MODIFICATION OF CORTICALLY EVOKED RHYTHMIC JAW MOVEMENTS BY REFLEX DEGLUTITION IN RABBITS

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Abstract In rabbits, lightly anesthetized with ether, tetanic stimulation of the superior laryngeal nerve (SLN) displaced the jaw toward opening and reduced the amplitude of cortically evoked rhythmic jaw movements. With increased intensity of stimulus, the effects became remarkable and the opened jaw movement ultimately ceased. Reflex swallowing in reaction to weak electrical stimuli of SLN or to a small amount of water squirted into the oropharynx yielded a brief and instantaneous cessation of rhythmic jaw movements with the jaw open. Strong electrical stimuli to the nerve or a squirt of relatively large amount of water into the oropharynx prolonged the duration of both swallowing and the cessation of rhythmic jaw movements for about 1.0 sec. Reflex swallowing yielded a burst of activity for about 300 msec in the mylohyoideus and silence for a longer period in the masseter. Spontaneous activity of the masseter was moderately decreased during the nerve stimulation and, when swallowing occurred, this decrease became prominent for a short period.

Deglutition and mastication are highly coordinated performances effected by many common gnatho-oro-pharyngeal muscles. In various species of vertebrates, including man, stimulation of the oral or pharyngeal mucosa or of the antero-lateral area of the frontal cortex readily elicits inter-coordinated rhythmic jaw movements (mastication) and swallowing (BREMER, 1923; KAWAMURA, 1972; MILLER and SHERRINGTON, 1915; SUMI, 1969; THEXTON, 1973). Rhythmic mastication is subserved by alternating activity of jaw closing and opening muscles, while swallowing is achieved by sequential excitation and inhibition in various muscles of the pharyngeal area. The muscles of jaw opening, *viz.* mylohyoideus, geniohyoideus, and digastricus, are prominently active in both swallow-

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ing and mastication. However, the pattern of activity is characteristic of each of these performances. The masseter, a muscle of jaw closing, however, reveals no activity in the dog, cat and monkey (DOTY and BOSMA, 1956) or becomes active only slightly in man (MØLLER, 1976; VITTI and BASMAJIAN, 1977) during reflex swallowing.

The present study on rhythmic jaw movements is concerned particularly with the change that occurs during coincidence of mastication and swallowing.

METHODS

Twenty-one adult rabbits (2.3–3.5 kg) were anesthetized with ether and tracheotomized. The rostral portion of the cerebral cortex was exposed bilaterally and covered with 2% agar in Ringer's solution. The animal was placed prone in a modified Horsley-Clarke apparatus and fixed rigidly at the skull, leaving the lower jaw free to move. The superior laryngeal nerve (SLN) was isolated, severed at its entrance into the larynx, immersed in warm vaseline, and enclosed in a bipolar platinum wire electrode.

The anterolateral area of unilateral cortex was stimulated through a paired silver wires of 80 μm in diameter, 2 mm apart from each other, and insulated with glass except for their distal 1.5 mm. The electrode tips only were placed in the cortex. Cortical or SLN stimulation was for about 30 sec with 0.2 msec electrical pulses at 30 or 50 Hz and 1–15 V. Reflex swallowing was also produced by squirting water (0.1–1.5 ml) into the oropharynx through a polyethylene tubing connected to a syringe.

Vertical movement of the mandible associated with cortically evoked rhythmic mastication was followed by means of a thread attached to the lower incisors, and rostral movement of the larynx associated with the pharyngeal phase of swallowing by another thread attached to the thyroid cartilage. The two threads were connected to strain gauges and the movements were recorded by a multichannel ink-writer. EMG's of the masseter (a jaw closer) and the mylohyoid (a jaw opener) were also recorded by a dual beam CRO and a kymograph camera.

RESULTS

1. Changes of cortically induced rhythmic jaw movements by reflex swallowing

Tetanic stimulation of the anterolateral area of the frontal cortex elicited frequent and rhythmic jaw movements that resembled mastication accompanied mostly with less frequent swallowing. The duration of each cortically elicited swallowing was less than 300 msec. Corresponding to this period, the rhythmic jaw movements were unchanged or the adjacent opening phase of the movements was slightly prolonged (Fig. 1A). A single swallowing elicited as a reflex by a squirt of water (*ca.* 0.2 ml) into the oropharynx showed a longer duration, and the coincident prolongation of the opening phase of the jaw movements was more

evident than in the case of swallowing elicited by cortical stimulation (Fig. 1B). As the volume of squirted water was increased, the duration of swallowing was increased further to 1.0 sec or longer. Accompanying this increase of the duration of swallowing, the displacement of the jaw became larger and its duration longer (Fig. 1C, D). At stimulation by maximal amount of water squirted (*ca.*

Fig. 1. Cortically evoked rhythmic jaw movements modified by swallowing. Upper trace: jaw movements, closing upward. Lower trace: rostral movement of the thyroid cartilage with pharyngeal phase of swallowing. Swallowing occurred during cortical stimulation alone (A) or elicited by squirting water (amount was increased from 'B' to 'E') into the oropharynx.

1.5 ml) for a single swallowing (a further increase in the amount of water resulted mostly in repetitive swallowing accompanied with or without gagging) the opening phase attained to about 1 sec (Fig. 1E). Resumption of previous rhythmicity of the jaw movements ensued after a few, small but gradually regaining strokes. However, following a prolonged jaw opening as such that attained to 1.0 sec, the amplitude of strokes was briefly increased (at $\times-\times$, Fig. 1E).

The electrical stimulation of SLN elicited repetitive swallowing (Fig. 2). The duration of each swallowing was prolonged as the stimulus intensity was increased or as a swallowing occurred later in the sequential order of repetition. Rhythmic jaw movements elicited by coincidental cortical stimulation was reduced in amplitude both throughout the SLN stimulation and at each swallowing. When stimulus intensity was relatively weak (*viz.* 50 Hz, 3 V), the swallow-associated opening phase of jaw movements was slightly prolonged, and the change showed slight variations in the schedule relation to the two performances (Fig. 2A). With moderate intensity of SLN stimulation (*viz.* 50 Hz, 6 V), the amplitude of rhythmic jaw movements was further reduced, the jaw shifted to an opened

Fig. 2. Cortically evoked rhythmic jaw movements modified by stimulation of SLN. Upper trace: jaw movement, closing upward. Lower trace: swallowing, rostral movement of the thyroid cartilage, downward. Onset of stimulation (arrow) same for A, B and C, continues throughout remainder of each record, intensity being 50 Hz, 3V for A, 50 Hz, 6 V for B and 50 Hz, 12 V for C.

position throughout the stimulation, and the movements were interrupted markedly with more prolonged swallows (Fig. 2B). With stronger SLN stimulation (*viz.* 50 Hz, 12 V), the displacement of jaw became profound and the movements were arrested not only coincident with swallowing but also during intervals between repetitive swallows (Fig. 2C).

2. Activity of jaw muscles during coincidence of cortically elicited rhythmic jaw movements and reflex elicited swallowing

With no cortical or reflex stimulation, masseter activity was tonic, whereas the mylohyoid was essentially inactive (Fig. 3A). At onset of sustained cortical stimulation, masseter activity ceased and the mylohyoid became active. Activities in the masseter and mylohyoid then alternated in reciprocal pattern characteristic of rhythmic mastication. During this rhythmic activity, when swallowing was produced by a squirt of water into the oropharynx, another burst of activity occurred in the mylohyoid with a suppression of activity in the masseter for about 500 msec (Fig. 3C). In the absence of cortical stimulation, a swallowing elicited by a squirt of water into the pharynx yielded a 300 msec burst of activity in the mylohyoideus and a longer silence in the masseter (Fig. 3B); the mylohyoideus activity preceded the onset of silence in the masseter. A swallowing produced by SLN stimulation in the absence of cortical stimulation similarly gave rise to both

Fig. 3. Modifications in the activity of masseter (upper trace) and mylohyoid (lower trace) during cortically elicited rhythmic jaw movements (A), during reflex swallowing elicited by a squirt of water into the oropharynx (B) and during coincidence of the two performances (C). Interrupted line indicates duration of cortical stimulation. Approximate timing of swallowing, shown by 's'. Time mark: 0.1 sec intervals.

Fig. 4. Modifications in the activity of masseter (upper trace) and mylohyoid (lower trace) by stimulation of SLN (indicated by interrupted lines). Cortically evoked rhythmic jaw movements preexisted in A, but not in B. Swallowing, produced during the nerve stimulation, shown by 's'. Time marks: 0.1 sec intervals.

the burst activity in the mylohyoideus and diminution of spontaneous activity in the masseter (Fig. 4B). Swallows elicited by SLN stimulation during cortically induced rhythmic jaw movements also interrupted the rhythmic activity in the masseter (Fig. 4A). This interruption varied in duration depending upon the temporal relation between swallowing and the preceding burst of rhythmic activity in the masseter, *i.e.*, the interruption was shortest when a swallow coincided with or occurred immediately after the onset of a burst of rhythmic activity in the masseter, whereas it became longer as a swallow occurred later. When a swallow preceded a burst of rhythmic activity in the masseter by 100 to 400 msec, then this burst was suppressed, resulting in a more prolonged interruption. Rhythmic bursts in the mylohyoideus followed those in the masseter in a stable reciprocal pattern (Fig. 4A, lower trace).

DISCUSSION

The brain stem organizations directly pertaining to generation of rhythmic activity of mastication and of swallowing are designated as the chewing center and the swallowing center, respectively, although their precise locus, extent and manner of operation are still undetermined. These two neuronal organizations can be

activated from various regions in the rostral brain and also from the oral and pharyngeal areas (DOTY, 1968; KAWAMURA, 1972). Stimulation of the rostral brain usually elicits rhythmic and frequent jaw movements (mastication) and less frequent swallowing (KAWAMURA, 1972; SUMI, 1969). These two performances can also be produced by stimulation of the peripheral structures, although depend upon the site and mode of stimulus applied. For example, light touch to the retropharyngeal wall, the epiglottis and the esophageal orifice readily evokes swallowing (SINCLAIR, 1970), whereas moderately heavy pressure applied to the dorsum of the tongue and hard palate evokes mastication (SHERRINGTON, 1917; THEXTON, 1973). Simultaneous peripheral and cortical stimulation enhances rhythmic mastication or swallowing (MORIMOTO and KAWAMURA, 1973; SUMI, 1969), and this facilitation is inferred to occur at the chewing center or the swallowing center. But cortically evoked swallowing is suppressed by stimulation of the lingual nerve innervating the dorsum of the tongue (SUMI, 1970), whereas cortically evoked mastication is suppressed by SLN stimulation (SUMI, 1969). Therefore, peripheral stimuli which evoke either of these performances seem to inhibit the other.

Electrical stimulations of SLN and lingual nerve (LN) also evoke various brief reflexes which follow each stimulus pulse at constant latency. These occur most frequently in the geniohyoideus, palatopharyngeus, thyrohyoideus and other muscles participating in deglutition (DOTY and BOSMA, 1956), and have been designated as elementary reflexes to distinguish them from the more elaborate reflex performance of swallowing and mastication. These brief reflexes may contribute to the general reduction in amplitude of cortically evoked rhythmic jaw movements and to the shifting of the jaw in the direction of opening during SLN stimulation. The jaw opening, which increases with stimulus intensity (Fig. 2), may reflect the variety of diameters (MILLER and LOIZZI, 1974) and of stimulus thresholds for the relevant nerve fibers in SLN. In addition, the sustained arrest of rhythmic jaw movements with strong SLN stimulation (Fig. 2C) may probably indicate a direct inhibition of the chewing center from high-threshold afferents of SLN. Reflex inhibition of the masseter which ensues from the afferents of the temporomandibular joint (ABE *et al.*, 1973), oral and pharyngeal structures (YU *et al.*, 1973) or periodontal mechanoreceptors (HANNAM and MATTEWS, 1968) probably has little role in the silence of the masseter associated with deglutition (Fig. 3B), since the swallow-associated silence of activity in the masseteric motoneurons can well persist after the movement of swallowing is abolished totally by gallamine triethiodide administration (SUMI, 1977).

The inhibition of rhythmic mastication that gives rise to jaw closing by noxious pinching of the paw, strong maxillary incisor pressure or rectal distension is attributed to a diffuse alteration of neuronal excitability mediated by the reticular formation (LUND and DELLOW, 1971), therefore differs to that described in the present paper. When judged simply from its action, the jaw may seem to close

during swallowing. However, it is not the case for the pharyngeal phase of swallowing as evidenced in Figs. 1 and 2. Therefore, closing of the jaw will occur only for the preparatory or voluntary phase of swallowing in which an intricate participation of the higher brain must be necessary; the animal used in the present experiments is inferred to have been free of these influences from higher levels.

Though more evidence is required to verify the mechanism of the phenomenon, it may be postulated that the swallowing center, activated from pharyngeal mucosa *via* SLN, effects suppression of the chewing center, since the rhythmic jaw movements ceased and the activity in the masseter diminished during reflex swallowing. Certain simple reflex linkages may also participate in the silence of the masseter.

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