

PHYSIOLOGICAL GUSTATORY SWEATING IN A WARM CLIMATE

BY T. S. LEE

From the Department of Physiology, University of Malaya, Singapore

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Gustatory sweating is sweating in response to certain foods, especially spicy foods and acids. Much work has been carried out on pathological gustatory sweating, such as the auriculo-temporal syndrome (Frey, 1923; Guttman, 1931; Needles, 1936; Langenskiöld, 1946), and on facial sweating resulting from cervico-thoracic ganglionectomies or upper limb sympathectomies (Wilson, 1936; List & Peet, 1938*a*; Haxton, 1948), but as far as can be ascertained there is no record of any systematic investigation of physiological gustatory sweating, beyond passing reference to the existence of such a phenomenon (Foster, 1895; List & Peet, 1938*b*).

METHODS

General plan of experiments. One hundred and nineteen experiments were carried out on forty-six healthy young men aged 19-36 years. Thirty-four experiments were carried out to study the distribution of gustatory sweating in response to chillies and six experiments to study the effects of repeated or continued stimulation with chillies. The sensitivity of different areas in the mouth to chillies was studied in a further eleven experiments, and fifty-three experiments were performed to investigate the effect of other types of chemical stimulation and of physical stimulation of the mouth. Four experiments were performed to investigate the nature of the secretory fibres responsible for gustatory sweating and eleven experiments to study the relationship between thermal and gustatory sweating.

In all experiments the subjects wore cotton trousers only. Before each test they washed their faces and upper parts of their bodies with cool water, and then they sat down on a chair under a fan providing an air movement of 40 m/min, but the fan was only switched on if visual observation or preliminary tests with starch and iodine revealed the presence of thermal sweating. The environmental temperature, unless otherwise stated, was always between 27 and 30° C with a relative humidity of 65-90%, and variations during any one test were always within 1° C and within 5% relative humidity. Radiation of heat from the surroundings was insignificant (Bedford, 1946). Thirty minutes were allowed to elapse, unless otherwise stated, before Minor's iodine was applied (see below) and before any experimental procedures were begun.

In those experiments in which a series of tests was carried out in succession on the same subject an interval of 15-20 min was always allowed to elapse between tests. During this interval the subjects rinsed their mouths thoroughly with water, and the next test was started only after all subjective and objective effects of the previous test had disappeared.

Gustatory excitants. Ripe, red chillies (*Capsicum minimum*) of an average weight of 0.6 g were used as the principal excitant. The chillies were grown by the author and specially selected for constancy of weight and ripeness. In most experiments a whole chilli was thoroughly chewed up by each subject and held in the mouth for 5 min. When quantitative studies were made, the chillies were broken up and applied as a thick paste to precisely defined parts of the mouth. Other chemical excitants included: (1) 10 ml. of a 50% cane-sugar solution (8 tests); (2) 5 ml. of 0.5% quinine hydrochloride (7 tests); (3) 5 ml. of 5% acetic acid (8 tests); (4) 5 ml. of 3% potash alum (6 tests); (5) 1 g of freshly ground pepper (8 tests); and (6) 0.5 g of thick mustard paste made from a well-known British commercial brand of mustard powder (3 tests). Each substance was left in the mouth for 5–8 min.

Physical stimulation of the mouth, pharynx, oesophagus, and stomach was produced in a number of ways. Three subjects filled their mouths with hot water at 52–54° C for periods of 5–20 min, changing the water at intervals of 1 min. Two subjects were given a beakerful of hot water to sip as fast as they could; the water was as hot as they could stand it, and one subject sipped 100 ml. of water at 73° C in 4 min, while the other sipped 200 ml. at 85° C in 5 min. In yet another experiment on another subject 150 ml. of oat gruel at 52° C was swallowed in 1 min. Two subjects were given a piece of sponge rubber to chew for 10 min. Another five subjects swallowed a Ryle's tube, which they did without any trouble in about 30 sec. Subjects who had difficulty in swallowing the tube were excluded, since vomiting and retching gave rise to sweating of a different nature.

Records of sweating. For the qualitative observation of sweating Minor's iodine method (1927) was used, which consists of painting the skin with a solution of iodine and dusting it with dry starch; this gives a blue reaction when sweating occurs. Iodine and starch were applied to the subjects' whole face and neck except the eye-lids. The pinnae of the ears and representative parts of the upper part of the body and upper limbs were similarly treated. On the scalp sweat could usually be seen in large drops but it could also be detected by running a dry finger through the hair, and objective evidence of sweating of the scalp was obtained with iodine and starch at the edges of the hair line (Fig. 1).

In regions of the skin where gustatory sweating had been demonstrated by Minor's method, the number of active sweat glands was counted by Randall's iodine and starch-paper technique (1946) with the following modifications. The starch-paper was prepared from Whatman no. 1 filter-paper which is highly absorbent. In order to fix the size and area in which the number of secreting glands was being counted, a circular window, 11 mm in diameter, was punched out with a cork borer from a piece of transparent adhesive tape, and the tape was affixed to the skin. The skin in the circular window was painted with iodine solution, and starch-paper was pressed against it for periods of 10 sec at intervals of 30 sec. Dark spots appearing on the paper corresponded to active sweat glands and they were immediately counted. A note was also taken of the size of the spots. When the number of active glands was large, the possibility of error in counting was eliminated by superimposing on the imprints a grid ruled on glass with lines 3 mm apart, the technique resembling that used in counting red blood cells, except that every spot in the whole field was counted. As a result of these modifications Randall's original method became a repeatable quantitative technique.

Other techniques. In order to check whether the secretory fibres were adrenergic or cholinergic, atropine sulphate 1 : 1000 in 0.9% saline and dihydroergotamine (Sandoz) 1 : 1000 were introduced into the skin by iontophoresis (Glaser & Lee, 1953).

In seven of the experiments on the relationship between thermal and gustatory sweating (see above) the subjects first chewed chillies at a room temperature of 28–29° C as described above, but the total time during which chilli remained in the mouth was prolonged slightly beyond 5 min. After an interval of 40–60 min thermal sweating was produced in these subjects by immersing the lower limbs in hot water at 43–45° C, and a high level of blood-flow through the limbs was maintained by exercising them (Barcroft & Dornhorst, 1949).

In further experiments on the relationship between thermal and gustatory sweating, the subjects were cooled by sitting in a constant temperature room at 13.5–15° C for 45–60 min until their mouth and finger temperatures were lowered by at least 0.5 and 10° C respectively, and

they were warmed by walking about in the midday sun for 15 min or by carrying out stepping exercises for 15 min in an attic at a temperature of 32° C in the presence of considerable radiation from the walls. The mouth temperatures were taken by means of a clinical thermometer placed under the tongue for 5 min and the skin temperature of the forehead, the chest and the tip of a middle finger were measured by means of a thermocouple (Glaser, 1949).

RESULTS

Regions affected by gustatory sweating

Twenty-five subjects were given a chilli to chew for 5 min, and twenty-four of these produced evidence of sweating by Minor's method. In twelve of these subjects the latent period from the time when chewing of a chilli started to the onset of sweating varied between 1 and 2 min, and in the other twelve subjects the latent period was 20 sec or less. Table 1 shows the distribution of

TABLE 1. Regional distribution of gustatory sweating in an environment of 29–30° C

Regions sweating	No. of subjects
Nose and neck	1
Nose and upper lip	1
Nose, upper and lower lips and chin	1
Nose, nasolabial regions and upper lip	5
Nose, nasolabial regions, upper lip and auriculo-temporal regions	1
Nose, nasolabial regions, upper and lower lips, and auriculo-temporal regions	1
Forehead	1
Forehead and nasolabial regions	1
Forehead, auriculo-temporal regions and upper lip	1
Forehead, auriculo-temporal regions, nose, upper and lower lips	7
Forehead, nose, upper lip and ear lobes	1
Forehead, scalp, nose, nasolabial regions, upper and lower lips	1
Forehead, scalp and auriculo-temporal regions	1
Scalp, auriculo-temporal regions, nose, nasolabial regions and upper lip	1
No sweating	1

sweating, and it shows that the commonest regions where sweating occurred were the forehead, the auriculo-temporal regions, the nose, the nasolabial region, the upper and lower lips, the upper lip and the scalp. Sweating was always confined to the face and the scalp, and it was always bilateral and symmetrical, but different regions of the face did not begin to sweat at the same time and the sequence in which sweating appeared varied in different subjects. Fig. 1 shows sweating of the frontal and cervical hair-line, the auriculo-temporal regions, the nose, the nasolabial regions and the chin. Fig. 2 illustrates profuse sweating involving almost the whole face.

In nine subjects the experiment was repeated on another day, and it was found that in each subject sweating took place in the same places and in the same sequence as in the previous experiments. During the second experiment

chewing was extended in seven of these subjects for another 5 min by giving additional amounts of chillies after the first chilli had been voided from the mouth, and in three of these sweating was intensified in the regions which had been sweating before, while in two subjects such profuse sweating ensued that the different sweating regions merged with one another to cover almost the whole face; in the remaining two subjects further chewing of chillies had no added effect.

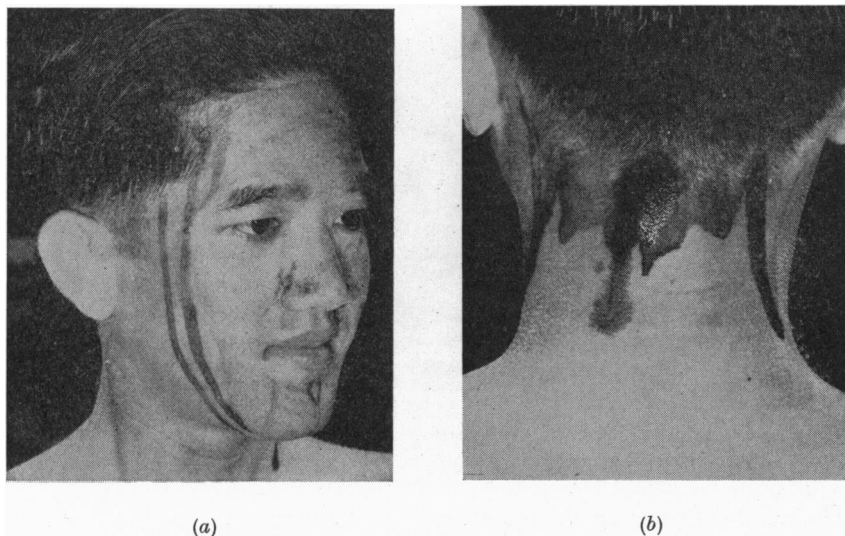


Fig. 1. Regions affected by gustatory sweating. (a) Front view, showing distribution of sweating. Note sweat dripping down the face from the scalp. (b) Back view, showing sweat dripping down the neck from the scalp.

Concomitant physiological reactions. In every subject, including the subject who did not sweat, there was an immediate flushing of the face and reddening of the conjunctivae on chewing chillies. The flushing usually extended to the chest and shoulders, and was better observed in subjects with lightly pigmented skins. In nine subjects there was venous engorgement in the temporal regions. In every subject there was marked salivation accompanied by varying degrees of lachrimation (Fig. 2) and nasal discharge.

Effects of repeated and continued stimulation

In three experiments on three subjects a constant amount of chilli paste was painted over the whole of the roof of the mouth, the cheeks and the tongue, 7 times at intervals of 15–20 min, leaving the chilli in the mouth for $3\frac{1}{2}$ min each time, and in all three subjects the numbers of active sweat glands increased until the second or third test, after which there was a progressive decline. Fig. 3 illustrates this and it shows that the highest number of forty-

four active sweat glands was obtained in the second test, after which the number of active glands decreased, so that no more than thirteen glands became active at any one time in the sixth test and no more than fifteen in the seventh.

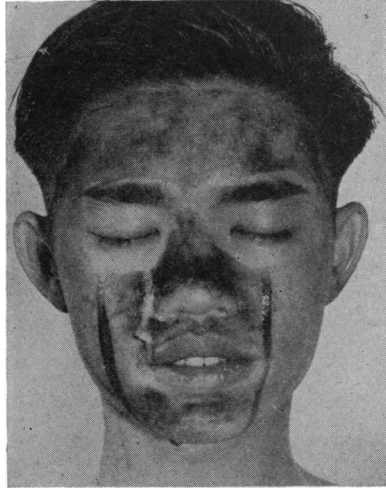


Fig. 2. An example of profuse gustatory sweating involving practically the whole face. Note the tears streaming down over the cheeks and the facial expression suggesting discomfort.

The effects of continued stimulation by chillies were studied in three experiments, the results of which are given in Fig. 4. Chilli paste was painted over the whole mouth of one subject and over the dorsum of the tongue in two others, so that the paste was in constant contact with the mucosa for 15 min. In all these experiments there was a distinct tendency for the numbers of active sweat glands to increase during the first 3 min and to decline slowly thereafter, so that after 15 min, sweating was absent in one subject and slight in the others.

In all six experiments the sizes of the sweat spots, and therefore the rates of sweating, showed changes parallel with the number of active glands, but there were minor irregular variations both in the number of active glands (Fig. 4) and their sizes. Subjective sensations of pain or pungency also decreased towards the end of repeated or continued stimulation.

Regions from which sweating could be elicited

In six experiments different areas of the mouth were in turn and at intervals of 15–20 min painted with chilli paste, taking care not to allow the paste to spread over other areas. The subjects kept their mouths open and allowed the saliva to drip into a beaker. The order in which the paste was applied to

different regions was randomized. The areas studied were: (1) the tip and edges of the tongue; (2) the dorsum of the tongue in front of the row of circumvallate papillae; (3) the hard palate; (4) the soft palate; (5) the posterior wall of the oro-pharynx; and (6) the inner walls of both cheeks. These areas are anatomically fairly well defined, and only a small amount of arbitrary

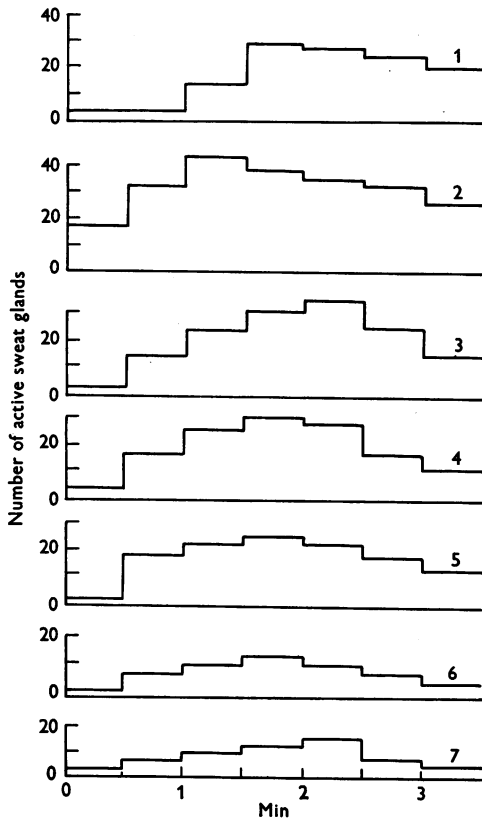


Fig. 3. Effects of repeated gustatory stimuli from the whole mouth on the number of active sweat glands in a circumscribed region. Numbers refer to successive tests at 15–20 min intervals.

judgement was necessary in their definition. The chilli paste was left on each area for $3\frac{1}{2}$ min and the numbers of active sweat glands were counted from the moment of first applying the paste.

In all experiments the largest number of active sweat glands was obtained when chilli was applied to the whole mouth. The individual regions in the mouth could be roughly classified into two groups, one consisting of relatively more sensitive areas, giving larger sweating responses and the other of less sensitive areas giving correspondingly smaller responses. The more sensitive areas were: (1) the tip and edges of the tongue; and (2) the soft palate. The

less sensitive areas were: (1) the dorsum of the tongue; (2) the posterior pharyngeal wall; (3) the hard palate; and (4) the inner walls of the cheeks. However, there was some individual variation because in two subjects stimulation of the dorsum of the tongue elicited a comparatively large sweating response, and stimulation of the posterior pharyngeal wall elicited a comparatively large response in one subject. Fig. 5 gives the results of a typical experiment, and it shows that the results did not depend on the order in which the different regions of the mouth were tested (cf. Fig. 3).

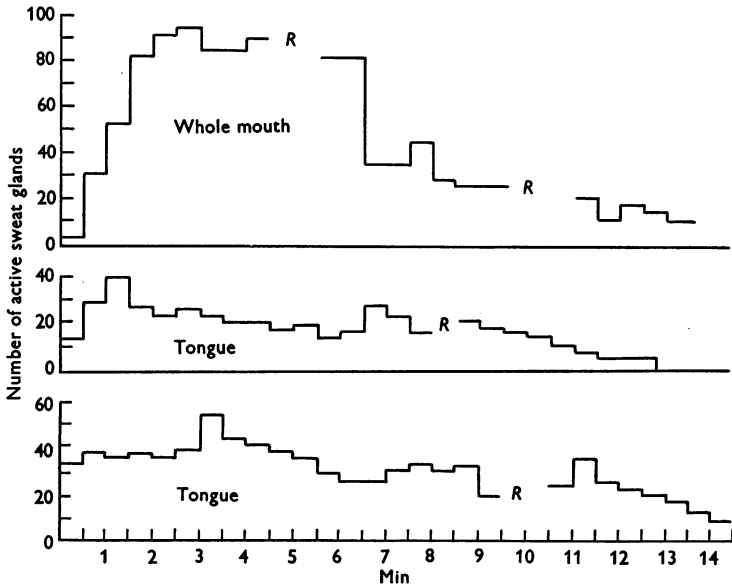


Fig. 4. Effect of prolonged stimulation of tongue or mouth by chilli paste. *R* signifies repainting with iodine.

The magnitude of the response was related to the degree of pungency experienced by the subjects when different areas were stimulated. This was shown very clearly when the tip of the tongue and the hard palate were compared. In the former region an intense burning sensation was associated with a high rate of sweating and in the latter a mild sensation was accompanied by correspondingly mild sweating. In three experiments, moreover, chilli paste was painted on the lips, and the presence of sweating was observed by Minor's qualitative technique. When in contact with the lips, chilli elicited intense pain, and this was accompanied by sweating in the same regions as those which were affected when chillies were placed in the mouth.

In twelve of the experiments on the distribution of sweating (see above) the subjects were asked to swallow the chilli after they had been holding it in the mouth for 5 min, but no further sweating was observed in any of these

subjects, although all of them felt 'hot in the stomach'. The absence of sensitive areas for gustatory sweating in the stomach was further demonstrated in two subjects who swallowed an amount of chilli paste equivalent to two chillies after their mouths had been anaesthetized by a 5% 'Borocaine' (benzamine borate) solution, and who showed no sweating after doing so.

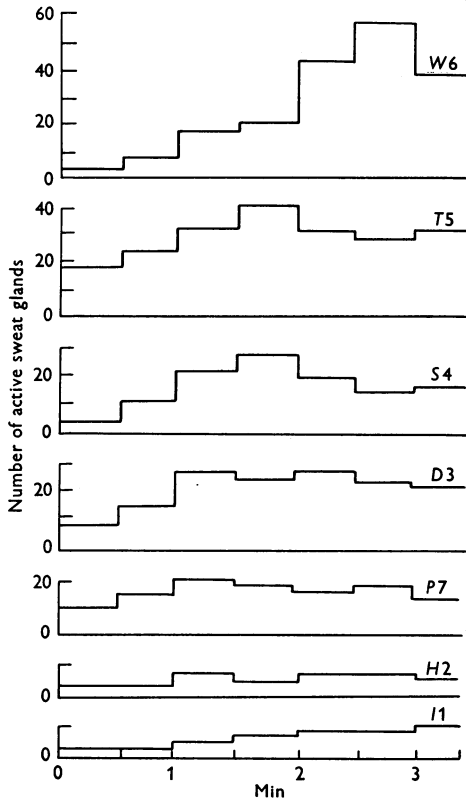


Fig. 5. Sensitivity of different regions of the mouth to stimulation with chilli. *W*, whole mouth; *T*, tip and edges of tongue; *S*, soft palate; *D*, dorsum of tongue; *P*, posterior pharyngeal wall; *H*, hard palate; *I*, inner walls of cheeks. Numbers indicate the order in which regions were tested.

Rates of salivation. Saliva was collected and its volume measured in the six subjects in whom various parts of the mouth were painted with chilli paste. There was some correlation between the volume of salivary secretion and the amount of sweating elicited from each region, but this did not apply to the posterior pharyngeal wall, stimulation of which was followed by production of more saliva than when the whole mouth was stimulated in four subjects and of an equal volume in two. The volumes of saliva were very high. In four subjects they exceeded 20 ml. in 3 min when the whole mouth or the pharynx

was stimulated, and they only fell below 5 ml. in 3 min in six out of the forty-two tests that were carried out.

Effects of other stimulants

Five per cent acetic acid solution produced slight sweating of the forehead accompanied by a transient flushing of the face in two out of eight subjects, and pepper produced slight sweating in three out of eight subjects. Solutions of 50% cane sugar, 0.5% quinine and 3% potash alum did not produce sweating in any of the eight subjects tested, although all of them sweated when chilli was given. Mustard elicited no sweating in the three subjects tested, although two subjects produced flushing of the face, lacrimation and nasal secretion. Water at 52–54° C held in the mouth did not produce any sweating, and a similar negative result was obtained when hot water at 73–85° C or oat gruel at 52° C was swallowed. Neither of the two subjects who chewed sponge rubber produced any sweating, and the five subjects who swallowed a Ryle's tube also did not sweat.



Fig. 6. Inhibition of gustatory sweating by introduction of atropine into the skin. Dihydroergotamine was introduced by iontophoresis into a circular area on the right side of the subject's forehead and atropine into a circular area on the left side. Note complete absence of sweating on the atropinized area.

Nature of secretory fibres

In four subjects, adjoining or symmetrical areas of the face, which had been shown to sweat in response to chilli, were treated by iontophoresis with atropine and dihydroergotamine respectively. Atropine inhibited sweating in all four subjects and dihydroergotamine had no effect in any of them. Fig. 6 illustrates the action of these two drugs on gustatory sweating in one subject, and it shows complete inhibition of sweating by atropine.

Comparison of gustatory and thermal stimuli

In seven subjects sweating in response to gustatory and thermal stimuli was compared, and the subjects were so selected that all regions of the face and the scalp known to produce gustatory sweating were represented among them. After immersion of the feet and legs in a hot-water bath, the regions that started to sweat first were invariably the same as those which first responded to the chewing of chillies, and the order in which sweating began in other regions was exactly the same as in gustatory sweating. In two subjects gustatory sweating began after a comparatively long latent period and the sweating was mild, and these subjects showed the same features when they sweated after immersion of their limbs in hot water. Fig. 7 illustrates the close correspondence between regions affected by thermal and gustatory sweating.

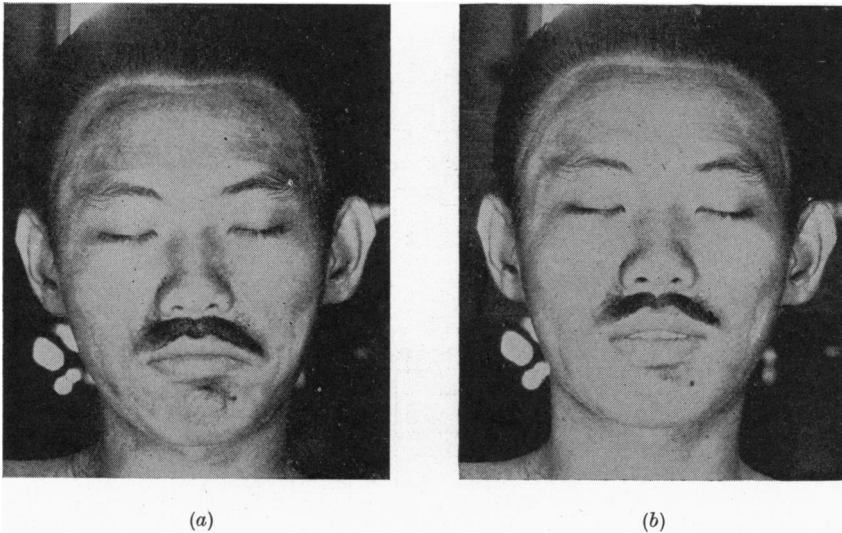


Fig. 7. Similarity in the regions affected by gustatory sweating and thermal sweating. Note painful expression when mouth contains chillies. (a) Gustatory sweating. (b) Thermal sweating.

Table 2 summarizes four experiments in which the subjects were cooled and warmed by various means before chewing chillies, and it gives the skin and mouth temperatures after cooling or warming as well as the maximum numbers of active sweat glands in the same area after each change of environment or activity. Both the temperature values and the maximum numbers of active sweat glands varied in the same direction, so that when the temperatures rose the numbers of secreting sweat glands increased, and when the temperatures decreased the sweating was either reduced or completely abolished. The

time interval between placing chillies in the mouth and the onset of sweating also decreased by warming. Fig. 8 demonstrates the inhibition of sweating after the subject sat still at an environmental temperature of 14° C for 45 min,

TABLE 2. The relationship between the maximum number of active sweat glands elicited by the presence of chillies in the mouth and the skin and mouth temperatures

Subject	Condition	Temperature (° C)				Max. no. of sweat glands
		Forehead	Chest	Finger	Mouth	
AC	Before cooling	34.7	33.4	35.2	36.8	69
	After cooling	32.5	29.6	23.2	36.0	9
	On warming	34.7	34.0	34.7	36.8	143
JC	After cooling	32.0	31.5	21.0	35.9	0
	On warming	34.3	34.5	32.0	36.5	0
	On further warming	34.7	34.3	33.3	36.9	34
	After cooling again	32.5	33.0	23.2	36.4	3
JA	Before cooling	35.5	34.7	34.7	37.5	59
	After cooling	32.8	31.8	21.8	37.0	22
BK	Before exercise	35.2	34.3	35.0	37.1	5
	Immediately after exercise	34.0	35.5	35.5	37.4	19
	95 min after exercise	35.2	35.0	35.5	37.2	3

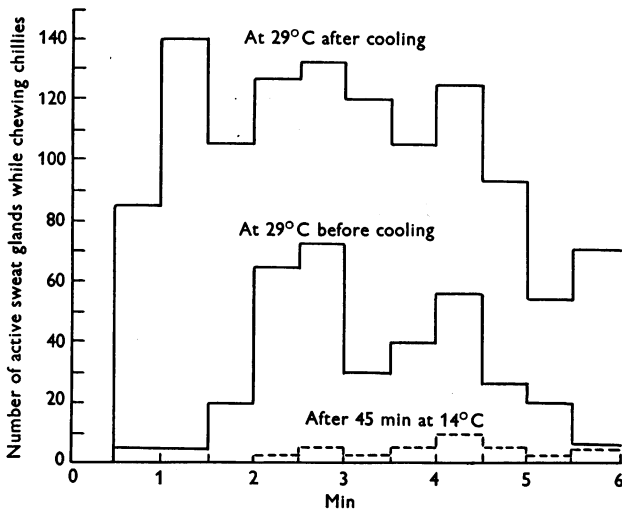


Fig. 8. Effect of different environmental temperatures on gustatory sweating in a representative area of the face.

and it shows that the onset of gustatory sweating was delayed and the number of active glands reduced by cooling. After leaving the cold room, sweating in response to the same gustatory stimulus increased. This corresponded to sweating observed after cooling (Glaser & Lee, 1953) and it was probably a central nervous phenomenon superimposed on gustatory sweating.

DISCUSSION

Characteristics of physiological gustatory sweating. It may be concluded that in a tropical climate sweating of the head almost invariably takes place when chillies are in contact with the mouth, but that sweating is difficult to elicit by other gustatory stimuli, while mechanical and thermal stimuli are ineffective. Although there were large individual variations both in the regions of the head affected by sweating and in the intensity of the response, the results suggested that under constant conditions and in any one individual, gustatory sweating always involves the same regions. In the present experiments sweating was always bilateral and symmetrical, whereas in most cases of pathological gustatory sweating only one side is affected (Uprus, Gaylor & Carmichael, 1934; Wilson, 1936; List & Peet, 1938*a*; Haxton, 1948) and this, coupled with the present findings of marked concomitant responses (such as flushing, salivation and lacrimation), suggests that there may be a fundamental difference between pathological and physiological gustatory sweating.

As may be expected, gustatory sweating conforms with known characteristics of reflex responses. Thus the finding that more and more sweat glands became active in response to a constant stimulus until a maximum number was reached suggests that recruitment took place, and the observation that the rate of secretion also increased suggests facilitation. With continued stimulation, however, both the number of active glands and the apparent rate of secretion decreased, and this suggests adaptation in the receptors, which was borne out by the fact that the initial sharp burning sensation experienced by the subjects became duller towards the end of each test. Since a few minutes elapsed before any signs of adaptation were noticed, the receptors must have been of the slowly-adapting type. In thermal sweating a similar increase in sweating (Kuno, 1934; Randall & McClure, 1949) followed by an eventual decrease (Hancock, Whitehouse & Haldane, 1930; Gerking & Robinson, 1946) has also been shown to exist. It cannot be excluded, however, that fatigue in the reflex pathways played some part in the diminished response after repeated or continued stimulation with chilli. Exhaustion of secretory power in the sweat glands is unlikely to take place after such a short time (Randall, 1947). The relationship between gustatory and thermal sweating provides interesting examples of facilitation and of convergence on a final common pathway.

The sensory receptors. Capsaicine, the active constituent of chilli is a powerful irritant (Burkill, 1935). The fact that in the mouth, chilli caused a painful burning sensation and that when different regions of the mouth were stimulated the degree of sweating varied with the intensity of the burning sensation experienced, suggests that pain fibres may play a predominant role in the receptor mechanism of normal gustatory sweating. The appearance of

sweating when the lips were painted with chilli confirms the importance of pain fibres in gustatory sweating, since no taste fibres exist in these regions. This is further supported by the absence of any response when the taste receptors were stimulated with sugar, quinine and potash alum. Moreover, pepper and mustard were inferior excitants to chilli both with respect to pain and sweating. It seems possible to conclude, therefore, that the degree of response varied with the degree of burning sensation produced by the various stimulants, and that taste fibres played only a minor role in the production of physiological gustatory sweating. In pathological gustatory sweating taste fibres play a predominant part (Haxton, 1948) and this adds further weight to the opinion expressed above that the two conditions are fundamentally different. Since mechanical or thermal stimulation, such as that caused by chewing or swallowing a tasteless substance or warming of the mouth with hot water, did not produce gustatory sweating, it seems safe to conclude, further, that the exteroceptive sensory fibres of the fifth nerve carrying tactile, pressure and heat impulses are not the afferent mechanism.

The effector mechanism. The fact that atropine inhibited sweating and dihydroergotamine had no effect show that the sudomotor fibres responsible for gustatory sweating are cholinergic and are not different from those controlling thermal sweating (Dale & Feldberg, 1934; Chalmers & Keele, 1951), emotional sweating (Chalmers & Keele, 1951), and other forms of sweating from central nervous excitation (Glaser & Lee, 1953).

It could not be conclusively shown whether the same glands did indeed respond to gustatory as well as thermal stimulation, but the close correspondence in the pattern of both of these responses (Fig. 7) seems to justify the conclusion, that those sweat glands which participate in gustatory sweating have a low threshold for thermal sweating. If this is considered in conjunction with the findings that cooling of the body reduced or completely inhibited gustatory sweating, while warming the body increased it, the conclusion may be made that the neurones of sweat glands concerned in gustatory sweating were at a subthreshold level of excitation for thermal sweating and were fired off by a gustatory stimulus that would otherwise have had no effect. This seems to provide a satisfactory explanation of the fact that gustatory sweating is seldom seen in a temperate climate (List & Peet, 1938*a, b*; Haxton, 1948; Tankel, 1951), and that on the rare occasions when gustatory sweating is encountered in such a climate it is confined to small areas of the face.

SUMMARY

1. By using *Capsicum minimum* (chillies) as an excitant, gustatory sweating was elicited in forty-five out of forty-six young men in a tropical climate.
2. Randall's method for counting sweat glands was modified to give repeatable quantitative data.

3. Physiological gustatory sweating is symmetrical, and it is confined to the head and exceptionally the neck. The regions involved and the extent of sweating are constant in each person under the same experimental conditions, but there is much variation between different persons.

4. Gustatory sweating is invariably accompanied by flushing of the face and the upper part of the body, salivation, lacrimation and nasal secretion. The intensity of these reactions varies in different people.

5. Sweat gland activity in response to gustatory stimuli exhibits recruitment, facilitation and adaptation or fatigue.

6. The evidence suggests that the sensory receptors mediating gustatory sweating are pain fibres. Substances which stimulate the taste fibres without causing pain do not give rise to gustatory sweating. There is no evidence of any receptors for gustatory sweating in the oesophagus and stomach.

7. The sudomotor fibres are cholinergic.

8. Warming the body facilitates, while cooling the body inhibits or abolishes gustatory sweating, and the evidence suggests that the sweat glands which respond to a physiological gustatory stimulus have a low threshold for thermal sweating so that the gustatory stimulus merely causes secretion in sweat glands which are already at a subthreshold level of excitation for thermal sweating.

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