CORTICAL REPRESENTATION OF TASTE IN MAN AND MONKEY

I. Functional and Anatomical Relations of Taste, Olfaction, and Somatic Sensibility*

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INTRODUCTION

If we turn to modern text-books of neurology and physiology to determine the present teaching with regard to the cortical taste system, we find that they are nearly unanimous in locating the gustatory area in the temporal lobe, adjacent to the cortical olfactory area. "The cortical synapses for taste," state Jelliffe and White,[44] "are not completely worked out. In all probability they are contained in the rhinencephalon, reaching them by paths similar to, if not identical with, the olfactory." Grinker[35] speaks of the hippocampal formations "whose functions are undoubtedly gustatory and olfactory." Similarly, Villiger,[71] Wechsler,[73] Brock,[15] Best and Taylor,[8] and Bard[5] either locate the cortical taste area in the temporal lobe or hold that this location is most probable.

This paper presents a critique of the theories which have been advanced, and new evidence, based upon theoretical considerations, is offered as to the localization of the cortical taste area. The experimental parts of the inquiry will be presented in subsequent papers.

THE TEMPORAL LOBE THEORY

Experimental and clinical basis

Despite the striking unanimity of opinion with respect to the temporal lobe localization of taste, there is surprisingly little experimental and clinical evidence supporting this statement. Ferrier[26] was apparently the first to claim that the sense of taste is localized in the lower part of the temporo-sphenoidal lobe, in close anatomical relation to the center for smell. In his first experiments, on two monkeys, he found after bilateral destruction of this lobe not only loss of smell and of taste, but also an abolition of tactile sensibility

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of the tongue (pp. 183-92). Fourteen years later Ferrier[27] characterized these earlier experiments as "not very exact;" but when he repeated them on another monkey, he again observed a loss of taste and of smell persisting for three months after bilateral extirpation of the temporal lobe. Unilateral operation on another monkey caused diminished reaction on the contralateral side of the tongue (p. 186). Not only were these experiments few in number, but, as will be shown in a later communication, the effect of cortical lesions on gustation in the monkey can be measured only by frequently repeated examination of the same individual before as well as after operation. Moreover, figure 51 in Ferrier's first book[26] (p. 188) shows that besides the temporal lobe the adjacent region of the parietal lobe was damaged. Ferrier was cautious enough to emphasize that his experiments were not sufficient and that further work was necessary. Luciani[50] was also of the opinion that the gustatory area is in closest relation to the olfactory area. His statement was based on the observation that the gustatory capacity of one of his dogs seemed, after unilateral extirpation of the olfactory area, slightly impaired on the ipsilateral (*sic*) side of the tongue. This dog survived the operation for only three days, and the observation was made on one day only. Such is the *experimental* basis for the temporal lobe theory.

The *clinical* evidence is more impressive and comes largely from the occurrence of a peculiar type of epileptic seizure which is characterized by a "dreamy state" coupled with hallucinations of smell or of taste, or with tasting movements. Jackson,[40] who first described seizures of this type, called them "uncinate fits," and he stated that they elicited from the uncinate gyrus or its neighborhood, the uncinate region.[43]* This "odd association" (Wilson) of an elaborate psychical state with the crude sensations of smell or of taste has since aroused the interest of many neurologists. Most of them agree that uncinate fits are discharge phenomena from the uncus or pes hippocampi, and that this type of epileptic attack justifies localiza-

* The hallucinations occur usually before and sometimes without the "dreamy state." Instead of smell or taste, there may be "epigastric sensations," and spitting may occur instead of tasting movements (Jackson). Complex visual hallucinations are also a characteristic part of the uncinate fits. A description of such an attack may be quoted from Cushing[23]: ". . . As in a dream he saw, always to his left side, his father and some other men in an unfamiliar room engaged in a game of cards which ultimately led to an altercation. The scene would fade and leave him with bad taste and smell of something undescribably horrid." Objectively smacking and tasting movements occurred. This patient had a temporal lobe glioma.

tion of the sense of taste in the same region of the brain as the sense of smell, namely, in the uncus and pes hippocampi of the temporal lobe. However, for localizing the gustatory sense the value of uncinate fits is not so great as is often assumed. This will be demonstrated by a survey of the chief observations of gustatory hallucinations and of gustatory impairments in connection with lesions in the temporal lobe of man.

In none of the cases of gustatory hallucination or impairment reported by Jackson was there biopsy or post-mortem examination.* Spiller[66] recorded three cases of uncinate fits, one with gustatory hallucinations of tasting raw, unsalted beef, one with a gassy "taste," and one without gustatory disturbances. There was no operation or autopsy. Mills[54] observed gustatory impairment over the anterior two-thirds of the tongue in a case of a tumor in the left uncinate region, but a large part of the thalamus had been involved in the destructive process. Foster Kennedy[45] presented nine cases of temporosphenoidal lobe tumors with biopsy or autopsy. Olfactory disturbances occurred in six and gustatory disturbances in only three. These three cases do not confirm a temporal lobe localization, since the destruction was not confined to the temporal lobe. In one of the three cases, the uncus and pes hippocampi were intact. Knapp[47, 48] evaluated seven cases of temporal lobe tumors with regard to gustatory disturbances. He emphasized the fact that in temporal lobe tumors gustatory disturbances are less frequent than are olfactory disturbances. His first five cases showed intact taste and olfaction. One of the later two cases showed gustatory deterioration on the contralateral side of the tongue and there was a tumor in the right temporal lobe. However, the patient had suffered from contralateral facial palsy and atonia of the contralateral side of the tongue—symptoms which show that the damage was not confined to the temporal lobe.

In 1921 Cushing[23] collected 59 verified tumors which were situated largely within, or had chiefly deformed, the temporo-sphenoidal lobe. Ten of these cases are analyzed in Cushing's paper. Olfactory hallucinations were observed in four, but gustatory hallucinations were noted in only two of the ten cases. But even these two cases are of doubtful value as proof of the temporal lobe theory. One of the patients referred to peaches and roasted peanuts which he smelled and "tasted." It is possible that the term "taste" was used by the patient in the unsophisticated sense and was actually an olfactory sensation. The other patient experienced sensations like those given by peppermint, which is a tactile-olfactory sensory complex. The fact of paresthesias in teeth and fingers might be taken to mean an involvement of regions other than the temporal lobe.

* Jackson[41] presented one case in which autopsy disclosed a small softening in the uncinate gyrus. The uncinate fits were characterized by masticatory movements. Gustatory disturbances were not noted.

An extensive monograph on temporal lobe tumors was published by Artom[4] in 1923. Only one out of his eight cases showed gustatory disturbance. This was a dissociative disturbance since perception for sweet was lost and for bitter delayed on the right side of the tongue, and perception for salty was lost on the left side. Sour was readily perceived on the whole tongue. The post-mortem examination disclosed multiple gliomata in the frontal and parietal lobes, in the first temporal gyrus of the right hemisphere, and in the gyri marginalis, angularis, and temporalis inferior of the left hemisphere. Thus, the localizing value of this case is limited. Artom also collected the case reports of previous authors on temporal lobe tumors in which the uncus, gyrus hippocampi, lobus lingualis, or Ammon's horn was involved and in which gustatory disturbances were reported. He found only five cases, in all of which the damage extended beyond the temporal lobe, presenting: (case 1) hemianesthesia of the head, optic neuritis, and anatomically a tumor in the right temporal lobe with obliteration of the lateral ventricle (Mackay[51]); (case 2) bilateral choked disc and anatomically a compression of the frontal lobe by the tumor (Siebert[64]); (case 3) bilateral optic atrophia and a tumor in the temporal and frontal lobes and in the caudate nucleus (Schupfer[62]); (case 4) bilateral choked disc, bilateral facial disturbances of cerebral type, and a tumor in the left hippocampal gyrus with intact uncus, the gyri of the brain being flattened by generally increased pressure (Mingazzini[55]); (case 5) olfactory, gustatory, and tactile deterioration, and anatomically a temporo-parietal lobe tumor which compressed putamen and pallidum (Stern[68]). It seems hardly justified to base a temporal lobe theory of taste on these cases exhibiting highly advanced stages of tumor growth.* On the other hand, Artom reported nine cases with lesions of the gyrus hippocampi, partly accompanied by lesions in the uncus, hippocampus, or gyrus lingualis, in which no gustatory hallucinations or impairment had been observed.

Herzog[39] considered his observations as tending to support the localization of taste in the temporal lobe. He observed gustatory impairment in six of 33 patients with hypophyseal tumors. All of these patients, however, suffered from increased intracranial pressure, with optic atrophia, amblyopia, or blindness which might have contributed to the symptoms. A larger compilation of temporal lobe tumors, analyzed by Kolodny,[49] consists of 38 cases observed at the National Hospital, London. These were certified by post-mortem examination. Uncinate fits were seen in seven cases. Impairment of taste

* Dissociation of gustatory impairment was observed in as many as three of these five cases. It may be mentioned that Mingazzini's patient was addicted to drink and was a heavy smoker who had suffered from cerebral commotion ten years before the examination of taste. Each of these factors might have been responsible for the impairment of taste. Mingazzini concluded from this case that the gustatory pathways subserving salt and sour undergo a decussation but not the pathways for the other two taste qualities.

and smell was observed in three cases. One of these patients had a bilateral loss of smell and impaired taste; the second showed bilateral perseveration of smell and taste; in the third case, taste was completely absent on the entire ipsilateral side of the tongue although the trigeminal and the facial nerves were apparently not involved. These cases seem to support the temporal lobe theory. However, bilateral anosmia in unilateral temporal lobe tumors is known only as a neighborhood symptom. Ipsilateral loss of taste can hardly be explained by a cortical lesion. The taste disturbances in the three cases might well be neighborhood symptoms. It is significant that motor and sensory disturbances were observed in no less than 92 per cent of these cases and trigeminal neuralgias were found in ten. These facts emphasize the frequency of neighborhood symptoms in temporal lobe tumors. Study of these cases led Kolodny to the conclusion that "disturbancess of smell and taste are of no localizing or lateralizing value in tumors of the temporal lobe."

The uncus theory of taste localization has, however, rarely been questioned. Wilson,[74] who dealt extensively with the problem of "dreamy states," took it for granted that taste hallucinations were caused by uncus lesions. Marburg[52] considered it almost certain that the uncus and gyrus hippocampi represent the centers of taste as well as of smell (p. 1876). On the other hand, Foerster[28] reported olfactory and gustatory auras produced by lesions in the first temporal gyrus, i.e., in Brodmann's area 22 (see below, p. 732). Gibbs[33] analyzed the records of 1545 verified brain tumors, mostly from Cushing's clinics. The records contained 74 cases with olfactory and 32 cases with gustatory hallucinations. Gustatory hallucinations "occurred most frequently among cases in which the tumor involved the left caudate or left lenticular nuclei or the left thalamus and somewhat less frequently among cases in which the tumor involved the temporal lobe or the cerebellopontile angle." The study involved 197 temporal lobe tumors and 33 of the left caudate or lenticular nuclei and left thalamus. Frazier and Rowe[31] studied 51 verified tumors of the temporal lobe. They found olfactory disturbances in 21 per cent and taste disturbances in 13 per cent of 45 tested cases. They came to the conclusion that "the exact location of the cortex for taste and smell has not been definitely fixed"; but they accepted a temporal lobe representation. Penfield and Gage[57] observed uncinate fits, with an acid taste, in one case of an "infiltrating" tumor in the right temporal lobe, and an aura of a bitter taste and of epigastric sensations in another case in which the tumor extended from the postcentral gyrus into the temporal lobe.

The difficulty of evaluating tumor cases for localizing purposes has recently been demonstrated by Pichler's report[59] on three cases of tumor in the right temporal lobe, associated with taste disturbances. In each case the trigeminal nerve had been involved by the tumor.*

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* Two other cases showed such olfactory disturbances as are characteristic of uncinate fits. The tumors were located outside of the temporal lobe.

Marcus[53] considered his case unique and decisive because the lesion was the result of a bullet wound which had damaged the right hippocampus and its neighborhood and was accompanied by taste disturbances. The fact, however, that the injury had also affected the middle cerebral artery diminishes the value of the case.

Association of gustatory with olfactory disturbances in temporal lobe cases has been considered strong evidence indicating that the taste area is located in the temporal lobe near the olfactory centers. However, all writers agree that in temporal lobe lesions alterations of taste are less frequent than are olfactory changes and when the individual instances of gustatory disturbances are examined it is apparent that the evidence is far from conclusive. In none of the cases mentioned above which have been taken as proof for the temporal lobe theory of taste was involvement of neighborhood structures excluded. Due to the singular position of the temporal lobe within the brain, tumors in this lobe can exert a destructive effect (by pressure, softenings, or hemorrhage) in three directions; downward upon peripheral nerves and ganglia and upon the pons, medially upon the thalamus, striatum, and pathways in the internal capsule, and upward upon the frontal and parietal lobes. The survey of the literature shows clearly the frequency of such effects. In at least two directions—downward and medially—from the temporal lobe lie structures which subserve the gustatory sense. Some minor factors may also contribute to the assumption that gustatory disturbances are due to temporal lobe lesions, even though the taste area may lie outside this region. In further studies these factors should be considered. In some cases the reports do not rule out the possibility that the patient is making the familiar error of describing olfactory experiences as "taste"; taste deterioration may be assumed to be due to a brain process because the individual variations in, or physiological deteriorations of, taste, such as may be found in older people or induced by habitual smoking, are not taken in account.

This survey shows that clinical observations have furnished no proof for the temporal lobe theory of taste.

RELATIONS BETWEEN TASTE AND OLFACTION

Ferrier's experiments and the clinical cases mentioned have provided the basis upon which the temporal lobe theory is founded.

In view of the paucity of clear-cut experimental and clinical evidence it is pertinent to ask why the theory of temporal lobe localization of taste has been so generally accepted. The explanation is not difficult to discover. Since so few unequivocal experiments and clinical observations supporting a temporal lobe localization are available, it would seem that this theory has been accepted chiefly on deductive inferences. The temporal lobe theory seems logical because there is a *functional relation between gustation and olfaction*, and this has been taken to indicate a similar cortical representation. The argument runs something as follows. The senses of smell and of taste both respond to chemical stimuli and they operate in feeding activities. Psychologically, this cooperation is so close that often we do not know whether a stimulus is perceived by olfactory or by gustatory channels. Experiments are necessary to show that the characteristic property of an onion is detected more by smell than by taste; that the "smell" of denatured spirit (pyridine) is in fact mainly taste; that perception of chloroform gas is based on stimulation of both gustatory and olfactory sense organs; and that the rancidity of butter is not perceived by taste, but merely by olfaction. It is now generally accepted that there are only four taste qualities;—sweet, salty, sour, bitter. So much of what is popularly called taste is actually perceived by olfaction that Starling[67] has said, "The epicure with a fine palate has really educated his sense of smell and would be but little satisfied with the simple sensations derived from his tongue."

It is this close functional and psychological interrelation which has lead to the belief that the two "chemical senses" form basically one morphological and physiological unit, that they are merely divisions of a single chemical sense. Olfaction and gustation differ, according to Nagel[56] and more recent authors, only in that the sense of smell is stimulated by gases and the sense of taste by fluids. It is, therefore, understandable that the cortical taste center has been placed in the immediate neighborhood of the centers of smell, that is, in the temporal lobe. But it is evident that the data on which this theory has been based are much too meager to justify the general acceptance of such a localization and that the deductions advanced above have influenced opinion unduly. It will be shown below that there are functional as well as anatomical facts which strongly indicate a localization separate from that of olfaction; that is, a localization in the inferior part of the parietal lobe.

RELATIONS BETWEEN TASTE AND TACTILE SENSIBILITY

Although gustation and olfaction have in common a chemical stimulus and similar reflex and psychological expression, there is also an apparently still closer functional interrelation of taste and of somatic sensation from the tongue. Moreover, the gustatory system

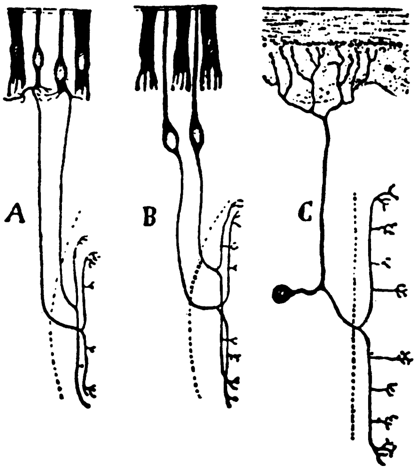

FIG. 1. The progressive centralization of the sensory cells in a phylogenetic series. A = earthworm; B = mollusk; C = vertebrates. (From Tilney and Riley, after Cajal.) The primary olfactory neuron is of type A; the gustatory and tactile neurons are of type C.

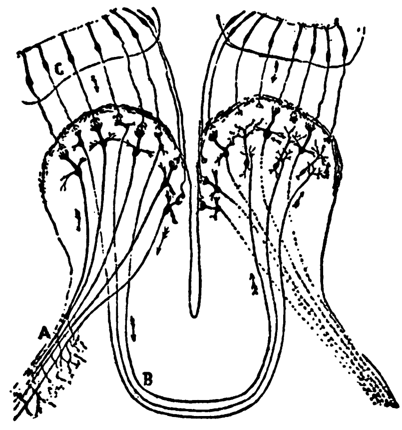

FIG. 2. Olfactory system. (From Ranson, after Cajal.) Note that olfactory stimuli act directly on the primary neuron (C).

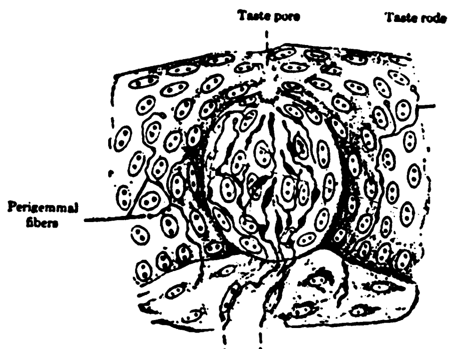

FIG. 3. Taste-bud of the hedgehog. (From Kappers after Boeke.) Two cells, a specific sensory cell and the primary neuron, are involved in gustation.

bears anatomically very little similarity to the olfactory system and, on the other hand, has essential points in common with the somato-sensory system. There are many reasons for believing that the cortical taste center is localized in the neighborhood of the cortical tactile representation of the parts carrying taste buds, i.e., tongue, soft palate, pharynx, and epiglottis. Five lines of evidence will be discussed briefly.

1. *Functional relations between taste and tactile sensibility.* Under biological conditions all gustatory stimuli act at

the same time upon organs for touch or pressure, and temperature. Tactile and gustatory perceptions may merge to build an intersensory complex impossible to analyze into its components. Salts, for example, in appropriate concentrations act at the same time on taste, touch, and pain nerve endings. Lye produces, seemingly, a simple "alkaline taste," but in fact this sensation is built up of gustatory, olfactory, pain, temperature, and touch perceptions (see v.Skramlik[65]). The astringent action of acids is not perceived by the gustatory sense but by tactile sensibility.

2. *Structure of the receptor.* The olfactory end-organ, even in man, retains the primitive type of structure which is characteristic of the receptor neurons of invertebrates, a single cell in the periphery performing both a receptive and a conductive function—the "neurosensory cell" of Retzius. The gustatory receptor, on the other hand, consists of a chain of two links, i.e., of special sensory cells which receive the stimulus and of nerve fibers (teledendrons) arborizing around them, which run to their *centrally* situated cell bodies, ganglion cells. The central location of the cell bodies of the first neuron is characteristic of the gustatory system as it is of the tactile sensory system.

3. *First-order neurons.* The primary olfactory axons form a purely sensory nerve. They remain unmyelinated. They develop from cells in the olfactory epithelium in the periphery. Their central processes connect with the olfactory lobe which is a part of the telencephalon. The gustatory fibers run in mixed sensory and motor nerves; they develop from ganglia and are myelinated. Their central processes connect with the myelencephalon. Gustatory fibers run in cerebral nerves which either conduct tactile sensory impulses in man, or did so in earlier phylogenetic stages.* The anterior two-thirds of the tongue in man is innervated, with regard to the gustatory function, by the facial nerve (chorda tympani†); the

* "In cyclostomes the somatic sensory fibers of the vagus and glossopharyngeus have retained their dorsal as well as their ventral branches, and consequently distribute to the dorsal and ventral parts of the lateral areas in the region of the gill arches. . . Sensory branches of the facial are found on the surface of the head caudal to the orbit and beneath it. . ." (Ariens Kappers,[3] p. 350.) Some observers, as Cushing and Oppenheim, believe that in man also sensory fibers are present in the facial from the anterior two-thirds of the tongue.

† Schwartz and Weddell[63] found that in a small percentage of cases these taste fibers run not in the chorda tympani but in the greater superficial petrosal nerve to the geniculate ganglion.

posterior third of the tongue by the glossopharyngeal nerve; the taste buds of the pharynx and epiglottis by the vagus. From the soft palate, taste fibers run through the nervi palatini and form, together with the chorda tympani, the intermedial nerve (see Kleist[46]). Each of these different nerves carries all of the four qualities of taste, though in different distribution.

Whether the trigeminal nerve carries gustatory fibers is still a controversial subject. A positive answer might be taken as further evidence that gustation is a derived tactile sense. That the trigeminal fibers conduct taste impulses (von Economo[24]) is not generally accepted. Cushing[21] found, after unilateral extirpation of Gasser's ganglion in some of his 13 patients, a diminution or loss of taste on the corresponding side of the tongue, but for no longer than a few weeks, with complete recovery after this period. Cushing's view that the trigeminal nerve takes no part in the conduction of taste impulses has been supported in some degree by more recent experiments of Wirtanen and Olmsted.[75] After division of the Vidian nerve in five cats, and after extirpation of Gasser's ganglion in a dog, these authors found no degeneration of taste buds. On the other hand, Carmichael and Woollard[20] point out that in man, after destruction of Gasser's ganglion, loss of taste and intact taste respectively have been reported about equally. They observed 17 cases of alcohol injection into the Gasserian ganglion and found in 10 of them a complete loss of taste on the anesthetic side of the tongue; in "several" of these cases the injection had been performed more than a year prior to testing. The other seven cases retained their gustatory faculty. The authors were unable to present an explanation for this discrepancy. However, it seems likely that this discrepancy indicates a normal variation and that in man the trigeminal nerve carries taste impulses in about 50 per cent of cases. If such a normal variation exists it might be taken as evidence, along with the fact that the facial nerve conducts tactile impulses, at least in lower forms, that taste is a derived tactile sense, so that further similarity might be expected in secondary and tertiary neurons.*

The gustatory fibers run through the respective facial, glossopharyngeal, vagal, and sphenopalatinal ganglia (also partly through

* In fishes close anatomical relation between taste and touch has been demonstrated by Herrick[38]: ". . . the facial lobe . . . sends a strong tract downward . . . for the purpose of effecting correlation between the two modalities of cutaneous sensation, taste and touch."

the trigeminal ganglia—see above) and enter the medulla oblongata and pons. They terminate either in the nucleus of the tractus solitarius, or, according to Kappers, in the nucleus intercalatus.

4. *Second-order neurons.* Pontine lesions with gustatory disturbances have been described by Pfeifer,[58] by Harris and Newcomb,[36] and others. Other clinicians (see Brodmann's review[17] and Strauss[69]) have observed gustatory alterations after lesions of the thalamus. Gibbs[33] reported gustatory hallucinations caused by tumors in caudate and lenticular nuclei and thalamus. Adler[1] published a case of progressive diminution of taste on one-half of the tongue, produced by a small tumor, which was located in the medial part of the thalamus and extended into the arcuate and median center nuclei. Olfaction was intact. Adler believes that the gustatory fibers terminate in the thalamus medial to the secondary trigeminal pathway. Projection fibers for taste to thalamus and hypothalamus have also been described on the basis of anatomical studies. The existence of such fibers, however, has not been definitely established (see Ranson,[60] Kappers,[3] Walker[72]). Kappers[3] observes that "little is known of the details of ascending gustatory connections in any form above fishes" (p. 409).

This short survey suggests that the gustatory pathway not only runs in the neighborhood of tactile fibers within the medulla oblongata and pons, but probably also terminates adjacent to them in the thalamus. It suggests, furthermore, that the anatomical situation of the first gustatory neurons is entirely different from that of the first olfactory neurons, which are built up by the oldest part of the brain, the archipallium. The olfactory nervous system represents from its beginning in the mucosa, over its unmyelinated fibers to its termination in the archipallium, a primitive form of sensory nervous system. With regard to the level of its development, the olfactory system of man is different from all the other sensory systems, including that subserving the sense of taste (see Börnstein[11]).

5. *Sensory-motor relations.* The sensory projections from the extremities and face terminate in man in the postcentral gyrus immediately behind the motor areas for the corresponding segments (Cushing,[22] Foerster,[29] Bard[5]). Thus, the motor and sensory areas for the face are in close topographical as well as functional relations. Gustatory sensation, like the somatic sensations from mouth parts, is related to chewing and tongue movements. A similar cortical location of the two types of sensation might, therefore, be expected,

i.e., a location of the gustatory area just behind the motor areas for tongue movements and chewing in the inferior part of the postcentral convolution.

Conclusion. From considerations such as the above, it was believed that the functional relations which taste bears to tactile function predicate a convergence in the cortex of these two kinds of sensation rather than of the gustatory and olfactory pathways. The anatomical similarity of the gustatory and tactile system at the level of the sense organs, of the peripheral nerves, and of the primary synapse is, of course, an even stronger basis for assuming a retention of their similarity at the level of the cortex in the form of a contiguous cortical representation in the parietal operculum.

EXPERIMENTAL AND CLINICAL EVIDENCE INCOMPATIBLE WITH TEMPORAL LOBE THEORY

In reviewing the literature critically, it is surprising to find that the balance of experimental evidence actually does not support the temporal lobe localization. Thus, Sanger, Brown and Schäfer[18] failed to confirm Ferrier's original experiments on the monkey. In man, von Bechterew[7] found in one case that bilateral destruction of nearly the whole hippocampal gyrus and of a part of Ammon's horn and uncinate gyrus had left the gustatory function undisturbed. Henschen[37] collected 18 cases in an effort to localize the cortical taste area in man, reaching the conclusion that hippocampus and Ammon's horn seem not to subserve the sense of taste, but he did not regard this conclusion as decisive. Other experiments and observations point directly to a representation of the sense of taste in a definite region of the cerebral cortex, separated from the sense of smell. Two such theories have been advanced.

INSULA THEORY

Some authors believe that the *anterior insula* is the cortical area for the sense of taste. This theory was based originally on the experiments of Bechterew's pupil, Gorschkow,[34] who found, in 43 dogs, that gustatory disturbances follow destruction of the anterior-inferior parts of the gyri sylviacus, ectosylvius, and compositus anterior. In applying these results to man, Bechterew suggested that the cortical taste area is probably located near the motor areas for tongue movements, chewing, and swallowing, i.e., "in the region of the operculum in the neighborhood of the insular gyri." But Bechterew was not able to provide a more precise localization, for no clinical evidence was available at that time except some cases of pseudobulbar paralysis with affection of the parietal operculum, in which, as Bechterew says, "more or less pronounced" gustatory alterations were reported. Campbell,[19] from an anatomical consideration, held that the area in the human brain which corresponds to Bechterew-Gorschkow's taste area in dogs is not the parietal operculum but the anterior insula. Campbell, therefore, advanced the tentative hypothesis that the cortical taste area is located there. This theory has received support from Adler,[2] who observed a case of a tumor in the first temporal gyrus and extending into the region of the insula. She emphasized, in support of the insular theory, that gustation was impaired without damage to tactile sensibility or to olfaction. However, it is conceivable that a tumor in the insula might exert pressure on the inferior part of the parietal operculum without affecting the somatic sensory tongue area, provided the latter is more superiorly situated.

Tilney and Riley[70] suggested that the anterior insula is related both to gustation and olfaction, and pointed out that the anterior insular region is histologically related to the olfactory cortex.

PARIETAL OPERCULUM THEORY

Ten years before the Bechterew-Gorschkow localization of the cortical taste area in the parietal lobe, Gad[32] and his pupil Schtscherbak[61] found loss of taste* in rabbits after bilateral destruction of that cortical area which also subserves voluntary swallowing movements. This report remained unnoticed in the literature until Bremer[14] localized the cortical taste area of rabbits in the masticatory area. Ectors,[25] in Bremer's laboratory, found changes in the oscillogram of the masticatory area when the mouth of the rabbit was stimulated with quinine, but he also obtained this effect by stimulation of the olfactory sense organ. Ectors considered this result to be an expression of the "habitual synergy of the olfactory and gustatory activities."

The writer has described in preliminary communications a series of cases in support of the parietal operculum theory. Marked

* Bitter was the only taste quality examined in these experiments.

gustatory disturbances were demonstrated by semi-quantitative methods in cases of brain injury caused by bullet wounds in which the lesions involved the parietal operculum. On this basis the cortical taste area was localized at the foot of the postcentral gyrus, a region corresponding to Brodmann's area 43.* Owing to the closeness of the "taste area" to the masticatory area in the precentral gyrus and to the primary auditory field in the transverse gyri of the temporal lobe, the gustatory disturbances usually appear as a part of a syndrome held to be characteristic of injuries in this region. This syndrome was described as the "taste, chewing, hearing triad" (Fig. 4). These findings were corroborated by Kleist[46] from further cases. Foerster[30] confirmed the connection between the parietal operculum and gustatory function by electrical stimulation in conscious subjects in the course of intracranial operations. However, he did not detect loss of taste in man after unilateral extirpation of the parietal operculum. Foerster refers to Adler's case and holds that the question of the localization of the cortical taste area is not yet settled.

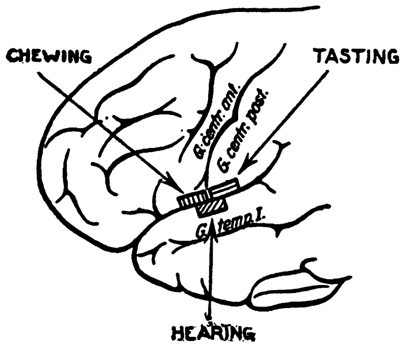

FIG. 4. Topographical basis of the taste-chewing-auditory triad. (After Börnstein.)

CONCLUSIONS

There remain, then, three rival theories of localization of the cortical taste area in man; i.e., the temporal lobe, the anterior insula, and the parietal. It has been brought out above that the alternatives to a parietal operculum localization have little basis in clinical, experimental, and anatomical data. In a subsequent paper of this series, semi-quantitative methods for the examination of gustatory sensibility will be described and a detailed report on the application of such methods to a series of cases of injury to the parietal operculum will be made. In a further communication, experiments on the cortical representation of taste in the monkey will be presented.

* In one of these cases, epileptic seizures began with gustatory aura on the side of a gustatory impairment.

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