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Activity of neurons located in the region of the hypoglossal motor nucleus during swallowing in sheep

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Summary. Extracellular activity of swallowing neurons (SN) in the region of the hypoglossal (XIIth) motor nucleus was studied in sheep anesthetized with halothane. Eighty six SN exhibited a discharge closely linked to swallowing electromyographic (EMG) activity of the geniohyoïd (GH) muscle induced by stimulation of the superior laryngeal nerve. Swallowing activation persisted after motor paralysis, indicating that this activity did not result from sensory feedback. SN were classified into two groups. *Group I SN* (N = 66) discharged a burst of up to 12 spikes for 50–300 ms during the response of GH. Mean frequencies ranged from 10 to 60 Hz, peak instantaneous frequencies from 10 to 100 Hz. Thirty two SN were antidromically activated by stimulating the XIIth nerve. Mean latencies of antidromic spikes were 2.6 ms and 2.4 ms for SN sending their axons in the medial and lateral branches respectively of XIIth nerve, corresponding to conduction velocities of 50.4 m/s and 53.7 m/s. The other 34 group I SN were located at sites with large antidromic field potentials obscuring the identification of unitary antidromic spikes. Thirty group I SN, 16 antidromically activated and 14 in areas with large field potentials, were histologically located in the XIIth motor nucleus between the transverse planes 1 mm caudal to 2 mm rostral to the obex. Group I SN are likely motoneurons supplying GH and tongue musculature. *Group II SN* (N = 20) were never antidromically activated by XIIth nerve stimulation, and were all located in the reticular formation adjacent to the lateral edge of the XIIth motor nucleus, particularly in transverse planes within 1 mm of the obex. During swallowing, group II SN exhibited an activation (10–50 spikes) lasting from 100 to 370 ms and generally starting before the onset of GH activity. Mean frequencies ranged from 60 to 200 Hz, and peak instantaneous frequencies from 120 to 400 Hz. Central microstimulation of group II SN evoked in the ipsilateral XIIth nerve a synaptic potential with a latency 0.8 to 1.3 ms longer than that induced by directly stimulating the XIIth motor nucleus. In addition, stimulation of group II SN was also effective in eliciting EMG activity of the contralateral GH. These results suggest that group II SN are interneurons involved in the bilateral activation of GH and tongue muscles.

Key words: Swallowing – Hypoglossal motor nucleus – Parvicellular reticular formation – Unit activity (extracellular microelectrodes) – Sheep

Introduction

Swallowing is a complex motor sequence involving the coordinated contraction of several muscles of the mouth, pharynx, larynx and esophagus. This motor sequence is centrally programmed by the medullary swallowing centre (Doty 1968; Car and Roman 1970; Jean 1972; Dubner et al. 1978; Miller 1982; Jean 1984; Kessler and Jean 1985; Roman 1986) which contains swallowing neurons (SN) including interneurons and motoneurons, the activity of which produces the motor sequence. This pattern of activity is unaltered by paralysis. In sheep, SN are located mainly in two regions (Jean 1972): a dorsal region including the nucleus of the tractus solitarius (NTS) and the adjacent reticular formation (2–4 mm rostral to the obex), and a ventral region corresponding to the nucleus ambiguus and the surrounding reticular formation (3–6 mm rostral to the obex). Other SN are located in the trigeminal (Vth) motor nucleus and the adjacent reticular formation (motoneurons and

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interneurons; Car and Amri 1982), and the hypoglossal (XIIth) motor nucleus which contains motoneurons supplying tongue musculature. In contrast to SN located in the ventral region of the swallowing centre, and in and around the Vth nucleus, the types of SN (motoneurons and interneurons) in the region of the XIIth nucleus have not been established. Some data were obtained by Sumi (1964, 1969, 1970) in cat and rabbit, but mainly by means of unitary recordings from the XIIth nerve. In the rat, Kessler and Jean (1985) recorded discharges from SN in the region of the XIIth motor nucleus; however, the cells were not identified as motoneurons or interneurons by antidromic invasion using stimulation of the XIIth nerve. The aim of the present work was to study the activity of SN located in the region of the XIIth motor nucleus, in order to demonstrate the existence of both motoneurons and interneurons. A preliminary report has been presented (Amri and Car 1985).

Methods

This study was performed on twenty-eight anesthetized adult sheep.

Surgical procedure

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 the anesthesia. The geniohyoïd (GH) and occasionally the anterior digastric (DG) muscle were exposed via a medial incision of the skin under the jaw. The XIIth nerve was dissected along the ventral border of the styloglossus (SG) muscle. This dissection was sometimes extended to the two main peripheral branches of the XIIth nerve, the lateral supplying the hyoglossus (HG) and SG muscles (retractors of the tongue), and the medial innervating the genioglossus (GG; main protrusor of the tongue) and GH muscles (see Lowe 1981). The superior laryngeal nerve (SLN) which contains laryngeal afferents involved in triggering swallowing was dissected at its exit from the thyroid cartilage.

For rhombencephalic exposure, the animal held in a prone position with the head firmly supported. The skin was incised along the midline of the skull. Following removal of the occipital bone and cerebellum, the dorsal surface of the medulla oblongata was exposed and covered with warm liquid paraffin. At the end of the surgical period, the head was placed in a stereotaxic apparatus specially adapted to sheep. An adequate level of anesthesia, indicated by pupillary constriction, was maintained throughout the experimental period with an inspired halothane concentration of 1–1.5%. All wounds were regularly infiltrated with a 2% procaïne solution. Body temperature and heart rate were continually monitored.

Electrical stimulation

Bipolar platinum electrodes were used to stimulate the SLN and XIIth nerves. For stimulation of medullary structures, tungsten microelectrodes with 1–2 µm tip diameters and impedances of 2–5 MΩ at 1,000 Hz (Haer) were used. The electrodes were connected to a stimulator through a high frequency isolation unit (WPI). Stimulus parameters were 0.5–2 V, 0.02–0.2 ms pulse duration for nerves, and 20–50 µA, 10–50 µs pulse duration for central stimulation.

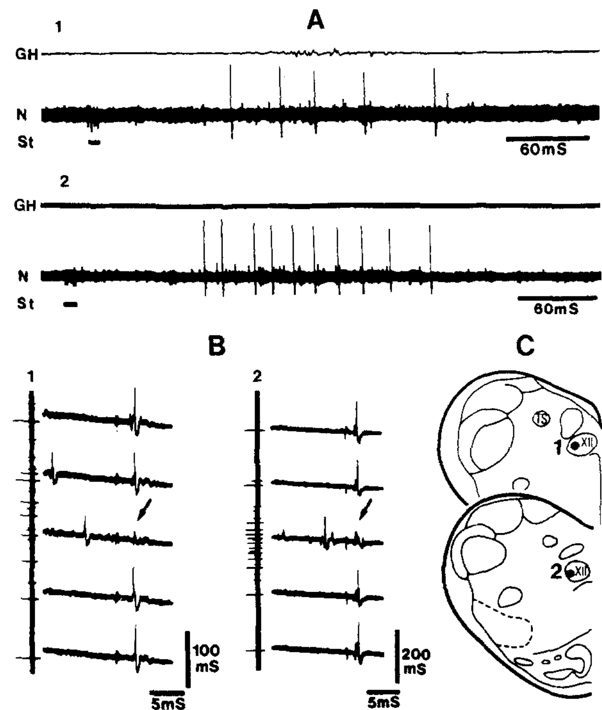

Fig. 1. A, B Activity of group I SN. GH, EMG activity of geniohyoïd muscle; N, activity of the neuron; St, stimulation. **A** Activation of two neurons (1 and 2) by SLN stimulation (4 pulses at 500 Hz). Animal lightly curarized in 1, deeply in 2. Swallowing activation greater (more spikes and higher frequency) in 2 than in 1. In both, a short latency response is absent. **B** Same neurons as in **A**. Collision test between orthodromic spike and antidromic spike elicited by stimulation of XIIth nerve (1.5 V; 0.1 ms). Antidromically evoked spike on horizontal trace; swallowing activity on vertical record. Antidromic spikes (arrows) fail when orthodromic spike precedes stimulation within critical delay. **C** Location of neurons indicated by filled circles

Recordings

Electromyographic (EMG) activity of GH was recorded with paired copper wires, insulated except at the tip, inserted into the muscle. Extracellular activity of neurons during swallowing was recorded with tungsten microelectrodes of 1 µm tip diameters and impedances of either 9–12 MΩ or 2–5 MΩ at 1,000 Hz (Haer). Potentials were amplified and monitored or filmed from an oscilloscope.

Histological controls

Medullary recording and stimulating sites were marked by electrocoagulation (200–300 µA DC for 5 s) and later located from unstained frozen 50 µm thick sections.

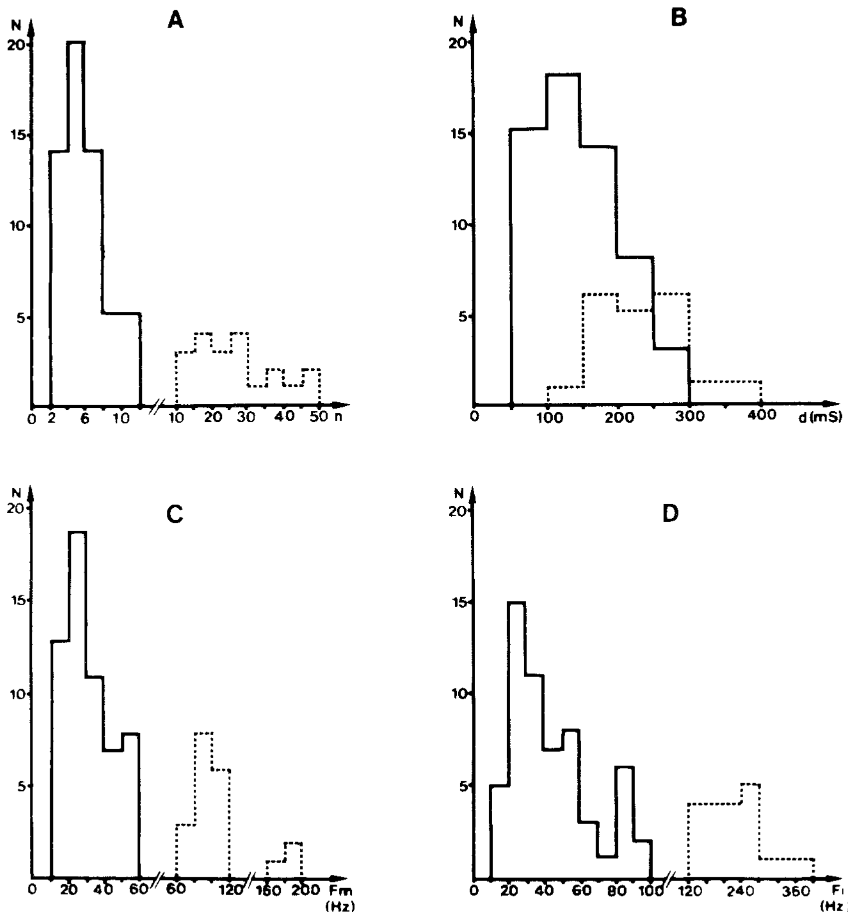

Fig. 2A–D. Histograms of discharge characteristics of SN. For each histogram: N = number of cells. Solid lines: group I SN (N = 58); 8 neurons discharging with either a single spike or 2 spikes with irregular intervals excluded. Broken lines: group II SN (N = 20). Note change of scale for abscissae of **A, C, D. A** Number of spikes (n) during swallowing activation. **B** Duration (d) of swallowing activation. **C** Mean firing rate (Fm). **D** Peak instantaneous frequency (Fi). Note absence of overlap between firing rates of the two groups of SN

Curarization

During studies of unitary activity of SN in the region of the XIIth motor nucleus, the animals could be curarized by i.v. injections of gallamine triethiodide (Flaxedil), in order to prevent activation of neurons by sensory feedback resulting from contraction of swallowing muscles (see Car and Amri 1982). Curarization was generally light (0.5–0.7 mg/kg) in order to allow weak EMG activity of the GH (swallowing muscle) to persist. Deep curarization (2 mg/kg) abolishing EMG of the GH was sometimes used, but always after the discharge of the recorded neuron had been related to reflex swallowing (EMG activity of GH).

Identification of motoneurons

Motoneurons supplying the GH and tongue muscles were identified by antidromic activation following stimulation of the ipsilateral XIIth nerve. The following criteria were used: (1) collision between antidromic and orthodromic spikes. To perform this test, the antidromic response was elicited during swallowing activity induced by SLN stimulation. Thus, when an orthodromic potential preceded the nerve stimulation within an appropriate time interval (critical delay), no antidromic response was obtained (Fuller and Schlag 1976; Schlag 1978; Barillot et al. 1980; Lipski 1981); (2) the antidromic response had a short fixed latency and could follow high frequency stimuli (300–500 Hz); (3) spikes elicited by nerve stimulation had identical waveforms to those during swallowing activity.

Results

Activity and location of swallowing neurons

We recorded in 22 sheep the extracellular activity of 86 SN discharging typically with a burst of spikes (swallowing activation) linked to reflex swallowing (EMG activity of GH) induced by SLN stimulation (short trains of pulses at 30 Hz, or 2–4 pulses at 500 Hz). In all 31 SN in which SLN stimulation elicited swallowing activation, activity persisted after complete paralysis (Fig. 1A2, Fig. 5B) and was therefore determined only by central mechanisms.

SN were divided into two groups. *Group I SN* (N = 66) were never spontaneously active and discharged only in association with EMG activity of GH. Swallowing activation (Fig. 1A; Fig. 2) was characterized by a burst of 1 to 12 spikes (5.4 ± 2.6; mean ± SD) and, for bursts containing at least 2 spikes, a burst duration of 50 to 300 ms (140.8 ms ± 63.6) and a mean firing rate of 10 to 60 Hz (30.8 Hz ± 13.2) with a peak instantaneous frequency of 10 to 100 Hz (42.5 Hz ± 22.9). Moreover, 4 SN were also

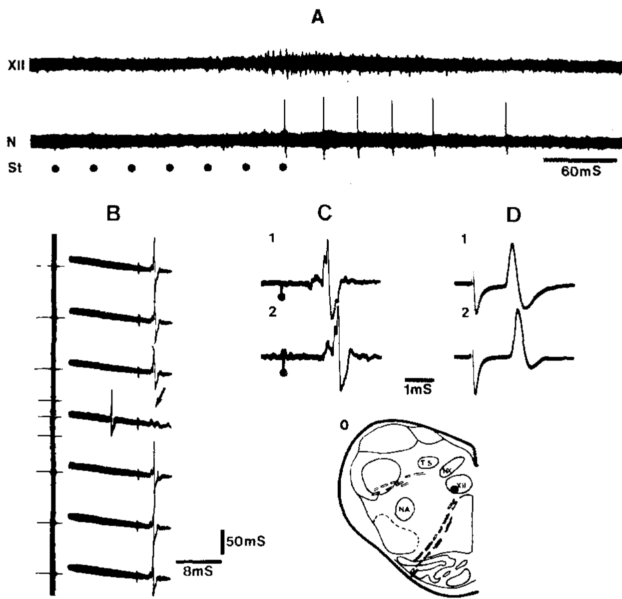

Fig. 3A–D. Conduction velocity of a group I SN calculated by stimulation or recording at two different sites. Location of neuron indicated by filled circle on transverse section of medulla at level of obex. **A** XII, activity of XIIth nerve; N and St as in Fig. 1. Swallowing activity elicited by SLN stimulation at 30 Hz. **B** Collision test by stimulating (1 V; 30 µs) the medial branch of XIIth nerve. Antidromic spike fails after stimulation following orthodromic spike (arrow). **C** Antidromic potentials due to stimulating (1 V; 50 µs) entire XIIth nerve in 1, and its medial branch in 2. Distance between the two stimulating sites: 16 mm. Difference in latency (0.33 ms) corresponds to a conduction velocity of 48.5 m/s. **D** Compound action potentials recorded from the common trunk (1) and the medial branch (2) of XIIth nerve following stimulation (50 µA; 10 µs) at location of unit. Latency difference (0.27 ms) corresponds to a conduction velocity of 59.2 m/s for the fastest fibers

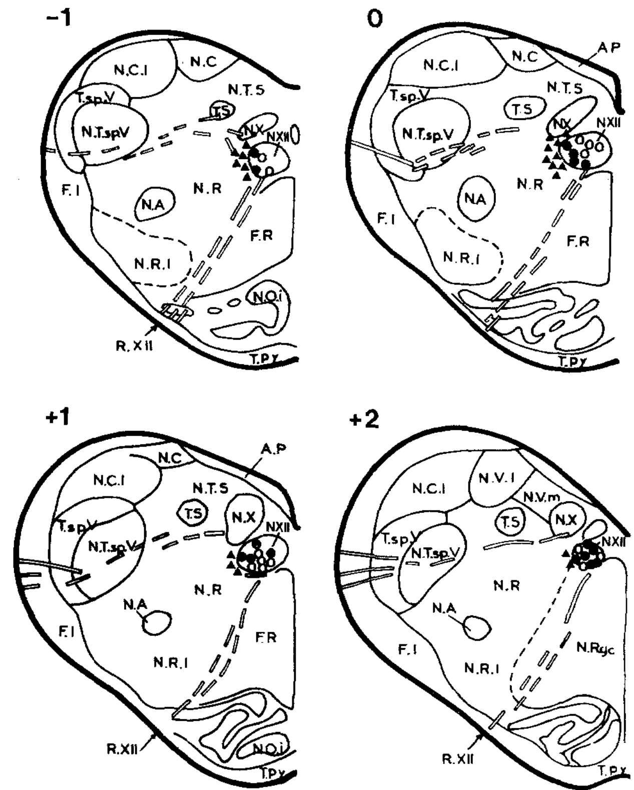

Fig. 4. Location of SN. Transverse hemisections of medulla oblongata, relative to obex (0 mm). *Filled circles*: group I SN antidromically activated by stimulation of the entire XIIth nerve (N = 3) or its peripheral branches (N = 13). *Open circles*: group I SN located at sites with large antidromic field potentials obscuring unitary antidromic potentials (N = 14). *Filled triangles*: group II SN (N = 20). AP: area postrema; Fl: fasciculus lateralis; NA: nucleus ambiguus; NC: nucleus cuneatus (Burdach); NCl: nucleus cuneatus lateralis (Von Monakov); Ni St: nucleus intercalatus (Staderini); NOi: nucleus olivaris inferior; NR: nucleus reticularis medullae oblongatae; NRgc: nucleus reticularis gigantocellularis; NRI: nucleus reticularis lateralis; NTS: nucleus tractus solitarius; NTspV: nucleus tractus spinalis n. trigemini; NVl: nucleus vestibularis lateralis; NVm: nucleus vestibularis medialis; NX: nucleus dorsalis n. vagi; NXII: nucleus n. hypoglossi; RX: radices n. vagi; RXII: radices n. hypoglossi; TPy: tractus pyramidalis; TS: tractus solitarius; TspV: tractus spinalis n. trigemini

activated at short latency (10–15 ms) by stimulation (2–4 pulses at 500 Hz) of the ipsilateral SLN.

Thirty two group I SN, most discharging at a mean frequency less than 40 Hz (25 neurons), were antidromically activated (collision test) by stimulating the ipsilateral XIIth nerve or one of its peripheral branches (Fig. 1B). The latency of the antidromic spike depended on the site of stimulation: 2.2 ms ± 0.3 for the common trunk (N = 9), 2.4 ms ± 0.2 for the lateral branch (N = 11), and 2.6 ms ± 0.7 (N = 12) for the medial branch. The mean conduction velocities of group I SN, calculated from the latencies of the antidromic spikes and an estimated distance of 13 cm, were 50.4 m/s ± 13 and 53.7 m/s ± 4.8 for the SN sending their axons through the medial and the lateral branches respectively of the XIIth nerve. These values are in accordance with those obtained using stimulation (Fig. 3C) or recording (Fig. 3D) at two different sites. The 34 remaining group I SN were recorded from regions in which stimulation of the XIIth nerve evoked a large field potential obscuring the unit's activity, even when the stimulus intensity was reduced.

Thirty group I SN, 16 antidromically activated by XIIth nerve stimulation and 14 recorded from regions in which the same stimulation evoked a large field potential, were localized by electrocoagulation (Fig. 4). They were all located in the XIIth motor nucleus, between the transverse planes 1 mm caudal to the obex to 2 mm rostral to the obex, with a predominant representation in the rostral part of the nucleus. We observed no difference in the locations of SN with axons in either the lateral or medial branch of the XIIth nerve. From their stereotaxic

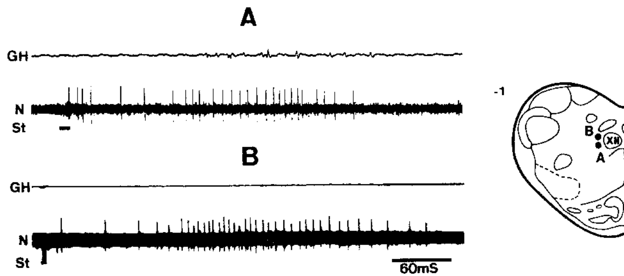

Fig. 5A, B. Activity of group II SN. Abbreviations as in Fig. 1. **A**, **B** Recorded from different animals during swallowing induced by stimulating the ipsilateral SLN (4 pulses at 500 Hz in **A**, 1000 Hz in **B**). Animal curarized in **B**. Recording sites indicated by filled circles on transverse section of medulla, 1 mm caudal to obex. Note the short latency response (~ 10 ms) followed by the swallowing activation at high frequency in **A**, and the prolonged discharge at high frequency in **B**

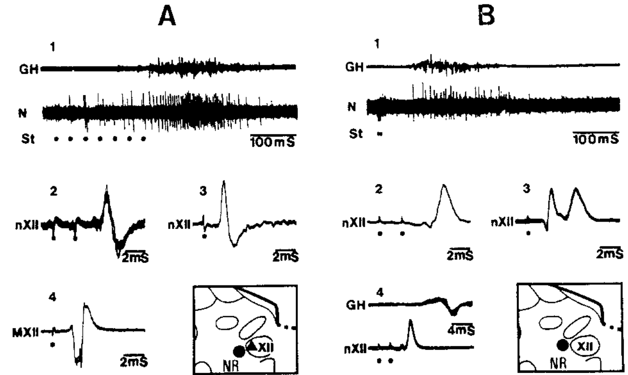

Fig. 6A, B. Effects of microstimulation at the level of SN recording sites. **A**, **B** Recorded from different animals. Abbreviations as in Fig. 1; n XII, global potential of XIIth nerve; MXII, XIIth motor nucleus activity. **A1** Swallowing activation elicited by SLN stimulation (7 pulses at 30 Hz). **A2** Synaptically evoked potential (latency 2.7 ms, 5 superimposed sweeps) to stimulation (50 μA, 50 μs, 2 pulses at 500 Hz) at the site of unit activity (filled circle in inset). **A3** Directly evoked response (latency 1.6 ms) to stimulation (25 μA, 50 μs, single pulse) of the ipsilateral XIIth motor nucleus (filled triangle). Note latency difference (1.1 ms) between **A2**, **A3**. **A4** Antidromic field potential recorded from motor nucleus by stimulating (2 V, 0.1 ms) ipsilateral XIIth nerve. **B1** Activation by SLN stimulation (3 pulses at 500 Hz). **B2** Potential synaptically evoked by ipsilateral stimulation (25 μA, 50 μs, 2 pulses at 500 Hz) at the site of unit activity (filled circle on inset). **B3** Stimulation at the same site at increased intensity (100 μA, 50 μs, single pulse) inducing a response with two components corresponding to direct and synaptic activation of motoneurons. **B4** Experimental conditions as in 2, but at a slower sweep speed and with EMG of contralateral GH

coordinates, the other 36 group I SN were also probably located in the XIIth nucleus.

Eighteen neurons did not discharge during reflexly induced swallowing and 2 (with axons in the medial branch) had spontaneous activity which was suppressed during swallowing; 7 of these neurons were activated antidromically by stimulation of the medial branch, 10 by the lateral and 3 by the entire XIIth nerve.

Group II SN (N = 20) were never antidromically activated by stimulating the ipsilateral XIIth nerve. Moreover, such stimulation did not evoke a field potential large enough to obscure unitary activity. Seven neurons were spontaneously active. During swallowing (Figs. 2 and 5), group II SN exhibited an activation lasting from 100 to 370 ms (218.2 ms ± 61.9) consisting of 10 to 50 spikes (25.1 ± 11.2) and generally starting before the onset of EMG activity (Fig. 5A; Fig. 6A1). The mean firing rate ranged from 60 to 200 Hz (104.6 Hz ± 36.7) and the peak instantaneous frequency from 120 to 400 Hz (214 Hz ± 75.7). Furthermore, 11 group II SN were activated at short latency (9 ms ± 1.8; range, 7–12 ms) by stimulation of the ipsilateral SLN (2–4 pulses at 500 Hz; Fig. 5A).

All group II SN were located in the parvicellular reticular formation, very close to the lateral edge of the XIIth motor nucleus, particularly in transverse planes within 1 mm of the obex (Fig. 4).

Effects of central microstimulation

In 6 sheep we tested the effects of central stimulation, delivered through the recording microelectrode, on the activity of either the ipsilateral XIIth nerve or swallowing muscles. Single pulses of low intensity applied at recording sites of group I SN always induced a short latency (1.65 ± 0.14 (mean ± SD); range 1.5–2 ms) compound action potential in the XIIth nerve (Fig. 3D, Fig. 6A3); this potential followed high frequency stimulation of the XIIth motor nucleus. In contrast, identical stimulation applied to group II recording sites evoked no response in the XIIth nerve. Only by using a train of pulses (2–3 pulses at 500 Hz) was a response obtained (Fig. 6A2, B2); the average latency was 2.59 ms ± 0.31 (range, 2.3–3.3 ms). This latency was longer than that required for direct activation of motoneurons of the XIIth nucleus (latency difference: 0.8–1.3 ms; Fig. 6).

Similar results were obtained by recording EMG activity of the ipsilateral GH; the latency of the EMG evoked by stimulating the XIIth motor nucleus was less than that following stimulation of the reticular formation adjacent to it (3–3.5 ms versus 4–4.5 ms). Moreover, stimulation of the reticular formation was also effective in eliciting activity of the contralateral GH muscle (latency 6.5–7 ms; see Fig. 6B4), as well as of the ipsilateral anterior DG muscle (latency 3–4 ms).

Discussion

In the region of the XIIth motor nucleus, we recorded the activities of 86 SN discharging during swallowing induced by SLN stimulation; in addition, 20 neurons antidromically activated by the XIIth nerve (N = 3) or its peripheral branches (N = 17) failed to discharge indicating that not all motoneurons of the XIIth nucleus were activated during reflexly induced swallowing. Two groups of SN were identified. *Group I SN* (N = 66) were either antidromically activated (N = 32) by stimulation of the XIIth nerve (common trunk or peripheral branches), or located in regions in which the same stimulation evoked a large field potential obscuring the identification of unitary antidromic spikes (N = 34). Thirty recording sites were marked by electrocoagulation, 16 at sites with antidromically evoked spikes and 14 at sites with large antidromic field potentials. All were located within the XIIth motor nucleus, particularly in its rostral part (see Fig. 4). The stereotaxic coordinates of the other 36 group I SN indicate that they were likely located in the XIIth nucleus. All these features indicate that group I SN are motoneurons. Since evidence for γ motoneurons within the XIIth motor nucleus and for muscle spindles in the tongue musculature of subprimates has not been reported (Blom 1960; Porter 1968; Bowman 1971; Morimoto et al. 1972; Lowe 1981; Kitamura et al. 1983) we believe that group I SN are all α motoneurons supplying GH and tongue musculature. During swallowing, most motoneurons, like those of the Vth motor nucleus (Car and Amri 1982), discharged at low frequencies (< 40 Hz; Fig. 2). Kessler and Jean (1985), however, never observed mean firing rates inferior to 40 Hz in the rat.

Our data show that motoneurons of the lateral and medial branches of the XIIth nerve, supplying respectively HG-SG and GG-GH muscles (see Lowe 1981), were activated during reflexly induced swallowing. The mean latencies of antidromically evoked spikes were similar for the two pools of motoneurons. This agrees with the results of Sumino and Nakamura (1974) and Lowe (1978) which show no difference in the mean latencies of antidromic responses between motoneurons of protrusive (GG) and retractive (HG-SG) muscles. However, the standard deviations of the mean latencies from our data suggest that the pool of swallowing motoneurons of the lateral branch is more homogeneous than that of the medial branch. The medial branch seems to contain motoneurons having both the fastest and slowest conduction velocities. The former are probably motoneurons of the GH muscle since, in the rat, motoneurons of the XIIth motor nucleus range in size from 10 to 34 μm in diameter (Odutola 1976) and, in the same species, Kitamura et al. (1983) report that motoneurons supplying the GH have a mean diameter of 28.7 μm ± 4.4 (SD) indicating that they are the largest in the motoneuronal pool. This feature has been confirmed in cat (Uemura et al. 1979). Moreover, our values of the conduction velocities of SN belonging to the XIIth motor nucleus are in accordance with those (24–60 m/s) measured by Porter (1968) in cat, but slightly higher than those (35.5 ± 8.7 m/s for protrusive motoneurons and 36.5 ± 11.6 m/s for retractive motoneurons) estimated by Lowe (1981).

Group II SN (N = 20) were never antidromically activated by XIIth nerve stimulation and were all located in the reticular formation near the ventrolateral edge of the XIIth motor nucleus. These features indicate that group II SN are interneurons or premotor neurons. During swallowing, they discharged at frequencies higher than motoneurons; a similar result has been reported for the pontine SN (Car and Amri 1982). In addition, group II unlike group I SN were generally activated with a short latency (7–12 ms) following ipsilateral stimulation of SLN. Kessler and Jean (1985) report that, in rat, stimulation of SLN evokes both an initial activation (latency 7–12 ms) and a later high frequency (up to 250 Hz) discharge of SN in the region of the XIIth nucleus. They did not, however, identify these cells as motoneurons or interneurons.

Many electrophysiological and histological studies (Green and Negishi 1963; Porter 1965; Sumi 1969; Sumino and Nakamura 1972; Lowe 1978; Brodal 1983) indicate the existence of interneurons in the vicinity of the XIIth motor nucleus. The functional significance of these interneurons remains unclear. Central microstimulation (see Fig. 6) showed that the latencies of the potentials recorded from the ipsilateral XIIth nerve to stimulation of the recording sites of group II SN were longer (0.8–1.3 ms) than those produced by direct stimulation of the XIIth motor nucleus. This latency difference corresponds to one or two synaptic delays. In addition, microstimulation of the reticular formation can activate contralateral motoneurons and even trigeminal motoneurons, since EMG activities were recorded from the contralateral GH muscle (see Fig. 6B4) and the ipsilateral DG muscle which is also involved in swallowing (Car and Amri 1982). All these responses may result from stimulation of interneurons excitatory to ipsilateral and contralateral hypoglossal motoneurons, as well as to trigeminal motoneurons. This interpretation is consistent with several neuroanatomical studies. Aldes (1980); Borke et al. (1983); Travers and Norgren (1983);

Takada et al. (1984) have found labeled neurons bilaterally in the reticular formation close to the ventrolateral edge of the XIIth motor nucleus after HRP injection within this nucleus in rat and cat. Moreover, Travers and Norgren (1983) showed labeled neurons in the reticular formation near the XIIth nucleus after injection of HRP within the trigeminal motor nucleus in rat. In addition, electrophysiological (Sumino and Nakamura 1974; Lowe 1978) and neuroanatomical (Borke and Nau 1985) data suggest that neurons located in the reticular formation adjacent to the XIIth nucleus exert inhibitory effects on trigeminal motoneurons. GG motoneurons exhibiting spontaneous discharges modulated by the respiratory rhythm are inhibited during swallowing (Lowe and Sessle 1974); in our study we found that the spontaneous activities of 2 motoneurons of the medial branch of XIIth nerve were suppressed during swallowing. Finally, facilitatory and inhibitory interneurons located in the reticular formation adjacent to the XIIth motor nucleus may be involved in the bilateral coordination of tongue motoneurons during swallowing.

In conclusion, our data demonstrate the existence of both swallowing motoneurons and interneurons in the region of the XIIth motor nucleus. This organization is similar to that previously described at the level of the Vth motor nucleus.

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References

Aldes LD (1980) Afferent projections to the hypoglossal nucleus in the rat and cat. Anat Rec 196: 7A

Amri M, Car A (1985) Activité des neurones déglutiteurs de la région du noyau moteur de l'hypoglosse. J Physiol (Paris) 80: 40A

Barillot JC, Bianchi AL, Dussardier M, Gauthier P (1980) Study of the validity of the collision test. Application to the bulbospinal respiratory neurones. J Physiol (Paris) 76: 845–858

Blom S (1960) Afferent influences on tongue muscle activity. A morphological and physiological study in the cat. Acta Physiol Scand (Suppl 170) 49: 1–97

Borke RC, Nau ME, Ringler RL Jr (1983) Brain stem afferents of hypoglossal neurons in the rat. Brain Res 269: 47–55

Borke RC, Nau ME (1985) The ultrastructural identification of reticulo-hypoglossal axon terminals anterogradely labeled with horseradish peroxidase. Brain Res 337: 127–132

Bowman JP (1971) The muscle spindle and neural control of the tongue. Implication for speech. Thomas, Springfield, Ill, 160 p

Brodal A (1983) The perihypoglossal nuclei in the macaque monkey and the chimpanzee. J Comp Neurol 218: 257–269

Car A, Roman C (1970) Déglutition et contractions oesophagiennes réflexes produites par la stimulation du bulbe rachidien. Exp Brain Res 11: 75–92

Car A, Amri M (1982) Etude des neurones déglutiteurs pontiques chez la brebis. I. Activité et localisation. Exp Brain Res 48: 345–354

Doty RW (1968) Neural organization of deglutition. In: Handbook of physiology, Sect VI, Vol IV. Alimentary canal. Am Physiol Soc, Washington, pp 1861–1902

Dubner R, Sessle BJ, Storey A (1978) The neural basis of oral and facial function. Plenum Press, New York, 483 p

Fuller JH, Schlag JD (1976) Determination of antidromic excitation by the collision test: problems of interpretation. Brain Res 112: 283–298

Green JD, Negishi K (1963) Membrane potentials in hypoglossal motoneurons. J Neurophysiol 26: 835–856

Jean A (1972) Localisation et activité des neurones déglutiteurs bulbaires. J Physiol (Paris) 64: 227–268

Jean A (1984) Control of the central swallowing program by inputs from the peripheral receptors. A review. J Autonom Nerv Syst 10: 225–233

Kessler JP, Jean A (1985) Identification of the medullary swallowing regions in the rat. Exp Brain Res 57: 256–263

Kitamura S, Nishiguchi T, Sakai A (1983) Location of cell somata and the peripheral course of axons of the geniohyoïd and thyrohyoïd motoneurons: a horseradish peroxidase study in the rat. Exp Neurol 79: 87–96

Lipski J (1981) Antidromic activation of neurons as an analytic tool in the study of the central nervous system. J Neurosci Meth 4: 1–32

Lowe AA (1978) Excitatory and inhibitory inputs to hypoglossal motoneurons and adjacent reticular formation neurons in cats. Exp Neurol 62: 30–47

Lowe AA (1981) The neural regulation of tongue movements. In: Progress in neurobiology, Vol 15. Pergamon Press Ltd, London, pp 295–344

Lowe AA, Sessle BJ (1974) Genioglossus activity during respiration, jaw opening and swallowing in cat and monkey. Brain Res 21: 417–422

Miller AJ (1982) Deglutition. Physiol Rev 62: 129–184

Morimoto T, Hamada T, Kawamura Y (1972) Mechanoreceptors in the geniohyoïd muscle of cat (cited by Kitamura et al. 1983)

Odutola AB (1976) Cell grouping and Golgi architecture of the hypoglossal nucleus of the rat. Exp Neurol 52: 356–371

Porter R (1965) Synaptic potentials in hypoglossal motoneurons. J Physiol (Lond) 180: 209–224

Porter R (1968) Antidromic responses of hypoglossal motoneurons. Exp Neurol 20: 624–634

Roman C (1986) Nervous control of swallowing and oesophageal motility in mammals. J Physiol (Paris) 81: 118–131

Schlag J (1978) Electrophysiological mapping techniques. In: Robertson RT (ed) Neuroanatomical research techniques. Academic Press, New York, pp 385–404

Sumi T (1964) Neuronal mechanisms in swallowing. Pflügers Arch 278: 467–477

Sumi T (1969) Functional differentiation of hypoglossal neurons in cats. Jpn J Physiol 19: 55–67

Sumi T (1970) Activity in single hypoglossal fibers during cortically induced swallowing and chewing in rabbits. Pflügers Arch 914: 339–346

Sumino R, Nakamura Y (1972) Identification and location of inhibitory interneurons with synapses on hypoglossal motoneurons. The Physiologist 15: 279A

Sumino R, Nakamura Y (1974) Synaptic potentials of hypoglossal motoneurons and a common inhibitory interneuron in the trigemino-hypoglossal reflex. Brain Res 73: 439–454

Takada M, Itoh K, Yasui Y, Mitani A, Nomura S, Mizuno N (1984) Distribution of premotor neurons for the hypoglossal nucleus in the cat. Neurosci Lett 52: 141–146

Travers JB, Norgren R (1983) Afferent projections to the oral motor nuclei in the rat. J Comp Neurol 220: 280–298

Uemura M, Matsuda K, Kume M, Takeuchi Y, Matsushima R, Mizuno N (1979) Topographical arrangement of hypoglossal motoneurons: an HRP study in cat. Neurosci Lett 13: 99–104

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