

## Mechanisms of Oral Sensation

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**Abstract.** Sensory nerves that supply mechanoreceptors in the mucosal lining of the oral cavity, pharynx, and larynx provide the substrate for a variety of sensations. They are essential for the perception of complex or composite sensory experiences including oral kinesthesia and oral stereognosis. Relevant to the concerns of the oral health care delivery specialist they also contribute to initiation of reflexes and coordination and timing of patterned motor behaviors. The response of oral mechanoreceptors to natural stimuli is determined to a large degree by morphological factors such as the nature of the relationship between nerve ending and certain cellular specializations, their distribution in the mucosa, the diameter of their primary afferent nerve fibers, and the central distribution of these fibers in the brainstem. Because of morphological similarities to certain cutaneous mechanoreceptors, the mucosal lining may be considered as an internal continuation of the large “receptor sheet” for localization and detection of mechanical stimuli. In some regions of the oral, pharyngeal, and laryngeal mucosa, this analogy is appropriate whereas in others, existing data suggest a different role consistent with regionally specific demands (i.e., initiation of protective reflexes).

**Key words:** Oral mechanoreceptors — Trigeminal nerve — Spinal trigeminal nucleus — Sensory nucleus — Nucleus tractus solitarius — Ventrobasal thalamus — Deglutition — Deglutition disorders.

Many of the receptor types located in the epidermis and dermis of the skin are also distributed throughout the mucosal layers of the oral cavity, pharynx, and larynx. Sensory nerves that supply mechanoreceptors in the mu-

cosa serve in a variety of capacities including sensation, composite sensory experiences (e.g., oral kinesthesia and oral stereognosis), reflex initiation, and modulation of patterned motor behavior. The functional repertoire of these receptors depends not only on their distribution in mucosal tissues but in the nature of the central termination of their primary afferent nerve fibers in the brainstem. In other words, peripheral and central factors are responsible for the ultimate effects of sensory stimulus transduction at the receptor.

This manuscript is concerned with examining the relationships between the distribution and functional role of tactile mechanoreceptors in various parts of the oral cavity, larynx, and pharynx. After a brief introduction to the general pattern of mucosal innervation, two basic lines of experimental evidence will be considered: first, data regarding the central representation of mechanoreceptors in the anterior oral cavity and how this information is routed for oral perceptual mechanisms; second, evidence that addresses the role of mechanoreceptor information in the production of complex patterned behaviors.

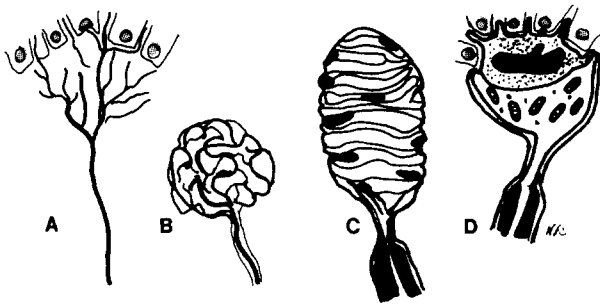
### Mechanoreceptor Morphology

Sensory receptors are distributed throughout the oral cavity, pharynx, and larynx. According to Munger [1,2], “All primates have a similar complement of corpuscular receptors in all of the oral mucosae including lips, palate, and dorsum of the tongue.” With respect to tactile mechanoreceptors, the mucosal lining is not particularly unique when compared to somatic cutaneous tissues. Therefore, from the perspective of receptor morphology, the sensory innervation of the mucosal epithelium, the underlying lamina propria, and when present, the submucosa may be considered to form a continuum with cutaneous surfaces (i.e., a receptor sheet).

The morphological classification of receptors provided here is based on a recent review by Munger [1].

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**Fig. 1.** Illustration of several types of sensory receptor endings. Free nerve endings (A) approach the epidermis where they separate and either end subepidermally or enter the epithelium to form intraepithelial "free nerve endings." The terminal ramification of a nerve fiber in simple corpuscular (glomerular) nerve ending is shown in (B). Although sensory corpuscles vary in size and developments, they all show the pattern of a complex terminal ramification of a nerve fiber among an organized collection of connective tissue cells (or Schwann cells). Receptors such as the Meissner's corpuscle (C) show a distinct lamellar arrangement of connective tissue cells. The Merkel cell neurite complex (D) is characterized by an association between a nerve fiber that ends in association with specialized granule-containing cells (Merkel cells) in the basal layer of the epithelium.

Other classifications have been offered [3,4] but the reader should be aware that apparent differences in opinion are often more semantic than substantive. Mucosal receptors include (1) corpuscular endings which include a variety of encapsulated receptors including the elaborate Meissner's corpuscle and a variety of smaller corpuscles which Munger [1] refers to as glomerular endings, (2) Merkel cell neurite complexes, (3) Ruffini-like endings, and (4) free nerve endings. Representative examples of 1–4 are shown in Figure 1.

### Distribution of Receptors in the Mucosae

The form of the epithelial lining, the underlying lamina propria, and the sensory nerves of the mucosae show regional differences [e.g., thickness of epithelium and underlying lamina propria, and presence (or absence) or a submucosa]. However, all mucosae possess a superficial plexus of the intraepithelial nerves and a deeper plexus in the lamina propria. The epithelia of the mucosae are more richly innervated and there are fewer complex endings in the lamina propria when compared with the skin. The epithelial innervation of the mucosae is common to all species and although the amount of innervation may show species-specific variations, the available forms of the sensory receptors are comparable. According to Dubner et al. [5] humans have the largest number and greatest variety of deep mucosal receptors.

### Specific Regional Distribution

One of the better documented examples of local regional specializations in receptor function is that associated with the taste buds. The concept that there are surfaces on the tongue that are more or less specialized for detection of certain taste substances (e.g., sweet, salty, sour, and bitter) is generally accepted. Another example of regional concentration of receptors with a specialized function is found in the tooth pulp where the predominant sensation elicited by stimulation is that of dental pain. It is possible that there are regional concentrations of functionally distinct tactile receptors in the mucosa. Differences in functional demands on the mucous membrane of the oral cavity led Ross et al. [6] to recognize a masticatory mucosa, a general mucosa, and the specialized dorsal surface of the tongue. A case will be presented later in this manuscript that certain regions of the pharynx and larynx are also specialized to accommodate specialized functional demands. However, there is clearly a need for more physiological evidence to firmly establish this point.

### Oral Cavity Receptive Field Size and Innervation Density

Innervation density (i.e., receptors/unit area, e.g.,  $\text{mm}^2$ ) on the cutaneous surface varies from one region to another. The lips and perioral tissues are among the most densely innervated cutaneous regions. The richness of peripheral innervation is reflected in the central nervous system by greater central representation of certain body parts. Tactile sensitivity also varies in different parts of the anterior oral cavity. Thresholds for detection of light touch are lowest on the tip of the tongue and hard palate [7]. Measures of two-point discrimination (i.e., ability to discriminate smaller differences between two points) show that the areas of greatest sensitivity are found in the tip of the tongue followed by the lips and the hard palate [8,9]. Receptor morphology in the periodontal tissues (i.e., gingiva and periodontal ligaments) and in the tooth pulp [5,10–12] has received extensive study. These receptors appear to be well suited for specialized sensory functions—the former in sensing bite force tooth displacement and the latter in signaling dental pain.

### Pharyngeal and Laryngeal Receptive Field Size and Innervation Density

The epithelia of the pharyngeal and laryngeal mucosae are more richly innervated than the skin and anterior oral cavity but deep receptors are fewer in number and are

generally less complex. The rich epithelial innervation is common to all species whereas there is a species hierarchy for deep receptors. The largest numbers and variety of deep mucosal receptors are found in humans [5]. The adult human nasopharynx contains relatively few organized endings; these include typical and modified Krause end bulbs (glomerular endings) and Meissner's corpuscles. The most richly innervated part of the pharynx is reported to be at the junction of the oral and nasal divisions. The receptors of the pharyngeal epithelium are predominantly free endings.

The larynx is supplied with two plexi of sensory nerves. Where the mucosa is not compressed, as over the arytenoid and cricoid cartilages, and is richly supplied with nerve terminals, a deep submucosal and superficial (proprial) plexus is the rule [5]. The receptors of the laryngeal and epiglottic epithelium are free endings and chemosensory nerve endings or taste buds. The base of the laryngeal face of the epiglottis is richly innervated. By contrast, the lingual face of the epiglottis is sparsely innervated and contains only free endings. The highest density of receptors is in the supraglottic mucosa nearest the arytenoid cartilages. The presence of two sensory plexi in the larynx and epiglottis as compared with one in the pharynx, suggests that sensibility is more acute or more highly organized in the larynx.

### Specific or Selective Properties

In considering the receptor complement in any organ or tissue, one cannot always attribute discrete functions to each morphological class of receptor. There is abundant evidence that functional diversity does not always require structural diversity. Some specialized endings obviously do possess a degree of stimulus specificity. For example, the role of the Meissner corpuscle in detection of vibration flutter and the Merkel neurite complex in tactile sensations are well documented. In contrast, morphologically identical free nerve endings represent a functionally heterogeneous population of fibers capable of transducing stimuli of multiple modalities. That is not to say that all free nerve endings are multimodal but that free nerve endings, which may respond to one modality, are morphologically indistinguishable from those that respond to other modalities. Free nerve endings in the pharynx and larynx contribute to sensations of pain (e.g., sore throat) and the ability to discriminate hot and cold liquids. Superficial receptors in the pharynx and larynx are also capable of initiating a variety of reflexes and more complex behaviors including respiratory arrest [5]. Morphologically similar receptors located in the epiglottis and glottis more than likely serve to initiate swallowing.

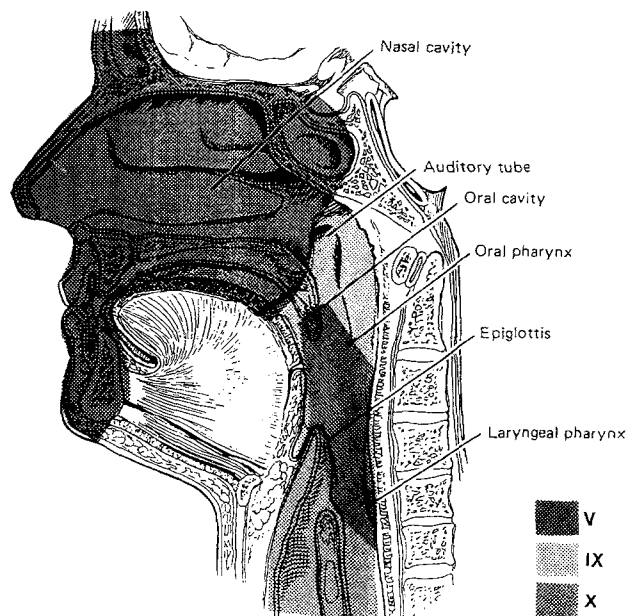


Fig. 2. This sagittal section through the head shows the peripheral distribution of the trigeminal (V), the glossopharyngeal (IX), and vagus (X) nerves along the tongue and the mucosae of the oral cavity, pharynx, and larynx. The darkened area between the oral and laryngeal pharynx represents overlap between IX and X. Adapted from Hiatt and Gartner [71], with permission.

### Primary Afferent Neurons

Sensory receptors in the oral cavity pharynx and larynx are innervated by fibers of the trigeminal (V), the facial (VII), the glossopharyngeal (IX), and the vagus (X) nerve. The cell bodies of the afferent fibers are located in sensory ganglia associated with these nerves. The V territory continues from the face and lips into the lining mucosa of the vestibule, includes the teeth, the periodontium, the areas overlying the hard palate, and the anterior part of the soft palate, and in humans extends to the superior portion of the nasopharynx in front of the tubal orifice. The glossopharyngeal nerve and the pharyngeal branch of the vagus nerve are the primary sources of sensory innervation of the pharynx. The sensory nerve supply to the larynx and epiglottis is primarily through X. There is some overlap in the innervation of the pharynx and larynx (Fig. 2).

### Response Properties—Afferent Physiology

A single primary afferent neuron has a peripheral process (the nerve fiber) that terminates in a variable number of receptor endings. It is believed that the endings of a single fiber are generally all of the same morphological type. However, the same may not be true for the func-

tional properties of these receptors. The functional properties of single primary afferent units have been studied by teasing individual fibers of different nerves, recording in the sensory ganglia, or more recently, by intraaxonal penetration of single axons that are subsequently labeled by intraaxonal injection with histochemically demonstrable anatomical tracers such as horseradish peroxidase (HRP). Single fiber studies of sensory nerves innervating the anterior oral cavity have been concerned with a range of topics including studies of the functional properties of receptors that innervate the mucosa, the tooth pulp, and in the surrounding periodontal tissues [for reviews see 5,13]. Many of these receptors produce a frequency-coded response in the afferent fibers to code stimulus intensity. However, patterns of activation are also important to the central nervous system in a variety of neural functions.

To study the properties of sensory endings supplying laryngeal structures, Storey [14] recorded from single fibers teased from the cat superior laryngeal nerve (SLN); he recorded 506 units from 40 cats. The most commonly encountered types of units were classified as proprioceptive (responsive to pressure applied over a laryngeal muscle or displacing cartilages), tactile (responsive to forces  $<0.3$  g applied to the mucosa), pressure (responsive to forces  $>0.3$  g and lacking responses to air puff), and water receptors. In addition, a number of other units were encountered that were only active during swallowing or showed hybrid or mixed characteristics (multimodal responses). Water receptors were activated by application of water to specific receptive fields. These same units either showed no response or had an attenuated response when the receptive field was tested with dilute saline or other test substances. Several manipulations led to the suggestion that the water response was chemically mediated (e.g., withdrawal of cations or anions from the receptor surface). There was a large overlap between fibers that showed responses to water and tactile stimuli. Storey argued that chemotransducer and mechanotransducer sites were different since the sensitivity of the two types of stimuli varied with different anesthetics. Laryngeal mechanoreceptors were also affected by thermal stimulation. Some tactile units show an increase in frequency to a thermal stimulus, others a fall, and still others no change. In most cases, firing frequency of tactile units increased with cold stimulation ( $20^{\circ}$ ), but units with proprioceptive receptive fields more commonly showed decreased firing frequency. The distribution and functional contribution of laryngeal and pharyngeal receptors with thermal sensitivity merit more study.

Knowing whether a single receptor, or a sensory unit consisting of several receptor endings, typically respond to more than one stimulus modality is critical to our understanding of the role of mucosal endings in perceptual mechanisms as well as in understanding their contri-

bution to oral motor behavior. It has not been fully resolved whether specific behavioral responses elicited in the pharyngeal and laryngeal mucosae depend upon activation of a unique population of mucosal receptors across large receptive field area, a specific pattern of afferent activation, or simply upon the total amount of afferent discharge in more focused regions [14,15]. It would be useful to know if stimulation of broad areas with specific combinations of afferent stimulation might in some way compensate for focal damage to areas with high innervation density. Considerations of this type have potential significance in developing and assessing treatment strategies used in patients suffering from dysphagia.

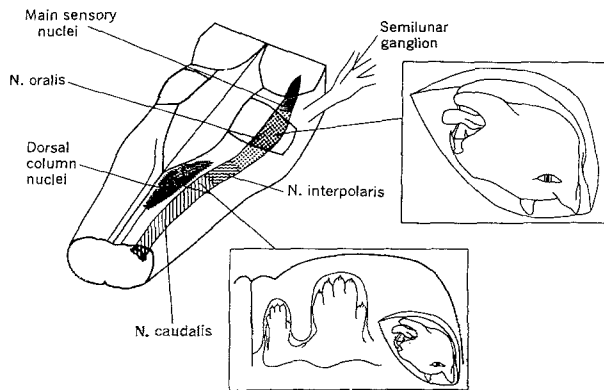
## Central Factors

### *Spinal Tract V*

The central processes of ganglion cells innervating the oral mucosa enter the pons via the sensory root of the trigeminal nerve and contribute to the spinal (descending) tract of the trigeminal nerve. Located in the dorsolateral region of the brainstem, the spinal tract extends from the pons to the second or third cervical spinal cord segment where the caudalmost fibers overlap with Lissauer's tract (dorsal longitudinal fasciculus). Fibers of the spinal trigeminal tract terminate in the adjacent trigeminal nuclei. Many of the larger diameter fibers of the trigeminal root bifurcate and ascend to terminate in the principal sensory nucleus, located in the pons. The descending branches of these fibers contribute to the spinal tract together with other fibers of the trigeminal root. Typically, the fibers in the spinal tract collateralize in course contributing terminal arbors in the morphologically defined subdivisions of the trigeminal sensory nuclei.

Afferent fibers of cranial nerves VII, IX, and X enter the brainstem at their respective medullary levels and most of these contribute to formation of a fiber bundle known as the solitary tract and terminate in the nucleus of the solitary tract. Many of these fibers are involved in gustation but many of the solitary tract afferents have a mechanosensory function. Some of the afferent fibers from these cranial nerves join the dorsal aspect of the spinal trigeminal tract, also contributing mechanosensory input to the trigeminal nuclei. Because of the embryological origin of the tissues they innervate, the small contingent of fibers that enter the trigeminal tract would technically be classified as visceral afferents.

Both the trigeminal and the solitary nuclei have distinct cytoarchitectural subdivisions. Within these subdivisions there also exists elaborate topographic organizations with respect to representation of different regions of the oropharynx and larynx. The general topographic or somatotopic representation in the trigeminal subnuclei is well documented. Fibers from different regions of the



**Fig. 3.** Drawing shows the location of the sensory components of the trigeminal brainstem nuclei including the principal (main) sensory nucleus, the components of the spinal trigeminal nucleus, and the somatotopic map of an inverted hemiface. Note that the oral cavity is oriented medially. Note also that perioral regions have a much greater central representation than regions around the eye and ears. This greater central representation is a reflection of the higher peripheral innervation density. Adapted from Mountcastle [72] with permission.

face are organized in the tract and subjacent nuclei in the form of an inverted hemiface (Fig. 3). Cells that respond to sensory stimulation of the oral cavity are medially located in the trigeminal nuclei whereas stimulation of more lateral and posterior facial structures excite cells in the lateral part of the nuclei. One of the important functions of the trigeminal system is in providing the substrate for perceptual processes involving the face and oral cavity. The following discussion will consider evidence regarding the properties of central trigeminal circuits consistent with this function.

Marfurt [16] described the terminal projection sites of afferents coursing in single nerve branches that supply the oral cavity via transganglionic transport of HRP. His experiments revealed that each area of the cat's head and face was represented as a longitudinal column that extended throughout most of the trigeminal brainstem nuclear complex. Later studies that relied on transganglionic transport of HRP [17–20] focused specifically on oral cavity representation in the trigeminal nuclei. These studies described complex patterns of representation of intraoral structures in both the rostral and caudal parts of the trigeminal nuclei. This mapping of peripheral structures in central sensory nuclei, which contains neurons that project this pattern rostrally in ascending pathways, is characteristic of central circuits involved in perception.

Extracellular recording of single brainstem neurons is a useful method to evaluate the response properties of central neurons that receive inputs from peripheral receptors. Combined with data from anatomical studies, extracellular recording permits one to begin an evaluation of the functional contributions of oropharyngeal and laryngeal afferents. Most recording studies [21–32] support the anatomical data showing that the oral cavity is

represented throughout the rostrocaudal extent of the trigeminal sensory nuclear complex and that this pattern is relayed to the thalamus from certain regions of the trigeminal nuclei.

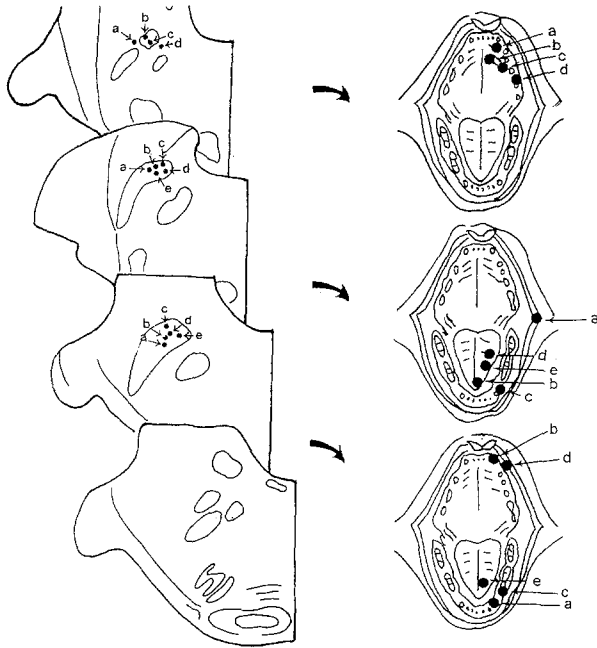
An important relationship of central neurons that receive primary afferent input is the extent that multiple sources of peripheral input converge on these cells. One might ask whether these cells are specific with regard to modality (i.e., are the cells responsive only to touch or temperature, etc.) or to location of the receptive field (i.e., is the receptive field size small, large, continuous, or discontinuous). It seems almost intuitive that neurons involved in the most discriminative types of sensory functions have small receptive fields, show little convergence, and are precisely mapped throughout central circuits. The pioneering work of Mountcastle [33] has amply demonstrated the existence of central circuits with these spatial- and modality-specific properties.

For afferent inputs to contribute to perceptual mechanisms they must terminate on neurons that project this information to the thalamus where it is relayed again to reach the cerebral cortex. Antidromic stimulation has been used to identify extracellularly recorded neurons that project to the thalamus [27,30]. We have used these methods to characterize response properties and spatial relationships of neurons that possibly contribute to perception and more complex experiences such as oral kinesthesia [30]. In these studies, peripheral nerve stimulation and systematically applied tactile stimulation (e.g., brush, pressure, and pinch) were used to identify single neurons in the brainstem. The receptive field size and locations mapped and the response properties were determined for each cell. Projection of trigeminal brainstem neurons to the thalamus was determined by antidromic stimulation of stimulating electrodes implanted in the ipsilateral and contralateral thalamus. After each experiment, brainstem recording sites were reconstructed from histologic sections.

#### *Oral Cavity Representation in the Rostral Brainstem*

The most rostral component of the trigeminal sensory complex is the principal sensory nucleus. It is dorsolateral to the trigeminal motor nucleus in the pons. Its rostrocaudal extent is slightly greater than that of the trigeminal motor nucleus. The feline principal sensory nucleus ( $V_p$ ) has been described in a number of studies [18,25,27,28,34,35]. It has been subdivided into a dorsal region ( $V_{pd}$ ) containing small densely packed neurons and a more loosely aggregated ventral region ( $V_{pv}$ ) which extends caudal to the trigeminal motor nucleus and overlaps with the more dorsally situated oral subnucleus of the spinal trigeminal nucleus.

The great majority of cells in the  $V_{pd}$  have peripheral receptive fields in the oral cavity including the ante-



**Fig. 4.** A series of drawings made from transverse hemisections through the principal sensory nucleus (left). The upper drawing represents the most rostral section and successively more caudal sections follow. The recording sites of ipsilateral trigeminothalamic neurons in recording sites in  $V_{pd}$  are indicated on the left and the intraoral receptive fields of each unit (a-e) are shown on the right side of the figure. From Ro and Capra [30] with permission.

rior part of the tongue, mandibular and maxillary periodontal ligaments, hard palate, and buccal mucosa (Fig. 4). Although most of these neurons were activated by light touch or pressure and had discretely localized receptive fields ( $<1 \text{ cm}^2$ ), cells that respond to noxious stimuli have been identified in this area. Most of the units with periodontal receptive fields in the principal sensory nucleus were slowly adapting with some spontaneous activity. The response frequency to mechanical stimuli was related to the direction and magnitude of applied forces. Cells located in the feline  $V_{pd}$  appear to project exclusively to the ipsilateral thalamus. In contrast, neurons in the  $V_{pv}$  with intraoral receptive fields project to the contralateral thalamus. Therefore, some species have a dual or bilateral projection of sensory information from the anterior oral cavity to thalamus.

Trigeminothalamic neurons in the principal sensory nucleus have been identified by making central injections of HRP and looking for retrogradely labeled cells in the brainstem. Bilateral projections to the thalamus from the principal sensory nucleus have been documented in many species including cats, nonhuman primates, and man [36-39]. However, this projection appears to be mainly contralateral to the rabbit and the rat [37]. Figure 5 shows distribution of ipsilateral trigeminothalamic neurons seen after a unilateral injection of

HRP is made into the ventroposteromedial nucleus of the thalamus. The labeled neurons ipsilateral to the injected side are located in  $V_{pd}$ . Neurons contralateral to the injected side are scattered in  $V_{pv}$  (not shown). Another point that emerged from the anatomical studies was that practically all the cells of the principal sensory nucleus, regardless of nuclear location, projected to one or the other side of the thalamus.

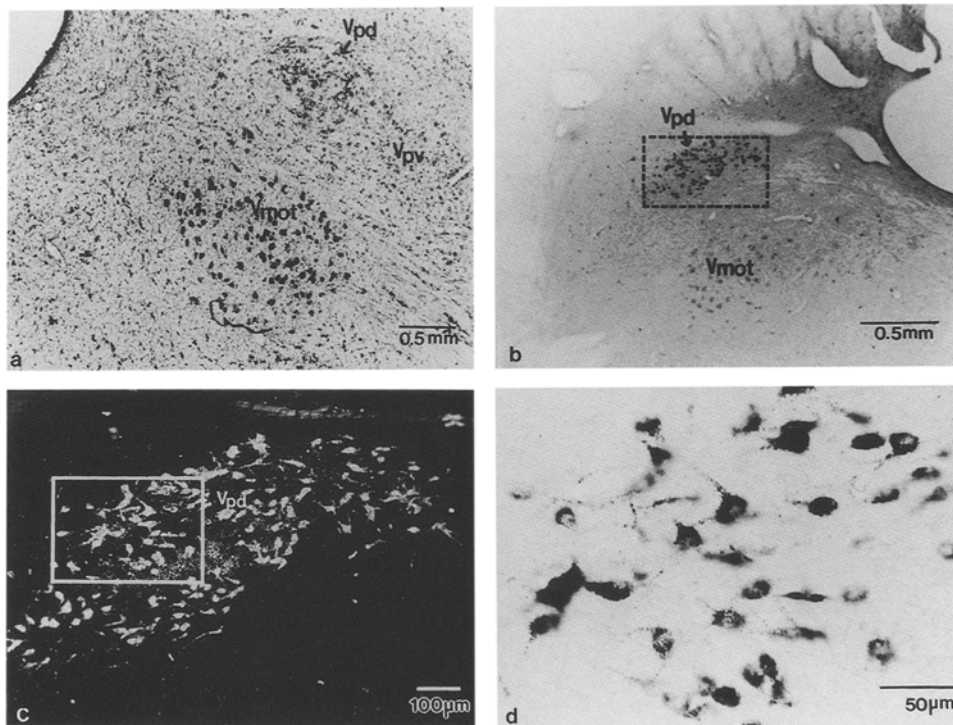
The large myelinated fibers that terminate in  $V_p$  are known to innervate more complex corpuscular receptors (e.g., Meissner's corpuscles) and glomerular receptors in the oral mucosa. This nucleus also receives input from a variety of receptor endings in the periodontal ligaments including several modified Ruffini endings [10,12]. The receptive field properties of most intraoral units recorded in the feline  $V_p$  under barbiturate anesthesia, are small and show little convergence, and most of these cells project to the thalamus. Therefore, the principal sensory nucleus has all of the characteristics to serve as an important link in the transmission of the most discriminative types of sensory information from the oral cavity.

#### *Oral Cavity Representation in the Caudal Brainstem*

The spinal trigeminal nucleus in oral sensory mechanisms also contains many neurons with properties not unlike those observed in the principal sensory nucleus. The spinal trigeminal nucleus is generally subdivided into an oral, an interpolar, and a caudal subnucleus on the basis of cytoarchitectural criteria. Cells with intraoral receptive fields are found in all three subdivisions including neurons with receptive fields in the periodontium, the oral mucosa, the hard and soft palate, and the mucocutaneous junction of the lip. Some of the periodontal units showed very specific directional and force responses applied to one tooth whereas others responded to stimulation of multiple teeth. It has been suggested that the caudal part of the interpolar subnucleus contains many neurons with functional properties similar to cells in the principal sensory nucleus which project to the thalamus. Trigeminothalamic projections from the spinal trigeminal nucleus are exclusively contralateral. Although the oral cavity is represented throughout the rostrocaudal extent of the nucleus, the number of thalamic projection neurons varies from one region to another [27,29].

#### *Laryngeal and Pharyngeal Representation in the Brainstem*

The central representation of the pharynx and larynx has not been studied as extensively as the anterior oral cavity. Sweazey and Bradley studied the responses of neurons to mechanical, thermal, and chemical stimulation of the



**Fig. 5.** Photomicrographs showing the cytoarchitectural features of  $V_p$ . The compact clustering of cells in  $V_{pd}$  located dorsal to the trigeminal motor nucleus ( $V_{mot}$ ) contrasts sharply with the cellular density in  $V_{pv}$  in cresyl violet-stained transverse sections. The distribution of HRP-labeled neurons in rostral  $V_{pd}$  that results from an injection placed in ipsilateral VPM (**b–d**). A higher power darkfield photomicrograph (inset) shows cytoarchitectural features of labeled cells (**b**) and the brightfield photomicrograph (**d**) shows a higher magnification (inset) of **c**. Adapted from Ro and Capra [30] with permission.

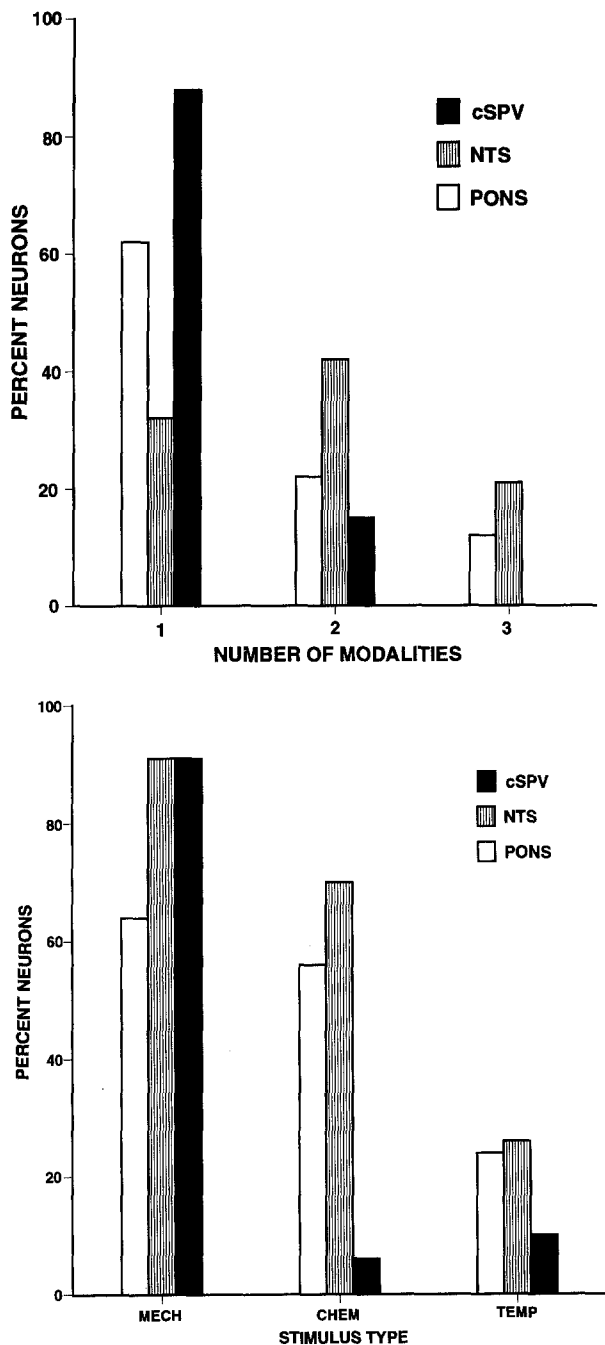
epiglottis and upper airways in rostral pons [31], in the caudal parts of the trigeminal nucleus [32], and in the nucleus solitarius of lambs [40].

In addition to input from the trigeminal nerve, the caudal subnucleus interpolaris and the rostral subnucleus caudalis receive afferent terminations from cranial nerves VII, IX, and X [40,41]. Their caudal recording sites included the nucleus tractus solitarius, the caudal part of the interpolar nucleus, and the rostral part of the caudal subnucleus. They identified neurons in the lamb trigeminal nucleus that responded to mechanical and thermal stimulation of the pharynx and larynx. Some of the cells showed multimodal responses but convergence was most often reflected in receptive field size. Convergence of different receptive fields was rare. In many respects, the properties of central neurons that received input from the posterior oral cavity and upper airway and terminated in the trigeminal nucleus had similar responses to trigeminal neurons that receive input from the anterior oral cavity. The somatotopic pattern in the trigeminal nucleus of the lamb was the same as reported for other species (inverted hemiface). Palatal representation was ventral to tongue representation.

Recordings in the pons were preferentially directed toward a region known to receive both upper air-

way and intraoral input. Most of their rostral recordings were made just dorsomedial to and overlapping the medial border of the principal sensory nucleus and rostral subnucleus oralis, an area designated as PONS. This area may include the supratrigeminal region described in other species and adjacent parts of the reticular formation. Multimodal responses and convergence of different receptive fields was rarely observed in the trigeminal nuclei proper. The majority of the neurons recorded in the trigeminal nucleus were activated primarily by mechanical stimuli. A few trigeminal units responded to thermal stimuli, and chemical stimuli were rarely effective. In contrast to units recorded in the trigeminal nucleus, mechanical, thermal, and chemical stimuli were effective in activated cells located medial to the trigeminal nucleus in PONS and within the solitary nucleus. Many more of these showed multimodal responses. Figure 6 summarizes the results of these experiments with regard to modality representation in different brainstem nuclei.

Another important point that emerged from the studies by Sweazey and Bradley was that units with the smallest receptive fields, reflecting input from regions with the highest innervation density, innervated the epiglottis. Table 1 summarizes the receptive field sizes they



**Fig. 6.** A summary of neurons that respond to mechanical, chemical, or thermal stimuli or some combination of these stimuli that were recorded in the caudal spinal trigeminal nucleus (cSPV), the nucleus tractus solitarius (NTS), or the more rostral trigeminal nucleus and adjacent reticular formation (PONS) in lambs. Note that most of the neurons recorded in cSPV are unimodal and responded to mechanical stimuli. Most of the multimodal units were found in NTS and PONS. Adapted from Sweazey and Bradley [31], with permission.

measured from different mucosal regions. It would be interesting to know whether the greater innervation density in this region is associated with differences in 2-point tactile discrimination and the ability to localize stimuli or

**Table 1.** Mean receptive field size for neurons isolated in the lamb brainstem

| Location         | Receptive field size* |
|------------------|-----------------------|
| All cSpv neurons | 130.7 ± 17.2          |
| Palate           | 132.3 ± 28.0          |
| Tongue           | 143.9 ± 28.7          |
| Epiglottis       | 22.1 ± 2.6            |
| All PONS neurons | 258.3 ± 34.6          |
| Palate           | 296.3 ± 149.3         |
| Anterior tongue  | 291.5 ± 56.5          |
| Posterior tongue | 273.5 ± 65.2          |
| Epiglottis       | 29.2 ± 5.4            |

This table summarizes the receptive field sizes of neurons with receptive fields located in the oral cavity, pharynx, and larynx, recorded in the caudal trigeminal nucleus and in the PONS (see text) of lambs. Receptive field sizes are means ± SE and are stated in mm<sup>2</sup>. Data from cells with convergent receptive fields are not included. From Sweazey and Bradley [31] with permission.

just an area with enhanced sensitivity to light touch. One scenario is that multimodal information originating in oropharyngeal and laryngeal receptors converge on interneurons in the nucleus tractus solitarius and adjacent reticular areas that are involved in reflex initiation and activation of the swallowing pattern generator whereas other fibers from the epiglottis, perhaps relayed through the trigeminal nerve, provide for perceptual dimensions of the stimulus. Neurons showing a great deal of primary afferent convergence and having relatively large receptive fields would seem more suited for initiation of reflexes and more generalized functions (e.g., arousal, affect). Such generalizations are useful but the reader must keep in mind the important caveats that estimates of receptive field size and the extent of convergence are heavily influenced by a number of experimental variables, notably, the use of different anesthetic agents. Convergence has been amply demonstrated in the trigeminal nuclei and this has been cited as an important central mechanism for referral of orofacial pain [23,24]. An exciting line of evidence clearly shows that variety of influences such as deafferentation injuries can produce changes in receptive field properties of neurons [5] (i.e., there is a certain plasticity to all of these maps). An obvious example of deafferentation occurs in the patient with Wallenberg's syndrome if the infarction includes the spinal trigeminal tract and nucleus. Thorough understanding of how cases of "deafferentation" seen in the clinic affect the normal functions of the mucosae are critical to realizing the potential for interventions designed to treat the patient with swallowing disorders of central origin.

#### *Oral Cavity Representation in the Ventrobasal Thalamus*

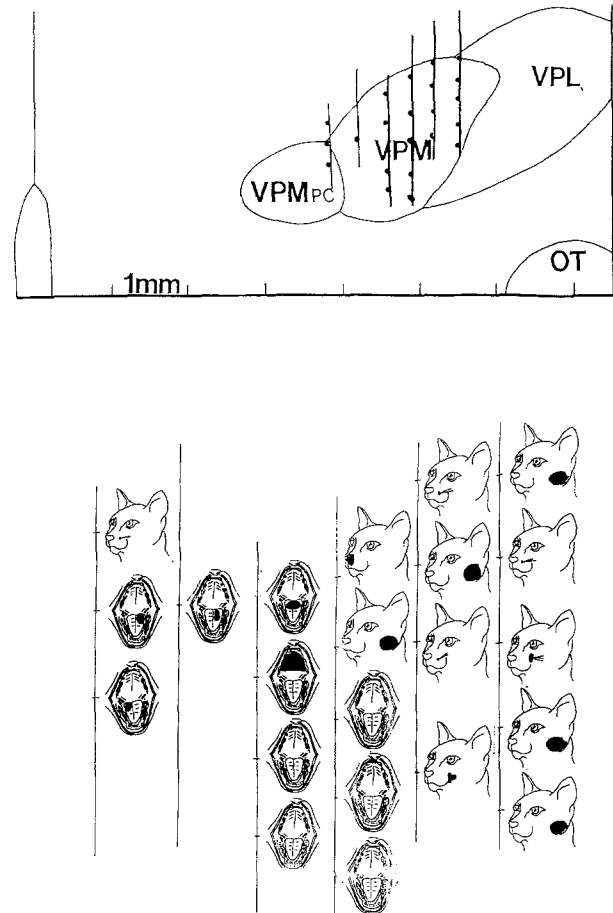
The site for thalamic relay of most information traveling in ascending somatosensory pathways is the ventrobasal



nucleus which consists of the ventroposterolateral (VPL) and ventroposteromedial (VPM) nucleus. Microelectrode studies of the receptive fields of single and multiple units in the ventrobasal thalamus confirm that most of the information from the face and oral cavity terminates in VPM [36]. Jones and Friedmann [36] demonstrated that ipsilateral and contralateral intraoral regions are represented in separate parts of the VPM in monkeys. A highly organized somatotopic map is preserved from the lower brainstem, which is consistent with the role of these circuits in the most discriminative types of sensation, including two-point tactile discrimination. We have conducted preliminary studies of this region in anesthetized cats (unpublished observations). In these experiments, thalamic neurons were activated by stimulation of the face and intraoral structures with brush, pressure, pinch, and electrical stimulation of trigeminal nerve branches. Forty-three single neurons were identified. In addition, we recorded multiple unit activity evoked from intraoral stimulation in 28 additional sites. Reconstruction of the recording sites suggested that the most medial part of VPM receives the input from the ipsilateral and contralateral oral cavity whereas input from the contralateral facial skin, hair, vibrissae, and muscle projects more laterally (Fig. 7). The receptive field sizes of the single units were quite varied and were generally smaller for neurons receiving input from areas known to have a high innervation density. A few cells with bilateral receptive fields, usually of the tongue or palate, were identified. The crossed and uncrossed projections of the trigeminal sensory nuclei provide the oral cavity with significant bilateral representation in the thalamus. Presumably this bilateral representation is relayed to the cerebral cortex where information is distributed to regions involved in the most complex types of sensory functions.

#### *Sensory Modulation of Oral Motor Function*

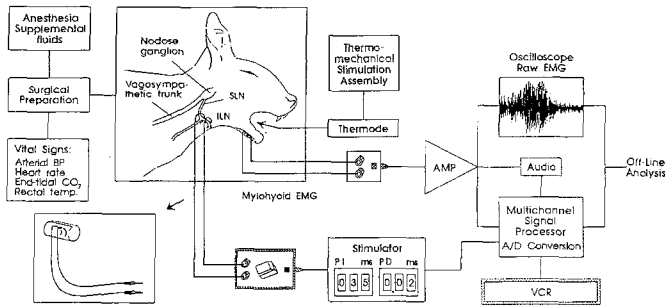
In addition to providing information for perceptual mechanisms, oropharyngeal and laryngeal afferents are the afferent link for reflexes, and are also capable of modulating more complex patterned behaviors. Chewing and swallowing involve significant coordination between the muscles of mastication, tongue muscles, and muscles in the cervical region [5]. The basic patterns for mastication and swallowing are thought to be controlled by central pattern generators [42,43]. However, patterned behaviors are subject to modulation from peripheral afferent input and from suprasedgmental regions such as the cerebral cortex. In a review of peripheral effects on the swallowing program, Jean [44] reported that peripheral stimuli can modify the amplitude and duration of the electromyogram (EMG) recorded from buccopharyngeal muscles, and mentions that the presence of a food bolus strongly excites vagal fibers in anesthetized rats or con-



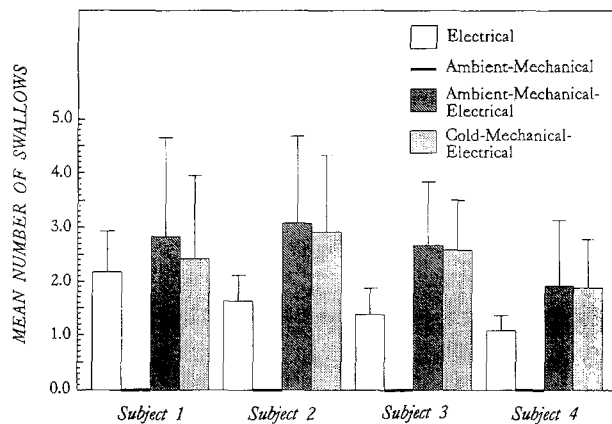
**Fig. 7.** Summary of the receptive fields of single and multiple units observed in ventroposteromedial nucleus of the thalamus in a single medial to lateral series of electrode penetrations made in one experiment. Note the presence of ipsilateral, bilateral, and contralateral receptive fields in the most medial parts of VPM (blackened areas on figurines in lower part of the drawing).

scious sheep. Afferent inputs may induce excitation or inhibition of neurons in the central (swallowing) network. What remains to be answered are the specific activation patterns and modalities represented by the afferents that produce these central effects.

The normal stimulus for the onset of pharyngeal swallowing is the arrival of a liquid or food bolus but several forms of peripheral stimulation are capable of eliciting swallowing. These include electrical stimulation of cranial nerves or their branches [45–48], laryngeal water stimulation [14,15,49], and oropharyngeal mechanical stimulation [50–52]. The rate of swallowing produced by electrical stimulation of one nerve may be facilitated by simultaneously stimulating other nerve branches, either on the same side or contralateral to the first stimulus. Simultaneous electrical stimuli just below or at threshold applied to two different nerves, each capable of producing a reflex response, may summate to produce a reflex response [53].



**Fig. 8.** Schematic diagram showing the experimental setup that was used in an experiment [59] that evaluated the effects of different thermal stimuli applied to the feline pharyngeal mucosa while simultaneously stimulating the internal laryngeal nerve (ILN). SLN = superior laryngeal nerve.



**Fig. 9.** Results on swallowing observed by electrical, mechanical, concurrent cold mechanical and electrical, and concurrent ambient mechanical electrical stimulation of the pharyngeal region. ANOVA for repeated measures indicated a significant main effect in number of swallows ( $F = 66.47$ ;  $p < 0.05$ ) during combined stimulation conditions. Tukey's HSD test revealed that the two forms of thermomechanical-electrical stimulation evoked significantly more swallows than electrical stimulation alone.

Cold probing (bilateral light stroking with an ice-cold laryngoscope) of the base of the anterior faucial pillar has been reported to improve "pharyngeal transit times" in some patients with dysphagia [54–57]. This procedure is referred to as "thermal stimulation" or "thermal sensitization" [54,56,57]. Despite the reported facilitating effect of thermal sensitization, the optimal temperature ranges or stimulus conditions have not been systematically studied. In addition, not all workers agree that this is an effective therapy [58]. A recent study attempted to determine whether swallowing responses elicited by unilateral electrical stimulation of the internal laryngeal nerve (ILN) could be facilitated by applying various forms of mechanical stimulation in an adjacent nerve territory and whether temperature of the mechanical test instrument might be an important variable [59]. In

other words, an attempt was made to dissect out the contribution of two afferent modalities (thermal and mechanical) in the elicitation of swallowing responses.

Ambient (25.3°C) or cold (8.9°C) probing of the region equivalent to the anterior faucial pillar was performed with a thermode in cats (Fig. 8). Frequency of probing and total distance traversed by the probe was constant for all experiments. The mechanical stimulus alone did not produce swallowing in the anesthetized cat although more posterior probing was effective. The lack of swallowing from the more anterior stimulation site does not preclude the possibility that afferents in this region may contribute to facilitation of swallowing in combination with other types of afferent stimulation. Electrical stimulation of the ILN was performed according to previously described methods [46] (30-sec pulse train, 0.2 msec; 30 Hz) at threshold (defined here as the lowest current required to produce swallows). A partially randomized repeated measures design was used to verify (1) threshold to electrical nerve stimulation before each trial and to test three additional experimental conditions including (2) ambient-mechanical stimulation, (3) concurrent ambient-mechanical and electrical stimulation, and (4) concurrent cold-mechanical and electrical stimulation. Suprahyoid EMG and visual confirmation were used to document the onset and occurrence of full swallows.

Although mechanical stimuli alone did not generally elicit swallows, analysis of variance (ANOVA) for repeated measures indicated a significant main effect in number of swallows ( $F = 66.47$ ;  $p < 0.05$ ) during combined stimulation conditions (Fig. 9). Tukey's HSD test revealed that the two forms of thermomechanical-electrical stimulation evoked significantly more swallows than electrical stimulation alone. However, the tested thermal conditions were not significantly different among conditions with respect to number of swallows or onset latency.

A tentative conclusion based on these results is that central summation of mechanical and electrical stimuli is responsible for the observed facilitation. However, a number of alternative mechanisms operating at the single neuron level may be proposed and tested in the laboratory. There is a need for further studies to systematically evaluate modality representation in the pharyngeal and laryngeal mucosae and to study the effects of manipulating these inputs on swallowing performance. With respect to thermal stimuli, the effects of a wider range of temperatures and perhaps, more importantly, the direction and rate of change of thermal stimuli should be tested for effects on initiation of swallowing. However, such studies conducted in animal models should take into account morphological and functional differences in feeding mechanisms among species [60,61].

## Future Strategies and Clinical Relevance

The sensory innervation of the oral cavity provides us with a complex palette of sensory experiences including touch, pressure, 2-point discrimination, taste, and temperature. All of these sensations contribute to more complex sensory phenomena such as oral stereognosis [62,63]. Various tests of sensory function have been applied to the anterior oral cavity (e.g., two-point tactile discrimination and oral stereognosis) in normal subjects and patients with pathological speech [8,9]. Not all of these studies support a critical role for sensory influence on complex oral motor behavior [5,64,65]. However, it is clear that sensory input is capable of modulating complex motor patterns or contributing to learning of oral motor patterns [5,66–69], though it is difficult to evaluate the significance of observations based on experimental deafferentation either by lesioning or by injections of local anesthesia. In many cases, the fundamental behavior is not abolished but certain aspects of the total oral motor pattern are altered. Subtle deficits may exist that are beyond our test instruments to measure, particularly with development of initial patterned behavior in infancy. Undetected deficits in young patients may have profound implications in the oromotor performance in later years.

Knowledge gained from the basic science laboratory regarding sensory mechanisms can be useful when interpreted from the perspective of potential clinical significance. Much more work is needed in the area of neuronal mechanisms that lead to the overt behaviors seen in the clinic. A careful consideration of how tactile mechanosensory and thermal information impinging on the mucosae is gated in the central nervous system, comparable to studies of cutaneous regions and the anterior oral cavity, has yet to be performed. In addition to aiding in diagnosis, this type of information could lead to the design and optimization of reliable and valid therapies to improve care of the patient with oral sensorimotor impairments.

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