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Projections from the medullary swallowing center to the hypoglossal motor nucleus: a neuroanatomical and electrophysiological study in sheep*

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Neurons of the hypoglossal (XIIth) motor nucleus participate in swallowing, but nothing is known of the input to these cells from swallowing interneurons (SIN) belonging to the medullary swallowing center (SC). After electrophoretic injection of horseradish peroxidase within the XIIth motor nucleus in sheep, labeled neurons were found principally in the ipsilateral ventrolateral reticular formation, 1–4 mm rostral to the obex which corresponds to the ventral region of the SC. Labeled cells were observed in the region of the nucleus of the tractus solitarius (dorsal region of the SC), predominantly when the injection site of HRP extended beyond the XIIth nucleus. The projections of ventral SIN to the XIIth nucleus was confirmed electrophysiologically. Twenty-seven of 98 tested SIN were antidromically activated (latency: 2.7 ± 1.5 ms) by stimulating the XIIth nucleus. Twenty-one of these were histologically localized in the ventral SC, and only one in the dorsal SC. The other 5 SIN were located in the ventral group according to their stereotaxic coordinates. Our data show that SIN in the ventral reticular formation, part of the medullary SC, project to the XIIth motor nucleus; we suggest that ventral SIN are command interneurons for the different pools of motoneurons involved in swallowing.

INTRODUCTION

Swallowing is a motor sequence centrally programmed by neurons belonging to the medullary swallowing center (SC)[7,11,12,15,17,22,25]. In sheep, the SC contains swallowing interneurons (SIN) located mainly in two regions[15]: a dorsal region including the nucleus of the tractus solitarius (NTS) and the adjacent reticular formation, 1.5–4 mm rostral to the obex, and a ventral region corresponding to the reticular formation near the nucleus ambiguus (NA) which contains swallowing motoneurons supplying the musculature of the pharynx, larynx and esophagus (see refs. 11, 15 and 25). Dorsal SIN are involved in programming the swallowing motor sequence[15], but the function of ventral reticular SIN has not been clearly established. However, some ventral SIN project to swallowing neurons located in the trigeminal (Vth) motor nucleus[3].

Other neurons involved in swallowing are located in the hypoglossal (XIIth) motor nucleus[9], but nothing is known of the connections between SIN and hypoglossal motoneurons. The aim of the present study was to establish the source of inputs to the XIIth motor nucleus by means of a retrograde tracer and antidromic invasion of SIN.

MATERIALS AND METHODS

This study was performed on 26 anesthetized adult sheep.

Surgical preparation

A short-lasting barbiturate anesthetic (sodium thiopentone, 25 mg/kg) was administered intravenously. After tracheotomy, the animal was venti-

* A preliminary report of these findings has been previously published[2].

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lated 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 typically less than 100/min. The geniohyoid (GH) and mylohyoid (MH) muscles, which discharge during swallowing, were exposed via a medial incision of the skin under the jaw. The superior laryngeal nerve (SLN) which contains laryngeal afferents involved in triggering swallowing was dissected via a ventromedial approach. The XIIth nerve was exposed for 5–6 cm central to its division into the two branches supplying the retractor and protrusor muscles of the tongue.

For the rhombencephalic exposure, the animal was prone 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 was exposed and covered with warm liquid paraffin. After surgery, the head was placed in a stereotaxic apparatus adapted to sheep. All wounds were regularly infiltrated with a 2% procaine solution. Body temperature and heart rate were continually monitored.

Electrical stimulation

Bipolar platinum electrodes were used to stimulate the SLN and XIIth nerves. The XIIth motor nucleus and SC were stimulated via steel bipolar concentric needles and tungsten microelectrodes, respectively. The needles had outside diameters of 0.4 mm and contained an axial wire (0.1 mm) such that the interelectrode distance was 1 mm. The tungsten microelectrodes had tip diameters of 1–2 μm and impedances of 2–5 MΩ at 1000 Hz. We stimulated the XIIth nucleus either to antidromically identify SIN that project to this nucleus or to obtain a compound action potential of XIIth nerve, the latency of which was then compared with that resulting from stimulation of the SC (ventral region). The difference in latency would indicate the probable nature (number of synapses) of the pathway between ventral SIN and the XIIth nucleus. The site of SC stimulation was based on the stereotaxic coordinates and the presence of unitary activity associated with swallowing.

Stimulating electrodes were connected to stimulators through high frequency isolation units (WPI). Stimulus parameters were 0.5–3 V, 100–200 μs pulse duration for nerves and XIIth motor nucleus, and 50–150 μA, 20–50 μs pulse duration for the SC.

Recordings

Electromyographic (EMG) activities of GH and MH were recorded with paired copper wires, insulated except at the tip, inserted into the muscles. Antidromic field potentials within the XIIth motor nucleus following XIIth nerve stimulation were recorded by bipolar concentric needles identical to those used for stimulation. Extracellular activities of SIN were recorded by tungsten microelectrodes of 1 μm tip diameters and impedances of 9–12 MΩ at 1000 Hz. Potentials were amplified and displayed on an oscilloscope for visual observation and filming.

Histological controls

Medullary stimulating and 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 studies of unitary activity of SIN, the animals could be curarized by i.v. injections of gallamine triethiodide (Flaxedil) in order to prevent activation of neurons by sensory feedback caused by contraction of swallowing muscles[8]. Curarization was generally light (0.5–0.7 mg/kg), in order to allow weak EMG activity of the GH and MH to persist. Deep curarization (2 mg/kg) abolishing EMG was occasionally used but always after the discharge of a recorded neuron had been related to reflex swallowing (EMG activity of GH or MH).

Identification of SIN projecting to the XIIth motor nucleus

These neurons were identified by antidromic activation following stimulation of the XIIth motor nucleus. Two concentric bipolar electrodes were inserted, at an angle of 15–20° from the vertical plane, into the lateral part of the nucleus, 1 mm caudal and 1 mm rostral to the obex. These regions contain swallowing motoneurons[9]. The electrodes were considered correctly placed when a large antidromic field potential was recorded following stimulation of the XIIth nerve. In addition, stimulation of XIIth motor nucleus via either electrode with a single pulse

elicited an EMG response of the GH.

The following classical criteria were used for establishing the antidromic invasion of SIN: (1) 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 stimulation of the XIIth nucleus within an appropriate time interval (critical delay), no antidromic response was obtained[4,13,19,26]; (2) the antidromic response had a short latency and could follow high-frequency stimuli (300–500 Hz); (3) spikes elicited by XIIth motor nucleus stimulation were identical to those during swallowing activity.

Retrograde tracing

HRP (Sigma, type IV) dissolved in saline solution containing 2% dimethylsulfoxide was electrophoretically injected into the XIIth motor nucleus of two sheep via a micropipette of tip diameter 40 μm. Microelectrophoretic injections were made by passing positive DC current (10–20 μA) for 5–8 min. Correct micropipette placement was determined from stereotaxic coordinates established by first mapping the antidromic field potentials elicited by stimulation of the XIIth nerve on the contralateral side.

Fifteen to 20 h later, the heads of the two sheep were perfused through the carotid arteries with a saline solution (2 liters) containing procaine (0.1%) and heparin (5000 IU). This was followed by 8 liters of a mixture of paraformaldehyde (1%) and glutaraldehyde (3%) in a 0.1 M phosphate buffer (pH 7.3). The rhombencephalon was removed, postfixed for 5–6 h in the same solution and soaked for 16 h in a 4 °C phosphate buffer containing 30% sucrose. The tissue was then frozen and cut into sections (45 μm) in the frontal plane. For histochemical demonstration of HRP, the sections were immediately treated with tetramethylbenzidine[21]. The sections were then mounted onto gelatinized slides and counterstained with Neutral red. They were studied microscopically under bright- and dark-field illumination.

RESULTS

Retrograde tracing

Electrophoretic injection of HRP within the XIIth motor nucleus, 1 mm caudal to the obex (Fig. 1, M1 and M2) provided injection sites extending beyond the XIIth motor nucleus in M1 and limited to the XIIth motor nucleus in M2. In M1, HRP extended rostally to the obex and laterally to the adjacent parvocellular reticular formation, to the dorsal motor nucleus of the vagus (Xth), but not to the nucleus tractus solitarius (NTS). We analyzed medullary regions between 1 and 4 mm rostral to the obex, in

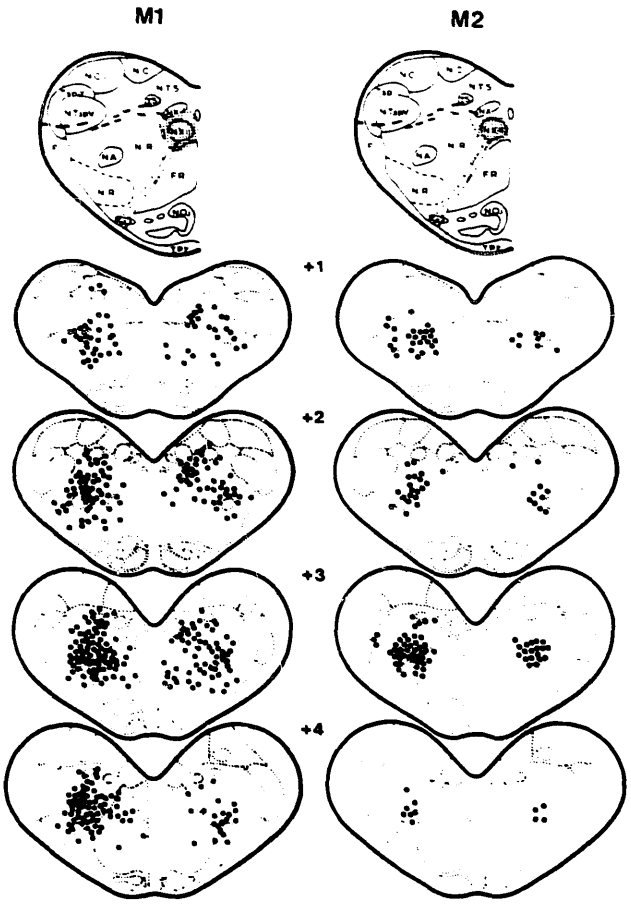

Fig. 1. Localization of HRP labeled neurons. M1 and M2 obtained from two sheep. HRP was electrophoretically injected in the region of the XIIth motor nucleus. Injection sites indicated by the stippled area on the hemisections of the medulla, 1 mm caudal to the obex. Dots in transverse sections of the medulla (respectively 1, 2, 3 and 4 mm rostral to the obex) indicate positions of labeled neurons; each section includes the cell bodies from 10 successive histological slices. Note that density of retrogradely labeled neurons is higher in M1 than in M2. Fl, fasciculus lateralis; F.R, formatio reticularis; N.A, nucleus ambiguus; N.C, nucleus cuneatus (Burdach); N.C.l, nucleus cuneatus lateralis (Von Monakov); N.O.i, nucleus olivaris inferior; N.R, nucleus reticularis medullae oblongatae; N.R.l, nucleus reticularis lateralis; N.T.S, nucleus tractus solitarius; N.T.spV, nucleus tractus spinalis n. trigemini; NX, nucleus dorsalis n. vagi; NXII, nucleus n. hypoglossi; T.Py, tractus pyramidalis; TS, tractus solitarius; T.sp.V, tractus spinalis n. trigemini.

which the SC is located. HRP-labeled neurons (Fig. 1) were found bilaterally, with an ipsilateral predominance, in the parvocellular reticular formation, the adjacent gigantocellular reticular formation, the NTS and the nucleus of the tractus spinalis of the Vth nerve. Some labeled neurons were also observed in the reticular formation close to the contralateral XIIth and Xth motor nuclei. When the injection site was restricted to the XIIth nucleus (Fig. 1, M2) the labeled neurons were mainly located ipsilaterally in the ventral part of the parvocellular reticular formation adjacent to the NA, i.e. in an area corresponding to the ventral region of the SC (Fig. 2).

Electrophysiological study

In 24 sheep, we recorded the extracellular activities of 98 SIN during swallowing induced by stimulation of ipsilateral or contralateral SLN (train of pulses at 30–50 Hz or 2–4 pulses at 500 Hz). According to their stereotaxic coordinates, 26 SIN were located in the dorsal region of the SC and 72 in the ventral region. All SIN discharged with a burst of spikes closely linked to reflex swallowing indicated by EMG activity of GH (Fig. 3A). In addition, stimulation of the ipsilateral SLN induced a short-latency activation in all 26 dorsal SIN (latency 2–4 ms; see ref. 15), but in only 29 of 43 tested ventral SIN (latency 5–9 ms).

Twenty-seven SIN were antidromically activated (collision test) by stimulating the ipsilateral XIIth motor nucleus (Fig. 3B). The average latency was 2.7 ± 1.5 ms; coupled with an estimated conduction distance of 6 mm, the mean conduction velocity was 2.2

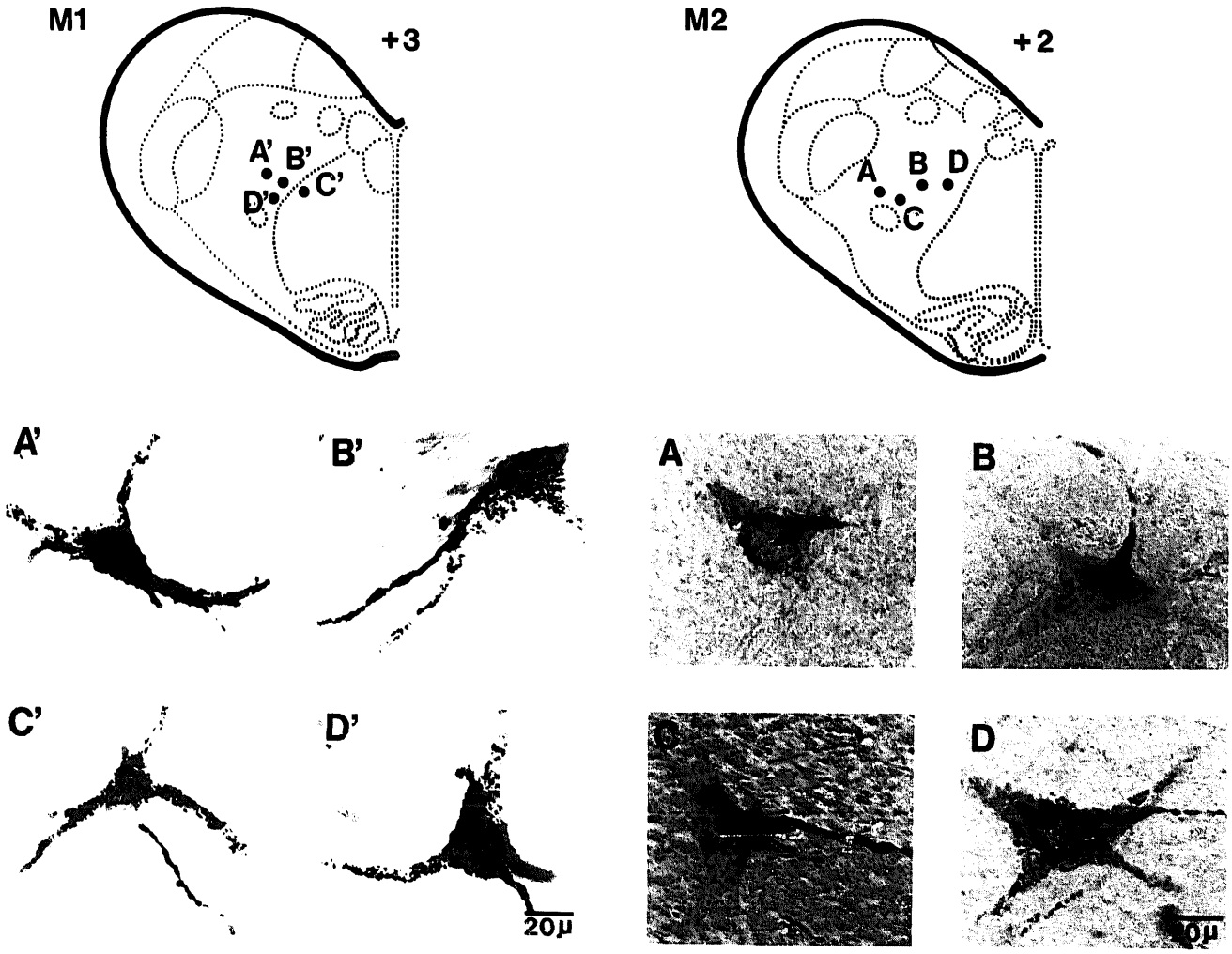

Fig. 2. HRP-labeled neurons in the ventrolateral reticular formation. A, B, C, D and A', B', C', D' represent bright-field photomicrographs of HRP-positive neurons corresponding, respectively, to M2 and M1 (see Fig. 1). Location of each neuron indicated by a dot on the transverse hemisection of the medulla (2 and 3 mm rostral to the obex).

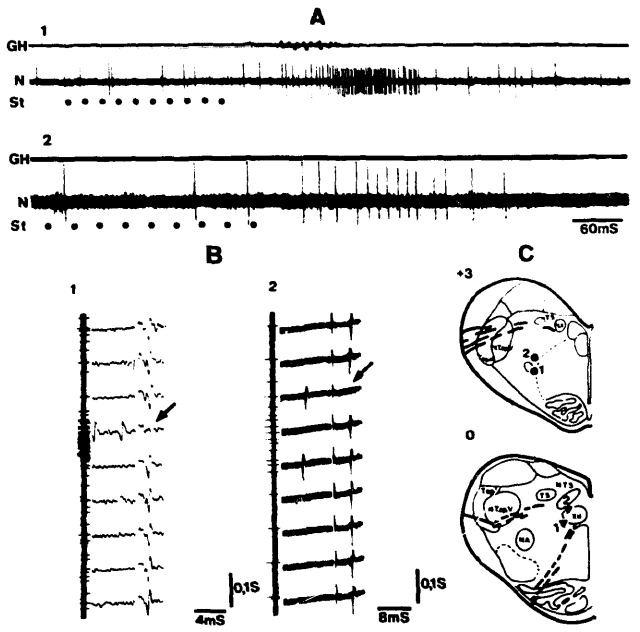

Fig. 3. Medullary swallowing neurons antidromically activated by stimulating the XIIth motor nucleus. A: activation of two neurons (1 and 2) during swallowing induced by superior laryngeal nerve stimulation at 30 Hz (0.5 V; 0.2 ms). Animal lightly curarized in 1, deeply in 2. GH, EMG activity of geniohyoid muscle; N, extracellular activity of neuron; St, stimulation. B: same neurons as in A. Collision tests between orthodromic spikes of swallowing discharges and antidromic spikes elicited by stimulating (2 V; 50 μs) the ipsilateral XIIth motor nucleus. Antidromically evoked spikes on horizontal traces, swallowing discharges on vertical traces. Note absence of antidromic spike (arrows) when a spontaneous spike precedes XII stimulation during appropriate time interval (critical delay). C: transverse sections of medulla showing, top, the recording sites (filled circles) 3 mm rostral to the obex, and bottom, the stimulating sites (filled triangles) at the level of obex.

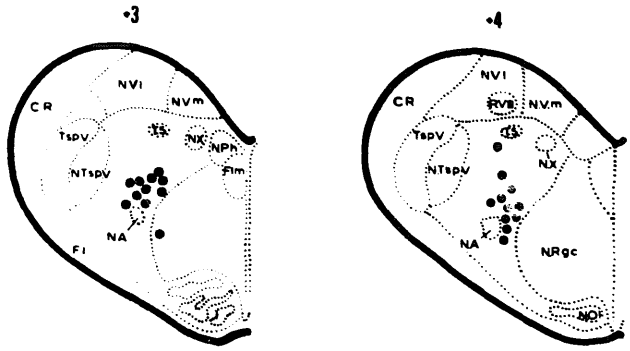

Fig. 4. Location of medullary swallowing neurons antidromically activated by stimulating the XIIth motor nucleus. Responsive neurons (n = 22) are indicated by filled circles on hemisections, 3 and 4 mm rostral to the obex. Note that, except for one neuron, the antidromically activated neurons are located in the ventrolateral reticular formation (ventral region of the swallowing center). CR, corpus restiformis; Flm, fasciculus longitudinalis medialis; N.P.h, nucleus prepositus hypoglossi; N.R.gc, nucleus reticularis gigantocellularis; N.V.l, nucleus vestibularis lateralis; N.V.m, nucleus vestibularis medialis; R.V.III, radices descendentes n. vestibuli. For other abbreviations, see Fig. 1.

± 1.2 m/s. The sites of 22 antidromically activated SIN were marked by electrocoagulation. Only one SIN was located in the region of the NTS; the remaining 21 were located in the reticular formation principally around the NA 3–4 mm rostral to the obex (Fig. 4), i.e. in the ventral region of SC. The other 5 SIN were also located in this ventral region, according to their stereotaxic coordinates.

Thirteen of the antidromically activated ventral SIN exhibited a short-latency response (6.9 ± 1.7 ms) following stimulation of the ipsilateral SLN. Moreover, in the 21 cases in which we made simultaneous measurements of GH EMG and ventral SIN discharge during reflexly induced swallowing, the activity of 17 neurons (80%) always preceded the EMG (Fig. 3A). In the other 4 cases, the swallowing discharges were phasic and occurred either slightly before or simultaneously with the EMG. In no case did ventral SIN activity appear after the onset of EMG activity.

Stimulation through the microelectrode of the region in which antidromically activated SIN were present induced a compound action potential in the ipsilateral XIIth nerve with a latency (4–4.5 ms) 2–3 ms longer than that resulting from direct stimulation of the XIIth motor nucleus (Fig. 5).

Eight neurons antidromically activated by stimulation of the XIIth motor nucleus either did not discharge during SLN-induced swallowing (5 neurons) or exhibited a suppression of spontaneous activity (3 neurons: Fig. 6). None of these neurons were activated at short latency by ipsilateral SLN stimulation.

DISCUSSION

Our anatomical data show that the region of the XIIth motor nucleus containing swallowing neurons[9] receives projections, mainly ipsilateral, from medullary neurons located in regions corresponding to the SC. Injection of HRP restricted to the XIIth nucleus resulted in the labeling of cells primarily in the ipsilateral parvocellular reticular formation surrounding the NA, i.e. in the ventral region of the SC. Fewer

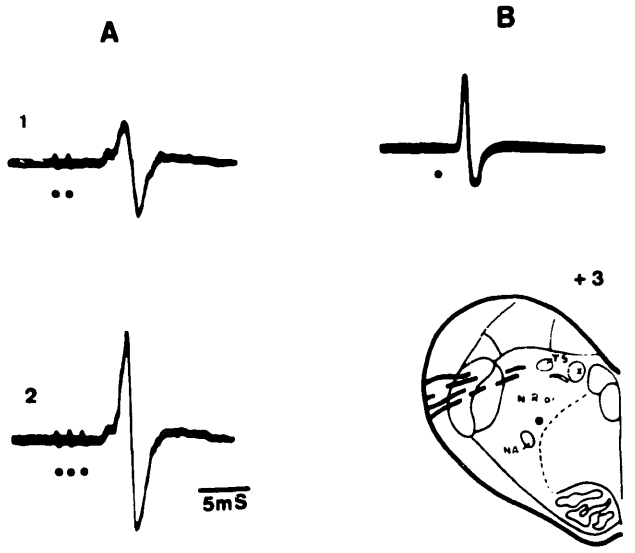

Fig. 5. Compound action potentials induced in the XIIth nerve by stimulating the ipsilateral ventrolateral reticular formation (A) and the XIIth motor nucleus (B). All records obtained on the same animal. A: XIIth nerve responses induced by stimulating (150 μA; 50 μs; 2 pulses at 1000 Hz in A_1 and 3 pulses at 100 Hz in A_2) the reticular formation. Stimulating site indicated by a filled circle on map (3 mm rostral to obex). Note facilitation of the response in A_2. B: nerve response to stimulation (100 μA; 50 μs; single pulse) of the ipsilateral XIIth motor nucleus at the level of obex. Note the difference between latencies of synaptically (A) and directly (B) evoked potentials (4 vs 2 ms).

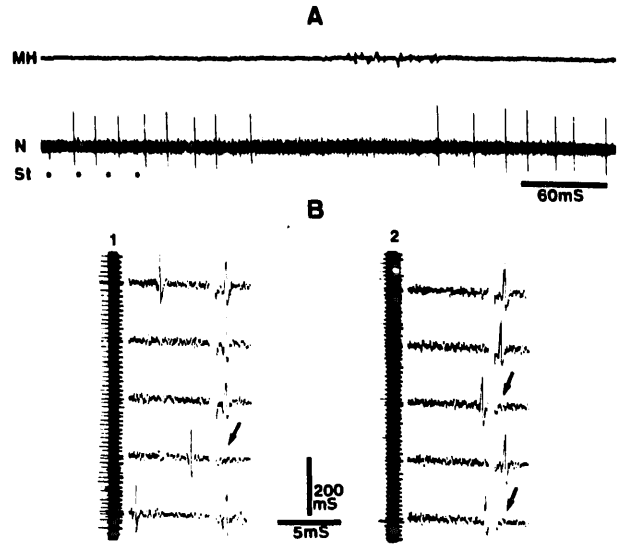

Fig. 6. Reticular neuron inhibited during swallowing. MH, EMG activity of mylohyoid muscle; N and St, as in Fig. 3. Animal lightly curarized. A: stimulation of the SLN (0.5 V; 0.2 ms; 30 Hz). Note inhibition of spontaneous activity during swallowing. B_1 and B_2: collision tests between orthodromic spikes of spontaneous discharges and antidromic spikes induced by stimulating (3 V; 0.1 ms) the ipsilateral XIIth motor nucleus at the level of obex. Note suppression of antidromic spikes (arrows).

retrogradely labeled cells were found in the dorsal region including the NTS, but their number increased when the injection site of HRP extended beyond the XIIth motor nucleus (Fig. 1, M1). This last result suggests that input to this nucleus from the NTS terminates primarily, if not exclusively, in the perinuclear region of the XIIth motor nucleus, a region containing SIN[9].

These findings are in agreement with those obtained by other workers[5,23,30] reporting projections to the XIIth nucleus from the caudal half of the NTS on the basis of retrograde uptake of HRP injected within the XIIth nucleus of rat. Takada et al.[28], using a similar procedure in cat, observed few labeled cell bodies in the NTS when HRP injection was confined to the XIIth nucleus. Moreover several workers have observed extensive labeling of cells in the parvocellular reticular formation after injection of HRP in the XIIth nucleus in rat[1,5,10,30] and cat[1,28]. In addition, anterograde labeling with tritiated leucine shows direct connections between the lateral reticular formation and the XIIth motor nucleus in rat[10], cat[14] and sheep[16]. Cells of the medullary reticular formation constitute the main source of input to the XIIth nucleus in rat[6,29]; our neuroanatomical data support and extend this conclusion to sheep.

Our electrophysiological data show that all but one of the 27 SIN antidromically activated by stimulating the XIIth nucleus were located in the ventral reticular formation, 3–4 mm rostral to the obex (Fig. 4). This result clearly indicates that SIN of the ventral region of the SC send their axons to the XIIth motor nucleus. However, only 26 of 72 (36%) ventral SIN tested responded to stimulation of XIIth nucleus; the remaining 46 may project to areas other than those stimulated, or to the other motor nuclei involved in swallowing (for example the Vth motor nucleus)[3]. Eight neurons antidromically activated by XIIth nucleus stimulation either did not discharge or decreased their activity during swallowing. Although located in the same region as SIN, they may be involved in functions other than swallowing (e.g. respiration or mastication).

Other data[20,24,27] indicate that the parvocellular reticular formation acts as a site of convergence of peripheral and cortical fibers. These premotor neurons in turn transmit integrated responses to hypoglossal motoneurons. Our data provide no direct evi-

dence for axonal terminals of ventral SIN on hypoglossal motoneurons or interneurons located near the XIIth motor nucleus. However, stimulation in regions known to contain SIN induced a compound action potential in the XIIth nerve with a latency 2–3 ms longer than that produced by direct stimulation of the XIIth motor nucleus (Fig. 5). This difference in latency is similar to the mean latency of the antidromic spike recorded from SIN following stimulation of XIIth nucleus. Moreover, aggregates of silver grains, typical of axon terminals, appear on the cell bodies of hypoglossal motoneurons after injection of tritiated leucine into the ventrolateral reticular formation in sheep[16]. Both electrophysiological and neuroanatomical data, therefore, are consistent with the existence of monosynaptic connections between ventrolateral reticular SIN and hypoglossal motoneurons.

In conclusion, our data suggest that swallowing neurons of the XIIth motor nucleus receive direct projections from SIN located in the ventrolateral reticular formation (ventral region of the SC). In addition, the swallowing discharge of most ventral SIN (80%) preceded the onset of GH EMG activity. These and previous[3] results suggest that ventral SIN act, within neuronal network which programs swallowing, as command interneurons for XIIth and Vth motoneurons. They may serve a similar function for motoneuronal pools in the facial nucleus and NA.

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