

INTERRELATION BETWEEN RHYTHMIC MASTICATION AND REFLEX DEGLUTITION AS STUDIED ON THE UNITARY ACTIVITY OF TRIGEMINAL MOTONEURONS IN RABBITS

Tadaaki SUMI

*Department of Physiology, Fujita-Gakuen University School of Medicine,
Toyoake, Aichi, 470-11 Japan*

Abstract Cortically evoked rhythmic mastication was variously modified by stimulation of the superior laryngeal nerve and by elicitation of reflex swallowing in rabbits under light ether anesthesia. The recording of the unitary activity was made from motoneurons in the motor nucleus of the trigeminal nerve or from motor fibers in the trigeminal nerve to study the neural mechanism subserving such modification.

1. In the absence of rhythmic mastication, spontaneous activity was consistently present in most masseteric (jaw closing) motor units, but was, however, scarce in the mylohyoid (jaw opener) units.
2. During stimulation of the superior laryngeal nerve, the activity in the masseteric motor units ceased, whereas that in the mylohyoid units discharged a continuous train of impulses.
3. When a swallow was elicited by a squirt of water into the pharynx or by stimulation of the superior laryngeal nerve, there ensued also a silence lasting 250 to 800 msec in the masseteric motoneurons, while a discharge of many impulses lasting 200 to 500 msec occurred in the mylohyoid motoneurons. The duration of these changes in both masseteric and mylohyoid motoneurons depended upon the duration of swallowing which varied with the amount of water or the intensity of stimulus applied.
4. During cortically evoked rhythmic mastication, the masseteric motor units discharged bursts of impulses in phase with jaw closing, whereas the mylohyoid motor units fired with jaw opening. When reflex swallowing was superimposed, the bursts of masseteric units were replaced by silence, while those of mylohyoid units discharged many impulses; and the rhythmic activity of mastication was interrupted.
5. Mechanical stimulation of the oral and pharyngeal mucosa produced a steady discharge of impulses in the mylohyoid motor units, whereas it

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produced a silence of spontaneous activity in the masseteric motor units.

6. The patterns of activity of the trigeminal motoneurons during rhythmic mastication and their changes both by reflex swallowing and by stimulation of the superior laryngeal nerve persisted after motoparalysis.

7. Based on these findings, the neural organizations involved in the phenomenon and their way of operation are discussed.

Rhythmic jaw movements (mastication) and deglutition are produced together by stimulation of the anterolateral area of the frontal cerebral cortex (KAWAMURA, 1972; MORIMOTO and KAWAMURA, 1973; SUMI, 1969a). Deglutition occurs reflexly by stimulation of the pharyngeal and laryngeal mucosa (DOTY, 1968; MILLER and SHERRINGTON, 1915; SINCLAIR, 1970), whereas mastication occurs by oral, palatal or periodontal stimulation (BREMER, 1923; SHERRINGTON, 1917; THEXTON, 1973); the two movements share many muscles in their achievement. Recently, changes of cortically evoked rhythmic jaw movements by reflex swallowing have been studied both mechanographically and electromyographically (SUMI, 1977). However, due to methodological limitations, the study has left the following points unsolved: (1) What are the patterns of activity of jaw closing or jaw opening motoneuron during rhythmic jaw movements and reflex swallowing and those during alteration of rhythmic jaw movements by reflex swallowing; (2) What is the role of the afferents from the oral and pharyngeal structures activated secondarily by the movement of swallowing in the swallow-associated alteration and (3) Neuronal mechanisms subserving the interrelation between rhythmic mastication and reflex swallowing.

The present investigation endeavors to gain further insight into these questions by recording the activity of the relevant motoneurons.

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METHODS

Forty-five adult rabbits were used. They were tracheotomized and maintained under light ether anesthesia. The rostral half of cerebrum was exposed bilaterally and covered with 2% agar in Ringer's solution. The animal was placed either prone or laterally on a modified Horsley-Clarke apparatus and fixed rigidly at the skull and the maxilla, leaving the lower jaw free to move. The cortical electrode was of a pair of silver wires, 80 μ m in diameter, 2.0 mm apart and insulated with glass capillaries except for 1.5 mm of the distal end. The tips were thrust into the pia and cortex in the delimited anterolateral area of the forebrain. Using a spiral wire, the electrode was suspended and thus a further mechanical injury to the brain was prevented. The superior laryngeal nerve (SLN) was isolated, severed at the entrance into the larynx, immersed

in warm vaseline and enclosed with a bipolar platinum wire electrode.

Cortical and SLN stimulations were applied for 10 to 30 sec with electrical pulses of 0.2 msec, 1 to 15 V and 20 to 60 Hz, to induce rhythmic mastication and reflex swallowing. An interval of about 2 min elapsed between each trial of cortical stimulation. When necessary, a single stimulus of varying strengths was delivered. Reflex swallowing was also produced by squirting various amounts of water into the pharynx through polyethylene tubing connected to a syringe. Vertical movement of the lower jaw or the activity of either the masseteric (jaw closer) or the mylohyoid (jaw opener) muscle associated with rhythmic mastication, and rostral movement of the thyroid cartilage associated with swallowing were monitored consistently and, when required, recorded simultaneously with the neuronal activity concerned (see below).

Under microscopic control and with the use of a pair of watchmaker's forceps, single efferent fibers were isolated at the severed end of the masseteric and the mylohyoid nerves. They were then immersed in warm liquid paraffin (35–37°C), placed on a 60 μ m platinum wire to record unit activity.

In some experiments the animal was decerebellated and the unit activity was recorded from neurons of the motor nucleus of the trigeminal nerve. In these cases glass-insulated silver wires with a tip diameter of 1–5 μ m were mounted on a micromanipulator and inserted perpendicularly into the floor of 4th ventricle. A silver plate of about 8.5 cm² was sewn tightly under the skin of the neck to serve as the indifferent electrode. Trigeminal motoneurons were identified by certain features of antidromic activation, *i.e.*, consistent elicitation of a single spike after a constant latent period not exceeding 1.0 msec when their peripherally severed axons were stimulated. In most cases, activities of motoneurons for both jaw closing and opening were displayed simultaneously on a dual beam CRO and photographed on a moving film. In other cases, the activity of each motoneuron was recorded together with the motion of either the jaw or the thyroid cartilage or with EMG's of either the masseter or the mylohyoideus during rhythmic mastication and swallowing. Auditory monitoring of the action potentials was also employed routinely.

Stimulus-bound responses were photographed on a moving film or in single frames. In the latter case, the responses were often superimposed. In fifteen animals, motoparalysis was induced by gallamine triethiodide (3 mg/kg, *i.v.*) in an attempt to determine whether the behavior of motoneurons could be altered by lack of afferent impulses associated with swallowing. In these experiments, artificial respiration was employed.

RESULTS

Eighty-nine units were recorded from either the motor axons or cells in the motor nucleus of the trigeminal nerve; 58 were of the masseteric and 31 of the mylohyoid motoneurons. The masseteric units tended to show a steady

activity even in the absence of jaw movement, whereas the mylohyoid units showed a little or no "spontaneous" activity. The activity was mostly regular and continuous for the masseteric neurons, but irregular and sporadic for the mylohyoid neurons. In two mylohyoid motoneurons, rhythmic activity was locked in phase with inspiration.

1. Patterns of activity of the masseteric and mylohyoid motoneurons during reflex swallowing

Spontaneous discharge of impulses occurring in the masseteric motoneurons ceased for a short period corresponding to reflex swallowing induced by a squirt of water into the pharynx (Fig. 1, A and B, left, upper traces). The arrest of discharge lasted for 250 to 800 msec, very often 400 to 600 msec, depending on each neuron and on the duration of each swallow. In 6 out of 58 masseteric motor units, however, no alteration was found (Fig. 1, A, right, upper trace). Two other units showed slight increase in their spontaneous firing during swallowing. All of 31 mylohyoid motoneurons consistently yielded a burst of many impulses (Fig. 1, A, lower traces and B, right, upper trace) or, when spontaneous activity preexisted, their rate of discharge increased dramatically for a period lasting from 200 to 500 msec, depending on the unit and the duration of the swallow (Fig. 1, A, left, lower trace). Onset of such increased activity of the mylohyoid neurons concomitant with swallowing preceded the silence in the masseteric neurons by a few tens of msec.

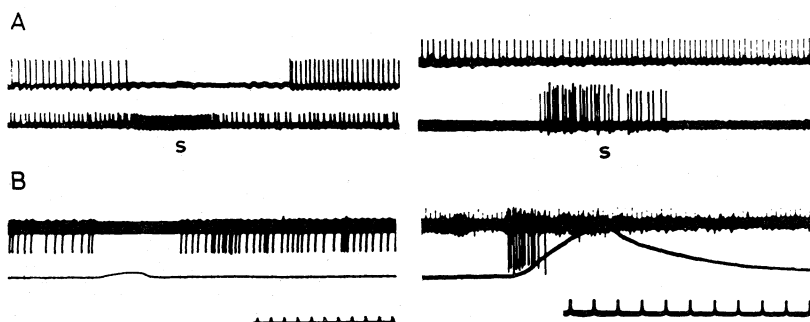


Fig. 1. Activity of trigeminal motoneurons during reflex swallowing. Swallowing was produced by squirting water into the pharynx (A and B, left) and by stimulation of SLN (B, right). In A, activity of single masseteric (upper traces) and mylohyoid (lower traces) motor nerve fibers recorded simultaneously; elicitation of swallowing (S) was confirmed by observation. In B, activity led from cells of jaw closing (left) or jaw opening (right) neuron in the trigeminal motor nucleus; swallowing indicated by upward deflection of each lower trace. Small, regular pulses seen in B, right, upper trace denote stimulus artifacts. Time marks in 0.1 sec divisions; that at right bottom applies all records except B, left.

2. *Effects of electrical stimulation of SLN on activity of the masseteric and mylohyoid motoneurons*

Continuous stimulation with repetitive electrical pulses to SLN reduced the "spontaneous" discharge of impulses in some masseteric motoneurons, whereas it increased in the activity of many mylohyoid motoneurons. When the latter neurons was silent before stimulation, a train of impulses was produced. During the stimulation, and when swallowing occurred, the masseteric motoneurons reduced the activity and often attained complete silence (Fig. 2, upper trace), while a burst of many impulses was elicited in the mylohyoid units (Fig. 2, lower trace). Thus, there existed two kinds of inhibition in the masseteric motoneurons and excitation in the mylohyoid motoneurons; stimulus-bound and swallow-bound inhibition for the masseteric neurons and stimulus-bound and swallow-bound excitation for the mylohyoid neurons. The stimulus-bound inhibition in the masseteric motoneurons and the stimulus-bound excitation in the mylohyoid motoneurons showed a lower threshold as compared to the other responses. In fact, stimulation with weak repetitive pulses, as such being insufficient to elicit swallowing, readily yielded a continuous cessation of "spontaneous" firing in the masseteric motoneurons, while an increased number of impulses appeared in the mylohyoid motoneurons. Stimuli at lower frequencies produced only the stimulus-bound responses in the two motoneurons (Fig. 3, A, top record), and when the frequency of stimuli was increased to elicit swallowing the swallow-bound responses were superimposed (Fig. 3, A, middle and bottom records). A single electrical stimulus to SLN produced inconsistent effects in the masseteric motoneurons, but a conspicuous response of multiple spikes in the mylohyoid motoneurons. Such response of multiple spikes in the mylohyoid motoneurons lasted for 50 to 60 msec after a latency of about 10 msec or longer. In contrast to those described above, 6 mylohyoid motoneurons ceased their firing for 20 to 90 msec depending on each neuron after each stimulus; the cessation began earlier than the excitatory response described above. The mylohyoid neurons that yielded such stimulus-bound inhibition reduced their "spontaneous" firing when repetitive stimuli were applied to the SLN, although they showed a burst discharge of many impulses when a swallow occurred (Fig. 3, B, lower trace). A few mas-

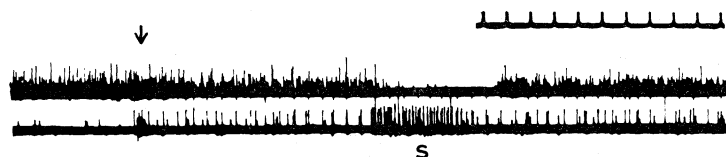


Fig. 2. Behavior of masseteric (upper trace) and mylohyoid (lower trace) motor nerve fibers to stimulation of superior laryngeal nerve with repetitive electrical pulses, onset shown by arrows and continued throughout. At "S" swallowing occurred during the stimulation. The intensity of stimuli was 3 V and the frequency 20 Hz. Time marks in 0.1 sec divisions.

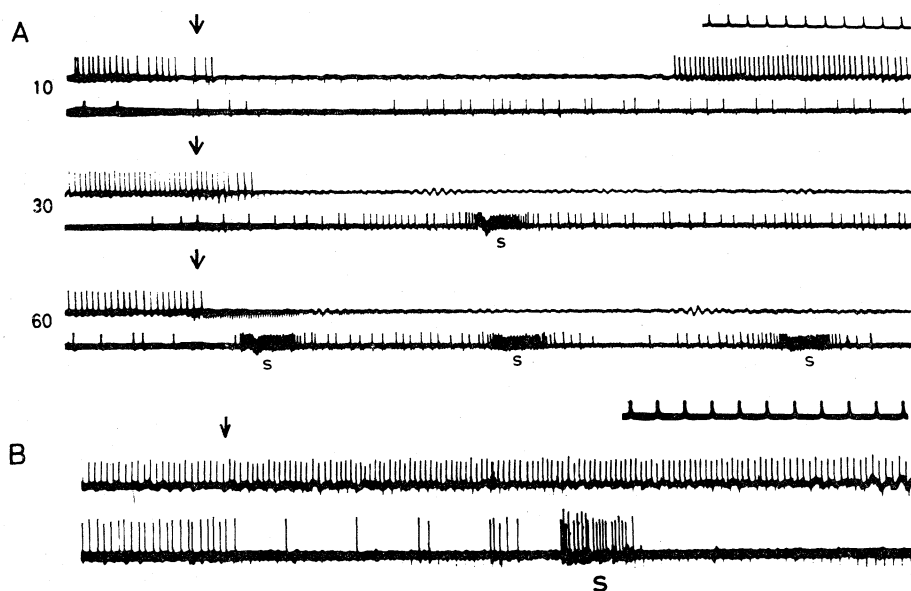


Fig. 3. Different types of changes in activity of masseteric (upper trace of each record) and mylohyoid (lower trace of each record) motor nerve fibers by tetanic stimulation of SLN. The intensity of stimuli was 3 V for all records; the frequency for A was shown by number at left of each record, and that for B 20 Hz. The stimulation began at arrows and continued throughout; swallowing occurred at "S." Time marks in 0.1 sec divisions.

seteric motoneurons revealed no alteration either with stimulation of SLN or with swallowing (Fig. 3, B, upper trace).

3. Activity of masseteric and mylohyoid motoneurons during cortically elicited rhythmic mastication coincided with reflexly elicited swallowing

During rhythmic mastication, the masseteric and mylohyoid motoneurons displayed alternate bursts of impulses corresponding to the phases of jaw closing and opening; number of impulses and duration of discharge in each burst varied among individual units. When a swallow was elicited reflexly by stimulation of SLN or by a squirt of water into the pharynx during this rhythmic activity, another burst of a much larger number of impulses, *i.e.*, a discharge of higher rate and longer duration (300–400 msec), was produced in the mylohyoid motoneuron (Fig. 4, lower trace). This burst discharge of impulses during swallowing is seen as if it concealed or overwhelmed the preexisted rhythmic burst discharge of mastication. Contrastingly, however, the burst discharge of mastication in the masseteric motoneurons disappeared for a period longer than the burst discharge during swallowing in the mylohyoid motoneurons (Fig. 4, upper trace at S₂). Furthermore, this interactive influence upon the masseteric motoneurons



Fig. 4. Reciprocal activity of masseteric (upper trace) and mylohyoid (lower trace) motor nerve fibers during cortically evoked rhythmic mastication and change associated with reflex swallowing occurring repetitively (S_1 , S_2 , and S_3) to stimulation of superior laryngeal nerve (40 Hz, 3 V), onset shown by arrow. Time mark in 0.1 sec divisions.

began apparently later than the start of the discharge during swallowing in the mylohyoid motoneuron (Fig. 4, upper trace at S_1). The delayed onset and the longer duration of the influence was comparably present when the masseteric motoneurons ceased their spontaneous activity during swallowing in the absence of rhythmic activity of mastication as shown already in Figs. 1 and 2. The duration of cessation of rhythmic bursts of mastication in the masseteric motoneuron depended on the temporal relation between swallows and the preceding masticatory activity of the motoneuron. The interruption was shortest when the burst of mastication in the masseteric motoneuron occurred simultaneously or occurred after about 50 msec or less than the start of the burst discharge of impulses of the mylohyoid motoneuron for swallowing. It became longer as the burst of mastication in the masseteric motoneuron preceded the start of discharge of swallowing in the mylohyoid motoneuron. The prolongation of interruption of rhythmic masticatory bursts in the masseteric motoneuron occurred also when a swallow was produced by an increased amount of squirting water or by electrical stimuli of SLN with an increased intensity. In every case, the duration of interruption was not equal to a multiple of the length of one masticatory cycle in the rhythmic bursts of masseteric motoneuron. A comparable prolongation of the discharge of impulses of swallowing in the mylohyoid motoneurons ensued similarly; two mylohyoid motoneurons discharged many impulses for 300 msec when a swallow elicited by stimuli of SLN at 1.5 V and 50 Hz, but they discharged for 710 msec when the intensity of stimuli was increased to 15 V with the frequency kept unchanged.

4. *Effects of motoparalysis on the influence of swallowing upon masseteric and mylohyoid motoneurons*

Spontaneous firing of masseteric motoneurons ceased concomitantly with swallowing elicited either by a squirt of water into the pharynx (Fig. 5, A, upper trace) or by electrical stimulation of SLN (Fig. 5, B, upper trace). In the latter case, however, swallowing occurred repetitively, and the cessation of the neuronal activity preceded the first swallow in the sequence and continued throughout the stimulation. The alterations in the discharge of the masseteric motoneurons could still be produced similarly after paralysis induced by administration of

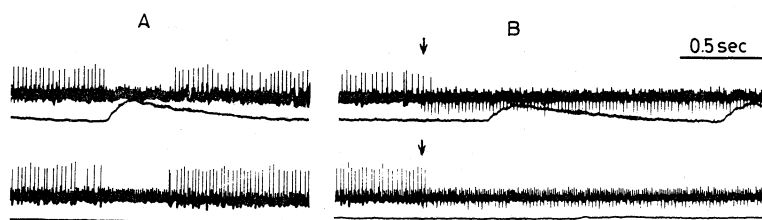


Fig. 5. Spontaneous activity of masseteric motor nerve fiber and change during swallowing elicited by squirting water into the pharynx (A), and during tetanic stimulation (50 Hz, 5 V) of superior laryngeal nerve (B), onset shown by arrow. Upper and lower sets of records were taken before and after motoparalysis. Each upward deflection in lower trace of upper two records indicates swallowing. The unit of small spikes reveals no alteration in its activity either during swallowing or stimulation of the nerve.

gallamine triethiodide (Fig. 5, A, and B, lower traces). Of the masseteric motoneurons examined, five units revealed no alteration in their spontaneous discharge with SLN stimulation *per se*, but ceased only with swallowing. There were still six others that yielded no change either with swallowing or SLN stimulation (Fig. 5, A and B, unit of small spikes). In any event, the pattern of discharge for each motoneuron remained unaltered after motoparalysis. As described above, the influence of swallowing on the discharge of a masseteric motoneuron that yielded burst activity of rhythmic mastication was moderate when swallowing was produced by introduction of a small amount of water into the pharynx (Fig. 6, A), but it lasted longer when elicited by a larger amount (Fig. 6, B). These changes in the rhythmic activity of masseteric motoneurons were retained after motoparalysis (Fig. 6, lower sets of traces). Similarly, the mylohyoid motoneurons that yielded a characteristic burst discharge of many impulses with reflex swallowing in the presence of rhythmic activity of mastication also retained their behavior after motoparalysis (Fig. 7, B, lower trace). Under the last condition, there was

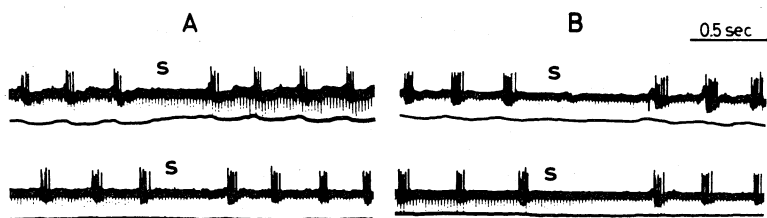


Fig. 6. Cortically evoked rhythmic activity in masseteric motor nerve fiber in phase with jaw closing (downward deflection in lower traces) and change during swallowing elicited by squirting water into the pharynx before (upper set of records) and after (lower set of records) motoparalysis. Approximate timing of swallowing is shown by "S." At "S" in B the amount of water was larger than that in A.



Fig. 7. Changes in activity of masseteric (upper trace) and mylohyoid (lower trace) motor nerve fibers by squirting water into the pharynx with (B) or without (A) preexistence of cortically evoked rhythmic mastication. All records taken during motoparalysis. At "S" modification by swallowing is seen. Time mark in 0.1 sec divisions.

no actual movement, however, the activities of neurons both with rhythmic mastication and reflex swallowing could be identified from their consistent elicitation by cortical and peripheral stimulations as well as from characteristic pattern. The onset of the burst discharge of swallowing in mylohyoid motoneurons preceded momentarily the onset of the masticatory burst in masseteric motoneurons (compare upper and lower traces at S in Fig. 7, B). The masseteric burst was interrupted shortly after its onset, remained silent thereafter and reappeared about 800 msec after the beginning of the interruption. The length of this interruption was various and irrelevant to the length of one cycle in the rhythmic bursts of mastication; the rhythmic masticatory activity was reset after the interruption.

Particularly noteworthy is the fact that the two masseteric motoneurons, the one spontaneously active and the other silent (Fig. 7, A, upper trace), revealed similarly the burst activity of rhythmic mastication when the frontal cortex was stimulated (Fig. 7, B, upper trace). Furthermore, under this condition they were equally influenced when swallowing was elicited by squirting water into the pharynx (Fig. 7, B, upper trace). The spontaneously active masseteric motoneuron, however, revealed no such influence when swallowing occurred in the absence of cortically evoked activity of rhythmic mastication, *i.e.*, the motoneuron exhibited the influence of swallowing only when the rhythmic activation of mastication coexisted.

5. Changes in activity of masseteric and mylohyoid motoneurons produced by mechanical stimulation of the oral and pharyngeal mucosa

Spontaneous activity of the masseteric motoneurons was reduced greatly or arrested completely when a steady pressure was applied to the oral and pharyngeal

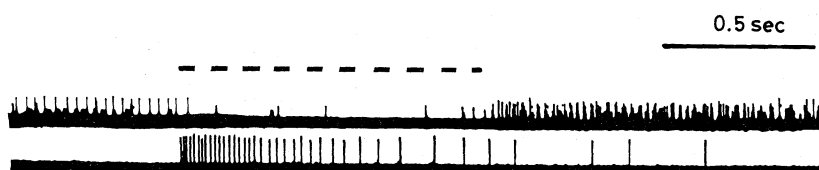


Fig. 8. Behavior of masseteric (upper trace) and mylohyoid (lower trace) motor nerve fibers during continuous touch, shown by broken line, of pharyngeal mucosa.

mucosa (Fig. 8, upper trace). On the other hand, the activity of the mylohyoid motoneurons was enhanced or, if no spontaneous activity existed, a continuous discharge of impulses appeared (Fig. 8, lower trace). Such changes in activity of each motoneuron lasted throughout or beyond the period of stimulation.

Burst activity occurring in phase with jaw closing during cortically evoked rhythmic mastication in the masseteric motoneurons was suppressed when the pressure was applied similarly to the mucosa of the tongue. During this suppression of the neural activity, however, the rhythmic movement of mastication was still retained, though reduced slightly both in its amplitude and frequency.

DISCUSSION

The existence of many spontaneously active motor fibers in the masseteric nerve and the scantiness of such fibers in the mylohyoid nerve imply that the jaw is usually closed. When swallowing occurs, all of 31 mylohyoid motoneurons examined discharged for a period ranging from 200 to 500 msec, whereas 50 out of 58 masseteric motoneurons ceased their activity for as long as 800 msec. These two facts are fully concordant with previous observations that the jaw opens during pharyngeal phase of reflex swallowing in rabbits (SUMI, 1977). Various receptors found in the masticatory muscles (KAWAMURA, 1974; SZENTÁGOTHAI, 1948), the temporomandibular and aryepiglottic joints (ABE *et al.*, 1973; ANDREW, 1954), the tongue (KAWAMURA, 1974; NAKAMURA *et al.*, 1970) and the mucosa of oro-pharyngo-laryngeal areas (STOREY, 1964; THEXTON, 1973; YU *et al.*, 1973) can all be influenced by the movements of mastication and swallowing. However, the swallow-associated interruption in the activity of masseteric motoneurons still persisted after all muscular movements were prevented by gallamine triethiodide administration (Figs. 5 and 7). Therefore, the afferents that could be influenced secondarily by the movement of swallowing play no or, if any, a little role in the elicitation of this interruption.

Stimulation of the SLN readily elicits reflex swallowing. It also leads to a continuous arrest in many masseteric motoneurons, while it activates 25 out of 31 mylohyoid motoneurons. The mylohyoid motoneurons show a tendency for each discharge of impulses to follow after each stimulus in the train (Fig. 2, lower trace). The response of stimulus-bound inhibition is also present in a few

mylohyoid motoneurons. These findings may indicate the existence of a reflex pathway of simple linkage other than the pathway that intercalates the swallowing center. This segmental reflex arising from the SLN may play some roles in a reduction in the amplitude of cortically evoked rhythmic mastication and a shift in the jaw position toward opening as reported in a previous paper (SUMI, 1977). The intramedullary pathways of the segmental reflex probably involve more than one synapse, since multiple peaks and troughs of EPSPs and IPSPs occur in the masseteric and the mylohyoid motoneurons with a long latency after stimulation of the lingual (GOLDBERG, 1972) or the dental nerve (KIDOKORO *et al.*, 1968; SUMINO, 1971). A similar pathway from the lingual nerve and the SLN is shown in the hypoglossal motoneurons that participate in both mastication and swallowing (PORTER, 1967; SUMI, 1969b).

When reflex swallowing is superimposed upon cortically evoked rhythmic mastication (Figs. 4 and 7), the masseteric and mylohyoid motoneurons that are discharging reciprocally in phase with closing and opening the jaw seem to convert their pattern of activity from that of mastication into that of deglutition. Firstly, this alteration in a pattern is inferred to be caused by the influences of the swallowing center exerting upon the chewing center, since (1) the rhythm of mastication, as indicated by the masseteric motoneuron activity, is lost for a time which depends on the timing (and duration) of swallowing in relation to the phase of rhythmic mastication (Fig. 4); (2) the rhythmic activity of mastication is reset after the interruption (Figs. 4 and 7); (3) the start of swallowing, indicated by the mylohyoid motoneuron activity, precedes the arrest of the masseteric motoneuron activity (Fig. 7). Secondly, the fact that the changes in activity of both masseteric and mylohyoid motoneurons by swallowing occur consistently in the absence of rhythmic activity of mastication (Fig. 1) may imply a direct influence from the swallowing center upon the relevant motoneurons.

Electrical stimulation of the SLN with the highest stimulus intensity arrests rhythmic mastication completely (SUMI, 1977). Excitation of the low threshold, large, myelinated fibers of the SLN produces an inhibition of respiration, and the medium sized fibers elicit swallowing; the function of the high threshold, small, myelinated or unmyelinated fibers are not clear yet (MILLER and LOZZI, 1974). From these findings it can be inferred that (1) the large fibers participate in the activation of the segmental reflex terminating on both masseteric and mylohyoid motoneurons, (2) the medium sized fibers contribute to the elicitation of swallowing, and (3) the small sized fibers suppress the chewing center.

When the swallowing center is activated, the brain stem respiratory neurons convert the pattern of their activity into that of swallowing; an interaction is postulated from the swallowing center onto the respiratory center (HUKUHARA and OKADA, 1956; SUMI, 1963). Therefore, it seems probable that stimulation of the SLN with supramaximal intensities may lead to the arrest of chewing center as a result of summation of the effects arising from two sources; one arises from

the swallowing center, as it does in the case of interaction of respiration by swallowing, and the other from afferent fibers of high threshold in the SLN. Noxious or strong stimulation of the pharynx elicits gagging, retching or vomiting, together with the jaw opening designated as the "pharyngo-mandibular reflex" (KAWAMURA, 1972 and refer Fig. 8). On these occasions, when the chewing center is already in operation, its rhythmic activity would be suppressed by the gagging or the vomiting center.

In the majority of human subjects examined (MØLLER, 1976), masseteric EMG's reveal a slight activation during swallowing, and this does not correspond to the existence of only 2 out of 58 masseteric motor nerve fibers showing the comparable behavior in rabbits. The motoneurons of reverse behavior, *i.e.*, masseteric neurons that yield a slight increase in their activity during swallowing or mylohyoid neurons that are inhibited during stimulation of SLN (Fig. 3, B, lower trace), are obscure in their physiological significance. In the trigeminal motoneurons of cats, alpha and gamma neurons are distinguished; many neurons of each type respond differently to stimulation of various central and peripheral sites (SESSLE, 1977a,b). However, in the present study, the changes in activity of both masseteric and mylohyoid motoneurons associated with rhythmic mastication and reflex swallowing have not been analysed in the relevance of such alpha and gamma neurons.

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