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Effects of lingual nerve and chewing cortex stimulation upon activity of the swallowing neurons located in the region of the hypoglossal motor nucleus

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This study focuses on motoneurons and interneurons in the region of the hypoglossal nucleus (XIIth) related to swallowing and chewing. In sheep anesthetized with halothane, we have used extracellular microelectrodes to study the effects of stimulation of the superior laryngeal nerve (SLN), the lingual nerve (LN) and the chewing cortex (CCx) upon activities of the swallowing neurons (SNs). Ipsilateral stimulation (1–5 pulses at 500 Hz) of the peripheral afferents or CCx did not generally induce a short latency activation of the hypoglossal swallowing motoneurons (Group I SNs) since only 4 motoneurons (69 tested) were activated by the SLN, 4 motoneurons (56 tested) by the LN and none by the CCx. In contrast, the same stimulations were more effective with swallowing interneurons (Group II SNs) located in the reticular formation close to the XIIth motor nucleus since 12 neurons (30 tested) were activated with short latencies (9 ± 1.8 ms; mean latency ± S.D.) by the SLN, 9 neurons (21 tested) by the LN (latency: 8 ± 1.8 ms) and 5 neurons (18 tested) by the CCx (latency: 13 ± 1.7 ms). Seven neurons were activated by two or three modes of stimulation indicating the existence of convergent inputs upon some Group II SNs. During chewing movements induced by a prolonged stimulation (20–40 Hz) of the CCx, 10 Group I SNs (16 tested) versus only one Group II SN (8 tested) were found to fire in association with the jaw opening. Moreover, 3 motoneurons and 4 interneurons inactive during swallowing discharged during chewing movements. Our data suggest that: (1) the peripheral and cortical signals primarily converge on interneurons located in the reticular formation adjacent to the XIIth nucleus; (2) this reticular formation contains interneurons mainly discharging during swallowing or during chewing and (3) the hypoglossal motoneurons generally discharge during both swallowing and chewing, but some motoneurons are specifically dedicated to swallowing or to chewing.

INTRODUCTION

Swallowing is a centrally programmed motor sequence resulting from the activity of hindbrain neurons (interneurons and motoneurons) belonging to the conceptually defined swallowing center[7,12,13,15,17,26,33]. In sheep the swallowing neurons (SNs) are mainly located in two regions of the medulla[15]: (1) a dorsal region including the nucleus of the tractus solitarius and the adjacent reticular formation, 2–4 mm rostral to the obex, and (2) a ventral region corresponding to the nucleus ambiguus, which contains motoneurons supplying the pharynx, larynx and esophagus[33], and to the ventro-lateral reticular formation[2,3]. Other SNs are located in the regions of trigeminal (Vth) and hypoglossal (XIIth) motor nuclei[8,9,12,13] which contain motoneurons supplying jaw and tongue musculatures respectively. Moreover, many studies[13,23] indicate that these muscles are also activated during chewing movements or during jaw opening reflex induced by stimulation of the lingual nerve (LN) suggesting some convergence of neural control for these different functions.

In previous work[8,9], we have studied the discharge characteristics of SNs located in the region of the Vth and XIIth motor nucleus in anesthetized sheep. Swallowing motoneurons of the Vth motor nucleus supply the mylohyoid, digastric (anterior body) and medial pterygoid muscles[8]; those of the XIIth motor nucleus supply the geniohyoid, styloglossus, and hyoglossus muscles[4]. Moreover, we have shown that jaw muscles and the same motoneurons of the Vth motor nucleus discharge: (1) during reflex swallowing induced by stimulation of the superior laryngeal nerve (SLN), (2) during rhythmic jaw movements induced by prolonged stimulation of the fronto-orbital cortex (chewing cortex, CCx), or (3) during jaw opening reflex induced by stimulation of the

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LN. The aim of the present work was to study the effects of LN and CCx stimulation upon activity of the tongue muscles and SNs located in the region of the XIIth motor nucleus, in order to demonstrate the existence of neurons involved in the different components of feeding behavior (swallowing and chewing) and possible mechanisms of interaction. A preliminary report has been previously presented[19].

MATERIALS AND METHODS

This study was carried out on 21 anesthetized adult sheep (body weight: 20–30 kg). Most of these animals were used for research described in a previous paper[9].

Surgical preparation

A short-lasting barbiturate anesthetic (sodium thiopentone, 25 mg/kg) was administered intravenously. After tracheotomy, the animal was ventilated by a respirator (Bird Mark 8) with a mixture of air and halothane (1.5–2%) to maintain anesthesia. Depth of anesthesia was adjusted to maintain pupillary constriction and a heart rate at approximately 100/min.

The jaw muscles and the extrinsic muscles of the tongue were exposed via a medial incision of the skin under the jaw from the symphysis menti to the pharynx. The geniohoid (GH) which is a suprahyoid muscle, and the hyoglossus (HG) and styloglossus (SG) muscles which are the retractor muscles of the tongue, were exposed close to their respective points of insertion on the hyoid and styloid bones. The genioglossus (GG), the main protrusor of the tongue, was approached submentally, close to its point of origin at the inferior spine of the mandible, after a short division (20 mm length) of the superficial mylohyoid (MH) muscles in the midline at the level of the MH raphe. The anterior digastric (Dig) and medial pterygoid (Pt) muscles, discharging respectively during jaw opening and closing movements, were exposed at their points of insertion on the internal surface of the jaw. This surgical preparation allowed to assess the tongue muscles in relation to jaw closing and opening muscles during both swallowing and chewing.

The SLN which contains laryngeal afferents whose stimulation can trigger swallowing[12,13,26,33] was dissected at its point of emergence from the thyroid cartilage. The XIIth nerve was prepared in the parotid region (common trunk), or more distally at the level of the two main peripheral branches, the lateral supplying the HG and SG, and the medial supplying the GG and GH. The LN which is a branch of the Vth nerve was dissected through an incision made in the lateral surface of the tongue musculature.

For exposure of the brain stem, the animal was held in a prone position with the head firmly supported. The skin was incised along the midline of the skull followed by removal of the occipital bone and cerebellum to expose the dorsal surface of the medulla oblongata. The surface was covered with warm liquid paraffin. After eye enucleation, craniotomy was performed in the fronto-orbital region to expose the CCx[6]. At the end of the surgical period, the head was placed in a stereotaxic apparatus specially adapted for sheep. All wounds were regularly infiltrated with a 2% procaine solution. Body temperature and arterial pressure were continually monitored.

Electrical stimulation

Bipolar platinum electrodes were used to stimulate the SLN, the LN and the XIIth nerves. The CCx was stimulated with two platinum electrodes (about 1 mm^2 of surface) placed on the cortex 2 mm apart. Stimulus parameters used were 0.5–1 V (0.2 ms) for the SLN, 1–5 V (0.2 ms) for the LN, and 10–15 V (0.5 ms) for the CCx. Stimulating electrodes were connected to stimulators through high frequency isolation units (WPI).

Recordings

Electromyographic (EMG) activities of tongue and jaw muscles were recorded with paired copper wires, insulated except at the tip, inserted into the muscles. Extracellular activities of neurons within the region of the XIIth motor nucleus were recorded by tungsten microelectrodes of 1 μm tip diameter and impedances of either 9–12 MΩ, or 2–5 MΩ at 1000 Hz. Potentials were amplified and displayed on an oscilloscope for visual observation and filming.

Histological controls

During experiments, medullary recording sites were marked by electrocoagulation (250 μA DC for 5 s) and later located from stained[18] 10–25 μm-thick transverse sections, or from unstained frozen 50 μm-thick sections.

Curarization

During recording of unitary activity of the SNs located in the region of the XIIth motor nucleus, the animals were, in some cases,

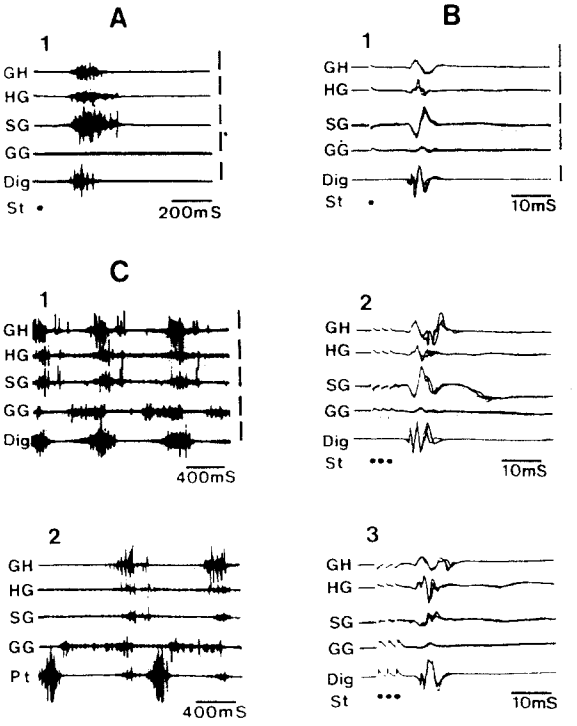

Fig. 1. Activities of extrinsic tongue musculature during swallowing, chewing and jaw opening reflex. EMG activity recorded from the geniohyoid (GH), hyoglossus (HG), genioglossus (GG), styloglossus (SG), anterior digastric (Dig) and pterygoid (Pt) muscles. Stimulation (St) is indicated by dots. A, B and C obtained from the same animal. A: EMG activities during swallowing induced by stimulation (0.5 V, 0.2 ms, 3 pulses at 500 Hz) of the SLN. Note the synchronous discharge of GH, HG, SG and Dig muscles, but GG fails to discharge. Amplitude calibration: 500 μV. B: reflex responses (5 superimposed traces) induced by stimulation (3 V, 0.2 ms, single pulse in (1) and 3 pulses at 500 Hz in (2) and (3) of the ipsilateral (1) and (2) and contralateral (3) LN. Note the short latency EMG of GH, HG and SG muscles in phase with Dig EMG. Amplitude calibration: 250 μV for the GH, HG and SG muscles; 500 μV for the Dig muscle. C: EMG activities during chewing movements induced by prolonged stimulation of the fronto-orbital cortex (10 V, 0.5 ms, 30 Hz). (1) and (2) obtained during two chewing sequences identified by EMG of Dig (jaw opening) in (1), or EMG of Pt (jaw closing) in (2). Note EMG of the GH, HG and SG in phase with Dig, and the absence of EMG in the tongue muscles during Pt discharge. Amplitude calibration: 500 μV.

curarized by i.v. injections of gallamine triethiodide (flaxedil), in order to prevent activation of neurons by sensory feedbacks resulting from contraction of swallowing muscles[8]. Curarization was generally light (0.5–0.7 mg/kg) in order to allow weak EMG activity of the swallowing muscles to persist. Deep curarization (2 mg/kg) abolishing EMG was sometimes used, but always after the discharge of the recorded neuron had been related to reflex swallowing.

Identification of motoneurons

Motoneurons supplying the tongue muscles were identified by antidromic activation following stimulation of the ipsilateral XIIth nerve. The three following criteria were used. The first involved collision between antidromic and orthodromic spikes. To perform this test, the antidromic response was elicited during swallowing activity induced by SLN stimulation. When an orthodromic potential preceded the nerve stimulation within an appropriate time (critical period), no antidromic response was obtained[5,14,20,34]. The second approach involved the antidromic response having a short fixed latency and the ability to follow high frequency stimuli (300–500 Hz). The third criterion was based on the concept that the spikes elicited by nerve stimulation had identical waveforms to those during swallowing activity.

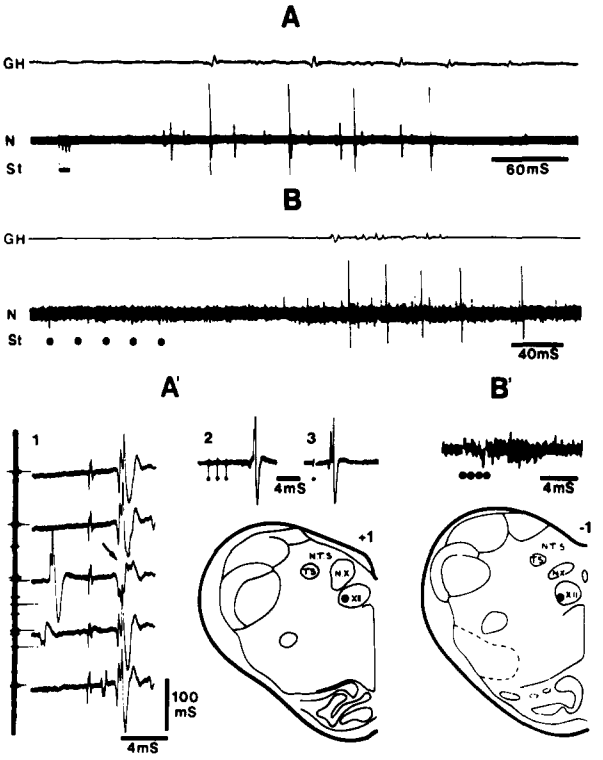

Fig. 2. Effects of LN stimulation on Group I swallowing neurons. A: swallowing activity in geniohyoid muscle (GH) and hypoglossal motoneurons (N) produced by stimulation of the SLN (St: 0.5 V, 0.2 ms, 4 pulses at 500 Hz). Recording site of motoneurons indicated by a filled circle on transverse map 1 mm rostral to the obex (+1) at bottom of figure. A′ (1): collision test between orthodromic spike of swallowing discharge (neuron with the greatest amplitude) and antidromic spike induced by stimulation (1.5 V, 0.1 ms) of the XIIth nerve (medial branch). Swallowing activity on vertical trace; antidromically induced response (field potential intermingled with the unitary spike) on horizontal trace. Note the absence of antidromically induced spike (arrow) after the occurrence of orthodromic spike. (2): activation of the neuron by ipsilateral stimulation of the LN (3 pulses at 500 Hz, 5 V, 0.4 ms). (3): antidromic activation of the neuron. B: swallowing activity induced by stimulating the SLN (0.5 V, 0.2 ms, 5 pulses at 30 Hz). Recording site indicated by a filled circle on transverse map 1 mm caudal to the obex (–1) at bottom of figure. B′: effect of LN stimulation (4 pulses at 1000 Hz, 3 V, 0.1 ms) on swallowing neuron. Note the absence of activation. Anatomical abbreviations: NTS, nucleus tractus solitarius; NX, nucleus dorsalis nervi vagi; TS, tractus solitarius; XII, nucleus nervi hypoglossi.

RESULTS

Electromyographical study

During swallowing induced by SLN stimulation (short train of pulses at 30 Hz or 1–5 pulses at 500 Hz), synchronous EMG discharges were recorded (latency ≥ 80 ms) from the suprahyoid (GH), jaw opening (Dig) and tongue retracting (HG, SG) muscles, while the tongue protruding (GG) muscle was generally inactive (Fig. 1A). SLN stimulation (1–5 pulses at 500 Hz) also induced a short latency (10–15 ms) evoked response from the tongue musculature (specially in the GG).

By stimulating (single pulse) the ipsilateral LN, reflex

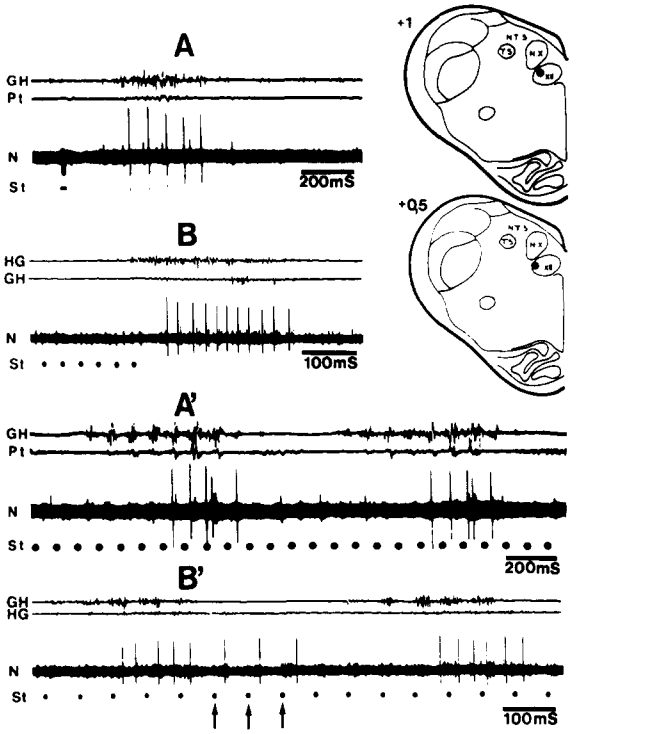

Fig. 3. Activation of Group I SNs during chewing. A: swallowing activity produced in the geniohyoid (GH) and pterygoid (Pt) muscles with discharge of a hypoglossal motoneuron (N) by stimulating the SLN (St: 0.5 V, 0.2 ms, 4 pulses at 1000 Hz). B: swallowing activity produced in hyoglossus (HG) and geniohyoid (GH) simultaneously with discharge of a hypoglossal motoneuron (N) after SLN stimulation (6 pulses at 30 Hz). A′ and B′: discharges of the same neurons during rhythmical jaw movements induced by prolonged stimulation (10 V, 0.5 ms) of the ipsilateral CCx. Note rythmic discharges of the SNs occurring at the end of jaw opening (EMG of GH), and short latency activation after the stimulating pulses (arrows) in (B′). Location of neurons indicated by filled circles on maps. Abbreviations as in Fig. 2.

EMG responses (latencies, 8–10 ms) were recorded from GH, HG and SG muscles, in phase with jaw opening reflex (EMG activity of Dig; Fig. 1B,1). The EMG responses were slightly increased when LN was stimulated with 2 or 3 pulses (Fig. 1B,2). Contralateral LN stimulation was also effective (Fig. 1B,3). Such responses of tongue extrinsic musculature were never obtained by stimulation (3–5 pulses at 500 Hz) of the ipsilateral CCx; but during a long lasting cortical stimulation (train of pulses at 20–40 Hz) which produced rhythmic chewing movements, the GH, HG and SG muscles discharged at about the same time essentially during jaw opening (EMG of Dig; Fig. 1C,1). The participation of GG in chewing was different: EMG activity of this muscle exhibited a longer duration than that of other tongue muscles, starting after jaw closing (EMG of Pt; Fig. 1C,2), and extending during jaw opening. The extrinsic tongue musculature was inactive during the active closing phase of the jaw (maximum EMG of Pt; Fig. 1C,2).

Microphysiological study

This study was performed on lightly curarized preparations (see MATERIALS AND METHODS). We studied the swallowing neurons (SNs) located in the region of the XIIth motor nucleus which discharged (burst of spikes) during reflex swallowing induced by SLN stimulation. These neurons were classified into two groups[9]: *Group I SNs* located in the XIIth motor nucleus (from 1 mm caudal to 2 mm rostral to the obex) and antidromically activated by stimulating the XIIth nerve; and *Group II SNs* never antidromically activated by XIIth nerve stimulation and located in the reticular formation close to the XIIth motor nucleus. Group I SNs were considered motoneurons while Group II SNs were labeled interneurons.

Group I SNs. Group I SNs (motoneurons) were generally not activated with short latency discharges (see Fig. 2A,B and Fig. 3A,B) by ipsilateral stimulation of the SLN (4 neurons activated out of 69 tested; latency, 10–12 ms). Only 4 Group I SNs (56 tested) were activated (latency, 6–8 ms) by ipsilateral stimulation of the LN (Fig. 2A′,2;B′). Axons of these motoneurons were found (antidromic invasion test) to run in the medial (Fig. 2A′, 1,3) or lateral branches of the XIIth nerve. Group I SNs were never activated (38 tested) by ipsilateral stimulation (single pulse or short train of pulses at 500 Hz) of the CCx. These results suggested that hypoglossal motoneurons which discharged during swallowing did not receive much synaptic inputs directly from the cortex or periphery. However, during prolonged stimulation inducing chewing movements, 10 Group I SNs (16 tested) presented a rhythmic discharge (burst of spikes) during jaw opening phase (Fig. 3A′,B′). During this prolonged stimulation, a short latency (15–20 ms) response was sometimes produced by the pulses (see Fig. 3B′).

Group II SNs. Group II neurons (interneurons) were more often activated at short latency by ipsilateral

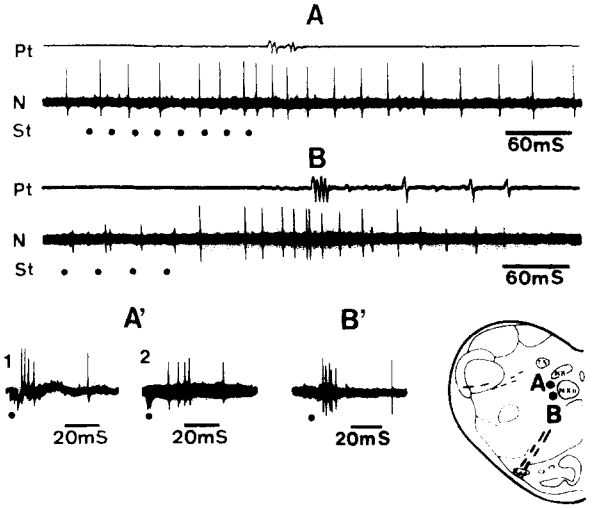

Fig. 4. Short latency activation of Group II SNs by stimulation of the LN and CCx. A: spontaneous firing rate of an interneuron (N) increased during swallowing produced by stimulation of the SLN (St: 8 pulses at 50 Hz) and indicated by EMG activity in pterygoid (Pt) muscle. A′ (1): activation of the interneuron with a short latency (5 ms) by stimulation (1 V, 0.5 ms, 3 pulses at 1000 Hz) of the ipsilateral LN. (2): activation of the same neuron (latency: 10 ms) by stimulation of the ipsilateral CCx (15 V, 0.5 ms, 2 pulses at 1000 Hz; 3 superimposed traces). B: phasic swallowing activity induced in an interneuron by stimulation of the ipsilateral SLN (4 pulses at 30 Hz, 1 V, 0.5 ms). B′: short latency (5 ms) activity reflexly evoked in the same interneuron by stimulation of the ipsilateral LN (single pulse, 1 V, 0.5 ms). Location of neurons indicated by filled circles on map, at the level of the obex (B) and 1 mm caudal (A). Abbreviations as in Fig. 2.

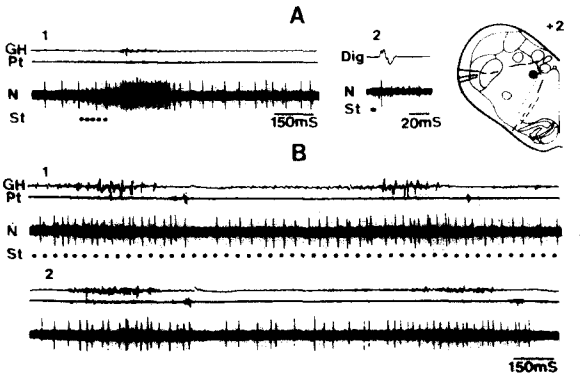

Fig. 5. Swallowing interneuron activated by stimulation of LN and during chewing movements. A (1): discharge of an interneuron (N) as compared to EMG activity of geniohyoid (GH) and pterygoid (Pt) muscles during swallowing induced by stimulation of the SLN (St: 5 pulses at 30 Hz, 1 V, 0.2 ms). (2): discharge of the same interneuron after stimulation of the LN (2 pulses at 1000 Hz, 1.5 V, 0.2 ms) which also evoked a short latency EMG activity (6 ms) in Dig (jaw opening). B: discharge of the same neuron during rhythmic jaw movements induced by prolonged stimulation (15 V, 0.2 ms, 25 Hz) of the CCx; chewing movements during the cortical stimulation in B (1), and after the train of pulses in B (2) (post discharges). Note the slight activation mainly during jaw opening (EMG of GH). Location of neuron indicated by filled circle on map.

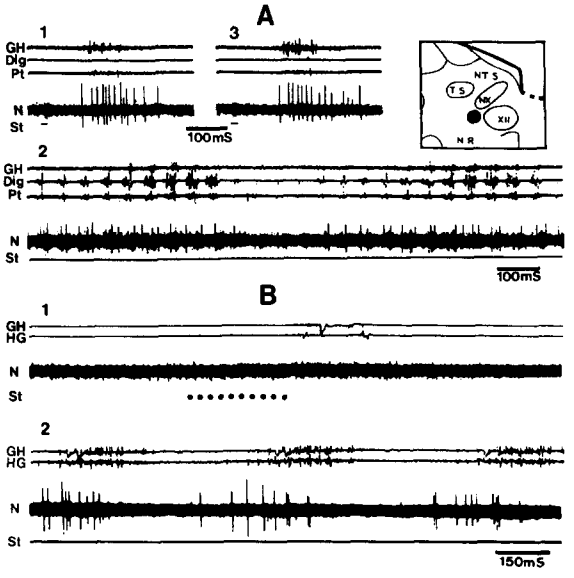

Fig. 6. Reticular interneurons activated during swallowing or chewing. A (1) and (3): activity of a reticular interneuron (N) as compared to EMG activity of geniohyoid (GH), digastric (Dig) and pterygoid (Pt) muscles during swallowing induced by stimulating the SLN (St: 5 pulses at 500 Hz) respectively before (1) and after (3) chewing movements. (2): rhythmic jaw movements induced by prolonged stimulation (12 V, 0.5 ms, 30 Hz) of the ipsilateral CCx. Note the absence of activation of swallowing interneuron and the presence of other neurons discharging during jaw opening. Location of neurons indicated by filled circle on inset (obex level). Abbreviations as in Fig. 2B (1): swallowing induced by stimulation of the SLN at 30 Hz and indicated by EMG activity of geniohyoid (GH) and hyoglossus (HG) muscles. Note the absence of neuronal discharge (N). (2): rhythmical jaw movements elicited by prolonged stimulation (12 V, 0.4 ms, 20 Hz) of the CCx. Note neuronal discharges occurring mainly during jaw opening (EMG of GH and HG).

stimulation of the peripheral afferents and CCx, since 12 neurons (30 tested) discharged by SLN stimulation (latency: 7–12 ms; mean, 9 ms ± 1.8, S.D.), 9 neurons (21 tested) by ipsilateral LN stimulation (latency: 6–12 ms; mean, 8 ms ± 1.8; Fig. 4A′, 1 and 4B′ and Fig. 5A, 2), and 5 neurons (18 tested) by CCx stimulation (latency, 10–15 ms; mean, 13 ms ± 1.7; Fig. 4A′, 2). Seven Group II SNs were found to be activated by two or three modes of stimulaton: 4 neurons by SLN and LN, 2 neurons by LN and CCx (Fig. 4A′) and one neuron by SLN, LN and CCx. In 8 Group II SNs tested during prolonged stimulation of CCx inducing rhythmic jaw movements, one neuron discharging spontaneously was rhythmically activated (slight increase of the firing rate) during the opening phase of the jaw (Fig. 5B); the remaining 7 neurons showed no modification of their activity during the jaw rhythmic movements (Fig. 6A).

Other neurons. Five neurons showing no activation during swallowing discharged rhythmically, in phase with jaw opening, during the chewing movements induced by the CCx stimulation (Fig. 6B); 3 of them were antidromically activated by stimulation of the XIIth nerve indicating that they were motoneurons. Moreover, 2 neurons whose spontaneous discharge was inhibited during swallowing were activated rhythmically during chewing movements (mainly during jaw closing). These neurons were not antidromically activated by stimulation of the XIIth nerve, and might correspond to interneurons.

DISCUSSION

Motoneurons and muscles of the tongue

Swallowing motoneurons of the XIIth motor nucleus (Group I SNs) are generally not activated at short latency by stimulation of the SLN (4 neurons activated out of 69 tested, i.e. 5.7%); this feature confirms the results obtained on motoneurons of the Vth motor nucleus[11]. On the other hand, SLN stimulation can produce EMG responses of short latency in the lingual musculature. Similar responses ('elementary reflexes') are reported in the GH (suprahyoid muscle active during jaw opening) of cat, dog and monkey[11]. Moreover, stimulation of the SLN induces in cat a response of the XIIth nerve, accompanied by a protrusion of the tongue[35]. Other investigations[21,27] have shown a reflex response in the GG by stimulation of the SLN; this result is consistent with our data. The tongue protrusion reflexly induced by stimulation of the SLN may correspond to a reflex protection of the upper airway since the GG is generally inactive during swallowing (see Fig. 1A).

Only 4 Group I SNs (56 tested, i.e. 7%) were activated by stimulation of the ipsilateral LN. Thus, in contrast with data obtained at the level of the Vth motor nucleus[11], swallowing motoneurons of the XIIth motor nucleus are not under the excitatory control of the lingual afferents. However, we have shown that stimulation of the LN induced reflex EMG responses in the tongue muscles. These responses are mainly due to the excitation of non-swallowing motoneurons. Other authors[40,41] recorded a global action potential on the medial and lateral branches of the XIIth nerve by stimulation of the LN. This stimulation was mainly effective with motoneurons of the tongue retractor muscles[22]. This feature is in accordance with our data indicating that EMG is more active in tongue retracting muscle (SG and HG) than in the tongue protruding muscle (GG, Fig. 1B). The antidromic field potentials elicited in the XIIth motor nucleus by stimulation of the lateral branch of the XIIth nerve were facilitated by a conditioning stimulation of the LN, whereas those induced by stimulation of the median branch were inhibited[28]. These results are confirmed by unitary recordings (intracellular microelectrodes) showing that LN stimulation produces EPSP in motoneurons supplying retractor muscles of the tongue, versus IPSP in

motoneurons supplying the protractor musculature[28, 29,32,38,43].

Stimulation of the CCx (1–5 pulses at 500 Hz) was not effective with either Group I SNs or with tongue muscles. However, 10 swallowing motoneurons out of 16 tested (i.e. 65%) were activated (bursts of spikes) by a prolonged cortical stimulation (20–40 Hz) inducing chewing movements. This activation was synchronous with the EMG activity in both tongue retracting (HG, SG) and jaw opening muscles (GH, Dig). In rabbit, most of the fibers of the XIIth nerve were activated during jaw closing[37]. Kaku[16] showed in rat that motoneurons of the protractor muscles discharged during jaw opening (or slightly before), whereas motoneurons of the retractor muscles are activated during jaw closing or the maximum jaw opening. Only this last point is consistent with our results on the swallowing motoneurons. In addition, our data confirm those obtained at the level of the Vth motor nucleus[1] where the same motoneurons were found to discharge during both swallowing and chewing. However, it shoud be noted that some swallowing motoneurons of the XIIth motor nucleus did not discharge during chewing, while other motoneurons inactive during swallowing exhibited a chewing discharge. Finally, we have indicated that during prolonged stimulation of CCx, swallowing motoneurons or tongue muscles could be activated at short latency ($\geqslant$ 15 ms) following the pulses of the train. Therefore, it seems that there might be two corticofugal pathways, one relaying through the chewing center and the other one impinging more directly on the motoneurons. A similar pattern has been described at the level of the Vth motor nucleus and jaw muscles[1,10].

Reticular interneurons

The excitatory effects (short latency activation) of peripheral afferents (SLN and LN) and fronto-orbital cortex (CCx) were greater upon Group II SNs. Twelve out of 30 tested (~40%) were activated by ipsilateral stimulation (1–3 pulses at 500 Hz) of the SLN, and 9 out of 21 tested (~42%) by LN stimulation. In addition, 4 Group II SNs discharged following stimulation of both the SLN and LN. Interneurons of the reticular formation adjacent to the XIIth motor nucleus were found to be activated by stimulation of the LN[22,32]. It is suggested[22] that afferent impulses of various origins (LN, SLN, glossopharyngeal and infra-orbital nerves) converge on these interneurons. This is consistent with other data showing that reticular interneurons near the XIIth nucleus are activated by stimulation of the masseter and alveolar nerves[39]. Moreover, 5 Group II SNs out of 18 tested (~28%) were activated at short latency by stimulation (1–5 pulses at 500 Hz) of the ipsilateral CCx; three of them also responded to the stimulation of the LN and/or SLN, indicating that corticofugal and peripheral impulses impinge on the same interneurons. This convergence has never been reported. Group II SNs located in the reticular formation very close to the XIIth motor nucleus may be excitatory or inhibitory interneurons for the XIIth motoneurons[9]. We think that Group II SNs activated at short latency by LN and/or CCx stimulation correspond to inhibitory interneurons for GG motoneurons. Motoneurons of the GG muscle are inhibited during swallowing[24] and we have shown that GG was generally inactive (see Fig. 1A). In addition, other authors[43] reported the presence of IPSP in the motoneurons of the GG during swallowing. IPSPs may be recorded from XIIth motoneurons by stimulation of the LN[29,43] or fronto-orbital cortex[42].

During chewing movement induced by prolonged stimulation of the CCx, only one swallowing interneuron (8 tested) discharged (weak increase of the spontaneous firing rate) during rhythmic jaw movements, independently of the stimulus pulses (Fig. 5B). In contrast to Group I SNs, Group II SNs of the reticular formation close to the XIIth motor nucleus are generally not involved in chewing. However, other reticular interneurons (4 neurons), inactive during swallowing or exhibiting an inhibition of their spontaneous activities, discharged rhythmically during chewing movements. These features seem to indicate that two different pools of interneurons are involved in swallowing and chewing. To our knowledge, the existence of interneurons active during chewing has never been reported in the parvocellular reticular formation very close to the XIIth motor nucleus (within 1 mm of the obex) since such reticular interneurons have previously been recorded only from the median part of the medullary reticular formation (4–7 mm rostral to the obex) in cat[31], from the lateral reticular nucleus in rabbit[25], and from the lateral ponto-bulbar reticular formation in rat[30].

In conclusion, our data indicate that the central swallowing pathway provides for convergence of peripheral and cortical inputs primarily in interneurons adjacent to the hypoglossal nucleus, and that interneurons devoted to swallowing are generally not activated during chewing. In contrast, hypoglossal motoneurons involved in swallowing are more isolated from peripheral and cortical inputs and can discharge during both swallowing and chewing. Other interneurons and motoneurons are specifically dedicated to chewing.

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