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OLFACTORY MODULATION OF HYPOGLOSSAL NEURON ACTIVITY

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INTRODUCTION

It has recently been shown that in the mediocaudal part of the XIIth nucleus, photic stimulation of the retina elicits the appearance of pronounced field potentials and responses of single neurons (15), correlated with significant variations in the electromyographic activity of extrinsic and intrinsic tongue muscles (16). With regard to the functional role played by this input, it has been suggested that tongue reflexes depending on visual stimuli are associated with the oral phase of digestion (15, 16).

The present study was designed to determine whether, besides visual, also olfactory inputs are involved in hypoglossal neuronal modulation. This possibility was suggested by the well known observation that olfaction can be associated with vision in evoking other reflex responses of the oral cavity, such as saliva secretion. In order to verify this hypothesis, hypoglossal neuron behavior in response to olfactory stimulation as well as a visual-olfactory convergence of these inputs on the same hypoglossal neuron were analyzed.

METHODS

Rabbits weighing 2 to 2.5 Kg were anesthetized throughout the experiments with α-D (+) gluco-chloralose and urethane at 50 and 400 mg/Kg respectively. The animals were tracheotomized, cannulated and fixed prone to a stereotaxic frame. The olfactory bulb, the cerebellum and obex were exposed by performing a craniotomy at frontal and occipital level, and a laminectomy at C_1-C_2 level. The hypoglossal nerve was exposed at mandibular angle level and mounted on bipolar Ag electrodes connected to an insulated stimulator. All exposed surfaces were covered with warm mineral oil and paraffin (37°C) and pressure points and wounds were injected with xylocaine (0.3%) every 40 min. The EKG and EEG were also monitored throughout the experiment. Two flexible catheters (1.6 mm diameter) were positioned a short way up the naris for olfactory stimulation. The animals were then paralyzed with Pavulon (pancuronium bromide) and artificially ventilated by the tracheal cannula.

The stimulation of the olfactory receptors was performed with a brief puff (7 sec) of air odorized with amyl acetate. This organic compound was chosen because it induces a significant response in the rabbit olfactive bulb (1, 26, 25, 29). The odorized puff was produced by means of a respiratory pump (Palmer) connected to a vaporizer (Socsil). The air stream, produced by the pump, was saturated with amyl acetate in the vaporizer

kept in a water bath at 20°C. The vaporizer was connected to the catheters inserted in the naris of the animal. The concentration of the odorant stimulus, expressed as a dilution of air saturated with the vapor at 20°C (12, 28, 25) was 10^{-2} of saturation. The nasal flow rate in the naris, considered equal to the flow rate out of the choanae (29), varied from 0.21 to 0.32 and 0.71 ml/sec. The volume and pressure of the puffs were measured at the outlet of the catheter. The puff volume varied from 1.5, 2.3 and 5 cc, and the correspondent puff pressure from 0.75, 1.15 and 2.5 cc H_2O/mm^2 respectively. These values represented the threshold stimulus (T), the 2T and the 4T for the olfactory bulbar neurons.

The stimulation of the retinae was by two conventional strobe units controlled by an external master time unit, the animals being kept in the dark. An intensity of 10 J and a frequency of 10 Hz was used. In all experiments, pupils were dilated by an ophthalmic mydriatic drug applied topically.

Extracellular recordings of the spontaneous electrical activity of the bulbar olfactory neurons and hypoglossal neurons were carried out by tungsten microelectrodes (700-900 KΩ) advanced by an electronic microdrive. The olfactory activity was recorded at rostro-intermedium level of the olfactory bulb. The approach to the XIIth nucleus was 0.7 mm rostral to the obex, 0.5 mm lateral to the midline and inclination angle 35°.

The spontaneous electrical activity of the bulbar olfactory neurons and hypoglossal neurons was analyzed before, during and after olfactory stimulation. The recording microelectrode was coupled through a cathode follower to a conventional preamplifier and to an oscilloscope for photography. Single spikes were converted to standard pulses which were fed to a Nicolet 1072 computer to produce frequency distribution histograms (FDHs). The evoked potentials and single hypoglossal unit responses to photic stimulation of the retinae were recorded before and during olfactory stimulation. Post stimulus time histograms (PSTHs) and cumulative frequency distributions (CFDs) were constructed.

All hypoglossal neurons were antidromically identified by electrical stimulation of the XIIth nerve. The recording spots were marked by an electrolytic lesion for the subsequent histological control. At the end of the experiment the animals were killed with a barbiturate overdose and the brain removed, fixed in Carnoy's solution, embedded in paraffin, serially cut and stained with cresyl violet.

The significance of changes in the spontaneous electrical activity and in evoked responses was statistically evaluated by Student's t-test for paired observations.

RESULTS

The spontaneous electrical activity of the bulbar olfactory neurons recorded before, during and after olfactory stimulation with amyl acetate was analyzed to obtain the threshold (T) for the olfactory neurons. Figure 1 shows a typical bulbar neuron response to olfactory stimulation. In basal conditions (B), the olfactory neuron fired at 3.7 spikes/sec, whereas during olfactory stimulation (C) the discharge rate significantly increased to 7.6 spikes/sec ($P<0.001$). The FDH and CFD of the neuron, constructed during 102.4 sec of analysis, showed 389 counts in basal conditions (D) and 778.2 counts during olfactory stimulation (E). In addition, the typical behaviour of the olfactory neurons is demonstrated by a continuous FDH during 3.71 min, showing the trend of the spontaneous electrical activity of the neuron recorded before, during and immediately after amyl acetate stimulation (F).

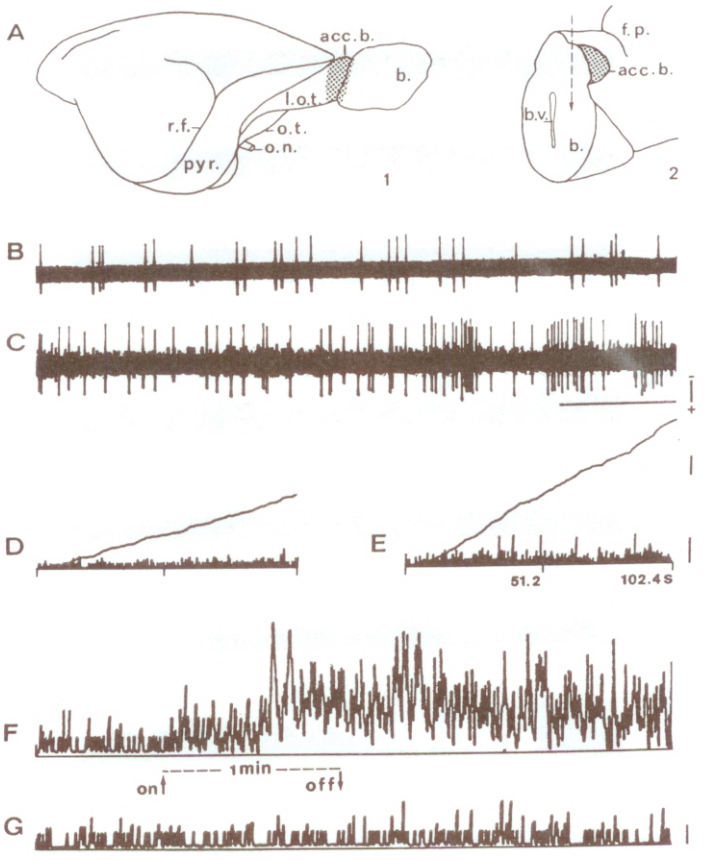

Fig. 1 – *Unit recordings from the olfactory bulb during olfactory stimulation with amyl acetate.*

A: 1, lateral view of the rabbit cerebrum; 2, medial view of a coronal section, carried out at the caudal level of the olfactory bulb, showing the laterality of the recording (arrow). acc. b: accessory olfactory bulb; b.: olfactory bulb; b.v.: bulbar ventricle; f.p.: frontal pole; l.o.t.: lateral olfactory tract; o.n.: optic nerve; o.t.: olfactory tubercle; pyr: pyriform lobe; r.f.: rhinal fissure. B: spontaneous electrical activity of a single olfactory bulbar neuron recorded in basal conditions, and C: during olfactory stimulation performed at threshold intensity (an air flow rate of 0.21 ml/sec and a concentration of 10^{-2} per cent amyl acetate vapor saturation). Horizontal calibration: 1 sec; vertical calibration: 500 μV.

Frequency distribution histograms (FDHs) and cumulative frequency distributions (CFDs) of the same unit recorded before (D) and during (E) olfactive stimulation. F: FDH of the same unit recorded before, during and after 1 min of stimulation (0.1 puffs/sec). The arrows mark the onset (on) and the end (off) of the stimulation. G: recovery (5 min after stimulation). Vertical calibrations: 1 count for FDHs and 100 counts for CFDs.

The olfactory stimulation with this acetate ester at 2-4 T intensity, significantly ($P<0.001$) modified the spontaneous electrical activity of the hypoglossal neurons by inducing several patterns of response. Figure 2 shows an example of inhibitory response. The spontaneous electrical activity of the hypoglossal neuron, which in basal conditions (A) fired at 5.5 spikes/sec was significantly reduced to 0.75 spikes/sec during olfactory stimulation with a 4 T odorized air puff (B). Recovery of the neuron occurred about 1 min after the end of stimulation (C). A continuous

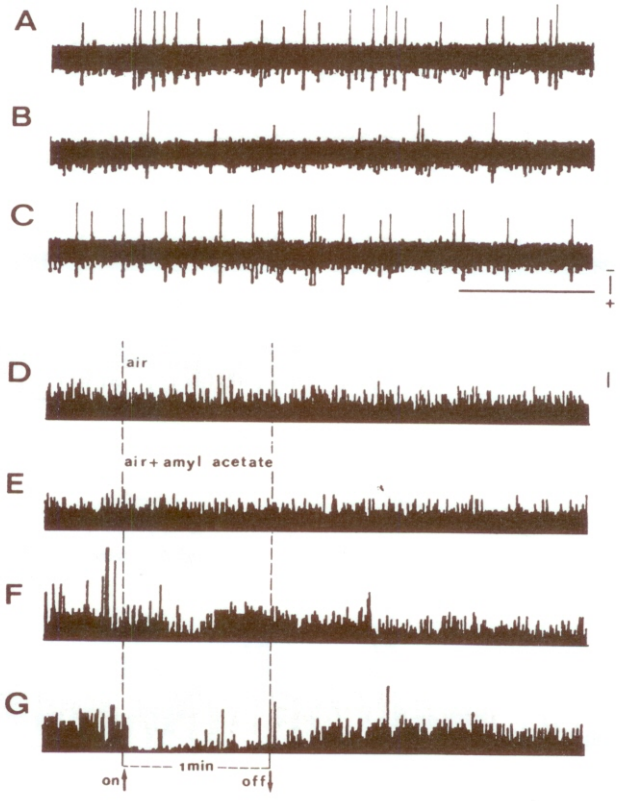

Fig. 2 – *Unit recordings from the hypoglossal nucleus during olfactory stimulation with amyl acetate.*

Spontaneous electrical activity of a single hypoglossal neuron recorded before (A), during (B) and after (C) olfactive stimulation (4 T for the olfactory bulbar neurons). Calibrations: as in Fig. 1.

FDHs of the same unit recorded before, during and after 1 min of stimulation (0.1 puffs/sec). D: with unodorized air puffs, at maximum air flow rate; E-G: with odorized puffs at increasing air flow rate (T, 2 T and 4 T respectively). Dotted lines and arrows mark the stimulation interval. Vertical calibration: 1 count.

FDH recorded before, during and immediately after olfactory stimulation at several intensities showed that the hypoglossal response was linearly correlated with the stimulation increase. An unodorized air puff at the maximal volume and pressure (D), like an odorized puff at the olfactory bulb threshold intensity (E), did not induce any modification in the spontaneous firing rate of the neuron. Only the odorized puff at 2 T intensity (F) and particularly at 4 T intensity (G) induced an inhibitory response. At 2 T intensity (F), the inhibitory effect of the olfactory stimulation ceased before the stimulation cut off, whereas at 4 T intensity (G), a longer effect was observed.

Figure 3 shows a typical example of excitatory response. The spontaneous discharge of a hypoglossal neuron, which in basal conditions fired at 17 spikes/sec (A), was significantly increased to 35 spikes/sec during a 4 T olfactory stimulation (B). Recovery of the neuron occurred about 1 min after the end of stimulation

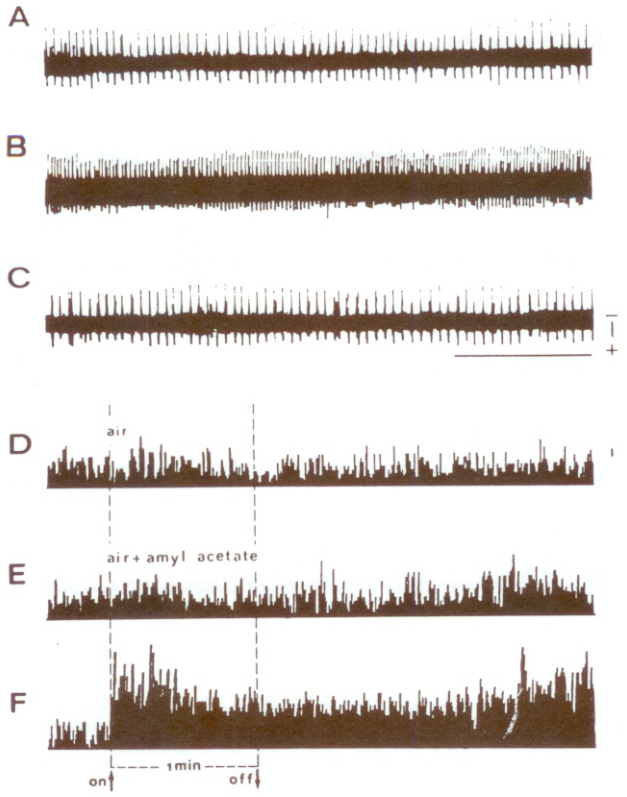

Fig. 3 – *Unit recordings from the hypoglossal nucleus during olfactory stimulation with amyl acetate.*

Spontaneous electrical activity of a single hypoglossal neuron recorded before (A), during (B) and after (C) olfactive stimulation (4 T for the olfactory bulbar neurons).

FDHs of the same hypoglossal neuron recorded before, during and after 1 min of stimulation (0.1/puffs sec). D: with unodorized air puffs, at maximum air flow rate; E-F: with odorized puffs at increasing air flow rate, 2 T and 4 T respectively. Symbols of stimulation and calibrations as in fig. 2.

(C). A continuous FDH recorded before, during and immediately after olfactory stimulation at several intensities showed that the strength of the neuronal response was linearly correlated with the intensity of stimulation. Stimulation with odorized puffs at 2 T intensity induced a slight increase in the spontaneous activity (E), whereas stimulation at 4 T induced a significant increase in the activity (105%) not only throughout the olfactory stimulation but also during a very long post-stimulation period, lasting about 2.25 min (F).

An analysis of the effect of the single odorized air puff shows that olfactory inputs can modulate the hypoglossal neuron activity in different ways. Figure 4 shows a hypoglossal neuron which at the beginning of stimulation responded with inhibition followed by excitation (B). During the stimulation, the hypoglossal neuron gradually reduced its response (C) and finally showed a strong and long-lasting inhibition after the stimulation ceased (D-E). Recovery was not seen until 5 min after the end of the stimulation (F). Some hypoglossal neurons showed

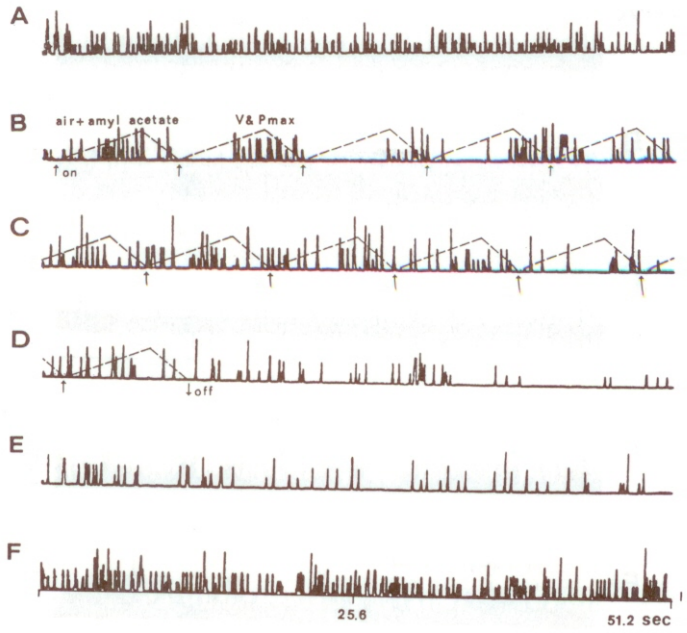

Fig. 4 – *Response pattern of a hypoglossal unit to single odorized puffs.*

FDHs of a single hypoglossal neuron constructed during 51.2 sec and recorded in basal conditions (A), during a 4 T olfactory stimulation (B-D), immediately following (D), 1 min (E) and 5 min (F) after olfactory stimulation. The arrows mark the start of each odorized puff indicated by the dotted lines. The puff applied for 10 sec reached the maximum volume and pressure (V&P max) after 7 sec. Vertical calibration: 1 count.

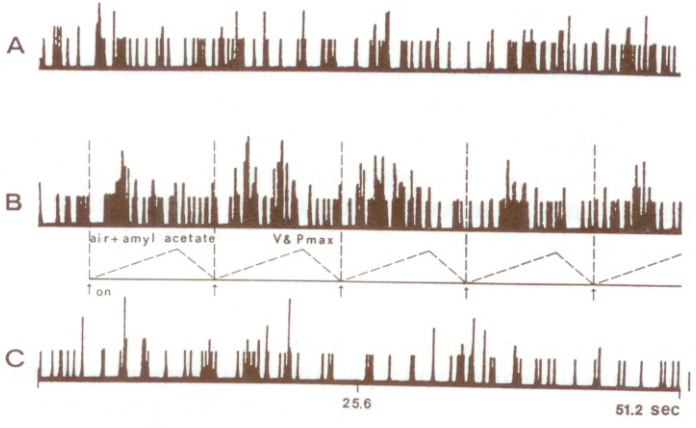

Fig. 5 – *Response pattern of a hypoglossal unit to single odorized puffs.*

FDHs of a single hypoglossal neuron constructed during 51.2 sec and recorded in basal conditions (A), during a 4 T olfactory stimulation (B) and 2 min after the end of stimulation (C). Vertical calibration: 1 count.

only a short lasting response to the olfactory stimulation as can be seen in Fig. 5 where a short-lasting excitatory response (B) followed by inhibition at the end of stimulation (C) is shown.

In order to examine the possibility of a convergence of visual and olfactory inputs on the hypoglossal neurons, the evoked potentials and single unit responses

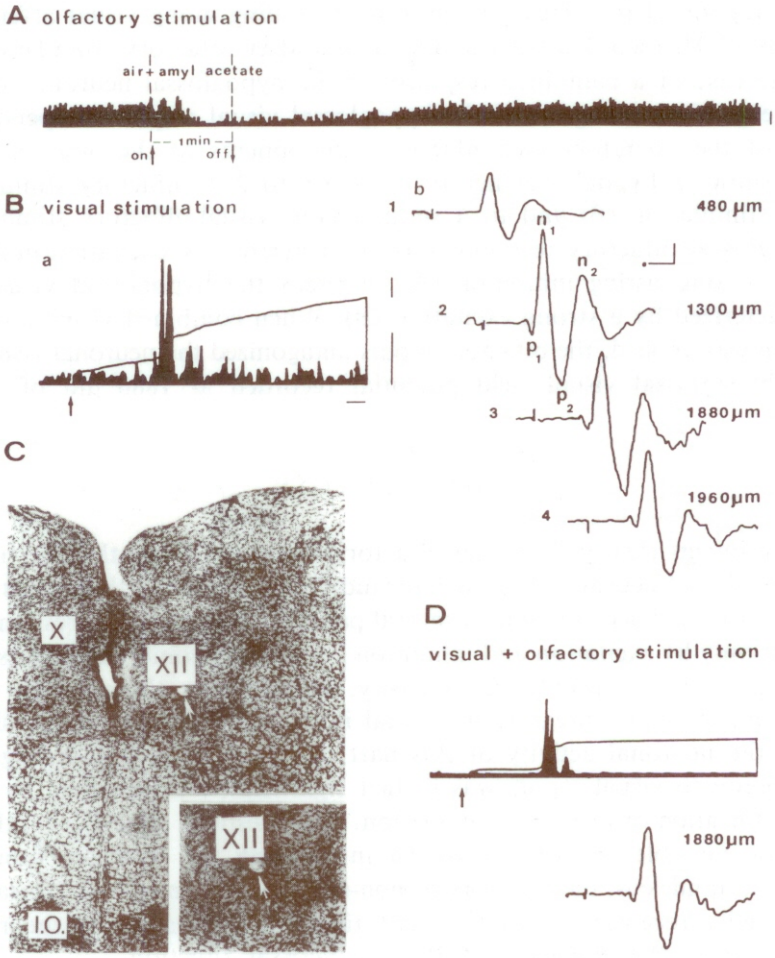

Fig. 6 – *Convergence of visual and olfactory inputs on the same hypoglossal neuron.*

A: Olfactory stimulation. FDH of a single hypoglossal neuron recorded before, during and after a 2 T olfactory stimulation, indicated by the arrows and dotted lines. Vertical calibration: 1 count.

B: Visual stimulation. *a*, PSTH and CFD of the same hypoglossal neuron to 100 consecutive photic stimulations of the retinae. Latency of the response was 45 msec. Horizontal calibration: 10 msec. Vertical calibrations: 10 counts for PSTH and 1 count for CFD. *b*, depth profiles of averaged field potentials by 16 consecutive photic stimulations of the retinae at 34.5 msec latency for p_1, 43,5 msec for n_1, 58.5 msec for p_2 and 67 msec for n_2. Horizontal calibration: 20 msec; vertical calibration: 0.5 mV. C: Histological cross section at the mediocaudal level of the hypoglossal nucleus showing the recording spot (arrow); X: vagus nucleus, XII: hypoglossal nucleus, I.O.: inferior olive. D: visual + olfactory stimulation. Response of the same unit and evoked potential to visual stimulation recorded during simultaneous olfactory stimulation (2 T). Calibrations as in B.

to photic stimulation of the retinae were recorded before and during olfactory stimulation. It was observed that olfactory input significantly modified the hypoglossal neuron response to photic stimulation. When the olfactory response of the hypoglossal neuron was congruent with the visual response, the olfactory influence synergized the visual hypoglossal response. On the other hand, when the olfactory response of the hypoglossal neuron was opposite to the visual response, the olfactory information antagonized the effect of the input travelling along visual afferences. The continuous FDH, recorded before, during and after olfactory stimulation, showed that in the case of a combined response of the hypoglossal neuron, the olfactory input synergized or antagonized the hypoglossal visual response depending on the duration of the excitatory and inhibitory components of the olfactory response. Figure 6 shows a hypoglossal neuron response to 2 T olfactory stimulation (A), to visual stimulation (B) and to a simultaneous visual-olfactory stimulation (D). The hypoglossal olfactory response was characterized by excitation-inhibition followed by a long-lasting inhibition (A), whereas the hypoglossal visual response was characterized by a strong excitation (B). When combined visual and olfactory stimulation was applied, the olfactory inputs antagonized the neuronal visual response and the hypoglossal visual field potential recorded at 1880 μm of depth (D).

DISCUSSION

These experiments clearly show that olfactory inputs modulate the electrical activity of the hypoglossal neurons of the mediocaudal part of the XIIth nucleus. Olfactory stimulation by amyl acetate induces several patterns of hypoglossal responses characterized not only by excitation and inhibition but also by combined effects, frequently dependent on the stimulation intensity. In addition, these results show that olfactory impulses can integrate the visual input which, as previously shown (15), modulate the neuronal activity of this part of the nucleus. The hypoglossal neuronal response to visual inputs was in fact significantly conditioned by the simultaneous application of olfactory stimulation. The questions arising from these results concern the possible pathways involved in carrying the olfactory inputs toward the hypoglossal nucleus, the olfactory or non-olfactory origin of hypoglossal responses to nasal cavity receptor stimulation and finally the question of the role played by this input in the economy of the hypoglossal function.

An olfactory-hypoglossal pathway has not yet been described, although olfactory pathways directed to the tegmentum of the mesencephalon, particularly to the interpeduncular nucleus, are well known (2, 33, 13, 24, 9). It has been suggested that the efferent fibers from this nucleus descend into the brainstem and act as a pathway for unspecified olfactory reflexes (2, 33). The axons of the neurons of the interpeduncular nucleus make the peduncular-tegmental pathway which contacts the tegmental region where the nucleus of the longitudinal medial fasciculus is found. According to Huber and Crosby (11) the olfactory signals might reach the rhombencephalic neurons by this way. Another study, on the afferent and

efferent connections of the preoptic area, went a step further, showing not only reciprocal connections with the interpeduncular nucleus and the gigantocellular reticular nucleus, but also confirming the efferent connections with the dorsal motor nucleus of the vagus and demonstrating a link with the nucleus of the solitary tract (8). In addition, it has also been shown that the hypothalamic area, which receives olfactory inputs through the fornix, not only contacts the interpeduncular nucleus but also projects to some brainstem structures as well as to the nucleus of the solitary tract (31).

An analysis of the dendritic arborization of the hypoglossal neurons by Golgi's method (27), by retrograde tracers and electron microscopic preparations (4, 6, 7) and by conjugates of horseradish peroxidase with cholera toxin (32), showed that dendritic cell processes (the «external dendrites» of Cajal) extended 800 to 1000 μm into the adjoining reticular formation, the trigeminal sensory nucleus, the medial longitudinal fasciculus and the solitary nucleus and tract. Experiments by electrical stimulation (23) showed that the hypoglossal nucleus receives inputs from the medial and lateral reticular formation, the trigeminal sensory nucleus and the nucleus of the solitary tract. Therefore, it is likely that olfactory inputs could reach the neurons of the hypoglossal nucleus by these pathways.

It must be remembered that odorized stimulation involves not only olfactory receptors, but also other nasal receptive structures such as the vomeronasal organ and the trigeminal system. In the most common laboratory animals, odorants are experienced also through these last two structures, which may therefore be activated by the chemical stimulation with amyl acetate and may in turn be involved in the hypoglossal olfactory response. In fact, the accessory olfactory bulb which, through the olfactory dorso-medial pathway (2), receives input from the vomeronasal organ, contacts the dorsal hyppocampus (5, 10) which is connected with the mamillar nuclei, interposed along the olfactory-hypoglossal pathway. On the other hand, the trigeminal afferences could use the spinal V nucleus-hypoglossal nucleus projection described by Borke *et al.* (4). A study of the olfactory, vomeronasal and trigeminal receptor responses to odorants showed that vomeronasal receptors responded better to molecular weight fatty acids and small aliphatic alcohols, and the trigeminal system to benzyl amine, while the olfactory receptors responded better to the longer chain acids and to all members of the acetate ester series (28, 29, 30). Experiments with trigeminal twigs indicated that the behavior of the trigeminal response was more like the vomeronasal than the olfactory receptor response (28). In addition, Tucker (30) obtained vomeronasal and trigeminal nerve twig responses to amyl acetate with an air flow rate and amyl acetate concentration at higher levels compared to those required for the olfactory nerve twigs. The choanal air flow rate was 32 times higher and, at the air flow rate used in the present experiment, also the amyl acetate concentration was 32 times higher. These findings and the significant olfactory bulb responses recorded in the present experiments support the hypothesis that the neuroepithelial cells of the olfactory mucosa must be involved and suggest an olfactory origin of the hypoglossal responses.

What is the functional role played by the olfactory inputs with regard to the

hypoglossal mechanism? Olfactory inputs, through the hypoglossal neuron modulation, may induce reflex responses in the tongue muscles associated with the oral phase of digestion concerned with the preparation of the oral cavity for food reception, in the same way as visual information (15, 16). However, with regard to the visual inputs an additional functional role has also been suggested based on the observation that the activity of the neurons localized in the mediocaudal part of the nucleus is modulated also by vestibular (14, 17, 18, 20, 21) and somatosensory information starting from forelimbs (19, 22). Consequently, visual messages could also participate in regulating the tongue posture affected not only by labyrinthine and somatosensory information, relating to the position of head and limbs, but also by changes in the visual field (15, 22).

In conclusion, our results show that: *i*) the same part of the nucleus which receives visual inputs also receives olfactory inputs; *ii*) visual and olfactory inputs converge on the same hypoglossal unit, and *iii*) olfactory messages can significantly condition the hypoglossal visual response. This physiological arrangement could allow tongue reflex adjustments which, together with the well known reflex salivary secretion dependent on visual and olfactory stimuli, could well complete the cephalic phase of digestion.

SUMMARY

Amyl acetate stimulation of the neuroepithelial cells of the olfactory mucosa induced significant responses in the olfactory bulb and modulated the spontaneous electrical activity of the hypoglossal neurons localized in the mediocaudal part of the XIIth nucleus. Olfactory stimulation induced several patterns of responses characterized by excitation, inhibition and combined effects frequently dependent upon the stimulation intensity. In addition, olfactory inputs converge with the visual inputs on the same part of the XIIth nucleus. The olfactory inputs inducing hypoglossal excitatory responses increased the hypoglossal excitation produced by visual stimuli and decreased its inhibition. *Viceversa*, the olfactory inputs inducing hypoglossal inhibitory responses decreased excitation and increased hypoglossal inhibition to photic stimulation of the retinae. The possible pathways involved in carrying the olfactory inputs towards the hypoglossal nucleus, and the olfactory or non-olfactory origin of the hypoglossal responses were considered. With regard to the role played by this input in the economy of the hypoglossal function, it was concluded that olfactory inputs, alone or together with visual inputs, may induce tongue reflex adjustments associated with the oral phase of digestion to prepare the oral cavity for food reception.

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