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RESPONSES OF HYPOGLOSSAL MOTONEURONS TO MECHANICAL STIMULATION OF THE TEETH IN RATS

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INTRODUCTION

The motoneurons of the hypoglossal (XIIth) nuclei provide the only source of somatic innervation of the intrinsic and extrinsic tongue muscles. Physiological studies have shown that exteroceptive and proprioceptive intraoral afferents modulate the activity of the hypoglossal neurons to control the tongue movements. Hypoglossal reflexes can be elicited by electrical stimulation of the lingual nerve (4, 27, 31, 32, 37) and by mechanical, chemical and thermal stimulation of the tongue surface (13, 39). Mechanical stimuli applied to the gingival mucosa are also able to modify the linguo-hypoglossal reflex (41). Other workers recorded synaptic potentials in the hypoglossal motoneurons following stimulation of the inferior alveolar and masseteric nerves (26, 27, 36). The alveolar nerves also contain low threshold large fibers connected with the mechanoreceptors involved in the tactile and pressure sensation of the teeth (34, 35).

The tooth mechanoreceptors located in the periodontal ligament respond to a pressure stimulus applied to the crown of the tooth (1, 10, 18, 28). Their function is, therefore, to signal the position of the bolus within the mouth and detect the load on the teeth during tooth contact in the course of mastication. Experimental studies have shown that during chewing movements the periodontal ligament receptors exert a feedback control over the trigeminal motoneurons, thus playing an important role in modulating the activity of the jaw muscles in the different phases of the mastication cycle (2, 8). It is not yet clear whether the afferent activity of tooth periodontal receptors, when naturally stimulated, contributes to control the displacement of the tongue in the mouth. In the present study, electrophysiological experiments were performed to investigate whether mechanical stimulation of the teeth could modulate the spontaneous electrical activity of single hypoglossal motoneurons. In addition, recordings of the unitary discharge were made from hypoglossal nerve and genioglossal muscle fibers.

METHODS

Thirty-five Wistar rats, weighing between 250 and 350 g were used for this investigation. The animals were anesthetized with ketamine (60 mg/kg i.p.) and maintained with additional injections as required. A ventral middle line incision of the skin from the mandibular symphysis to the hyoid bone exposed the underlying muscles, and further dissection up to the hypoglossal muscle exposed the branches of the XIIth nerve to the tongue. The medial branch was electrically stimulated by means of a pair of silver rings placed around the proximal nerve stump and connected to a Grass Stimulator (mod. S8). The exposed nerves were covered with cotton wool soaked in warm mineral oil and paraffin (35-37°C), and the electrode wires were stitched to the surrounding tissues. Each animal was then tracheotomized, paralyzed with Fazadon (1,1-azobis[3-methyl-2-phenyl 1H-imidazo-(1,2-α) pyridinium] dibromide), artificially ventilated and fixed to a stereotaxic frame in a prone position. The animal's head was held by the ear bars and the mouth was maintained in a half-open position by fixing the maxillar and mandibular bones. In twenty-five animals a craniectomy exposed the cerebellum from which the posterior half was removed by suction to expose the trigonum hypoglossi in the floor of the IV ventricle. Extracellular electrical activity from the single hypoglossal motoneurons was recorded with tungsten microelectrodes (0.9-1 MΩ) introduced into the hypoglossal nucleus by means of an electronic microdrive. Single motoneurons were antidromically identified by electrical stimulation of the homolateral XIIth nerve (0.1 msec duration, twice the threshold intensity to evoke the response, 1 Hz). A maxillar incisor was mechanically stimulated as follows: a rod was mounted on a microdrive device that allowed graduated movements in different directions. The end of the rod was formed to fit firmly around the tooth, adhesion was reinforced with dental cement. The microdrive was connected to a strain gauge (Ugo Basile 7005) for measuring the pressure applied to the tooth (1-25 g) in labio-lingual (la-li), linguo-labial (li-la), disto-medial (di-me) and medio-distal (me-di) directions. Since the mechanical pressure was applied manually, the timelag between application and realization of the planned stimulation varied (from 100 to 400 msec). For the same reason, the stimulus duration also varied (from 0.5 to 1 sec). In four experiments to evaluate the latency of the response, an automatic stimulating device was adapted to allow standardized mechanical stimuli to be delivered to the tooth (the planned stimulation was constantly reached in 4 msec). To this end, the soft iron core of an electromagnet was serially connected to the rod fixed to the tooth. When current from a stabilized D.C. power supply flowed through the coil, the soft iron core pressed on the rod, thus stimulating the tooth. The electrical potentials of the hypoglossal motoneurons and the artifact of mechanical stimulation of the tooth were amplified, displayed on a dual-beam oscilloscope and recorded on magnetic tape (Racal Recorders LTD) for subsequent analysis. At the end of the experiments the recording point was marked by an electrolytic lesion and the animals were killed with a barbiturate overdose. The brain stem was then removed, fixed, serially cut, stained and histologically examined to verify the recording site.

In four animals, the tooth-lingual reflex was studied by stimulating the upper incisor tooth and recording the reflex activity in the single fibers of the homolateral XIIth nerve and in the genioglossal muscle. A tungsten microelectrode was introduced into the medial branch of the XIIth nerve to record the electrical activity from the single fibers. In two non-paralyzed animals, the electromyographic (EMG) activity of the genioglossal muscle was monopolarly recorded by means of tungsten microelectrodes (insulated except at the tip, 200 μm diameter) inserted into the ipsilateral exposed muscle. The recorded electrical activity was amplified, displayed on the oscilloscope and stored on magnetic tape. The unitary discharge of the hypoglossal motoneurons, the electrical activity of the single fibers of the XIIth nerve, the electromyographic activity of the genioglossal muscle and the profile of the mechanical stimulus were displayed on a memory oscilloscope (Tecfen Computerscope ISC-16 program) for photography, or fed to a plotter for the analogic signals to be directly charted.

RESULTS

Hypoglossal motoneurons were identified by spike potentials evoked by electrical stimulation of the medial branch of the ipsilateral XIIth nerve. An example of the antidromic spike potentials and spike collision is shown in Fig. 1A. The latency of spike response was 1.1 msec (the latency of all units ranged between 0.80 and 1.13 msec). Antidromic responses were recorded from the hypoglossal motoneurons localized in the ventral-caudal region of the nucleus whose axons, travelling in the medial branch, innervate the protrusive and intrinsic tongue muscles (genioglossus, vertical and transverse muscles). Fig. 1B shows the recording site on a histological cross-section of the hypoglossal nucleus made at caudal level; in this case, the electrolytic lesion, marked by the arrow, is located in the ventral part of the nucleus. The activities of a hypoglossal motoneuron and of a fiber detected from the hypoglossal medial branch are reported in Fig. 1 C-D, respectively. Varia-

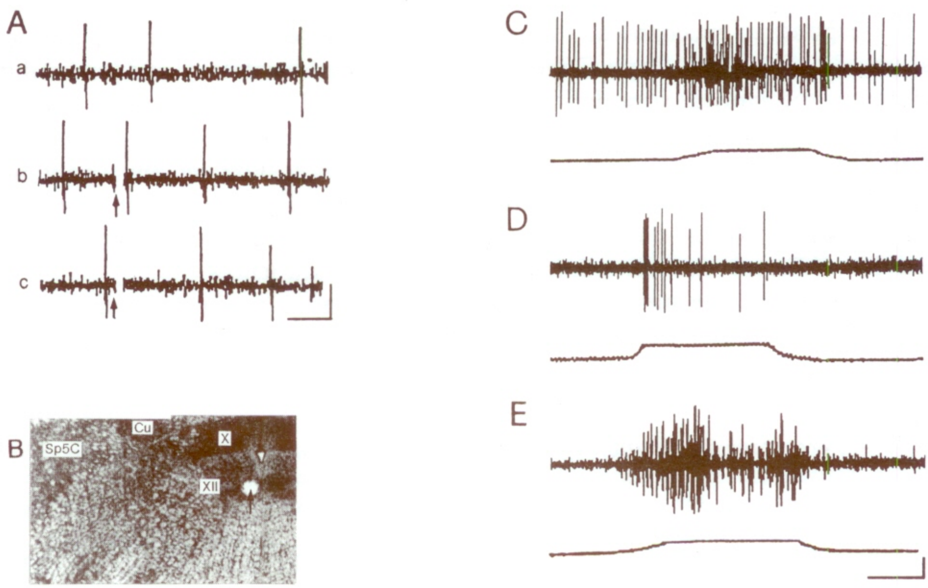

Fig. 1 - *Hypoglossal responses following mechanical stimulation of the homolateral incisor tooth.*

A: antidromic identification of the hypoglossal motoneuron by electrical stimulation of the XIIth nerve; a, spontaneous activity; b, antidromic response at 1.1 msec latency; c, collision, when the spontaneous spike preceded the antidromic stimulation by 1.32 msec. The arrows mark stimulation artifacts. Vertical calibration: 75 μV. Horizontal calibration: 5 msec. B: Histological cross section at the mediocaudal level of the hypoglossal nucleus showing the recording site in the ventral part of the nucleus. The arrow marks the electrolytic lesion. XII, hypoglossai nucleus; X, vagal nucleus; Cu, cuneate nucleus; Sp5C, spinal trigeminal nucleus.

C-E: the upper traces represent the electrical activity of a hypoglossal motoneuron (C), the unitary discharge of the XIIth nerve fiber (D) and the motor unit activity of the genioglossus muscle (E). The lower traces represent the profiles of the mechanical stimulation of the tooth applied in the labiolingual direction. Vertical calibrations: 75 μV for electrical activity and 10 g for mechanical stimulus. Horizontal calibration: 500 msec.

tions in the firing rate were recorded after a mechanical stimulus was applied to the crown of the homolateral upper incisor tooth. In this case, the responses were characterized by an increase in the motoneuron unitary discharge with recruitment of new units and by response of a hypoglossal fiber previously silent. Fig. 1 E shows genioglossal motor units which are discharging during mechanical stimulus (the resultant protrusive tongue movement was usually directed to exploring the site of stimulation). A hundred and fifteen out of 150 tested motoneurons localized in the ventral region of the hypoglossal nucleus responded to the mechanical stimulation of the tooth. Excitatory, inhibitory and complex responses were observed following tooth stimulation applied in various directions. In relation to the response patterns observed, the hypoglossal motoneurons can be subdivided into six main types as shown in Table 1. Figs. 2 and 3 report the response patterns of the hypoglossal motoneurons following mechanical tooth stimulation applied in various directions. Type A hypoglossal motoneurons responded with excitation to labio-lingual (la-li) and with inhibition to linguo-labial (li-la) stimulus direction (Fig. 2A). Opposite effects were observed in type B motoneurons (Fig. 2B), which did not respond to mechanical stimuli applied in disto-medial (di-me) or medio-distal (me-di) directions. Type C motoneurons showed excitatory and/or inhibitory responses to mechanical stimulation in all directions (Fig. 3A). Type D responded with excitation or inhibition to only one direction of stimulation (Fig. 3B). Twenty per cent of the responsive motoneurons (type E), not showing any spontaneous discharge at rest, were excited by tooth stimulation (Fig. 3C). Ten out of 115 responsive motoneurons, during one stimulation, showed complex responses characterized by different excitation-inhibition-excitation sequences.

The threshold of the mechanical stimulation for evoking hypoglossal responses varied from cell to cell within the range of 1-25 g. The latency of the responses, measured by using the electromagnetic method (Fig. 4, inset), ranged from 8 to

Table 1. — *Percentage distribution of the response types of all tested motoneurons (N = 115) following mechanical stimulation of the homolateral incisor tooth.*
The first two columns indicate the hypoglossal motoneuron types (TYPE) and the corresponding numbers (N.) The remaining columns indicate the stimulus direction: labio-lingual (LA-LI), linguo-labial (LI-LA), disto-medial (DI-ME) and medio-distal (ME-DI). E: excitation; I: inhibition; No: no response.

Type	N.	LA-LI	LI-LA	DI-ME	ME-DI	%
A	25	E	I	No	No	21.7
B	22	I	E	No	No	19.4
C	12	I or E	I or E	I or E	I or E	10.4
D	13	E	No	No	No	11.3
»	3	No	I	No	No	2.6
»	2	No	No	I	No	1.7
»	5	No	No	No	E	4.3
E	23	E	E	E	E	20.0
Complex	5	E-I-E	No	No	No	4.3
»	3	No	No	No	I-E	2.6
»	2		E-I-E	No	No	1.7

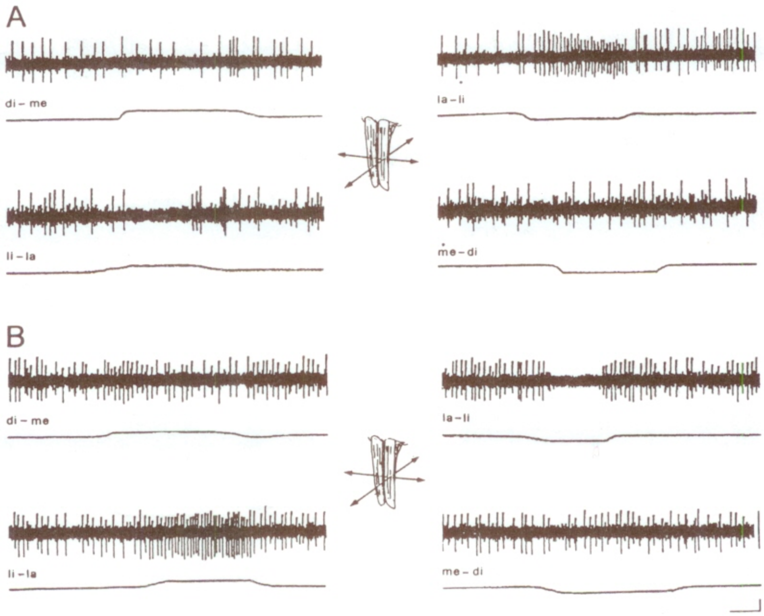

Fig. 2 – *Electrical activity of two hypoglossal motoneurons following mechanical stimulation of the homolateral incisor tooth.*

For each pair of recordings shown in this and the following figures, the upper trace represents the electrical activity and the lower trace shows the profile of the mechanical stimulation. The arrows indicate the stimulus directions on the tooth.

A: type A motoneuron responded with excitation to labiolingual (la-li) stimulus direction and with inhibition to linguo-labial (li-la). B: type B motoneuron responded with excitation to linguo-labial (li-la) stimulus direction and with inhibition to labio-lingual (la-li). Vertical calibrations: 250 μV for electrical activity and 10 g for mechanical stimulus. Horizontal calibration: 500 msec.

20 msec, varying with the stimulus intensity. The responsive motoneurons often showed phenomena of adaptation to the stimulus as in the example in Fig. 4. The spontaneous discharge was inhibited during short tooth stimulus (A) and the phenomenon of adaptation was clearly evident when the stimulus duration was increased (B-E).

DISCUSSION

The results reported in this paper have shown that the hypoglossal motoneurons, the fibers of the XIIth nerve and the genioglossus motor units, were modulated in their activity by mechanical stimulation of the ipsilateral incisor tooth. Recordings were made in anesthetized rats from motoneurons localized in the ventral region of the hypoglossal nucleus extending approximately 3 mm upward into the medulla oblongata from the pyramidal decussation. In this area there are motoneurons innervating the intrinsic and extrinsic geniohyoid and genioglossus

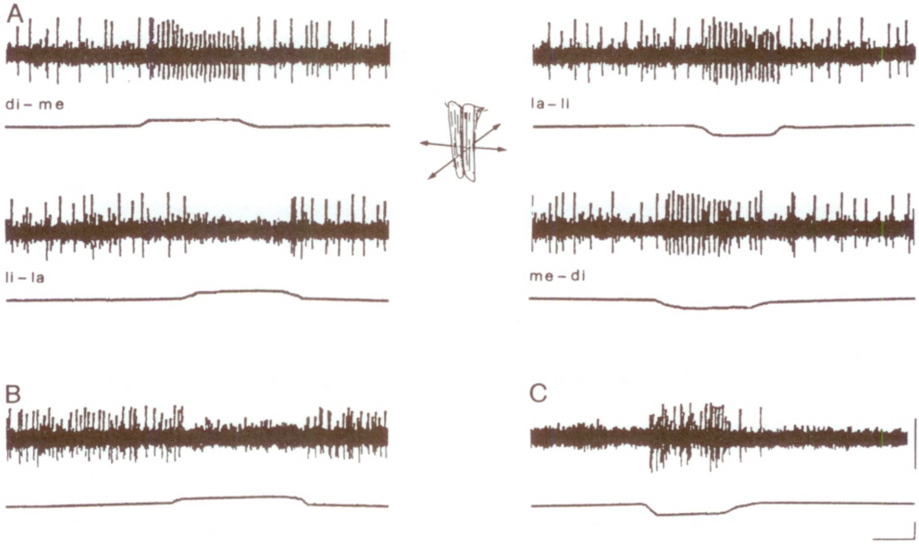

Fig. 3 – *Electrical activity of three hypoglossal motoneurons following mechanical stimulation of the homolateral incisor tooth.*

A: type C motoneuron showed excitatory and/or inhibitory responses to mechanical tooth stimulation in all directions: disto-medial (di-me), labio-lingual (la-li), linguo-labial (li-la) and medio-distal (me-di).
B: type D motoneuron responded with inhibition to linguo-labial direction of stimulation.
C: type E motoneuron not spiking at rest was excited by medio-distal tooth stimulation. Vertical calibrations: 250 μV for electrical activity and 10 g for mechanical stimulus. Horizontal calibration: 500 msec.

muscles functionally involved in the protrusive movements of the tongue (16, 29). Since the mechanical stimuli used in these experiments were at non-noxious intensities for human subjects, we postulated that the hypoglossal responses recorded following application of pressure to the tooth arose from the excitation of the periodontal receptors only.

Tooth mechanoreceptor stimulation affected the firing rate of 70% of the tested motoneurons (115 neurons). Twenty per cent of the responsive motoneurons, not showing any spontaneous discharge at rest, were excited by tooth stimulation. The studied motoneurons were affected by the direction of the stimulus. On the basis of the pattern of response according to the direction of the mechanical stimulus, the hypoglossal motoneurons were classified into five types. Complex responses have also been recorded, characterized by excitation-inhibition-excitation sequences during one stimulus direction. It is known that the afferent fibers from the mechanoreceptors travel in the alveolar nerves, arising in the cell bodies localized in the mesencephalic nucleus (7, 12, 17, 30) and the trigeminal ganglion (3, 15, 18, 25). Other workers showed that electrical stimulation of the low-threshold fibers travelling in the inferior alveolar nerve evoked synaptic potentials in the hypoglossal motoneurons characterized by a depolarization — hyperpolarization sequence or by hyperpolarization only (36, 38). The latencies of the electrical potentials suggested a disynaptic-polysynaptic linkage between the trigeminal sensory nuclei and/or the brain stem neurons and the hypoglossal nucleus (5, 6, 14,

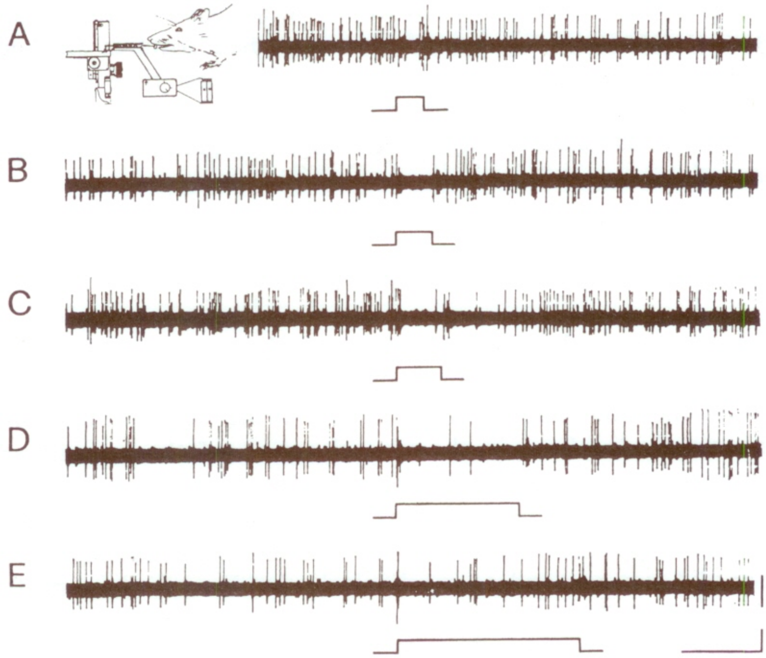

Fig. 4 – *Electrical activity of hypoglossal motoneurons following mechanical stimulation of the homolateral incisor tooth.*

Type D hypoglossal motoneuron responded with inhibition only during linguo-labial tooth stimulation. The electromagnetic method was used (see inset and Methods). The stimulus pressure intensity was maintained constant at 6 g, while the duration was gradually increased from 166 msec to 1100 msec (A-E). Vertical calibrations: 250 μV for electrical activity and 10 g for mechanical stimulus. Horizontal calibration: 500 msec.

26, 32). In addition, the cerebral cortex (33, 39), the glossopharyngeal and vagal nerves (11, 40), the solitary nucleus, the lateral and medial reticular formations (5, 6, 19, 36), visual and somatosensory inputs (20, 23), as well as vestibular afferents (21, 22, 24), modulate the activity of the hypoglossal motoneurons. Some relay stations of these afferent pathways are neurons responding to mechanical stimulation of the teeth. Excitatory and inhibitory effects were observed in different brain stem nuclei (5, 6, 19, 36) and in the bulbo-ponto-mesencephalic reticular formation mainly involved in controlling jaw movements during mastication and biting processes (8, 9, 30).

In the present study, the stimulus utilized was adequate to excite the tooth periodontal mechanoreceptors naturally. The wide range of latency (8-20 msec) of the hypoglossal responses suggests that different alternative polysynaptic pathways can be used to connect the tooth mechanoreceptors to the hypoglossal nuclei. The central excitatory and/or inhibitory pathways converge in the same hypoglossal motoneurons and their activation is dependent upon the time-spatial characteristic of the excitation of the tooth periodontal mechanoreceptors. However, in these experiments it was not possible to determine whether the cell bodies of the excited mechanoreceptors were in the mesencephalic nucleus or the trigeminal ganglion.

Consequently, the relative contribution of the mesencephalic and trigeminal ganglion mechanoreceptors to the hypoglossal responses requires further study.

In conclusion, the present results suggest for the first time that excitation of the periodontal mechanoreceptors, induced by pressure on the teeth, could provoke hypoglossal reflexes directed to adjust the tongue displacement in the oral space during mastication.

SUMMARY

Reflex discharges were evoked in the XIIth nerve single fibers and in the genioglossal muscle following mechanical stimulation of the homolateral incisor tooth in rats. The tooth mechanoreceptors affected the firing rate of 70% of the tested motoneurons mainly localized in the ventral region of the hypoglossal nucleus. Different types of response in relation to stimulus direction were recorded. Type A responded with excitation to labio-lingual and with inhibition to linguo-labial stimulus direction. Opposite effects were observed in type B motoneurons. However, these neurons did not respond to mechanical stimuli applied in medio-distal or disto-medial directions. Type C showed excitatory or inhibitory responses to mechanical stimulation in all directions. Type D only responded to one direction of stimulation. The stimulus was often able to excite motoneurons previously silent (type E). Some motoneurons showed complex responses to one sitmulus direction.

The results demonstrate that stimulation of the periodontal mechanoreceptors can evoke hypoglossal responses probably aimed at controlling tongue position in the mouth during mastication.

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