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Sensory components facilitating jaw-closing muscle activities in the rabbit

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Summary. The role of oral and facial sensory receptors in the control of masticatory muscle activities was assessed from the effect of acute deafferentiation on cortically induced rhythmic jaw movements (CRJMs) in anesthetized rabbits. When a thin polyurethane-foam strip (1.5, 2.5 or 3.5 mm thick) was placed between opposing molars during CRJMs, masseteric activities were facilitated in association with an increase in the medial excursion of the mandible during the power phase. The effects varied with the pattern of CRJMs, and the rate of facilitation was greater for small circular movements than for the crescent-shaped movements. Furthermore, the response of the masseter muscle was greater in the anterior half of the muscle, where muscle spindles are most dense, than in its posterior half. It was also demonstrated that the response increased with an increase in the thickness of the test strip. In contrast, the activities of the jaw-opening muscle were not affected significantly. The duration of masseteric bursts increased during application of the test strip and the chewing rhythm tended to slow down. However, the latter effect was not significant. After locally anesthetizing the maxillary and inferior alveolar nerves, the facilitative responses of the masseter muscle to the test strip was greatly reduced but not completely abolished. Lesioning of the mesencephalic trigeminal nucleus (Mes V) where the primary ganglion cells of muscle spindle afferents from jaw-closing muscles and some periodontal afferents are located, also reduced the facilitative effects. Similar results were obtained in the animals with the kainic acid injections into the Mes V 1 week before electrical lesioning of this nucleus. In these animals the effects of electrical lesioning of the Mes V could be attributed to the loss of muscle receptor afferents since the neurons in the vicinity of the Mes V were destroyed and replaced by glial cells, whereas the Mes V neurons are resistant to kainic acid. When electrical lesioning of the Mes V and sectioning of the maxillary and inferior alveolar nerves were combined in animals with a kainic acid injection into the Mes V, the response of the masseter muscle to application of the strip was almost completely abolished. From these findings, we conclude that both periodontal receptors and muscle spindles are primarily responsible for the facilitation of jaw-closing muscle activities. Furthermore, it is suggested that the transcortical loop may not be the only path producing this facilitation since similar effects were induced in animals with ablation of the cortical masticatory area (CMA), when the test strip was placed between the molars during rhythmic jaw movements induced by pyramidal tract stimulation.

Key words: Jaw movement – Masticatory muscle – Periodontal receptor – Muscle receptor – Trigeminal nerve – Cortical masticatory area

Introduction

As demonstrated in a previous paper (Inoue et al. 1989), patterns of rhythmic jaw movements and associated EMG activities during mastication were influenced by food consistency in the rabbit. Furthermore, they changed greatly following deprivation of oral and facial sensations. In particular, jaw-closing muscle activities were significantly reduced after combining sections of the maxillary and inferior alveolar nerves, whereas no significant changes were induced after sectioning the infraorbital and mental nerves. These results indicate that sensory inputs from intraoral receptors are more

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important for the regulation of muscle activities and jaw movements than are facial cutaneous receptors. However, the contribution of extraoral sensory receptors in the stomatognathic structures and the central compensatory mechanism cannot be neglected because animals deprived of intraoral sensations still maintained an ability to chew food, although their chewing behavior became clumsy. In order to identify the receptors mainly responsible for the regulation of jaw movements, we examined the effects of blocking the afferents from periodontal and muscle receptors, each being regarded as representative of intraoral and extraoral sensory receptors, respectively. For this purpose, cortically induced rhythmic jaw movements (CRJMs) of anesthetized animals were used as a model of chewing movements partly because they resemble normal chewing movements (for review, see Nakamura et al. 1980; Luschei and Goldberg 1981) and partly because it is easier in the anesthetized animal than in chronic cases to stimulate or destroy the afferents from certain kinds of receptors independently from others. We first examined the effects of intraoral stimulation on CRJMs and then blocked sensory inputs from the oro-facial areas. The maxillary and inferior alveolar nerves were anesthetized in order to block periodontal afferents, and muscle spindle afferents were blocked by making lesions of the trigeminal mesencephalic nucleus (Mes V) where their ganglion cells are located. The results demonstrate that jaw-closing muscle activities are facilitated during CRJMs by intraoral stimulation and also that this facilitative response was reduced by locally anesthetizing the maxillary and inferior alveolar nerves. During the preparation of this paper, Lavigne et al. (1987) reported that periodontal receptors provided positive feedback to jaw-closing muscles during rhythmic jaw movements in the anesthetized rabbit. The present results are thus in agreement with their results. On the other hand, information about the effect of Mes V lesion is available only for the monkey (Goodwin and Luschei 1975) and the rat (Daunton 1977). Since the Mes V neurons distribute in a long narrow zone, there is considerable risk of damaging the neurons in the surrounding structures during lesioning of this nucleus. It is thus necessary to differentiate the effects of Mes V lesions from those produced by the lesions of other structures. This problem is overcome by examining the effect of the Mes V lesion in animals which received a kainic acid injection along the Mes V. Kainic acid causes a degeneration of the neurons in the vicinity of the Mes V without affecting the Mes V neurons (Colonnier et al. 1979). The results indicate that muscle spindles also contribute to enhance jaw-closing muscle activities during chewing. The present study also tested whether the cerebral masticatory area (CMA) is required for the above positive feedback regulation of the masticatory system. Some of the results have been published previously in abstract form (Morimoto et al. 1987).

Methods

The experiments were conducted on fifty male rabbits weighing 2.0–2.5 kg. The surgical procedures were nearly identical to those described previously (Inoue et al. 1989), and only a brief summary is presented here. All surgery was performed after intravenous injections of urethane (500 mg/kg) and alpha chloralose (60 mg/kg), which were supplemented by injections of 2.5% sodium thiamylal (Isozol, Yoshitomi Pharm. Co., 0.2 ml/25 min). The level of anesthesia was maintained at such a level that the animals showed the constant rate of respiration (ca 40/min) and heart beat (ca 240/s), no apparent corneal reflex, no spontaneous eye movements, and no appreciable resting discharges of the masticatory muscles. The trachea was cannulated for artificial ventilation. Small screws were attached to the mentum to hold a phototransistor array for recording jaw movements by means of a He-Ne laser position detector (Morimoto et al. 1984). The head of the animal was fixed to a stereotaxic apparatus. For stimulation of the cortical masticatory area (CMA), the cortical surface was exposed between 0 and 8 mm anterior to bregma and mediolaterally between 3 mm lateral to the midline and the lateral edge of the cranium. The underlying dura was opened and the exposed surface was covered with warm liquid paraffin (37° C). To reduce brain pulsations, drainage of the cerebrospinal fluid was performed through an opening in the dura over the foramen magnum. The rectal temperature was maintained at 36–38° C with a heating pad and the electrocardiogram was continuously monitored. Pairs of teflon coated stainless steel wires were inserted unilaterally in all animals in order to record EMG activity from the masseter and digastric muscles on the side opposite cortical stimulation. Signals from EMG electrodes were amplified, displayed on an oscilloscope and recorded on magnetic tape. The data were later replayed and the magnitude of the integrated activities, the duration of the masseter and digastric bursts and the total cycle duration (TCL), whose reciprocal represents the frequency of cyclic movements, were analyzed with the aid of a signal processor (Nihondenki-Sanei, 7T-18).

Cortical stimulation

Glass-coated metal electrodes, having an impedance of 1–3 MΩ at 1 KHz, were used for the intracortical microstimulation. The reference electrode was placed on the cranium at the bregma. The stimulating electrode was vertically inserted from the dorsal surface into the right cortex. Square wave pulses of 0.2 ms duration, a frequency of 30 Hz and current intensity of less than 50 μA were used for evoking rhythmic jaw movements. The effective sites were searched in the right frontal cortex anterior to the bregma.

Intraoral stimulation

A thin polyurethane-foam strip which was held by an experimenter, was placed between opposing molars during CRJMs. Three test strips, 1.5, 2.5 and 3.5 mm thick and 2 mm wide, were prepared. The facial skin was excised from the mouth

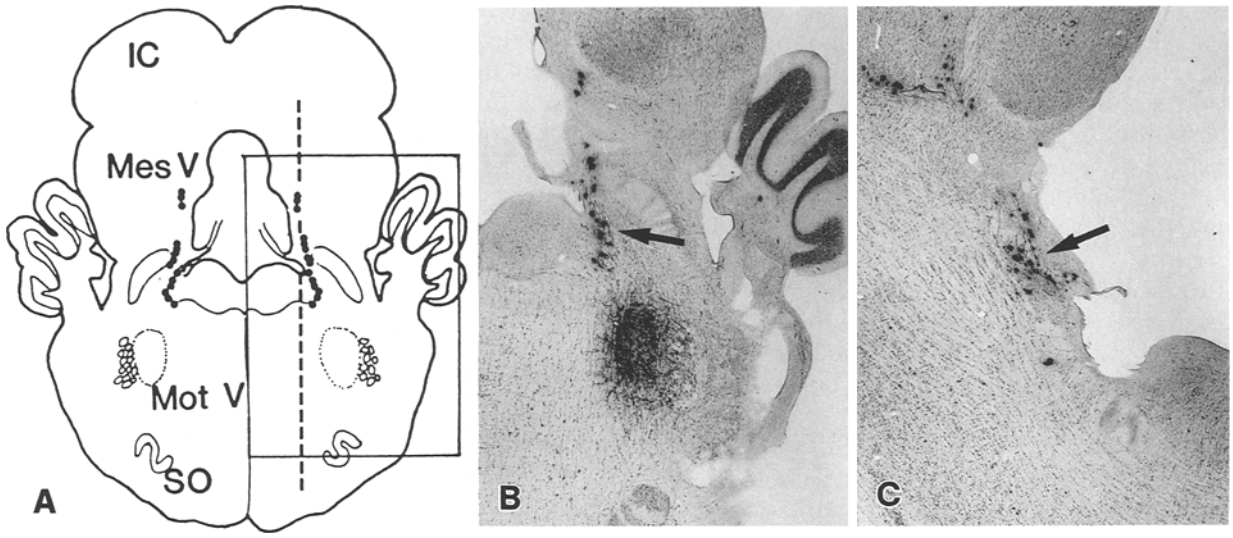

Fig. 1 A–C. Distribution of mesencephalic trigeminal neurons labeled by injection of WGA-HRP into the right masseter nerve. **A** Schematic representation of labeled neurons (black dots). Mes V: mesencephalic trigeminal nucleus; Mot V: trigeminal motor nucleus; SO: superior olive nucleus. Although the distribution is conveniently illustrated bilaterally, the cells were labeled only unilaterally. **B** Examples of HRP-labeled cells on the frontal section. The histological section corresponds to the square drawn in **A**. **C** Examples of HRP-labeled cells on the sagittal section approximately 2 mm lateral from the midline. The arrows in **B** and **C** indicate the lower cell group through which the descending fibers of the upper cell group pass

angle to the anterior edge of the masseter muscle, and the incised skin and mucous membrane on the maxillary part were sutured separately from their mandibular parts. The maxillary part was then deflected upward and connected to the stereotaxic apparatus using a surgical thread to expose the molars. All wound margins were anesthetized with topically applied xylocaine ointment or by small injections xylocaine hydrochloride. The lingual nerve was sectioned unilaterally or bilaterally in order to eliminate tongue sensations. The jaw movements and EMG activities were analyzed for 7 masticatory cycles in each trial. The mean values of the data obtained from 5 trials were compared with and without an application of the strip.

Local anesthetization of branches of the trigeminal nerve

The maxillary nerve was exposed at the bottom of the orbit after incision of the skin along the upper border of the zygomatic arch. In order to expose the inferior alveolar nerve in the mandibular canal, the periosteum with overlying soft tissues around the root of the molars and retromolar regions were removed, and the underlying bone was ground. For a topical application of anesthetics, a cotton ball soaked in lidocaine (2%) or bupivacaine hydrochloride (Marcain, Yoshitomi Pharm. Co., 0.25%) was placed on the exposed nerve bundles. The level of anesthesia was assessed by pinching the facial skin or by pricking the intraoral mucous membrane. The experiments were performed only when no reflex movements were elicited by such nociceptive stimulation. The recovery of the response was tested about 7 h after rinsing the nerves with saline.

Mesencephalic trigeminal nucleus lesion

The contribution of muscle spindle inputs to the control of jaw movements was assessed by examining the effects of lesioning the Mes V on the jaw movements and EMGs of masticatory muscles. In order to block muscle spindle afferents effectively, the course of the afferents was identified histologically in 2 animals with an injection of WGA-HRP into the unilateral masseter nerve. Perfusion and fixation of the animals and the subsequent TMB reaction of the brain slices (50 μm thick) were performed using the methods of Mesulam (1978). The Mes V spindle neurons were found to distribute in a long narrow zone in the pons and their descending fibers passed through the caudal group of Mes V neurons at the portion dorso-medial to the trigeminal motor nucleus (arrows in Figs. 1B, C). Hence, the afferents must be blocked effectively by making lesion at this portion. For this purpose, the Mes V neurons were first located physiologically by recording unit activities responding to passive jaw-opening and to electrical stimulation of the masseter nerve at latencies shorter than 1.5 ms, then lesioned by passing DC currents through the stimulating electrode (20 μA, 10 s). Destruction of the nucleus was estimated from the magnitude of the jaw stretch reflex elicited by jaw depression passively applied with the muscle stretcher. The Mes V lesion was performed in 5 animals and successful in 2 animals.

As described in the introduction, neurons in the vicinity of this nucleus may also be injured during lesioning of the Mes V. Hence, the possibility exists that the effects following the Mes V lesion are attributable to injury of these neurons rather than the destruction of Mes V neurons. In order to assess the true effect of the Mes V destruction, a total of 2 μl kainic acid (1.5 μg/μl) was injected along the Mes V with a Hamilton 10 μl syringe (tip diam., 200 μm). Since the Mes V neurons are resistant to kainic acid (Colonnier et al. 1979), only the neurons in the vicinity of the Mes V are injured by this procedure. After 1 week of survival, the Mes V was lesioned electrically. Any changes in the jaw-closing muscle activities following the electrical lesioning of the Mes V could be attributed to the loss of sensory inputs via this nucleus, rather than the destruction of neurons surrounding the Mes V. This method was applied to

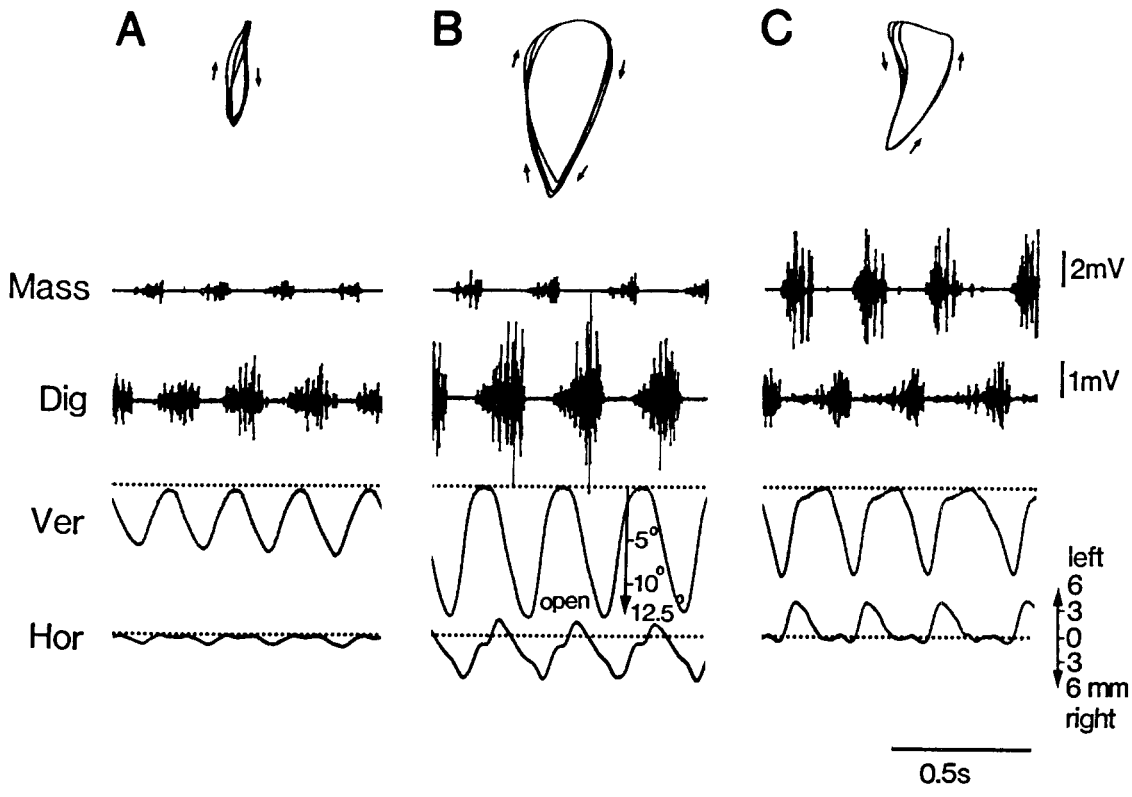

Fig. 2 A–C. Three typical patterns of cortically induced rhythmic jaw movements (CRJMs) on the frontal plane and associated EMG activities of masticatory jaw muscles. **A** Type A movement – small circular movements which are associated with small activities of the jaw-closing muscle and moderate activities of the jaw-opening muscle. **B** Type B movement – large circular movements characterized by relatively small activities of the jaw-closing muscles and large activities of the jaw-opening muscle. The jaw swung ipsilateral towards the cortical stimulation during the jaw-closing phase. **C** Type C movement – crescent-shaped movements which are associated with large activities of the jaw-closing muscles. Activities of the type C jaw-opening muscle varied from moderate to low in amplitude, depending on the site of stimulation. In contrast to type B, the jaw swung contralateral towards the cortical stimulation. This type of movement resembles natural chewing movements at the mastication stage in alert animals. The small arrows indicate the direction of jaw movements

15 animals and successful in 5 animals. For two of these 5 animals, a combined section of the maxillary and inferior alveolar nerves was performed simultaneously with the Mes V lesion. Two animals died after the kainic acid injection. In the remaining eight, both the kainic acid lesion and the subsequent eletrical lesion of the Mes V were incomplete. The data is from the former 7 animals. The extent of the lesion was histologically examined later. For this purpose, animals were deeply anesthetized, and perfused with saline through the ascending aorta, followed by 10% formaldehyde. After 2 or 3 days postfixation, the brain was removed from the skull, sectioned at 50 μm in the frontal plane and stained with cresyl-violet.

Statistical analysis

Paired *t* tests were performed for comparisons of the three variables (integrated EMG activities, burst durations, and chewing rate (TCL)) before and during the application of a strip between the molars during CRJMs, and also for comparison of the data before and during local anesthetization of the trigeminal nerve. The statistical significance was tested for a group of 6 animals. In each animal, the mean of the variables was first calculated from the data from 7 masticatory cycles before and during application of a strip or before and after local anesthetization in a trial. The data were then obtained as the mean of the total of 5 trials. Comparisons of the masseteric activities before and after Mes V lesioning were performed by *t* tests in each animal.

Results

Cortically induced rhythmic jaw movements (CRJMs)

Repetitive electrical stimulation of the CMA produced various patterns of rhythmic jaw movements from the region between 2 and 6 mm anterior to the bregma, betwen 5.0 and 7.5 mm lateral to the midline and between 0.5 and 3.5 mm from the dorsal surface. The region was smaller than that reported by Sumi (1969) and Lund et al. (1984), probably because we used weaker currents for the intracortical microstimulation than the other authors. Three typical patterns of CRJMs in the frontal plane and associated EMG activities are shown

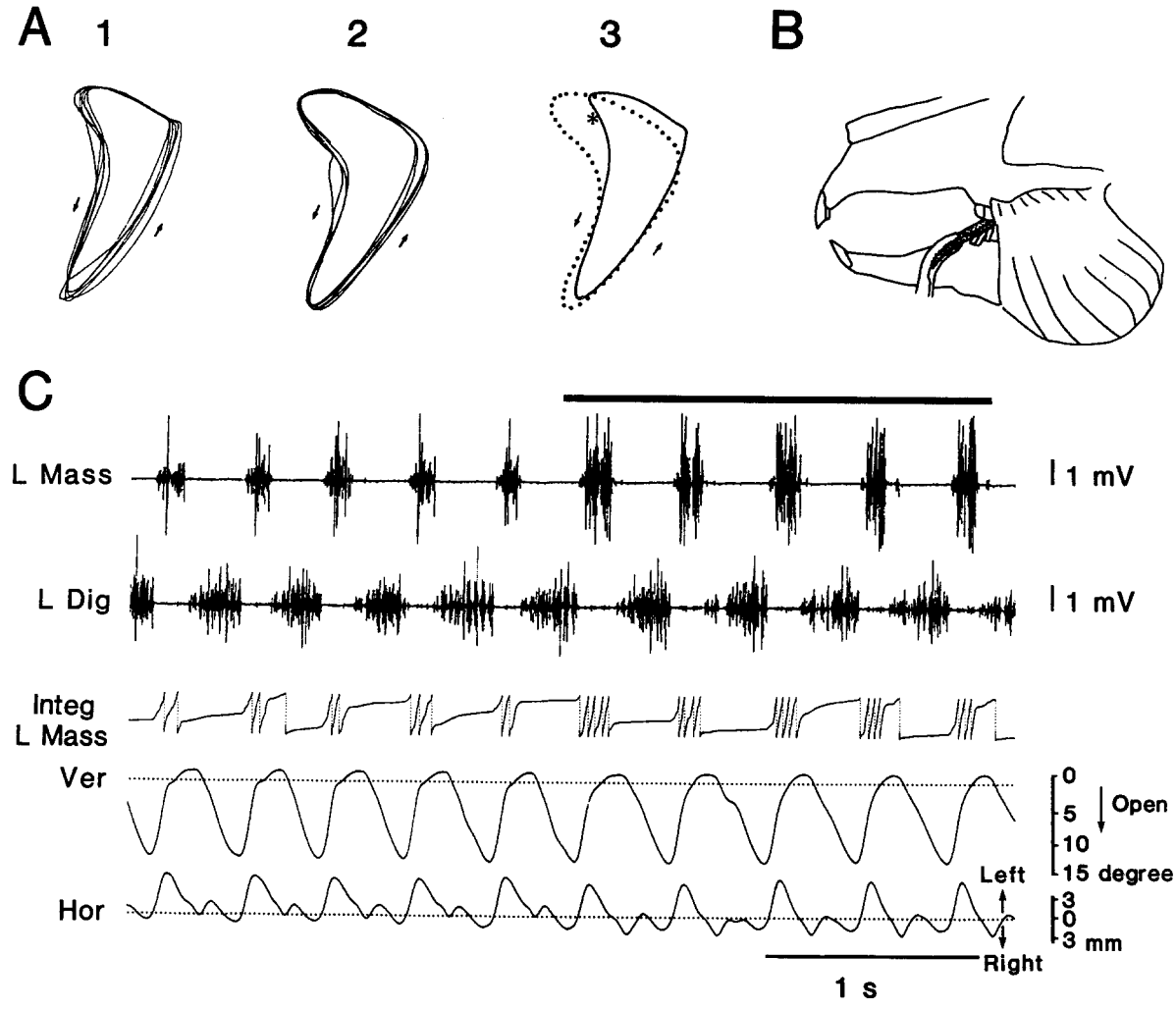

Fig. 3A–C. Modification of the pattern of CRJMs and associated EMG activities of masseter muscles during application of the test strip between opposing molars. **A** Patterns of jaw movements before (1) and during (2) application of the test strip, and their superimposed traces (3). The medial excursion developed during application of the strip. **B** The procedure for application of a polyurethane-foam strip between the molars using a forceps. **C** EMG activities of the masseter and digastric muscles recorded simultaneously with vertical and horizontal jaw movements. The thick bar indicates the period of test strip application. L Mass: Left masseter muscle; L Dig: left digastric muscle; Integ L Mass: integrated activities of the left masseter muscle; Ver and Hor: vertical and horizontal jaw movements

in Fig. 2. From the most dorsal part of the CMA, small circular movements with little horizontal excursion were induced (Fig. 2A). The dorso-ventral extent of the area producing this type of movement (type A) was about 0.5 mm. With advancement of the stimulating electrode, both the vertical and horizontal movements developed, producing large circular movements as shown in Fig. 2B (type B). The mandible swung ipsilateral to the cortical stimulation during jaw closure (Fig. 2B). The area producing type B extended dorso-ventrally in the range 1–1.5 mm. When the electrode was advanced ventrally, the pattern changed from circular to crescent-shaped movements (type C), and the mandible swung contralateral to the cortical stimulation during jaw closure (Fig. 2C). This type of movement resembled normal chewing patterns when grinding food between molars (Bremer 1923; Weijs and Van der Wielen-Drent 1982; Morimoto et al. 1985), and was composed of three phases: jaw-opening, jaw-closing and power phases. Each typical type of movement was also characterized by EMG activities of the masticatory muscles. Masseteric burst activities were small for type A (about 10% of the maximum value), slightly large for type B (about 20% of the maximum value) and maximum for type C. In accordance with large activities of masseter muscle during type C movements, the power phase developed and the animals

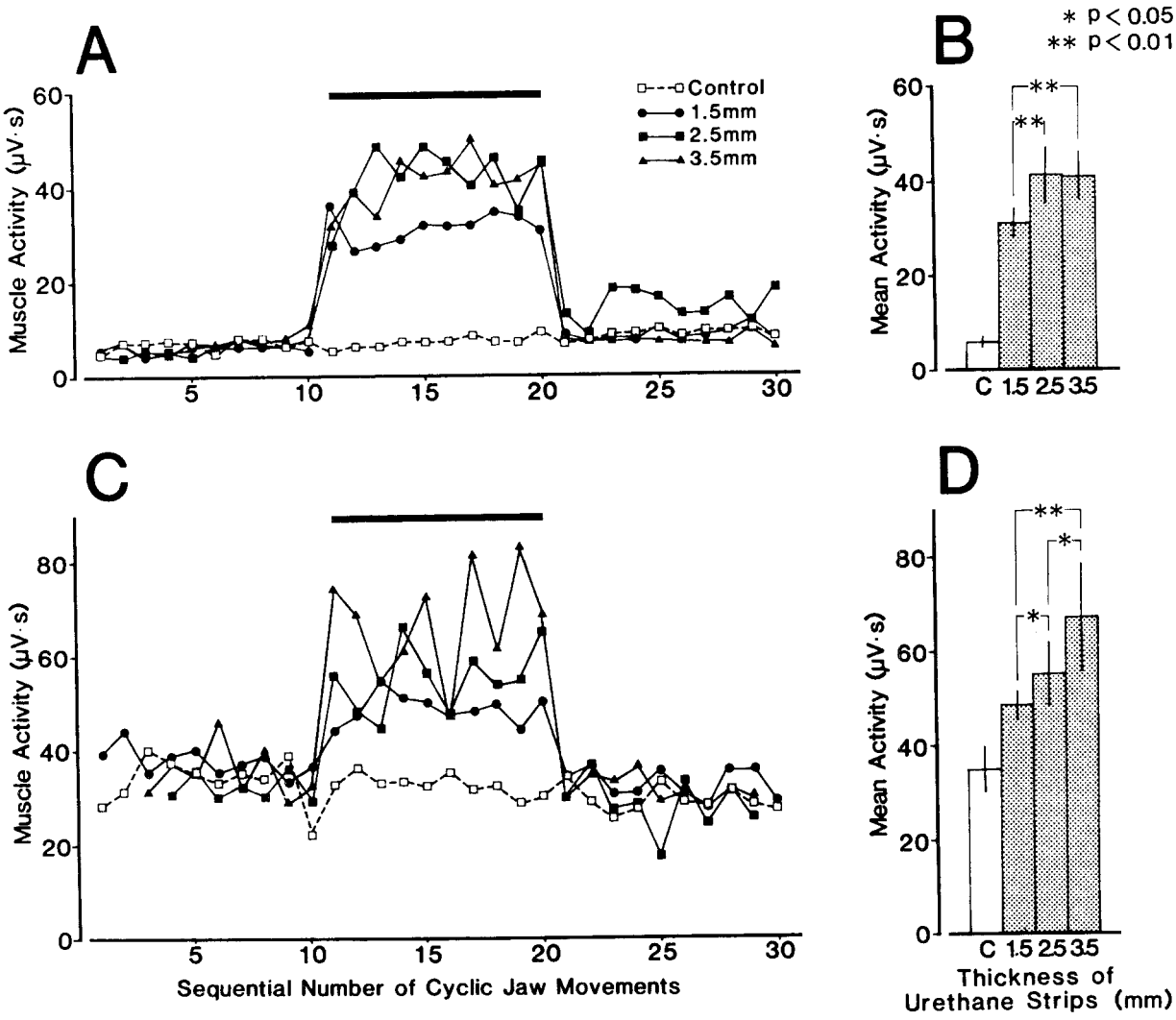

Fig. 4A–D. Masseteric responses to application of the test strips during CRJMs of different types, (**A**) type A; (**C**) type C. Three test strips 1.5, 2.5 and 3.5 mm thick were used. The ordinate shows the integrated activity of the masseter muscle and the abscissa indicates the serial number of cyclic jaw movements. Thick bars indicate the period of application of the strip. In **B, D** the mean and standard deviation of the masseteric activities when chewing strips of 3 different thickness were compared with each other

often gnashed the molars. In contrast, the power phase was indistinct in both types A and B. Digastric burst activities were moderate for type A (about 40% of the maximum value) and maximum for type B. For type C, they gradually decreased from moderate to small with advancement of the electrode and were minimal at the most ventral part of the CMA. Some variations of the typical movements, such as 8-shaped movements, large vertical movements with little horizontal excursion, etc. were evoked from the transitional zone between the areas producing type B and type C movements.

Jaw movements and EMG activities during application of a strip

The pattern of jaw movements and associated EMG activities were modified when a thin polyurethane-foam strip was placed between opposing molars during type C movements (Fig. 3B). The most prominent effects were a facilitation of masseteric activities during the jaw-closing or power phases (Fig. 3C) and medial excursions of the mandible during the power phase (Fig. 3A-2 and 3A-3). In small circular movements (type A), the horizontal excursion which was negligible before strip application, developed when chewing the strip simultaneously with the facilitation of masseteric activities. However, the pattern of CRJMs was never converted from type A to type C by applica-

Table 1. Comparisons of integrated EMG activities, burst durations and total cycle length (TCL) before and during application of either one of 3 different test strips during CRJMs in 6 animals

		Thickness of a test strip		
		1.5 mm	2.5 mm	3.5 mm
Mass. activity (% of control)	before	98.7 (±11.3)	99.8 (±16.6)	97.5 (±9.6)
	during	278.3 (±127.1)	317.0 (±142.5)	354.2 (±167.7)
	t	3.64*	4.09**	3.87*
Dig. activity (% of control)	before	97.7 (±8.8)	97.1 (±11.8)	101.8 (±8.4)
	during	93.3 (±7.8)	86.7 (±10.8)	88.6 (±17.5)
	t	0.82	1.69	1.48
Mass. duration (ms)	before	100.3 (±34.2)	101.8 (±31.5)	101.3 (±28.1)
	during	109.2 (±35.7)	125.5 (±35.9)	133.1 (±35.2)
	t	2.27	4.41**	5.03**
Dig. duration (ms)	before	178.2 (±44.4)	175.7 (±42.4)	176.3 (±43.9)
	during	169.5 (±43.1)	163.2 (±38.0)	160.7 (±46.5)
	t	1.39	1.46	0.92
TCL (ms)	before	332.7 (±37.2)	324.7 (±32.4)	325.7 (±32.1)
	during	345.8 (±43.8)	352.2 (±53.0)	348.2 (±55.2)
	t	1.87	1.96	2.00

For comparisons of the variables, paired t tests were performed. Single and double asterisks indicate significant differences at the level of 5% and 1%, respectively. t: t-value; Mass.: masseter muscle; Dig.: digastric muscle

tion of a strip. In contrast to these two types of CRJMs, large circular movements were not affected by this procedure because the strip was not firmly occluded between the molars during the power phase. Masseteric activities were compared before, during and after application of each strip (Fig. 4). The CRJMs of Figs. 4A and 4C were type A and type C, respectively, and they were evoked in the same animal. Masseteric activities during application of a 2.5 mm strip were about 10 times the value before application for the former (Fig. 4A) and about 2 times for the latter (Fig. 4C), implying that the rate of increase in the masseteric activities was greater for the small circular movements than for the crescent-shaped ones. However, the absolute maximum value was greater for the latter than for the former (Fig. 4B, D). Modifications of muscle activities, burst durations and the total cycle length (TCL) were statistically compared before and during application of the strip in a group of 6 animals (Table 1). It is apparent that the increment of both masseteric activities and masseteric burst durations are two conspicuous features of the changes which occurred during application of the strip. Furthermore, masseteric activities increased with an increase in the thickness of the test strip. On the other hand, digastric activity and its burst duration were not affected significantly. Although the duration of masseteric bursts increased significantly when chewing a strip 2.5 or 3.5 mm thick, the TCL did not increase significantly in either case.

The rate of the masseteric response varied with the recording site in the masseter muscle. Four sites were selected for recording, i.e., the anterior deep, anterior superficial, middle superficial and posterior superficial parts according to the classification of Weijs and Dantuma (1981). The effects were examined for type A and type C. In both types of CRJMs, the rate of increment of the masseteric response was in the following order: anterior deep > anterior superficial > middle superficial > posterior superficial part. Consequently, masseteric activity was recorded from the deep anterior part of the muscle throughout the experiments.

We also examined whether masseteric activities could be elicited by reflex by pressing the upper and lower molars with a hard wooden stick. No facilitation was induced in the masseter muscle by axial or horizontal pressure to the molars.

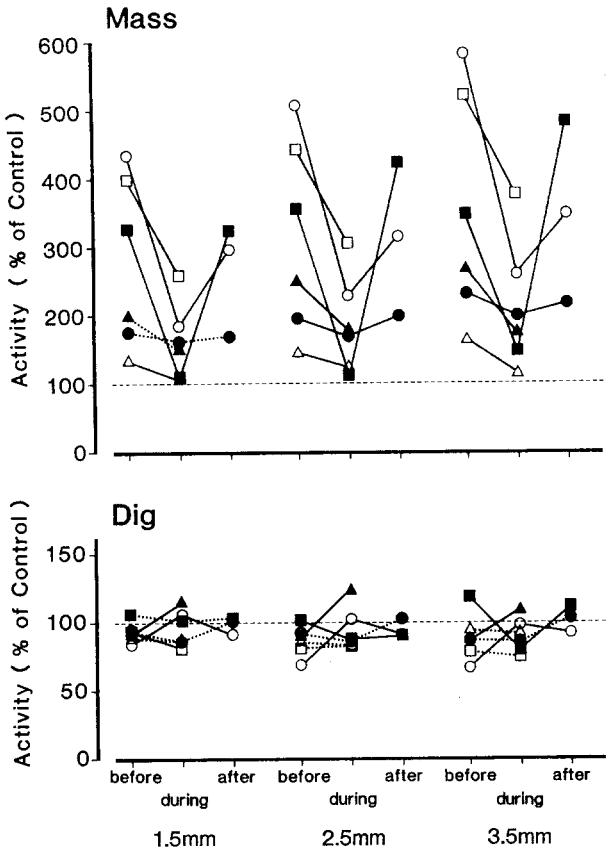

Fig. 5. The effect of locally anesthetizing both the maxillary and inferior alveolar nerves on the muscle response to application of a test strip. The results of 6 animals are represented by different symbols. Significant differences are represented by a solid line and insignificant differences by a dotted line. The masseteric responses were reduced by the topical application of local anesthetics, and recovered 7 hours after rinsing the nerves with saline. In contrast, digastric activities were not affected significantly by anesthesia

The effects of local anesthesia to trigeminal sensory branches on the masseteric response during CRJMs

Muscle activities and the duration of a single cycle (TCL) when chewing a strip were compared before and after topical application of local anesthetics to both the maxillary and inferior alveolar nerves in a group of 6 animals (Table 2). The results of each are shown by different symbols in Fig. 5. The notable change following local anesthesia was a reduction in the masseteric response to application of the strip. There were large individual differences in the effect, and it appears that the reduction was great when the pre-anesthetic value was high and vice versa (Fig. 5). However, the responses were never abolished even at such a deep anesthetic level that no jaw-opening reflex was induced by pinching the facial skin or pricking the oral mucous membrane. Seven hours after rinsing the nerves with saline, the responses recovered, though not completely, in three animals. In the remaining three, the pattern of jaw movements altered after local anesthesia and did not return to the preanesthetic phase. The effects on digastric activities were minor and not regarded as significant (Table 2). The TCL tended to decrease after local anesthesia (speed-up of the chewing cycle), but the effect was not significant except for the 1.5 mm strip.

Effects of Mes V lesion on the masseteric response

Since the masseteric response to application of the strip was not abolished after locally anesthetizing both the maxillary and inferior alveolar nerves, extraoral sensory receptors in the stomatognathic structures must also be responsible for this response. Muscle receptors, especially muscle spindles, are one of the most likely candidates for the responsible receptors. This possibility was examined by making a lesion in the Mes V where the cell bodies of the muscle spindle afferents are located. The results obtained from 7 animals are listed in Table 3. These animals were divided into 3 groups, depending on the kind of surgical operations executed. In the first group (Nos. 2 and 3), only the Mes V lesion was performed electrically, while in the second group (Nos. 14, 16 and 18) kainic acid was injected into the Mes V 1 week before the electrical lesioning of the Mes V. In the third group, both the Mes V lesions and the sectioning of the maxillary and inferior alveolar nerves were combined. Examples of the lesion at the anterior, middle and posterior parts of the Mes V are illustrated in Figs. 6A–C. Neurons around the Mes V, particularly the parabrachial nucleus and locus coeruleus, were killed by kainic acid and replaced by glial cells (Fig. 6E). Before making the electric lesion of the Mes V, both the stretch reflex-response which was elicited by depressing the mandible by 1 mm and also the facilitative response of the masseter muscle to application of a test strip were recorded (Fig. 7). After lesioning the left Mes V, the ipsilateral stretch reflex decreased greatly, while the contralateral reflex remained unaffected (Fig. 8). The facilitative responses of the ipsilateral masseter muscle to application of the strip were reduced to 80% of the control value after the lesion, the effect being significant ($t=2.85$, $P<0.05$). In association with such a reduction of the masseteric activities, the magnitude of the horizontal excursion at the power phase was decreased. In this animal, the response of the contralateral masseter muscle was also re-

Table 2. Comparisons of integrated activities, burst durations and total cycle length (TCL) before and after local anesthesia of the trigeminal branches in 6 animals

		Thickness of a test strip		
		1.5 mm	2.5 mm	3.5 mm
Mass. activity (% of control)	before	278.3 (±127.1)	317.0 (±142.5)	354.2 (±167.7)
	after	162.4 (±57.0)	187.2 (±71.7)	213.4 (±95.3)
	t	2.76*	2.87*	3.14*
Dig. activity (% of control)	before	93.3 (±7.8)	86.7 (±10.8)	88.6 (±17.5)
	after	97.3 (±12.5)	94.6 (±16.4)	90.2 (±12.9)
	t	0.66	0.92	0.16
Mass. duration (ms)	before	109.2 (±35.7)	125.5 (±35.9)	133.2 (±35.2)
	after	108.9 (±30.0)	115.8 (±28.1)	126.2 (±27.8)
	t	0.05	1.76	0.83
Dig. duration (ms)	before	169.5 (±43.1)	163.2 (±38.0)	160.7 (±46.5)
	after	153.3 (±32.9)	149.3 (±28.4)	135.0 (±22.8)
	t	3.16*	1.81	2.37
TCL (ms)	before	345.8 (±43.8)	352.2 (±53.0)	348.2 (±55.2)
	after	317.5 (±22.0)	317.7 (±28.8)	316.2 (±18.5)
	t	2.90*	2.39	2.00

For comparisons of the variables, paired *t* tests were performed. Single asterisk indicates significant difference at the level of 5%. *t*: *t*-value; Mass.: masseter muscle; Dig.: digastric muscle

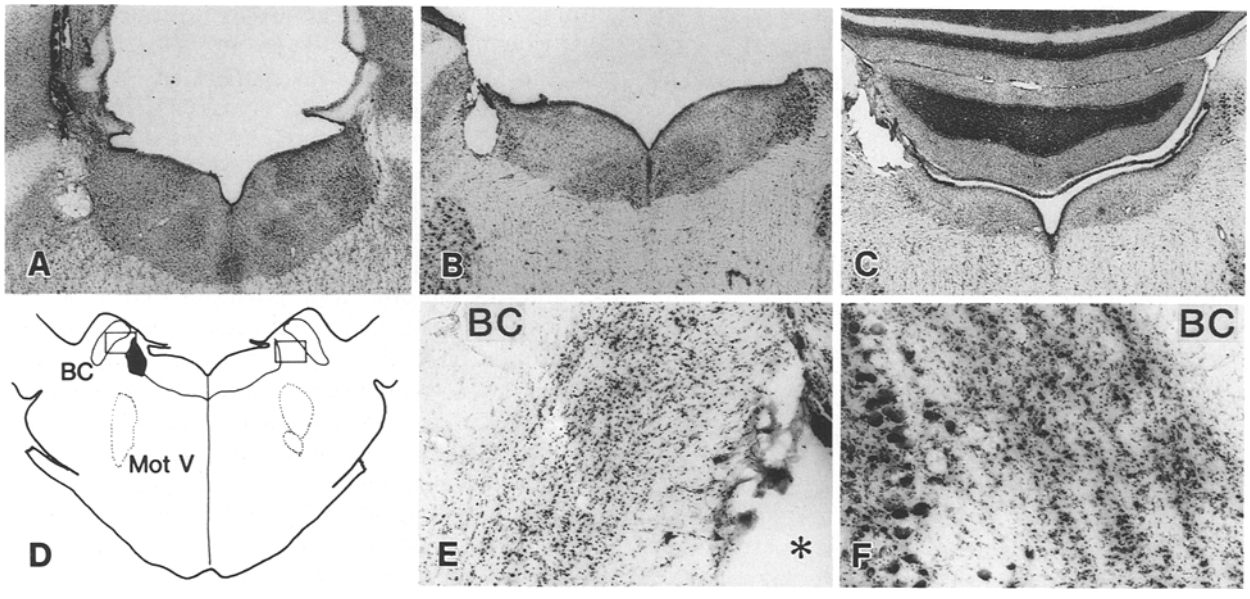

Fig. 6A–F. Low-power photomicrographs from 50 μm section of the brain-stem of the animal with chemical and electric lesions. Both lesions were made on the left side. **A–C** Represent the anterior, middle and posterior levels of the mesencephalic trigeminal lesion, respectively. High-power photomicrographs of **E**, **F** were taken from the areas illustrated by squares on the left and right sides of the schema shown in **D**. BC: brachium conjunctivum; Mot V: trigeminal motor nucleus. An asterisk in E shows the hole made by electrical lesion. It is noted that large neurons of the trigeminal mesencephalic nucleus (Mes V) and small neurons in the parabrachial nucleus and locus coeruleus are present on the right side (**F**), whereas such neurons are not found on the left side with kainic acid injection (**E**)

duced by 14% but this effect was insignificant ($t = 1.59$, $P > 0.05$). As shown in Table 3, the masseteric responses of the animals in the first and second groups were reduced to 75–85% of the control value after the Mes V lesion, irrespective of whether or not the kainic acid was injected into the Mes V. On the other hand, these responses were diminished almost completely in the third group. The results indicate that when the lesion of the

Table 3. Comparisons of the masseteric response to application of the 2.5 mm strip during CRJMs before and after the lesion of the mesencephalic trigeminal nucleus

Animal number	Kainic acid injection	Nerve section	Recording side	Rate of increase		Diff. between (A) and (B)
				Before lesion (A) (%)	After lesion (B) (%)	
2	–	–	I	236 (±33)**	179 (±25)**	$P<0.05$
			C	–	–	–
3	–	–	I	169 (±35)**	135 (±6)**	$P<0.01$
			C	–	–	–
14	+	–	I	339 (±38)**	287 (±25)**	$P<0.05$
			C	330 (±37)**	348 (±39)**	none
16	+	–	I	206 (±7)**	165 (±32)**	$P<0.05$
			C	335 (±50)**	288 (±33)**	none
18	+	–	I	326 (±38)**	251 (±30)**	$P<0.01$
			C	209 (±25)**	211 (±23)**	none
19	+	+	I	172 (±28)*	104 (±7)	$P<0.01$
			C	226 (±24)**	257 (±20)**	none
20	+	+	I	132 (±3)**	108 (±5)	$P<0.01$
			C	179 (±18)**	182 (±19)**	none

The rate of increase in the masseteric response during application of a strip is represented as a percent of the control values obtained without application of the strip. Values were mean ±S.D. $n=35$. I and C: EMG recording on the side ipsilateral and contralateral to the lesion of Mes V, respectively. Single and double asterisks indicate significant difference in the masseteric response before and during application of the test strip at the levels of 5% and 1% respectively. Diff.: Statistical significant difference in the rate of response before and after Mes V lesion. The animals were divided into 3 groups depending on the kind of surgical operations executed. In the first group (No. 2 and 3), only the Mes V lesion was performed electrically. In the second group (No. 14, 16 and 18), kainic acid was injected into the Mes V 1 week before the electric lesion of the Mes V. In the third group (No. 19 and 20), combined section of the maxillary and inferior alveolar nerves was performed in the animal both with kainic acid lesion and Mes V lesion

Mes V was combined with the section of the maxillary and inferior alveolar nerves, the facilitative responses of the masseter muscle was reduced more than by the nerve section alone. This added effect could be attributed to loss of the Mes V neurons rather than the destruction of the neurons in the vicinity of the Mes V since the latter had been injured by kainic acid injection performed 1 week before the electric lesion of the Mes V.

Responsibility of the transcortical reflex

The above facilitative response of the masseter muscle was examined to determine whether it was evoked via the transcortical feedback loop composed of peripheral sensory receptors, the CMA and trigeminal motor nucleus. For this purpose, the CMA and its surrounding area were ablated in the animal (Fig. 9B), and then rhythmic jaw movements were induced by stimulation of the pyramidal tract applied 5 mm posterior to the bregma (Fig. 9A). As shown in Fig. 9C, activities of the masseter muscle were still enhanced when chewing the strip.

Discussion

Modulation of jaw movements and masticatory EMG activities when chewing a test strip

The present study demonstrates that when a thin elastic strip was placed between opposing molars during CRJMs, masseteric activities were facilitated in association with the development of the medial excursion of the mandible during the power phase. These results are in accord with those reported very recently by Lavigne et al. (1987), except for the effect on the chewing rhythm. These authors showed that the chewing cycle was prolonged significantly when chewing a test material, whereas the change in the chewing cycle was not significant in the present study. The difference may have resulted from the difference in the material placed between the teeth. Lavigne et al. (1987) used a steel ball which is hard and could not be compressed during the power phase, while we used polyurethane-foam strips which were elastic and compressed during the power phase. Such a difference in the test material may produce a difference in

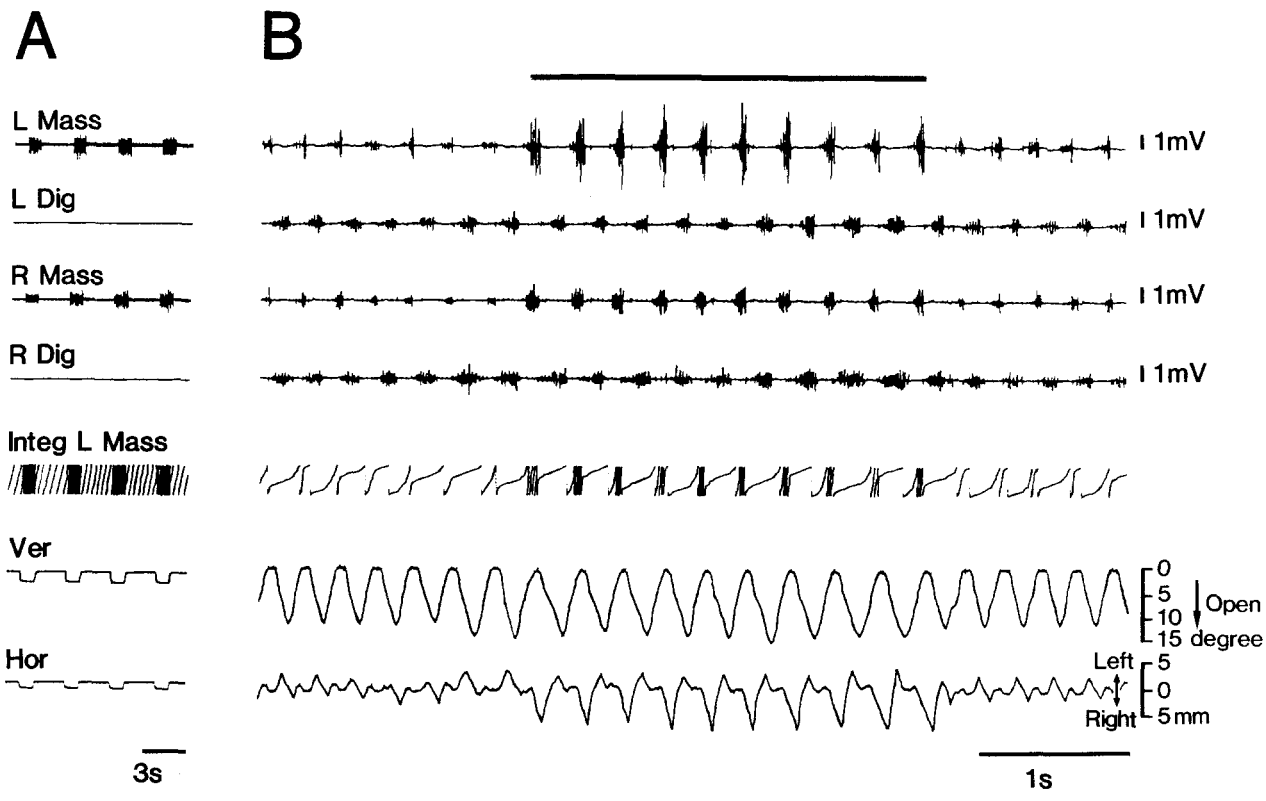

Fig. 7A, B. Responses of masticatory muscle to passive jaw-opening (**A**) and facilitative response of masseteric activities to the application of the test strip between the molars on the left side (**B**). The records were obtained before making an electrical lesion of the Mes V in the animal with kainic acid injection. The strip was applied during the period shown by the thick bar. L Mass and R Mass represent the left and right masseter muscles, respectively. L Dig and R Dig represent the left and right digastric muscles, respectively. Other abbreviations are the same as those in Fig. 3

the intermaxillary distance at the power phase, which affects the excitability of the sensory receptors in the mouth and the masticatory muscle as discussed below.

The response of the masseteric muscle to application of the strip was influenced by the pattern of CRJMs. The rate of increase in the masseteric response was greater for the small circular movement (type A) than for the crescent-shaped movement (type C), although the maximum activity was always greater for the latter than for the former. Without application of the strip, type C masseteric burst activities were about 10 times greater than those of type A. There might be less room for the masseteric activities to increase during application of the strip for the former than for the latter. On the other hand, such an increment of masseteric activities was not observed in the large circular movements (type B) because the strip was not firmly occluded between the opposing molars. The findings indicate that masseteric activities increase when jaw-closing movements were obstructed by the material inserted between the molars. Since the rate of the masseteric response was greater for the thick strip than for the thin one, the rate of facilitation is also dependent on the degree of obstruction. Such a mechanism may play an important role in the regulation of masticatory force according to food consistency. The large activities of the jaw-closing muscles are induced when chewing hard food rather than soft food. The present results suggest that such a difference in the muscle activities would be auto-regulated in accordance with the physical properties of the food.

In alert rabbits, the medial excursion of the mandible during the power phase and jaw-closing muscle activities develop with the hardness or toughness of the food as shown in the previous paper (Inoue et al. 1989). These features are similar to those observed for anesthetized rabbits, suggesting that the mechanism regulating masticatory muscle activity during chewing is similar in both animals. This preparation may be a useful model for exploring the sensory control mechanism of masticatory jaw movements under natural conditions.

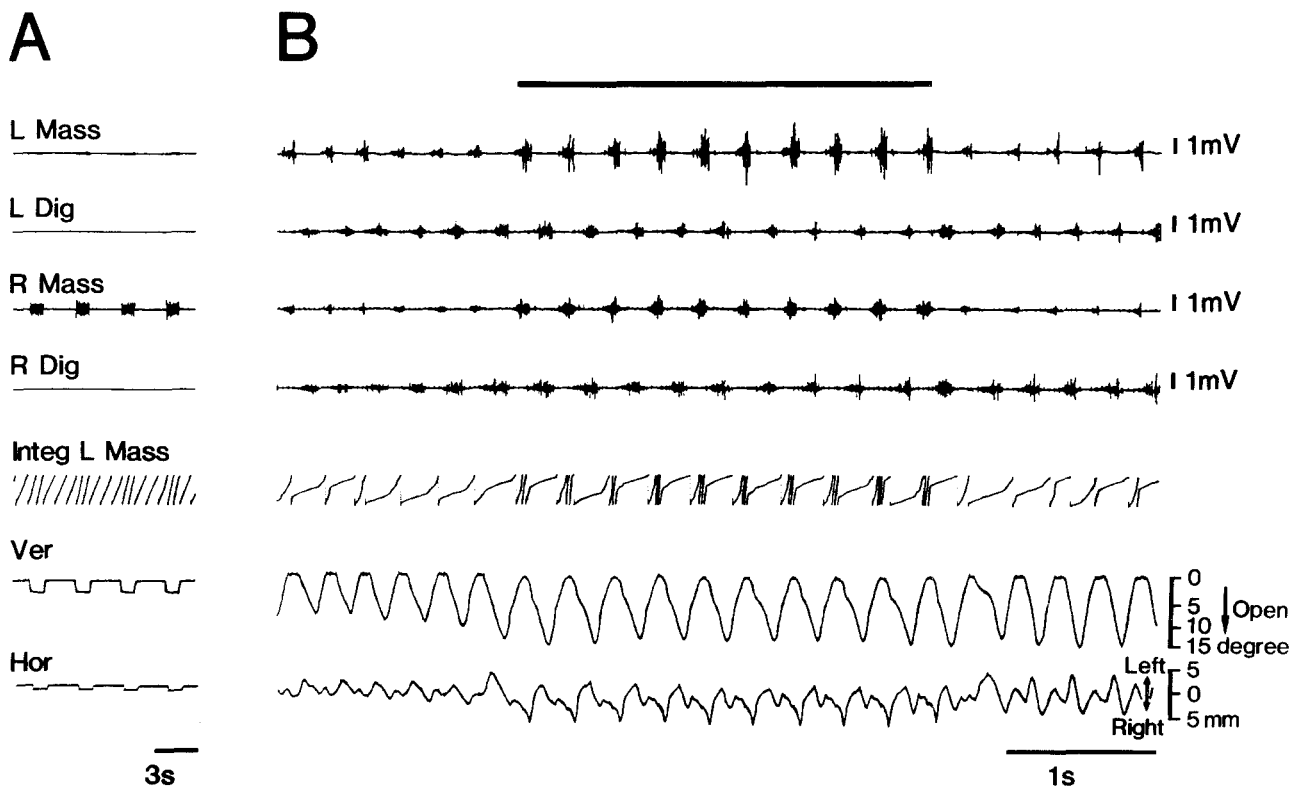

Fig. 8A, B. Stretch reflexes of the masseter muscles (**A**) and the responses of these muscles to application of the strip after the Mes V lesion in the same animal shown in Fig. 7. It is noted that the stretch reflex was greatly reduced but the response to application of the strip was well preserved on the side of the lesion

Receptors responsible for facilitation of masseter muscle activities when chewing a strip

In the present study, an anesthetic block of both the maxillary and inferior alveolar nerves greatly reduced the facilitative effects on jaw-closing muscle activities during application of the test strip. This finding also is in good agreement with that of the Lavigne et al. study (1987) using denervated rabbits. We further observed that the reducing effects on the masseteric activities disappeared with the recovery from local anesthesia, which confirmed that this effect was truly the result of blocking the sensory inputs via the maxillary and inferior alveolar nerves. These two nerves innervate the periodontium of both incisors and molars, gums, other oral mucous membranes, periosteum, facial skin, etc. Accordingly, the effects of the afferent nerve block are not necessarily due to the loss of periodontal sensations. Among the sensory receptors in these tissues, tactile receptors in the oral mucous membrane, tongue, and periosteum and also those at the corner of the mouth are excited during CRJMs (Appenteng et al. 1982a). As described in the experimental methods section, however, the structures where these receptors are located, were incised, removed, or denervated in the present study. Furthermore, the test strip was placed precisely between the molars during CRJMs without touching surrounding tissues. On the other hand, periodontal receptors were preserved following the surgical operation, and they must be stimulated most when chewing the strip. Appenteng et al. (1982b) reported that periodontal afferents were activated at the start of the power phase, which is suitable for augmentation of the subsequent jaw-closing muscle activities. The excitatory influences of periodontal receptors on the jaw-closing muscles are discussed in the next section.

When the Mes V was lesioned in the animal with a combined section of the maxillary and mandibular nerves, the masseter muscle hardly responded to an application of the strip during CRJMs. This observation alone does not indicate the contribution of muscle spindles because not all of the Mes V neurons are ganglion cells of spindle afferents (Jerge 1964) and also because loss of the masseteric response is possibly due to the lesion

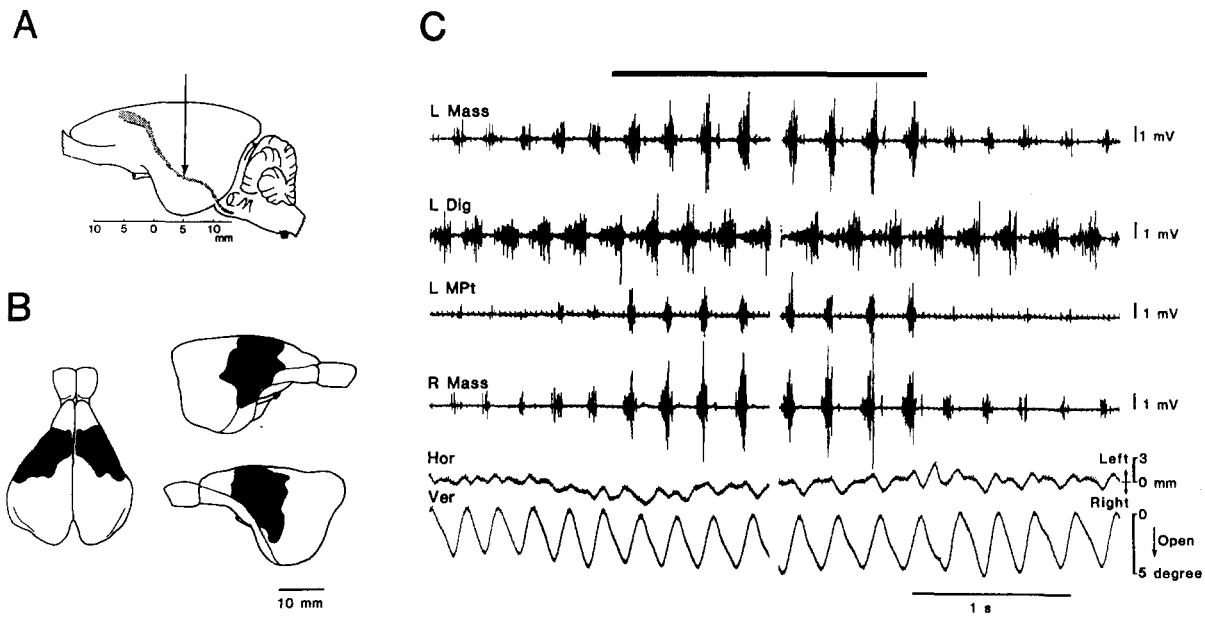

Fig. 9A–C. Facilitative response of the masseter muscle to application of the strip in the animal with ablation of the cortical masticatory area and its surrounding regions. **A** The portion to which repetitive electrical stimuli was applied to induce rhythmic jaw movements. The long arrow indicates the portion of stimulation in the pyramidal tract 5 mm posterior to the bregma. **B** The areas of cortical ablation. **C** Responses of masticatory muscles to application of the test strip between molars. The period of application is shown by a thick bar. Abbreviations are the same as those in Fig. 7

of structures in the vicinity of the Mes V. Although some neurons in the Mes V transmit intraoral mucosal sensations, they may not be responsible for the effects of the Mes V lesion since the structures in which the mucosal receptors lie were removed or denervated as discussed previously. Receptors in the temporomandibular joints may also not be responsible because their ganglion cells are found in the trigeminal semilunar ganglion (Lund and Matthews 1981), while little evidence has been presented to support the presence of ganglion cells in the Mes V. The contribution of Golgi tendon organs is also denied by Lavigne et al. (1987) since this type of receptors exerts inhibitory influences on the homonymous motoneurons, and thus the destruction of the Golgi tendon organs might result in a lack of inhibition of the jaw-closing motoneurons. On the other hand, the large majority of Mes V neurons other than periodontal afferents are ganglion cells of muscle spindle afferents (Passatore et al. 1983). Those neurons distribute longitudinally, making a narrow band along the lateral edge of the central gray. When the Mes V is lesioned electrically or when kainic acid is injected in this nucleus, structures around the nucleus may also be injured. Among the structures, the parabrachial nucleus was affected most by kainic acid injection. In this nucleus, there are relay cells transmitting taste and mechano-sensations from the oral cavity to the thalamic nucleus (Yamamoto et al. 1980; Ogawa et al. 1987), and the destruction of this nucleus produced ageusia (Ables and Benjamin 1960). Neurons in the locus coeruleus also could not escape from the lesion. This nucleus seemed to be concerned with the control of sensory inputs and their transmission to higher centers (Sasa et al. 1977), and stimulation of this nucleus generally inhibited activities of the interneurons in the spinal trigeminal nucleus. The possibility exists that when the above two nuclei were destroyed, sensory inputs from the oral-facial regions would be altered, which affected jaw muscle activities. Among the structures in the vicinity of the Mes V, supratrigeminal neurons were relatively free from the lesion. They responded to mechanical stimuli on the palate, gum, teeth, or tongue (Jerge 1963). They were also driven by passively applying cyclic jaw movements and thus supposed to relay proprioceptive information to the cerebellum or thalamus (Miyazaki and Luschei 1987). In addition, they were found to be interpolated in the trigeminal reflex path which made direct inhibitory synapses in the contralateral masseteric motoneurons (Nakamura et al. 1973) and also in the descending path from the amygdaloid nucleus to the contralateral trigeminal motoneurons (Ohta and Moriyama 1986). When this nucleus is lesioned, the excitabili-

ty of trigeminal motoneurons would be modulated. From histological examinations of the brain stem, however, this nucleus did not seem to be affected seriously even with the large Mes V lesion. Since the neurons of this nucleus exert inhibitory influences on jaw-closing motoneurons (Kidokoro et al. 1968a, b), the destruction of this nucleus may cause disinhibition of these motoneurons. This possibility may not occur because the present results were not in agreement with this assumption. Hence, the supratrigeminal nucleus may not be injured seriously. When the above results are considered together, the effect of the Mes V lesion may be attributed to the loss of spindle inputs, rather than the destruction of neurons in the vicinity of the Mes V. The contribution of muscle spindles is further supported by the finding that the augmentation of masseteric activity was greater in the anterior half than in the posterior half of the masseter muscle. Such a site-dependent change in the facilitative effects seems to agree with the fact that tonic stretch reflex activity of the masseter muscle of the cat was only seen in its deep anterior part (Taylor 1981), where muscle spindles distribute most densely (Lund et al. 1978).

Excitatory influences from periodontal receptors on the jaw-closing muscles

A number of studies have been performed on the effects of tapping or pressing the teeth on the masticatory muscle activities (Funakoshi and Amano 1974; Goldberg 1971, 1972; Lund et al. 1971; Sessle and Greenwood 1976). Most of these studies, however, examined the effect of incisor stimulation, and few reports are available on the effects of molar stimulation. Since food is crushed and ground between opposing molars during chewing, the influences from periodontal receptors from molars must be important for the regulation of masticatory jaw movements and masticatory force. Sessle and Gurza (1982) found that the tactile stimulation of molars as well as incisors and canines produced excitation of the upper and lower heads of the lateral pterygoid muscle in the monkey. As already described, Lavigne et al. (1987) reported that the amplitude and duration of the jaw-closing muscle EMGs increased when a steel ball (2 mm diam) was thrust between the anterior molars. This activation was attributed to the stimulation of the molar periodontal receptors. We were unable to induce reflex activation of the jaw-closing muscles by pressing the upper or lower molars either axially or horizontally. However, this does not necessarily mean that the periodontal-jaw muscle reflexes are not present in the rabbit's molars because the following two possibilities may occur. First, periodontal sensory inputs would be regulated by the centrally operating gate so that they could arrive at jaw-closing motoneurons only during the power phase of a masticatory cycle, and the pressure applied at rest may be ineffective. Excitatory connections from periodontal afferents to jaw-closing motoneurons are presumed. The second possibility is that the periodontal afferents of molars make inhibitory connection with jaw-closing motoneurons. Kidokoro et al. (1968a, b) showed that IPSPs were produced in masseteric motoneurons by the stimulation of low-threshold afferents in the inferior dental nerve via the supratrigeminal neurons. In addition, some supratrigeminal neurons are found to respond to mechanical stimulation on the teeth (Jerge 1963). It is hence possible that pressure stimulation to the teeth produce inhibitory influences on the jaw-closing motoneurons. Furthermore, it is reported that interneurons in the rostral and/or caudal parts of the trigeminal sensory complex which transmit low-threshold sensory inputs from the orofacial areas including periodontium, are mostly depressed throughout the masticatory cycle (Kim et al. 1985; Olsson et al. 1986). Consequently, it may not be excluded that suppression of the trigeminal periodontal interneurons reverses the above inhibitory path during chewing, which in turn enhances the activities of the jaw-closing motoneurons. Further studies are needed to clarify which one of these two possibilities is more likely.

Contribution of muscle spindles of jaw-closing muscles

As already mentioned, muscle spindle afferents may partly be responsible for the facilitation of jaw-closing muscle activities during application of the test strip. Several studies have been carried out on spindle discharges during mastication in awake animals (Taylor and Cody 1970; Cody et al. 1975; Goodwin and Luschei 1975; Matsunami and Kubota 1972; Larson et al. 1983) or during peripherally induced rhythmic movements in anesthetized animals (Appenteng et al. 1980; Taylor et al. 1981). These studies demonstrate that the discharges of primary spindle afferents increase with an increase in the EMG activities of jaw-closing muscles when the teeth contact food and the movements of the mandible slow down (Matsunami and Kubota 1972; Larson et al. 1981; Larson et al. 1983). We obtained similar results on the spindle discharges during CRJMs in the lightly anesthetized rabbit: some spindle afferents fired during the power

phase in addition to the beginning of the jaw-opening phase (unpublished observation). Futhermore, Appenteng et al. (1980) found that one type of the presumed fusimotor fibers, which they called "sustained" type, showed modulation of the firing frequency which was closely related to the jaw movements in the lightly anesthetized cat. The activity of the fusimotor neurons has also been recorded in the trigeminal motor nucleus of the alert monkey and these neurons discharged vigorously before and during contraction of the jaw-closing muscles when chewing food (Lund et al. 1979). The above reports indicate that fusimotor fibers are activated simultaneously with alpha motoneurons during rhyhtmic jaw movements. The question then arises of how effective spindle discharges are in exciting trigeminal motoneurons. Goodwin and Luschei (1975) reported that the lesion of the Mes V tract did not change either the rates or patterns of jaw movement during chewing or the timing of EMG activity in the alert monkey. The only change observed was that the animal preferred to chew on the contralateral side. The findings suggest that the contribution of muscle spindles to the excitation of the jaw-closing motoneurons during chewing is relatively minor. In contrast, the present results showed that loss of the spindle inputs reduced jaw-closing muscle activity when chewing a test strip, which is statistically significant. Goodwin and Luschei (1975) also observed in the monkey with a Mes V lesion that the peak amplitude of activity from the jaw-closing muscles was reduced in the postlesion records. However, this reduction was attributed to a change in the recording conditions between pre- and postlesion periods. In the present study, the recording conditions might not change appreciable since the time interval between the records in these two periods was shorter than 5 h. From the present results, we have concluded that excitation of the trigeminal motoneurons in the power phase is partly attributed to muscle spindle inputs during chewing. When the contraction of the jaw-closing muscles is obstructed by a load such as a tough piece of food, spindle afferent activity which is supported by fusimotor discharges, may increase alpha motoneuron activity through the stretch reflex arc. The excitation of masseter motoneurons may probably be elicited by the activation of the primary endings, rather than the secondary endings because the afferent discharges of the latter do not significantly increase with an increase in the extrafusal fiber activity (Appenteng et al. 1978; Larson 1981).

The present study also demonstrates that the masseteric burst activities tended to increase with an increase in the thickess of the test strip, which was particularly clear for crescent-shaped movements. This phenomenon may partly be accounted for by the "temporal template" theory of Taylor (1981), in which fusimotor drive is postulated to vary as a "temporal template" of the intended movements and the actual movement is compared continuously with this to give an error signal. If this mechanism works during CRJMs, the error signal of the spindles would be greater for a thick strip than for a thin one because the intermaxillary distance at the power phase must be greater for the former than for the latter, which increases jaw-closing muscle activities through the stretch reflex path. In other words, the thicker strip is a greater obstruction to jaw-closure than the thinner one during the power phase. The greater obstruction also activates the jaw-closing muscles via the periodontal positive-feedback loop since periodontal discharge varies in a load-dependent manner (Pfaffmann 1939; Johanson and Olsson 1976).

Minor effects of the Mes V lesion on the masseteric response to application of the test strip may not be attributed to the remaining contralateral innervation of the spindle afferents because recent HPR studies on spindle afferents revealed only ipsilateral distribution of their ganglion cell in the Mes V (Nomura and Mizuno 1985; Shigenaga et al. 1988). Passatore et al. (1979) reported that a single or repetitive stimulation of CMA in the lightly anesthetized rabbit modified the discharge frequency of the Mes V neurons. Accordingly, the possibility exists that the effects of the Mes V lesion are partly due to the loss of direct cortical influence on the Mes V neurons.

Transcortical reflex for the control of jaw muscle activation

Transcortical proprioceptive reflexes of the limb transmitted via the pyramidal tract neurons have properties similar to segmental proprioceptive reflexes, i.e., changes of muscle length elicit discharges of pyramidal tract neurons which oppose the changes in length and maintain stability (Conrad and Meyer-Lohmann 1980; Evarts and Fromm 1981). The projection of low-threshold muscle afferents from the masticatory muscle to the cerebral cortex has been reported in the cat and the monkey (Lund and Sessle 1974; Sirisko and Sessle 1983), and the possible transcortical response has been presented for the masticatory muscles (Marsden et al. 1976). Although decisive evidence is still lacking to show that muscle afferent inputs can drive the pyramidal tract neurons of the jaw motor area

or the CMA as has been proved on limb muscle afferents (Conrad et al. 1974; Tanji and Wise 1981), the biting force or masticatory force were reduced after decortication in rats and monkeys (Larson et al. 1980; Luschei and Goodwin 1975; Whishaw et al. 1981). In the face motor area of the monkey, a clear relationship was found between the rate of maintained discharges of cortical units and the force output of jaw-closing muscles for 25% of the activated cells during the isometric contraction task (Hoffman and Luschei 1980). These results suggest that some precentral neurons assist in regulating the tension output of jaw-closing muscles. In contrast, we found that after the CMA ablation, masseteric burst activities were still enhanced by insertion of a strip between the molars during the rhythmic jaw movements evoked by stimulation of the pyramidal tract. This result, however, does not deny the cortical regulation of masticatory force, but only shows that there may be other neuronal regulation mechanisms than those including the CMA. It is probable the masticatory force is regulated both via the transcortical loop and via the central pattern generator in the brainstem (Thexton et al. 1980, 1982), in response to food consistency.

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