the cochlea, whereas the spatial control of the application of the chemical stimulus to the tongue is impeded by involuntary muscle fibrillations and a moist, irregular surface.

The electrical method of taste stimulation permits a much better control of the temporal and spatial distribution of the stimulus. Almost any time/intensity pattern can be produced, rectangular impulses, linear or logarithmic changes of intensity, alternating current, etc. Metal electrodes ranging from pin-point size to several square centimetres can be applied to the tongue either by hand under visual control or by means of an acrylic tongue holder with the electrodes embedded in the inside wall (Føns and Osterhammel, 1966).

It has been the object of the present study to apply Békésy's principle of continuous threshold tracing to the electrical method of taste stimulation.

It seemed reasonable to expect that the information obtained by this

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method of automatic electrogustometry would have many valuable applications. A detailed and preferably quantitative knowledge of adaptation as a factor which can influence the response to taste stimuli is of the utmost importance to clinical and experimental taste examinations. A comparison of the electrical taste threshold tracings with Békésy's findings for chemical taste is another object of interest. The mechanism of chemical taste stimulation is still incompletely understood and even less is known about the mechanism of electrical taste. Any analogy between the two may therefore lead to new knowledge of the site of reception and the neurophysiological processes involved. Last but not least, the degree of adaptation varies so much from one sense organ to another that the importance of this basic principle in sensory perception can only be perfectly understood by comparing the different modalities. Adaptation in vision, hearing and cutaneous sensation has been thoroughly studied for many years but only few authors have investigated adaptation in taste (Békésy, 1965; Hahn, 1934).

Method

A transistorized constant current generator similar to the one described in a previous publication (Føns, and Osterhammel 1966) was used as a stimulator. Two wire-wound potentiometers mounted on the same axle were connected so that the current output varied with the square of the angle of rotation. The resulting time/intensity curve is in good accordance with the physiological variation of the sensitivity which is approximately logarithmically related to the current as measured in micro-amp (Føns and Osterhammel, 1968). The potentiometers were driven by a reversible electromotor connected with a press button which allowed the subject to increase or decrease the stimulus intensity. The gustometer used for clinical purposes covers a range of intensities from 0–300 micro-amp. In order to get a better graphic registration, the threshold tracings were limited to 0–200 micro-amp.

In preliminary experiments, the standard electrode (5 mm., flat, circular steel electrode) was found to give rather unstable tracings. This seemed to be due to involuntary tongue movements which brought the small electrode into contact with unadapted tongue areas. The problem was solved by using a 320 mm.^{2} electrode built into an acrylic tongue holder (Føns and Osterhammel, 1966).

The importance of the stimulating current was evaluated by tracing the threshold with two different gears on the electromotor. The resulting current change was 0–200 micro-amp./$3\frac{3}{4}$ min. and 0–200 micro-amp./23 sec.

In order to estimate the recovery time threshold tracings were recorded with interrupted as well as continuous current. When interrupted stimulation was used, the stimulus was of 500 m.sec. duration (Føns and Osterhammel, 1968) with intervals of 8, 4, 2, 1 and $\frac{1}{2}$ sec.

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Out of several subjects tested two were selected for the present publication. Determined with Krarup's procedure and his circular steel electrode (20 mm.^{2}) (Krarup, 1958), the thresholds were 15 micro-amp. for subject A and 57 micro-amp. for B. As opposite extremes of a normal range of intensities they were therefore considered representative. In sessions of 1–2 hours they were tested repeatedly with continuous and interrupted stimulation at the two different speeds of the engine.

The anodal stimulation usually preferred for clinical electrogustometry gives a lower threshold than cathodal stimulation. The polarity also affects the subjective taste sensation which is described as sour, metallic at the anode and uncharacteristic, pricking at the cathode. In order to reveal a possible relation between polarity and adaptation, the threshold tracings were repeated with the cathode placed on the tongue and the anode on the wrist.

Results

Fig. 1 gives the threshold tracings of subject A at the low speed of the engine. As the intervals of the interrupted current are shortened, the threshold increases slightly but a constant level is reached. Only with continuous stimulation does the threshold show a progressive increase over a period of 12 minutes.

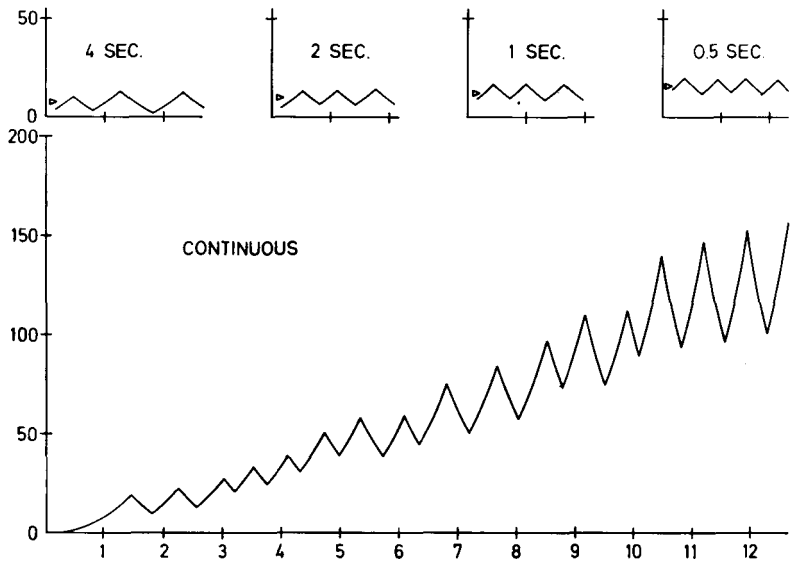


Fig. 1.

Threshold tracings of subject A at the low speed of the engine. The abscissa is given in minutes, the ordinate in micro-amp. Where a constant level was reached, the average was indicated by a small triangle.

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Subject B who had a considerably higher threshold showed completely different tracings (Fig. 2). Even with 8 sec. intervals, the threshold continued to grow and reached the maximum intensity of 200 micro-amp. in 7 minutes. The continuous current gave no response whatsoever.

When the rise time of the stimulating current was shortened to 0–200 micro-amp./23 sec., subject A showed no threshold elevation. Continuous current which causes the highest degree of adaptation gave the tracing shown in Fig. 3.

Subject B, on the other hand, showed a considerable threshold elevation, but in contrast to his tracings with the slow rise time, a constant level was now reached with interrupted stimulation and intervals of 8 and 4 sec. As the two tracings were practically identical, only one is given in Fig. 4. Intervals of 2 sec. or less gave steeply increasing tracings.

In both subjects cathodal stimulation gave somewhat higher threshold but the degree of adaptation was practically independent of the polarity.

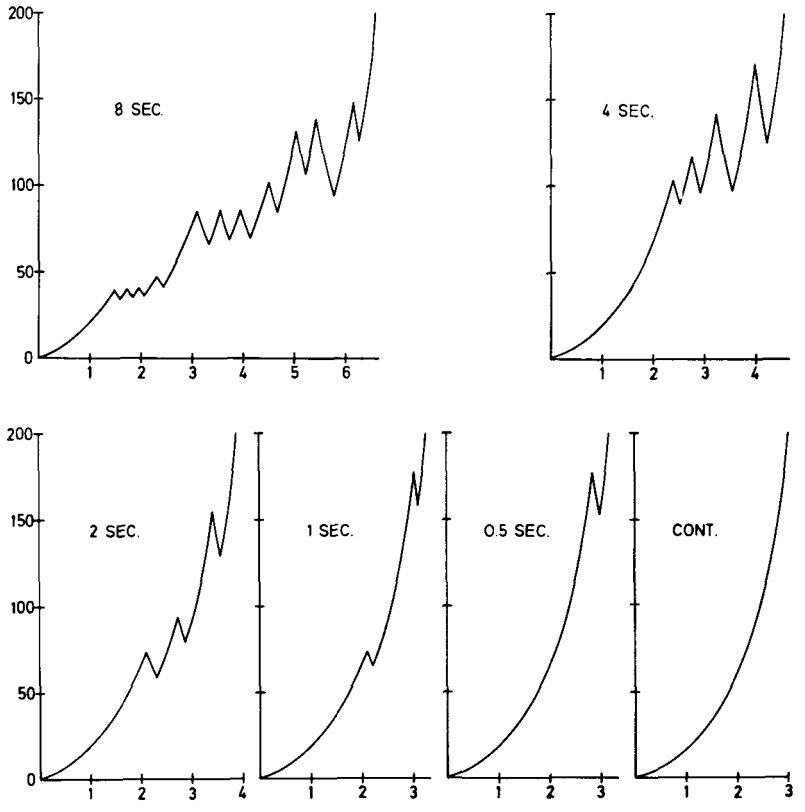


FIG. 2.
Threshold tracings of subject B at the low speed of the engine.

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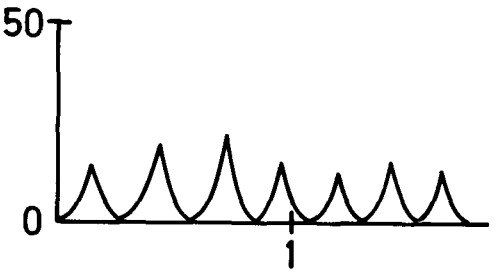


FIG. 3.
Subject A, continuous current. High speed of the engine (faster rise time).

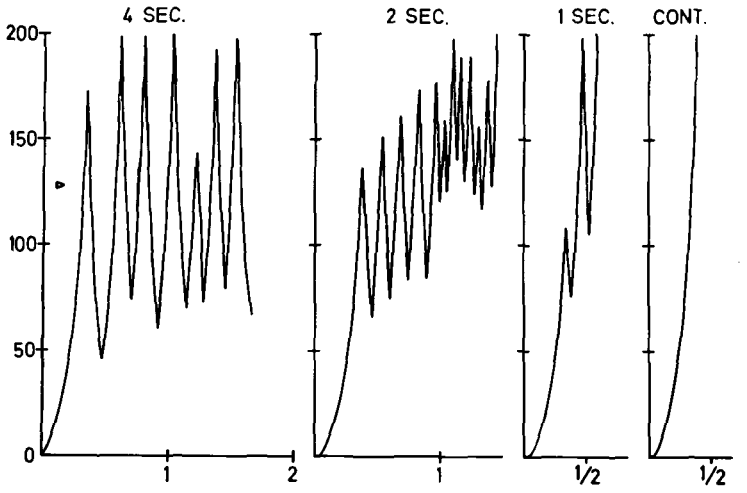


FIG. 4.
Subject B. High speed of the engine. With 4 sec. intervals, a constant level was reached and maintained for several minutes.

Discussion

The most obvious conclusion of these findings is that the sense of taste reacts to a maintained electrical stimulus with a high degree of adaptation. This is in accordance with the common experience that the sense of taste, being mainly exploratory, reacts to stimulatory changes rather than to maintained stimuli.

The threshold tracings obtained with constant current stimuli show a close resemblance to Bekesy's results for chemical taste. The fact that anodal as well as cathodal taste stimulation cause a degree of adaptation comparable to that of chemical taste permits the conclusion that the peripheral process which is responsible for the adaptation phenomenon is neither by-passed by the anodal nor the cathodal stimulus. The receptor

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cell and the free nerve endings have been suggested as alternative sites for the adaptation process as well as for the initiation of the electrical taste sensation. The present findings rule out the combination of the receptor cell as the site of adaptation and the free nerve endings as the site of reception in electrical taste. Gray and Matthews (1951) found that the elaborately encapsulated Pacinian corpuscle adapts faster than the nerve ending coming from it can accommodate. This points towards a specific, preneural end organ process in the explanation of the behaviour of this rapidly adapting tactile receptor. Regarding the initiation of the electrical taste sensation, we know that the electrical taste threshold is lower for the anode than the cathode, which is the reverse of the relation found for direct nerve stimulation. This has led to the assumption that the anodal stimulus might act on the receptor cell whereas cathodal stimulation might act directly on the free nerve ending. The present findings make it likely that electrical stimulation—anodal as well as cathodal—acts via the receptor cell.

The pronounced difference in adaptation rate between subjects A and B showed a remarkable correlation with their threshold levels. Subject A who had an unusually low threshold adapted much more slowly than B who had a rather high threshold. This correlation may only be apparent, brought about by the use of the threshold as a measure of the adaptation rate. Another possibility is that a common cause—e.g the number of active nerve fibres—decides the threshold level as well as the adaptation rate.

The rise time of the stimulating current was found to be of decisive importance to the threshold tracing. If the registrations had been limited to those given in Fig. 3, the conclusion would have been that electrical taste stimulation at threshold level did not cause any adaptation. Fig. 1 proves that a sufficiently slow rise time allows the adaptation process to run ahead of the stimulus increase. With the engine set at the slow speed, the stimulus intensity was doubled in approximately 30 sec. This is roughly the rise time used by Békésy for his chemical threshold tracing although he used a linear stimulus growth.

When interrupted, current stimulation is used, the variable duration of the intervals permits an estimation of the threshold recovery time. Here again the individual differences were so pronounced that average values would be of little interest. In Fig. 1, the threshold of subject A will be seen to recover almost completely in $\frac{1}{2}$ sec. The threshold of subject B did not recover completely even with 8 sec. interval and the engine geared to give the faster rise time (Fig. 4).

From these findings it will be evident that the parameters of adaptation —stimulus time and intensity, interval duration, recorded threshold level and individual differences—are so intricately related to each other that only a semi-quantitative evaluation is possible.

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To this should be added that for all the subjects considerable concentration and some experience with this special procedure was necessary in order to get reproducible results.

Summary

The electrical taste threshold was traced with continuous and interrupted current by means of a semi-automatic electrogustometer similar in principle to the Békésy audiometer. It was demonstrated that the sense of taste reacts to a maintained electrical stimulus with a pronounced degree of adaptation. This is true for anodal as well as cathodal stimulation. These findings make it likely that electrical taste stimulation acts via the receptor cell. With a sufficiently fast rise time of the stimulating current, a constant threshold level could be reached. Under such circumstances, the stimulus growth seemed to run ahead of the adaptation process which takes a certain time.

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