Bulbar gustatory responses to anterior and to posterior tongue stimulation in the rat

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Am. J. Physiol. 209(1): 105-110. 1965.—Amplitudes of neural responses in the nucleus of the fasciculus solitarius to stimulation of the tongue with quinine hydrochloride were analyzed using the response to NaCl as a reference standard. Three distinguishable areas were observed within the gustatory response zone of the nucleus. One area, responsive only to stimulation of the anterior region of the tongue, was at the anterolateral limit of the active zone. A second area, caudal and medial to the first, responded to both anterior and posterior tongue-region stimulation, the latter region yielding larger responses. Medial to both of the other areas was a third, highly responsive area, which responded only to posterior tongue-region stimulation.

METHODS

The results to be reported were obtained from 36 rats, both males and females, of the Sprague-Dawley and Wistar strains. Anesthesia was produced with sodium pentobarbital (60 mg/ml, 1 ml/kg, ip), and maintained with 0.1-μl doses as needed. The trachea was cannulated. The head was rigidly supported, and the medial portions of the occipital and interparietal bones, and the medial-caudal portion of the cerebellum were removed as previously described (11). The recording electrode was a single nickel chrome wire, 25.4 μ in diameter, insulated except at the tip. A three-coordinate manipulator positioned the electrode and drove it into the medulla oblongata under visual control. Silver ground and indifferent electrodes contacted muscle near the recording site. The multiunit neural activity was led to an electronic summator based on an RC circuit with a 0.75-set rise time, 5.63-set tall time; and finally into a recording milliammeter.

Electrolytic marker lesions were made by passing 4-10 μa dc for 5-12 sec, with the recording electrode cathodal. Brains which were studied histologically were embedded in paraffin, sectioned at either 10 or 20 μ, and stained with either a modified Weil method or with Luxol fast blue-cresylecht violet (5).

The anterior region of the tongue was placed in either a glass or a Plexiglas flow chamber through a snugly fitting rubber diaphragm, thus isolating it from stimuli applied to the posterior tongue. The posterior region was stimulated by one of two methods. For the first 15 animals a polyvinyl tube was attached to the head holder in such a way that liquids reached the circumvallate papilla. For the remaining 21 animals a polyethylene tube, 0.085-0.115 inch i.d., was introduced into the rear of the buccal cavity by blunt dissection through a skin incision made caudal to the angle of the jaw and ventral to the ear. The polyethylene delivery tube was passed out of the mouth and heat flared. The tube was then retracted into the mouth and held in place at the rear of the buccal...
FIG. 1. Ten-micron transverse section through the hindbrain of a rat. Arrow indicates an electrolytic lesion in the lateral division of the nucleus of the fasciculus solitarius, which marks the location of the exclusively anterior tongue response area. The lesion was produced by passing 4 μA dc for 12 sec, electrode cathodal. Luxol fast blue-cresylecht violet stain.

Local anesthesia of CT was produced by instilling 2% CarboCaine HCl into the ipsilateral auditory meatus through a polyethylene tube.

RESULTS

In the most rostral N.F.S. area, anterior tongue region stimulation produced responses in 25 rats from 37 responsive electrode tracks, but posterior tongue region stimulation was not effective. The median location of this "exclusively anterior tongue area" was 2.35 mm rostral to the obex, and 1.75 mm lateral to the median dorsal sulcus. In two of the above rats, marker lesions were placed at anterior area points, and were found in the lateral division of N.F.S., at the level of the corpus restiform, caudal to the extreme rostral limit of N.F.S., and rostral to the nucleus of n. hypoglossus (Figs. 1 and 2).

A second N.F.S. area gave responses to chemical stimulation of both the anterior and the posterior regions of the tongue. Such responses from both tongue regions were recorded in 18 rats from 23 responsive electrode tracks. This N.F.S. area, the "composite response area," had a median location 2.20 mm rostral to the obex and 1.65 mm lateral to the median dorsal sulcus (Fig. 2). These coordinates are significantly caudal and medial to the exclusively anterior area location. The brains of eight composite response area rats were studied histologically (Fig. 3). In each case, the electrolytic marker lesion was in the lateral division of N.F.S., slightly caudal to the anterior-posterior level of the lesions in the anterior response area.

In a third area, responses to posterior tongue region stimulation were recorded in four animals from six responsive electrode tracks while anterior tongue stimulation gave no response. The median location of this "exclusively posterior tongue area" was 2.25 mm rostral to the obex, 1.23 mm lateral to the medial dorsal sulcus (Fig. 2). The rostral coordinate does not differ significantly from those of either the anterior or the composite areas, but the exclusively posterior area is significantly medial to both other areas.

1 Medial coordinates differences, for anterior only area, P < .01 > .001; for composite area, P < .05 > .025, MWU.

2 Cook-Waite Laboratories, New York City. Each milliliter contains 20 mg mepivacaine HCl, 0.05 mg levo-norepinephrine, 4.0 mg NaCl, no more than 2.0 mg acetone sodium bisulfite, and a sufficient quantity of water for injection, up to 1.0 ml.
ANTERIOR AND POSTERIOR TONGUE TASTE RESPONSES

FIG. 2. Dorsal surface of hindbrain of rat. The brain was fixed in 10% formalin, and the cerebellum and dura were removed. Left side: Filled circles indicate locations of 37 electrode punctures in which exclusively anterior tongue responses were recorded. Circles with diagonals indicate 23 electrode locations in which responses were recorded from both anterior and posterior regions of the tongue (composite responses). Open circles indicate six electrode punctures in which exclusively posterior tongue responses were recorded. Right side: Filled ellipse represents the median location, plus and minus the quartile deviations, of the exclusively anterior tongue response area (2.35 ± 0.22 mm rostral to the obex; 1.75 ± 0.14 mm lateral to the median dorsal sulcus). Ellipse with diagonal represents the composite area (2.20 ± 0.31 mm rostral to the obex; 1.65 ± 0.20 mm lateral to the median dorsal sulcus), and open ellipse represents the exclusively posterior tongue response area (2.25 ± 0.37 mm rostral to the obex; 1.23 ± 0.28 mm lateral to the median dorsal sulcus). (Based on 36 rats.)

The N.F.S. areas differed in responsiveness to QHCl and NaCl (Figs. 4 and 5). The anterior tongue area gave only small responses to QHCl. In the composite area, responses to stimulation of the posterior region of the tongue with 0.01 M QHCl were significantly larger in absolute response magnitude than responses which were recorded at the same electrode position to anterior tongue stimulation. Responses to 0.1 M NaCl did not show this difference (Fig. 5). As Fig. 4 indicates, responses in the composite area to QHCl, taken relative to the response to NaCl for the same tongue region, were also significantly larger for posterior than for anterior tongue stimulation. Finally, in the exclusively posterior tongue response area, relative responses to QHCl were significantly larger than the relative responses in either the anterior or the composite areas.6

5 For 0.01 M QHCl, P = .025, Wilcoxon signed-rank test, one-tailed (WSR), Siegel, 1956 (op. cit.); for 0.1 M NaCl, P > .05, WSR.
6 For relative QHCI response in the composite area P < .01, WSR; in the exclusively posterior area, P < .02, MWU.

The cranial nerve branches which carry gustatory responses into the composite and anterior response areas were studied by anesthetizing the CT. In five animals, the response in the composite area to anterior tongue region stimulation disappeared completely within a few minutes, while the response to posterior tongue gustatory stimulation remained. These responses to gustatory stimulation of the posterior tongue tended to increase in magnitude after anterior responses disappeared. In one animal in which this increase was studied quantitatively, the composite area response to posterior tongue stimulation with 0.1 M NaCl was 9.5 ± 2.3 units (median ± quartile deviation) before CT block; 12 ± 2.3 units, after CT block. Responses to 0.1 M LiCl showed a similar trend.

In addition to the responses to gustatory stimulation, mechanical and thermal stimuli also produced activity in the solitary nucleus. Stroking the anterior region of the tongue with a glass rod gave responses in both the anterior and the composite areas of the nucleus (the posterior
portion of the tongue was not stimulated mechanically). With the tongue preadapted to H₂O at 25 C, H₂O responses were produced in both the anterior and composite areas when H₂O at 12 C flowed over the anterior region of the tongue, and responses were recorded in the composite area when H₂O at 12 C flowed over the posterior region of the tongue. The magnitudes of both the anterior area and the composite area responses to 12 C H₂O were comparable to the response magnitudes to 0.1 M NaCl. The exclusively posterior area of the solitary nucleus was not studied for thermal responses.

**DISCUSSION**

Discrete gustatory response areas were found in the N.F.S. One responded only to stimulation of the anterior portion of the tongue, a second only to posterior tongue region stimulation, while a third area responded to stimulation of both the anterior and the posterior tongue (composite area). The anterior tongue area was the most rostral and lateral of the three, the posterior area most medial, while the composite area had an intermediate position.

The existence and locations of the above N.F.S. areas confirm previous degeneration studies. In the rat, Torvik (12) found that evulsion of n. facialis (of which CT is a branch) and consequent damage to the geniculate ganglion produced degeneration primarily in the rostral zone of N.F.S. On the other hand, evulsion of both IX and n. vagus, with attendant damage to g. petrosum and g. nodosum, resulted in N.F.S. degeneration mostly caudal and medial to the CT-related degeneration zone in N.F.S. but with a clear area of overlap. Allen (1), who studied the guinea pig, reported that evulsion of IX and g. petrosum produced degeneration in N.F.S. which overlapped with the degeneration due to n. facialis evulsion, but was mostly medial-caudal to it. Essentially the same conclusions were reached by Aström (9) in his study of Golgi-stained mouse brains.

The several N.F.S. areas observed are located in agreement with Blomquist and Antem's report (3a) that electrical stimulation of CT in the rat evoked responses in the most rostral ipsilateral N.F.S., while responses to stimulation of IX were recorded in an ipsilateral N.F.S. area just caudal to, and overlapping with, the CT area of N.F.S. Further, the observation in the present paper that all gustatory response site marker lesions were in the lateral division of N.F.S. supports their suggestion (3a) that the medial and lateral divisions of N.F.S. may have different functions.

In the present experiment, the lesions marking the location of the composite response area were slightly caudal to anterior area marker lesions. This confirms the statistically significant difference between the rostral-caudal location of the anterior and the composite areas. All three areas differed significantly in medial coordinates. The absence of a significant difference, in the rostral-caudal plane, between the posterior and the other areas, may be due to the small number of posterior area responsive electrode tracks.

The results of the nerve-block procedures also confirmed the previous anatomical studies. If the anterior tongue area is primarily a CT termination area, then CT block should eliminate anterior area responses. This was observed. Further, if the responses to anterior tongue region stimulation which were recorded in the composite area represent CT input into this area, then CT block should eliminate composite area responses to anterior tongue stimulation. However, composite area responses to posterior tongue region stimulation should not be eliminated. This was also observed. It should be noted...
that the neurons of the anterior area may receive some IX input. Nonetheless, this possible input is clearly insufficient to produce a multiunit discharge detectable by the methods of this experiment. Along the same lines, units in the composite area may receive either dual (CT and IX) or single (CT or IX) input. This is an open question until single-unit recording is done. It was observed that a flow of H₂O over the anterior tongue region, during stimulation of the posterior tongue region, appeared to increase response magnitudes recorded in the composite area of N.F.S. This perhaps suggests a dual input. Since the H₂O wash of the anterior tongue would reduce CT “spontaneous activity” to a minimal level, some of the CT input may be inhibitory to those units in N.F.S. which received both CT and IX input. The possibility of inhibitory input from CT is consistent with the observed increase in magnitude of composite area responses to posterior tongue stimulation after CT block.

The partial overlap of the termination of CT and IX which was observed in N.F.S. in this experiment appears to be maintained in the thalamus. Responses to electrical stimulation of CT and IX are recorded in the medial subnucleus of n. ventralis of the rat dorsal thalamus by Emmers et al. (4). The area which responds to CT stimulation overlaps with the area responsive to IX stimulation. However, CT responses were centered anteriorly within the subnucleus, while IX responses were limited to the posterior half of the subnucleus.

It was previously observed that NaCl was a more effective stimulus than QHCl for CT responses, while the reverse was true for responses recorded from IX (2, 10). The present experiment indicates that this functional distinction between CT and IX is maintained in the areas of termination of these cranial nerves in N.F.S. Also, the N.F.S. area most highly responsive to QHCl (posterior) is spatially separated from the area in which NaCl is most effective (anterior). Thus, a QHCl solution flowing from the front to the back of the tongue would produce a spatial-temporal response magnitude pattern in N.F.S. First, small responses would occur in the anterior and composite areas, as the anterior tongue region innervated by CT was stimulated. Slightly later, as the QHCl solution reached the posterior region of the tongue, a larger response would develop in the composite area, and a relatively larger response would occur in the posterior area. In contrast, responses to an NaCl solution would have successive decreasing magnitudes in the same areas, though the temporal sequence would be similar. Such spatial-temporal patterns, which may be analogous to patterns found in the olfactory system by Mozell (7, 8), could have a role in the encoding of gustatory stimuli.

REFERENCES


