Reflex Activation of Extrinsic Tongue Muscles by Jaw Closing Muscle Proprioceptors

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Abstract Depression of the mandible in the decerebrate cat induced retraction of the tongue. The mechanism of this jaw-tongue reflex was analyzed by recording electromyographic activity from the temporal and styloglossal muscles as representative masticatory and extrinsic tongue muscles, respectively. Tongue muscle activity was elicited when the mouth was opened beyond 10° while the threshold for the masticatory muscle activities was around 2°. Neither sectioning of the masseteric nerve nor anesthetization of the temporomandibular joint capsule affected the tongue muscle activities. In contrast, exfoliation of the temporal muscle from the temporal bone greatly reduced the effects of jaw depression. When the isolated coronoid process of the mandible was stretched downwards, activities were evoked in the tongue muscle. Repetitive electrical stimulation at a frequency of 100 Hz to the temporal nerve activated the tongue muscle, and the threshold of reflex activation was between 1.3 and 1.7 times threshold of the temporal nerve. Vibratory stimuli applied to the mandible at frequencies below 130 Hz were also effective in evoking tongue muscle activity. However, when the frequency was above 135 Hz, tongue muscle activity was not induced although activity was still observed in the masticatory muscles. These results indicate that the jaw-tongue reflex is elicited mainly by proprioceptors in the temporal muscle, and that they may probably be the Golgi tendon organs and the secondary endings rather than the primary endings of the muscle spindle.

Coordination of the tongue and jaw movements during mastication is one of the most intricate biological control systems. Although the mechanisms for such coordination is presumably organized in the brain stem (MAGOUN *et al.*, 1933; MORIMOTO and KAWAMURA, 1973), the timing of the rhythmic movements may also be adjusted by peripheral inputs so as to maintain coordination between the jaw and the tongue. SCHOEN (1931) found that the tongue was retracted by pas-

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sive depression of the lower jaw in the cat, and named this reflex the jaw-tongue reflex (JTR). Furthermore, as tongue retraction was sometimes accompanied by increase in tension of jaw closing muscles, he assumed that excitation of proprioceptors in jaw closing muscles was responsible for the JTR. Recording electromyograms (EMGs) from the masseter and tongue muscles during jaw depression, KAWAMURA and MORIMOTO (1973) noticed differences in the pattern of the evoked EMG activities of these muscles. From this and other results, they supposed that the receptor subserving the JTR was different from the one contributing to the stretch reflex of the masseter, and suggested that proprioceptors in jaw closing muscles, particularly those in the medial pterygoid muscle, were responsible for the JTR. Recently, however, LOWE and SESSLE (1973) suggested that the joint receptors might play an important role in this reflex. In spite of the significance of this reflex in coordination between the jaw and tongue movements, only a few investigations have been done so far and some discrepancies have been found among them.

The purpose of the present study is to elucidate localization of the receptors responsible for this reflex and to identify their types.

METHODS

Thirty cats weighing between 2.0 and 3.5 kg were used. Tracheotomy, cannulation into the left brachial vein and further surgical operations were performed under ether anesthesia. The animals were fixed in a stereotaxic apparatus and decerebrated at the precollicular level. During precollicular transection, the carotid arteries were occluded temporarily. After decerebration ether inhalation was discontinued. Bilateral lingual nerves were cut so that responses in the tongue and jaw muscles might not be altered by excitation of sensory receptors in the tongue.

Application of mechanical stimuli to the mandible. A short metal stick was screwed into the mandible at the portion between the first and second molars. The shaft of the stick was coupled to an electromagnetic muscle stretcher (EMIC 513 A, Shin-nihon Sokki Co.) by which the mandible was moved up- and downwards in a ramp manner or vibrated at various frequencies. The amplitude of the jaw movement or vibration was regulated with a d.c. amplifier (EMIC 381 A, Shin-nihon Sokki Co.), and the frequency of vibration was controlled with a function generator (Kikusui Elec. Co., 458 A). The speed of the ramp movement of the jaw was fixed at 20 mm/sec throughout the experiments. In some experiments in which the movements greater than 8 mm in amplitude were needed, a d.c. motor (LAG-3005, Tokyo Automation Co.), whose shaft length could be adjusted in the range from 0 to 40 mm, was used as a driving device. This device was connected to another metal stick which was screwed into the mandible at the mentum. The jaw movements were recorded with an isotonic transducer whose rod was connected to this metal stick. After the experiments, the distance between the con-

dylar axis of the temporomandibular joint and the tip of the transducer's rod was measured and the amplitude of the jaw movement was expressed in terms of angles.

Recordings of EMGs from masticatory and tongue muscles. In most animals, the left masseter and temporal muscles were exposed after removal of the overlying facial skin. A pair of enamel-coated copper wires, 200 μm in diameter, were sewed in each muscle with an interpolar distance of about 10 mm. A concentric bipolar needle electrode was used for recording unitary EMG activity. In a few cats, EMGs were recorded bilaterally from these two muscles. For recording EMGs of extrinsic tongue muscles, the styloglossal, hyoglossal, and genioglossal muscles were prepared by a ventral approach. Responses were rectified and integrated with a time constant of 0.1 sec through an integrator (Nihon Kohden Co. RFJ-5). The jaw movement was recorded simultaneously with EMG activity on paper with an inkwriter. Unitary discharges were displayed on the screen of an oscilloscope and recorded on moving film with a continuous recording camera.

Electrical stimulation of the temporal nerve. The middle and posterior branches of the temporal nerve were sectioned at the cranial base after removing the temporal bone. The central stumps were stimulated with a sleeve-type stimulating electrode with an interpolar distance of 3 mm. The incoming volley was recorded in the trigeminal mesencephalic nucleus with microelectrodes filled with a 0.9% solution of NaCl.

RESULTS

When the mandible was passively depressed in the decerebrate cat, the tongue retracted and the radix was raised. EMG activities were evoked in the styloglossal and genioglossal muscles but were negligible in the hyoglossal muscle. In the present study, the styloglossal EMG was employed as an indicator to evaluate the JTR because this muscle was readily accessible by the ventral approach and electrodes could be attached to it without damaging the hypoglossal nerve.

Temporomandibular joint receptors do not participate in jaw-tongue reflex

Similar to the observation made by LOWE and SESSLE (1973) on the evoked genioglossal muscle activity, the styloglossal EMGs were diminished by injection of local anesthetics (2% Xylocaine sol., 0.4 ml) into the ipsilateral temporomandibular joint (TMJ) region, especially in front of the joint capsule. This result, however, does not necessarily mean that the TMJ receptors are responsible for the JTR because the nerve branches to the temporal and masseter muscles passing through this region may also be anesthetized. The following two procedures were used to examine whether or not the TMJ receptors contribute to this reflex. In the first study, the condylar process of the mandible was carefully isolated from the mandibular body without damaging the masseteric and auriculo-temporal nerves. When the mandibular body was depressed concomitantly with the iso-

lated condylar process, EMG activities were evoked in the styloglossal muscle as shown in Fig. 1A. In contrast, no activity was observed when only the isolated condylar process was rotated (Fig. 1B). In the second study, 0.2 ml of 2% Xylo-
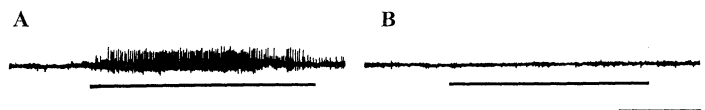

Fig. 1. Ineffectiveness of rotation of an isolated condylar process for evoking styloglossal muscle activity. A: Activity was evoked in the styloglossal muscle when the mandibular body was depressed downwards together with the isolated condylar process. B: No appreciable activity was evoked by rotation of the isolated condylar process alone. During the period indicated by an underlying bar, the jaw was depressed in A and the condylar process was rotated in B. Calibration: 200 μV. Time scale: 3 sec.

caine solution was injected into the ipsilateral TMJ capsule. The styloglossal muscle activity was not affected at all for more than 20 min after the injection. Later, 10% Xylocaine solution (0.2 ml) was also injected intracapsularly, but activity was still elicited in the styloglossal muscle. These experimental results suggest that the TMJ receptors are not important in evoking the JTR.

Contribution of muscle receptors in masticatory muscles to the jaw- tongue reflex

When the jaw was depressed, the masseter muscle was activated through the masseteric stretch reflex simultaneously with activation of the styloglossal muscle due to the JTR (Fig. 2A). After sectioning of the ipsilateral masseteric nerve, the
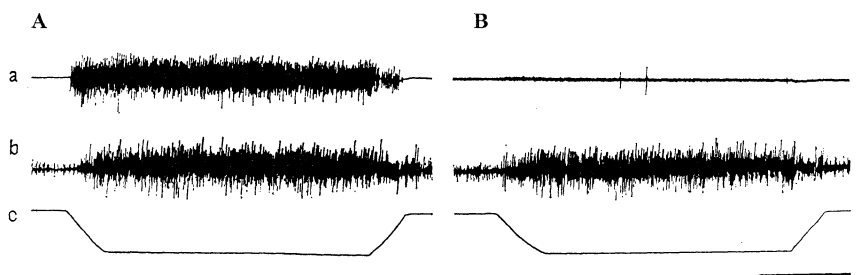

Fig. 2. EMG activity in the masseter and styloglossal muscles before and after section of the masseter nerve. A: Before section. B: After section. a: Masseteric nerve activities. b: Styloglossal muscle activities. c: Jaw movements. Calibrations: 400 μV for a, 300 μV for b, and 20° for c. Time scale: 3 sec.

masseter muscle activity completely disappeared but activity of the styloglossal muscle was hardly affected (Fig. 2B). On the other hand, when the insertion of the unilateral temporal muscle was exfoliated from the temporal bone, activities of the ipsilateral styloglossal muscle were greatly reduced whereas those of the contralateral muscle remained unaltered as shown in Fig. 3. These results indicate

that the receptors subserving the JTR are not in the masseter muscle but mainly exist in the temporal muscle and that the JTR operates unilaterally.
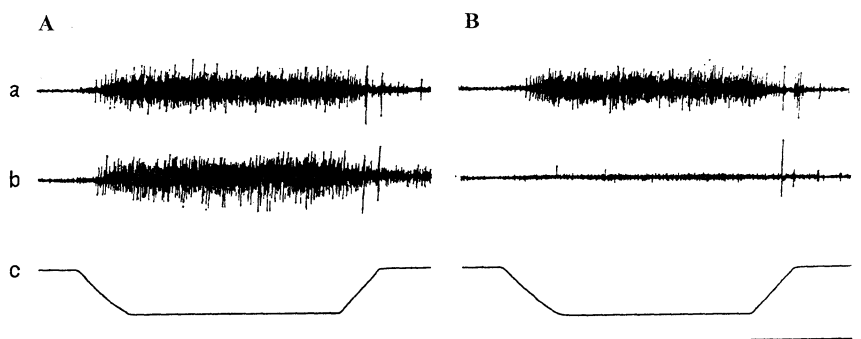

Fig. 3. Effects of exfoliation of the left temporal muscle from the temporal bone on activity of the bilateral styloglossal muscles. A: Before exfoliation. B: After exfoliation. a: EMGs of right styloglossal muscle. b: EMGs of left styloglossal muscle. Note that activity of the left styloglossal muscle was greatly diminished while that of the right styloglossal muscle was left unaltered. Calibrations for a and b: 200 μV. Time scale: 3 sec.

Since the other insertion of the temporal muscle anatomically is made with the coronoid process of the mandible, this process was carefully isolated from the mandibular body and pulled downwards by hanging a weight. Figure 4 shows activation of the styloglossal muscle evoked by hanging a weight of 150 g. The threshold was 110 g in this preparation. This finding reconfirmed contribution of the temporal muscle receptors to the JTR.
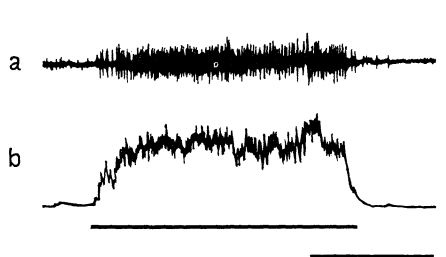

Fig. 4. Styloglossal muscle activity evoked by a downward stretch of the isolated coronoid process of the mandible. a and b: Actual response of the styloglossal muscle and its integration, respectively. The coronoid process was stretched during the period indicated by an underlying bar. Calibration for a: 100 μV. Time scale: 3 sec.

Finally, the middle and posterior branches of the temporal nerve were electrically stimulated at 100 Hz with 0.01–0.1 msec pulses. Unitary discharges were evoked in the styloglossal muscle at the stimulus intensity of 1.5 times threshold

of the temporal nerve (Fig. 5).   The threshold of the JTR ranged from 1.3 to 1.7
times threshold of the temporal nerve in 5 cats when the jaw closing muscles were
stretched by jaw depression.   However, it was 3 times higher than the threshold
without depressing the mandible.   The above-mentioned result indicates that the
diameter of the lowest threshold afferents subserving the JTR is rather thick.
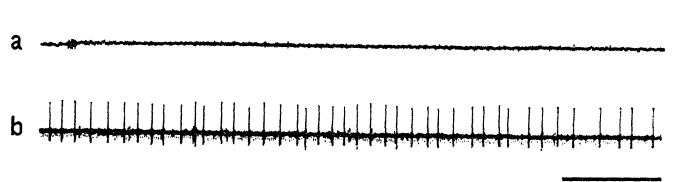

Fig. 5.   Single unit responses evoked in the styloglossal muscle by repetitive stimulation
    of the temporal nerve; Stimulus frequency, 100 Hz; Pulse width, 0.1 msec; Stimulus
    intensity, 1.5 times threshold.   The response was obtained under background facilitation
    by jaw depression. a: Control. b: During stimulation.   Calibrations for a and b:
    200 μV.   Time scale: 3 sec.

*Comparison of EMG activities between the styloglossal and temporal muscles during
depression of the lower jaw*

      In order to examine whether or not the muscle spindle in the temporal muscle
subserves the JTR, responses of the styloglossal muscle were compared with those
of the temporal muscle during depression of the mandible.   As shown in Fig. 6A,
the response of the styloglossal muscle increased without evoking an obvious
dynamic response to a ramp opening of the mouth and adapted very slowly during
a sustained opening of the mouth.   On the other hand, to the same jaw movement
the temporal muscle often showed a relatively large transient response at the be-
ginning of movements and it was followed by a slowly adapting response during a
sustained opening of the mouth.   In Fig. 6B, the magnitudes of the integrated re-
sponses of the styloglossal and temporal muscles are plotted against the degree
of mouth opening in 3 cats.   It is seen that the threshold for evoking activity in
the temporal muscle is below 2°, while that for evoking activity in the styloglossal
muscle was between 10° and 13° where the temporal muscle activity almost attains
its maximum.

      Since EMG activity, both in the styloglossal and temporal muscles, adapted
slowly during sustained opening of the jaw, the degree of adaptation was compared
between the two (Fig. 7).   In both muscles, the adaptation appeared in two phases;
the early and the late phases.   The period of the early adapting phase was about
3 min and was similar in both muscles, while the late phase of adaptation lasted
more than 15 min in the styloglossal muscle, surviving much longer than in the tem-
poral muscle.

      The ability to follow vibratory stimuli was also different between the tongue
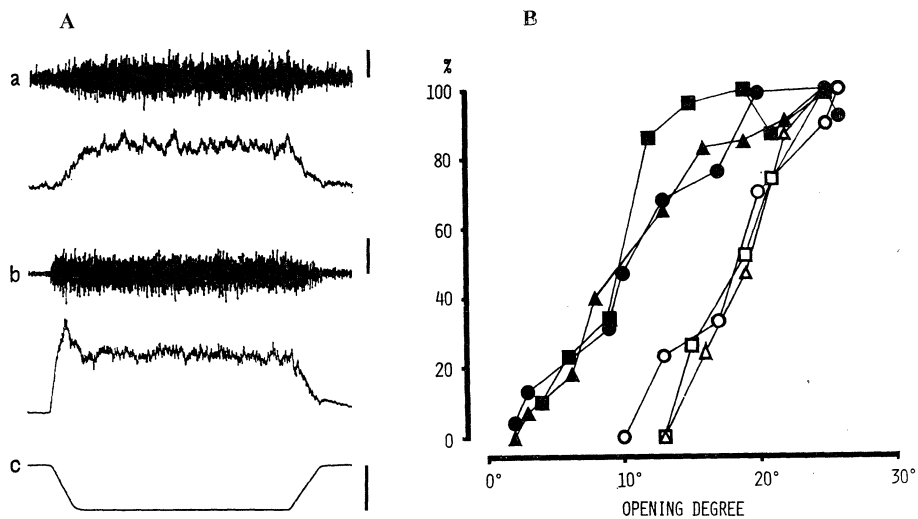
Fig. 6. A, Activity of the styloglossal and temporal muscles during passive depression of the lower jaw. a: Styloglossal muscle. b: Temporal muscle. c: Jaw movements. Downward deflection of the trace in c indicates mouth opening. The upper and lower traces of a and b show actual response and its integration, respectively. Activity of both muscles and the jaw movement were recorded simultaneously. Calibrations: 100 μV for a and b, and 20° for c. Time scale: 3 sec. B, Relations between response magnitudes and degrees of mouth opening. Circles, triangles, and squares indicate the data obtained from three different animals. The solid and empty symbols express temporal and styloglossal muscle activity observed in the same animal, respectively. Ordinate: Relative magnitude of the integrated responses. The area of the integrated response for 3 sec after termination of mouth opening was measured as the response magnitude. 100% is the maximal response in each record. Abscissa: Degress of mouth opening. Note apparent difference in the threshold degree of mouth opening between the styloglossal and temporal muscles.
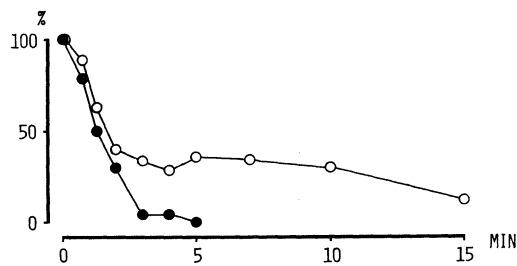

Fig. 7. Difference in the adaptation of EMG activity during sustained opening of the mouth between the styloglossal and temporal muscles. Ordinate: Relative magnitude of the integrated response of EMGs of both muscles; 100% is the response during 3 sec immediately after termination of mouth opening. Abscissa: Time after opening of the mouth. Solid circles: Temporal muscle. Empty circles: Styloglossal muscle. The time course of adaptation consisted of early and late phases. Activity in the styloglossal muscle survived longer than those in the temporal muscle.

and jaw closing muscles. The styloglossal muscle was strongly activated by a vibration at frequencies of 40–70 Hz (Fig. 8Bb). With increase in the frequency of vibration, however, the response of the styloglossal muscle decreased and it hardly followed frequencies higher than 130 Hz. In contrast, the temporal muscle could be activated even at 150 Hz with an amplitude of 35 μm (Fig. 8Ac).
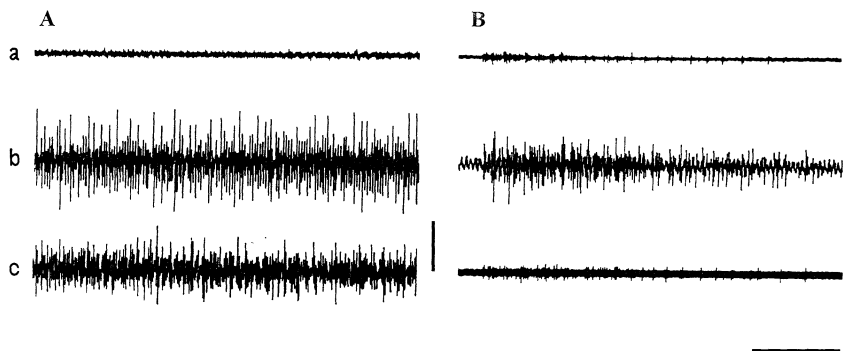

Fig. 8. Difference in responsiveness to vibratory stimuli applied to the mandible between the styloglossal and temporal muscles. A: EMGs of the temporal muscle. B: EMGs of the styloglossal muscle. a: Control. b and c: Responses to vibration at frequencies of 70 Hz and 150 Hz, respectively. Calibration: 100 μV. Time scale: 500 msec. The styloglossal muscle was often activated at the inspiratory phase of respiration (Ba). Vibratory stimuli not only enhanced this activity but also evoked discharges during the expiratory phase of respiration (Bb).

DISCUSSION

The present study indicates that the receptors subserving the JTR are present mainly in the temporal muscle. In contrast, LOWE and SESSLE (1973) assumed the contribution of the TMJ receptors to this reflex from the finding that genioglossal muscle activities evoked by jaw depression disappeared after bilateral injection of local anesthetics into the TMJ region. The discrepancy between LOWE and SESSLE (1973) and us will be explained based on the fact that the temporal nerve passes just in front of the joint capsule, and, therefore, even a small amount of anesthetic solution injected around the TMJ region might effectively block the conduction along the temporal nerve and thus diminish the JTR. As shown in the present experiment, rotatory movements of the isolated TMJ condyle could not produce any appreciable discharge in the extrinsic tongue muscle and moreover, intracapsular anesthesia of the TMJ did not block the JTR. Consequently, the TMJ receptors may not be responsible for the JTR. SCHOEN (1931) recognized that the tongue retracted simultaneously with spontaneous jaw closures in the cat and supposed that proprioceptors in the masticatory muscles were important for this reflex. He also found that the JTR was evoked even after bi-

lateral exfoliation of the masseter muscles from the mandible. Nevertheless, he maintained that an important role would be played by muscle receptors in the masseter muscle, although he did not neglect the contribution of receptors in other jaw closing muscles. From the present findings, it is assumed that the contribution of the masseter muscle proprioceptors must be very little, if any. In our previous study (KAWAMURA and MORIMOTO, 1973), it was suggested that the receptors in the medial pterygoid muscle were responsible for the JTR because electrical stimulation of the pterygoid nerve activated hypoglossal nerve fibers. In that study, current spread to the temporal nerve was not completely excluded when the pterygoid nerve was stimulated. In the present study, exfoliation of the temporal muscle from the temporal bone greatly diminished the styloglossal muscle activities of the JTR. Moreover, a downward stretch of the isolated coronoid process of the mandible activated the styloglossal muscle. Since these two procedures could be carried out without damaging the afferents from the joint receptors or from the medial pterygoid muscle receptors, it may be concluded that the receptors responsible for the JTR are located mainly in the temporal muscle.

Identification of receptor contributing to the jaw-tongue reflex. EMG activity of the styloglossal muscle in the JTR were different from those of the temporal muscle in the stretch reflex in the following several points: (1) The threshold for evoking the styloglossal muscle activity by passive jaw depression was much higher than that for evoking the temporal muscle activity. (2) The styloglossal muscle activity showed only slight dynamic response to the passive jaw depression in a ramp manner, while to the same movement of the jaw the temporal muscle activity often showed an apparent dynamic response. (3) Adaptation occurred more rapidly in the temporal muscle than in the styloglossal muscle during sustained opening of the mouth. (4) The styloglossal muscle was activated by vibratory stimuli at frequencies below 130 Hz, whereas the stretch reflex of the temporal muscle followed the frequencies higher than 150 Hz. In addition to these differences in EMG activity, it was found that repetitive electrical stimulation at a frequency of 100 Hz to the temporal nerve activated the extrinsic tongue muscle, and the threshold for this activation was between 1.3 and 1.7 times that of the lowest-threshold fibers in the temporal nerve under background facilitation by jaw depression. These results strongly suggest that the receptor for the JTR is not the primary ending of the muscle spindle responsible for the stretch reflex of the temporal muscle.

Among proprioceptors other than the primary ending, either the Golgi tendon organ or the secondary ending of the muscle spindle is a possible receptor for the JTR. The physiological properties of both receptors seem to meet requisites for the receptor contributing to the JTR. They are slowly adaptive to maintained stretch of the muscle if the length of muscle stretch is well above their thresholds, and also less sensitive to vibratory stimuli (BROWN *et al.*, 1967). Furthermore, the threshold of these endings to muscle stretches is known to be higher than that

of the primary ending (MATTHEWS, 1933; HUNT and KUFFLER, 1951; HUNT, 1954; LUNDBERG and WINSBURY, 1960; ALNAES et al., 1965). Of these two different kinds of sensory endings, the Golgi tendon organ seems to be a more appropriate candidate than the secondary ending. The threshold of the Golgi tendon organ in maintaining stretch is considerably higher than that of the secondary ending (LUNDBERG and WINSBURY, 1960). Sensitivity of the Golgi tendon organs to vibratory stimuli is found to be relatively high when the muscle is contracting and they can follow vibration with an amplitude of 100 μm and a frequency of 200 Hz (BROWN et al., 1967). JANSEN and RUDJORD (1965) found that the tonus of extensor muscles in the decerebrated animals increased due to spontaneous activation of the static and dynamic fusimotor-neurons. The animals used in the present study were decerebrated and they closed their mouths rather firmly at rest. Under these conditions, therefore, the tonus of the jaw closing muscles may also increase and it may raise sensitivity of the Golgi tendon organs in the masticatory muscles to vibratory stimuli. The threshold of the afferent fibers from the Golgi tendon organs (GIb) is relatively low compared with that of the afferents from the secondary endings (GII), and it is considered to be between 1.2 and 1.8 times threshold of the lowest-threshold afferents (GIa) (ECCLES et al., 1957; ECCLES and LUNDBERG, 1958). These properties of the Golgi tendon organ seem to be appropriate as those of a possible receptor for the JTR. However, the threshold of the JTR to electrical stimulation to the temporal nerve increased to more than 3 times that of the temporal nerve when the jaw was not depressed. This fact may mean that receptors other than the Golgi tendon organs are involved in elicitation of the JTR. Therefore, although the Golgi tendon organs in the temporal muscle seem to be mainly responsible for the JTR, the secondary endings may also play some part. It must be noted that the above discussion is based on the results of investigations on the Golgi tendon organs and the secondary endings in limb muscles because no data are available at present on the properties of these receptors in the masticatory muscles.

No convincing proof of the existence of the Golgi tendon organ in the masticatory muscles has been physiologically presented so far, but some morphological studies suggest their existence. From degeneration studies on the trigeminal mesencephalic nucleus, SZENTÁGOTHAI (1948) reported existence of the Golgi tendon organ in the masticatory muscles. KAWAMURA and HAMADA (1974) found at the musculotendinous junction of the temporal muscle an ending resembling the Golgi tendon organ; it is an encapsulated club-like ending provided with an accessory nerve fiber clinging to its body. Recently, TOULOUMIS et al. (1975) have reported existence of the Golgi tendon organs in the temporal and masseter muscles in kittens and also in young macaques. If Golgi tendon organs exist both in the temporal and masseter muscles in the adult cat, only the ending in the former muscle may have synaptic connections with hypoglossal motoneurons innervating extrinsic tongue muscles. The input of the JTR is thus considered to be strictly

restricted.

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