# Separate Relays of Tactile, Pressure, Thermal, and Gustatory Modalities in the Cat Thalamus.* (30821)

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Thalamic neurons that respond to stimulation of the cat tongue have been studied by Landgren(5). At the time of his studies, however, the borders of the thalamic projection regions for the chorda tympani, the ninth, and the lingual nerves were poorly defined. This situation as well as the use of glass electrodes could have been the major factors contributing to the difficulties in pinpointing the exact thalamic position of neurons within the nucleus that he studied. This in turn led him to believe that the neurons which relay various lingual modalities are intermingled in the arcuate nucleus of the cat thalamus.

Since the time of his studies, the borders of the thalamic projection regions for lingual afferents have been delineated(4), and consequently, single neurons in these regions could be localized more effectively. Under these conditions it was found that a clear topographic separation of modality specific neurons existed. Furthermore, the modality specificity was expressed to such a degree as to permit a division of that group of neurons which responded to mechanical stimulation of the tongue. Previous work indicated (2) that such neurons form a singular group. In the present study it was possible to distinguish between neurons that subserve touch from those that subserve pressure. This functional division was also associated with a distinctly separate localization of such neurons in the thalamus.

*Materials and methods.* Fifteen cats anesthetized with Nembutal were used for the study. In order to isolate electrophysiologically single thalamic neurons which respond to stimulation of the cat tongue, tungsten microelectrodes with a tip diameter of 1 to 3 $\mu$ were stereotaxically oriented to reach the thalamic region for the projection of lingual afferents. At various intervals of microdriving of the electrode, the tongue was stimulated alternately with several types of stimuli. Touch and pressure were applied by using a glass stylus with a thin but dull tip. Warm water at 42 to 45°C, cool at 20 to 22°C, and cold water at 5 to 8°C were applied by drop-squeeze bottles while a Yellow Springs tele-thermometer registered the tongue surface temperature continuously. A drop-squeeze bottle was used also for applying a solution to various localities of the tongue to test the neurons for their response to gustatory stimulation. This solution contained 4 different substances at the following concentrations: 0.01 M quinine hydrochloride, 1.0 M sucrose, 1.0 M sodium chloride, and 0.1 N hydrochloric acid. Although a number of authors(3) have reported that the cat tongue is quite insensitive to sweet substances, sugar was included in the mixture in order not to miss whatever meager stimulation it might effect. Any one application of a particular type of stimulus was, of course, preceded by thorough washing of the tongue with water at 35°C. The taste solution was also maintained at 35°C to exclude thermal stimuli when gustatory stimulation was intended. Whether or not touch or pressure played any role in the application of fluids to the tongue could be readily ascertained by testing the response of the same thalamic neuron to separate application of pure touch and pressure stimuli. Before an experiment was terminated, a tiny lesion was made in the place where the last neuron was localized. This was accomplished by passing a 0.1 ma DC current through the tip of the microelectrode for approximately 5 seconds. This lesion was later identified on Nissl stained coronal sections cut at 40 $\mu$ by the freezing technique. The position of the neurons studied in a particular preparation was reconstructed by re-

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FIG. 1. Response pattern of a thalamic neuron elicited by tactile stimulation of its peripheral field on the cat tongue. Dark column at beginning of the spike burst indicates the moment at which one of the barbs of the tongue was deflected. In records of this and the following figures negativity is downward.

lating their stereotaxic location to the stereotaxic positioning of the lesion.

*Results and discussion.* Although a couple of hundred thalamic neurons were found to respond to some form of stimulus, only 60

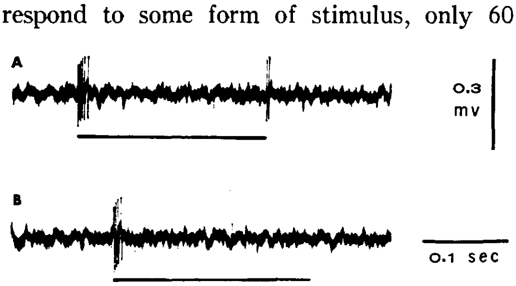


FIG. 2. Response patterns of a functionally specific tactile neuron of the thalamus elicited by application of pressure to a minute locus of the cat tongue. Duration of the stimulus is indicated by a continuous line under the active oscilloscope trace.

of them could be held at the tip of the microelectrode sufficiently long to test them thoroughly with all of the stimuli in the series. Thirty-three of these responded to touching of the tongue in a limited area, 8 responded to pressure, 10 to cooling, and 9 to the stimulation of the tongue by the mixture of taste solutions. No thalamic neurons were encountered that responded to warming of the tongue, although it was observed that some neurons which responded to cooling, decreased their spontaneous firing rate when the tongue was warmed. The peripheral receptive fields of the thalamic neurons were in most cases very restricted. Response patterns of a thalamic neuron to the stimulation of a particularly small peripheral field are illustrated in Fig. 1. These responses were elicited by quick deflection of one of the barbs located near the midline of the tongue. A similar deflection of other barbs in its near vicinity was ineffective. More than two-thirds of the neurons responsive to tactile stimulation of the tongue had as small peripheral fields as the one described. These neurons were located in the thalamus ipsilaterally with respect to the effective locus of stimulation. Neurons

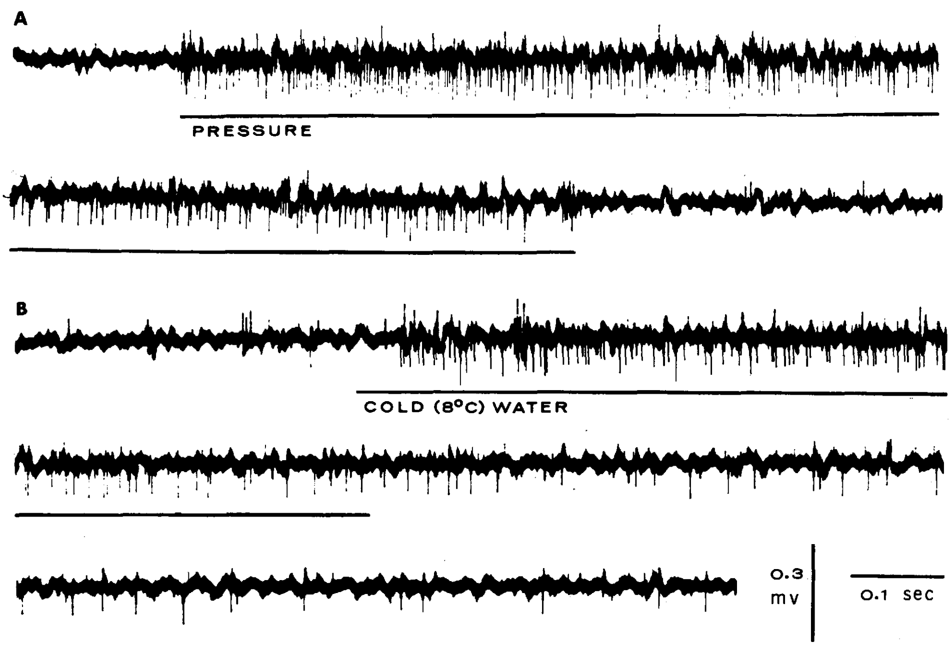


FIG. 3. *A*: Response pattern of thalamic neurons sensitive to pressure applied to a pinpoint locus on the edge of the cat tongue. *B*: Response of the same cluster of thalamic neurons as in part *A* to stimulation of the same locus of the tongue with ice water.

with a contralateral position in the thalamus had considerably larger peripheral fields, and a few neurons which received bilateral projections could be activated by tactile stimulation of almost any locus on the surface of the tongue. Regardless of the size of the peripheral field, all neurons that could be activated by tactile means showed similar response characteristics. Each stimulation was followed by a burst of spikes which terminated as suddenly as it began. These response characteristics remained virtually unaltered when the peripheral field of such a neuron was stimulated by pressure instead of touch. Response of a functionally specific tactile neuron to pressure is illustrated in Fig. 2. This neuron did not respond to pressure but with an "on" and an "off" burst of spikes, and sometimes, (Fig. 2B), there was only an initial "on" response. Such a response is qualitatively no different from the burst of spikes elicited by a tactile stimulus. Neurons which responded specifically to pressure remained active throughout the duration of the stimulus. This is illustrated in Fig. 3A. Although the record reveals responses of several neurons, their peripheral field was very restricted. It was not larger than a square millimeter in size and was located ispilaterally on the very edge of the tongue approximately 10 mm from the tip. This locus of the tongue was the effective peripheral field for 7 other similar recordings obtained from different experimental preparations. All of these pressure sensitive thalamic neurons had ipsilateral location in the thalamus. A very similar response was obtained (Fig. 3B) from the group of neu-

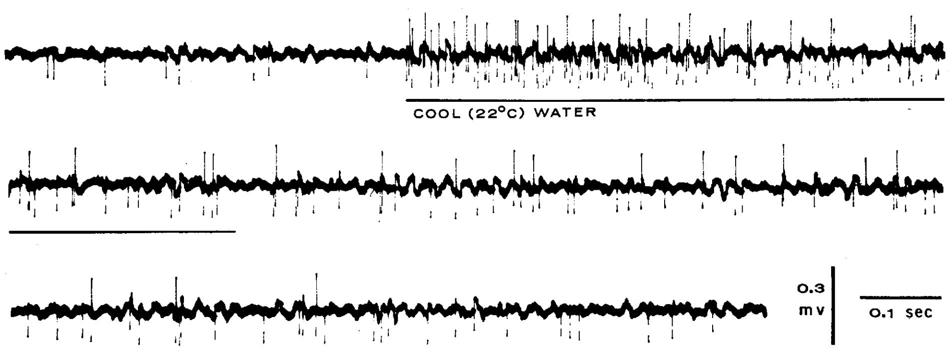


FIG. 4. Response patterns of thalamic neurons sensitive to cooling of a restricted locus of the cat tongue.

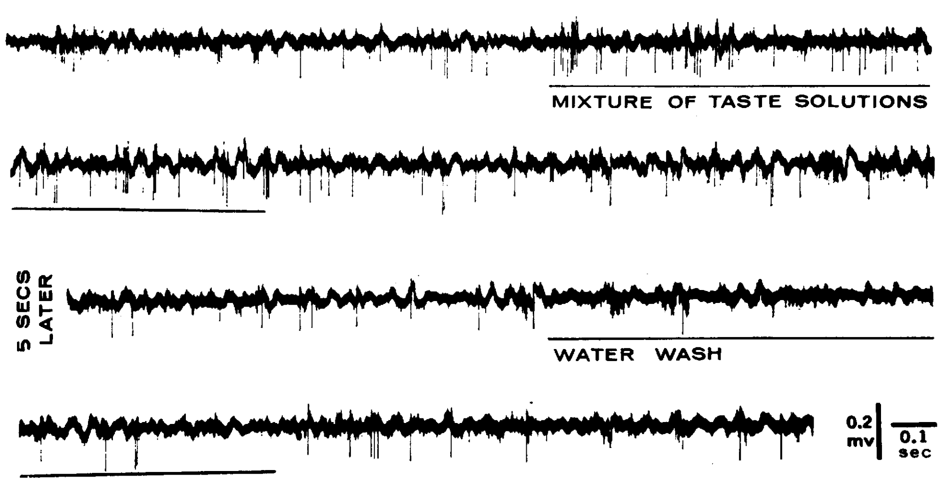


FIG. 5. Response pattern of thalamic neurons elicited by a mixture of taste solutions applied to a restricted locus on the cat tongue.

rons of Fig. 3A when this locus was rapidly cooled with ice water. Such a response persisted even after the tongue was precooled to approximately 22°C. This is in contrast to the responses of neurons which could be activated maximally when cooling of a particular locus on the tongue was done in the range from body temperature down to approximately 22°C. They did not respond to cooling in the range from approximately 22°C to 5°C, although they did respond to ice water if the tongue temperature was 35°C. Responses of such neurons are shown in Fig. 4. The recording electrode picked up spike activity of 2 neurons simultaneously. One of them was firing continuously at a slow pace, the other was usually silent. Both responded to cooling of the same locus of the tongue. If the jet of cool water was directed to a neighboring area, no response could be evoked. Tactile or pressure stimuli were ineffective. The neuron that discharged continuously is remarkably well suited for signaling the level of steady temperature while the phasically active neuron seems best suited for detecting temperature changes within a certain range. Thalamic location for most of the neurons that responded to these thermal stimuli was ipsilateral with respect to locus of stimulation; a few of them, however, were contralaterally located.

All neurons that responded to stimulation of the tongue by the mixture of taste solutions were spontaneously active but their frequency of firing increased considerably during stimulation. Although maximal response was obtained during the application of the taste solution, firing of the neurons at relatively high frequency persisted after the application was terminated. The solution had to be washed off before the firing diminished to approximately control levels. This response pattern is shown in Fig. 5. Some of these neurons could be activated by ice water, others could not. Tactile and pressure stimuli were ineffective. No neurons were encountered that responded to water as a taste stimulus.

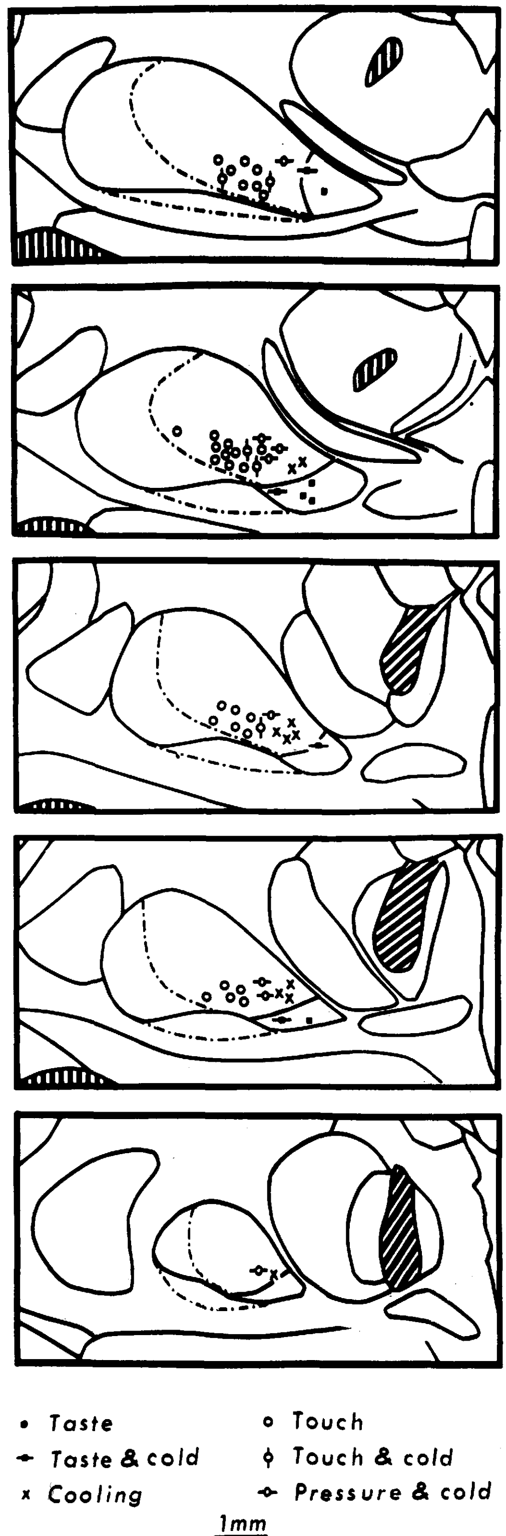


FIG. 6. Diagrams of a portion of the cat thalamus showing the individual position of the 60 thalamic neurons which were studied at 5 coronal levels.

The thalamic position of all 60 neurons is shown in Fig. 6. This figure consists of 5 diagrams which represent cross-sections taken at 0.3 mm distances through a portion of the cat thalamus. They are arranged in sequence along the anterior-posterior dimension vertically. The top section is the most anterior of the group. It is obvious that neurons which responded to a particular form of stimulation were grouped in clusters and were not dispersed randomly throughout a nuclear mass. Neurons activated by tactile stimuli were grouped in a lateral position with respect to those responding to pressure or cooling, even though all of them were found within the nucleus ventralis posteromedialis. This indicates that separate systems for touch and pressure exist. Consequently, any tendency to regard these sensory phenomena as modulations within one afferent system should be abandoned in favor of the view that touch and pressure are different sensory modalities.

Neurons for taste were found in a distinctly separate thalamic nucleus. In the human thalamus, Toncray and Krieg(6) named it the nucleus semilunaris accessorius. Although terminology for this nucleus with the cat and the monkey has varied, the term used by Toncray and Krieg appears the most satisfactory one also for these animals. Functionally, this nucleus is the thalamic relay nucleus for taste.

Finally, it is interesting to note that all thalamic neurons for taste investigated in this study had ipsilateral peripheral fields. This indicates that, contrary to the prevalent belief in a total decussation of the solitariothalamic tract(1), an ipsilateral pathway must exist. However, no pathway has yet been described anatomically which could serve such a projection.

*Summary.* An analysis was made of response patterns of 60 neurons in the cat thalamus which were modified by stimulation of limited loci of the tongue with tactile, pressure, thermal, and taste stimuli. This analysis revealed the following. 1. Except for the activity elicited by tongue stimulation with ice water, responses of the neurons were modality specific. 2. Tactile stimuli activated certain thalamic neurons which were grouped in a separate cluster from those responding to pressure. Such an organization indicated the existence of separate sensory systems for touch and pressure. 3. Neurons were found which were activated by lowering of the tongue temperature within a particular range. They did not respond to ice water if the tongue was precooled to 22°C. 4. Taste is relayed in a particular nucleus of the cat thalamus. Anatomically this nucleus has been described in the human thalamus as the nucleus semilunaris accessorius. It is suggested that this term be adopted for designating a homologous nucleus in the cat thalamus. 5. Since responses to taste stimuli were conveyed to the thalamus ipsilaterally, an ipsilateral pathway should exist. The anatomical description of such a pathway awaits future work.

1. Allen, W. F., J. Comp. Neurol., 1923, v35, 273.

2. Benjamin, R. M., Some thalamic and cortical mechanisms of taste. In Y. Zotterman, Ed., Proc. of 1st international symposium on olfaction and taste, Pergamon Press, Oxford, 1963.

3. Cohen, M. J., Hagiwara, S., Zotterman, Y., Acta physiol. scand., 1955, v33, 316.

4. Emmers, R., Anat. Rec., 1964, v148, 67.

5. Landgren, S., The thalamic and cortical reception of afferent impulses from the tongue. In G. E. W. Wolstenholme, M. O'Connor, Eds., Pain and itch, Ciba Foundation Study Group 1, Little, Brown & Co., Boston, 1959.

6. Toncray, J. E., Krieg, W. J. S., J. Comp. Neurol., 1946, v85, 421.

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