Regulation of Masticatory Force During Cortically Induced Rhythmic Jaw Movements in the Anesthetized Rabbit

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Hidaka, O., T. Morimoto, Y. Masuda, T. Kato, R. Matsuo, T. Inoue, M. Kobayashi, and K. Takada. Regulation of masticatory force during cortically induced rhythmic jaw movements in the anesthetized rabbit. J. Neurophysiol. 77: 3168–3179, 1997. To examine the relationships between masticatory force, electromyogram (EMG) of masticatory muscles, and jaw movement pattern, we quantitatively evaluated the effects of changing hardness of a chewing substance on these three variables. Cortically induced rhythmic jaw movements of a crescent-shaped pattern were induced by electrical stimulation of the cerebral cortical masticatory area in the anesthetized rabbit. The axially directed masticatory force was recorded with a small force-displacement transducer mounted on the ground surface of the lower molars. EMGs were recorded from the masseter and digastric muscles simultaneously with jaw movements. Five test strips of polyurethane foam of different hardness were prepared and inserted between the upper molar and the transducer during the movements. The peak, impulse, and buildup speed of the masticatory force increased with strip hardness, whereas duration of the exerted force did not vary with strip hardness. The integrated activity and duration of the masseteric EMG bursts also increased with strip hardness. The integrated EMG activity of the digastic bursts was weakly related to strip hardness, whereas the duration was not. The minimum gape increased with strip hardness, but the maximum gape did not. The horizontal excursion of the jaw did not vary in a hardness-dependent manner, although it was greater in the cycles with strip application than in the cycles without strip application. Deprivation of periodontal sensation by cutting the nerves to the teeth reduced the buildup speed of the force, maximum gape, net gape, and horizontal jaw movements. The denervation also elongated the masticatory force duration and that of masseteric EMG bursts. However, the rate of the hardness-dependent changes in the above parameters did not alter after denervation. The latency of the masseteric EMG response to strip application was evaluated before and after denervation. In both conditions, it was ≥6 ms in ~70% of the cycles and <6 ms in the remaining ~30%, which cannot be explained by a simple reflex mechanism. On the basis of the analysis of correlation coefficients, the masseteric integrated EMG seemed to be a good indicator of the peak and impulse of the masticatory force both before and after denervation. We conclude that periodontal afferents would be responsible for a quick buildup of masticatory force and that afferents other than those from periodontal tissue would contribute to the hardness-dependent change of masticatory force during cortically induced rhythmic jaw movements.

INTRODUCTION

Electromyographic (EMG) activity of the masticatory muscles and masticatory jaw movements are influenced by orofacial sensations arising during the chewing of foods of various properties (Thexton et al. 1980). It has been reported that in various animals including humans, EMGs of the jaw-closing muscles are greater when hard food is chewed than when soft food is chewed, although the relationship between muscle activity and food properties was not quantitatively evaluated in most of these reports (Horio and Kawamura 1989; Inoue et al. 1989; Luschei and Goodwin 1974; Plesh et al. 1986; Takada et al. 1994; Weijs and Dantuma 1981; Weijs and de Jongh 1977; Yamada and Haraguchi 1995). In anesthetized rabbits, the masseteric EMG activity was facilitated when a small steel ball or a thin polyurethane foam strip was placed between the opposing molars during cortically induced rhythmic jaw movements (CRJMs) (Lavigne et al. 1987; Morimoto et al. 1989). Furthermore, this facilitatory response was enhanced with an increase in hardness of the test strips, i.e., the harder the strip, the larger the masseteric activity (Liu et al. 1993). These findings suggest that the masticatory force is regulated automatically according to the hardness of food if the masseteric EMG activity is a good indicator of masticatory force. However, because the EMG activity is affected by various factors such as recording sites, degree of jaw opening (Lindauer et al. 1993; MacKenna and Turker 1983; Manns et al. 1979), and fatigue (Kawazoe et al. 1981; Maton et al. 1992), it is not known whether the EMG activity is always a reliable indicator of the force exerted between the teeth. Recording masticatory force is thus needed to know how muscles control masticatory force. More importantly, this would provide information on development of masticatory force in a masticatory cycle and on the temporal relationship between EMG activity and force. In the present study, the loading force during CRJMs was recorded with a force-displacement transducer that has been recently developed (Ogata et al. 1993). Then we quantitatively evaluated the effects of the hardness of a chewing substance on masticatory force, EMG activity of the masticatory muscles, and jaw movement pattern and examined the relationships between these three variables.

It has been previously reported that after section of the maxillary and inferior alveolar nerves, the masseteric bursts are reduced in conscious rabbits during chewing of food and in anesthetized rabbits during chewing of a test substance (Inoue et al. 1989; Lavigne et al. 1987). This reduction was ascribed mainly to the loss of periodontal sensation. However, the response to the test strips was not completely abolished by the denervation in the anesthetized animals (Morimoto et al. 1989). When muscle spindle afferents of the jaw-closing muscles were additionally blocked by le-
sioning the mesencephalic trigeminal nucleus, the remaining facilitatory response of the masseteric EMG bursts was nearly eliminated (Morimoto et al. 1989). Thus muscle spindles from the jaw-closing muscles as well as the periodontal receptors are likely involved in the regulation of the jaw-closing muscle activities during chewing. Because these two kinds of sensory receptors have different physiological properties, they may contribute to the force regulation in a different manner, in which the periodontal receptors transmit information on magnitude and direction of the load applied to the tooth (Appenteng et al. 1982), whereas the muscle spindles in the jaw-closing muscles are sensitive to the change in the intermaxillary distance (Inoue et al. 1981; Morimoto et al. 1995a). The periodontal receptors may excite the masseter muscle via the periodontal-masseteric reflex path (Funakoshi and Amano 1974; Lund et al. 1971; Yamamura and Shimada 1992), and the muscle spindles via the jaw-stretch reflex path (Chandler et al. 1985; Nakamura et al. 1976). The second purpose of this study is to clarify the different roles in the regulation of masticatory force between periodontal receptors and muscle spindles. For this purpose, cutting the nerves to the teeth, we quantitatively evaluated the response to variations in the hardness of a chewing substance.

Various patterns of CRJMs were induced depending on the site of stimulation in the right cerebral cortical masticatory area (CMA), as was reported previously (Bremer 1923; Lavigne et al. 1987; Liu et al. 1993; Lund et al. 1984; Morimoto et al. 1989). Only crescent-shaped jaw movements were employed here because they resemble normal molar chewing movements (Liu et al. 1993; Morimoto et al. 1985).

**Methods**

The surgical procedures were mostly identical to those described previously (Liu et al. 1993) and were reviewed and approved by the Osaka University Faculty of Dentistry Intramural Animal Care and Use Committee. Eight male rabbits weighing 2.5–3.5 kg were used. The animals were anesthetized by ketamine (16 mg/kg, Ketalar 10, Sankyo) and thiamyld sodium (20 mg/kg) injected via an auricular vein. After tracheal cannulation, anesthesia was maintained during surgery by a mixture of halothane and oxygen at such a level that neither apparent corneal reflex nor spontaneous eye movements were present. Small screws were attached to the mentum to hold a photodiode for tracing jaw movements by means of an optoelectronic recording apparatus (C2399, Hamamat Photonics, Hamamat, Japan). The head of the animal was fixed to a stereotactic apparatus by means of three skull screws in such a position that the lambda was 1.5 mm below the bregma (Sawyer et al. 1954). For the electrical stimulation of the CMA, the cortical surface was exposed between 1 and 7 mm anterior to the bregma and medially between 3 mm lateral to the midline and the lateral edge of the cranium. The rectal temperature was maintained between 36 and 38°C with a heating pad. An electrocardiogram was continuously monitored. Pairs of Teflon-coated stainless steel wires were inserted unilaterally to record EMG activities from the masseter and digastric muscles on the side opposite to the cortical stimulation. Masseteric activity was recorded from the deep anterior part of the muscle throughout the experiment on the basis of the results of our previous study (Morimoto et al. 1989).

**Masticatory force recording**

The axially directed masticatory force was measured with a small S-shaped transducer (length 8.5 mm, width 4 mm, height 4.1 mm) (Fig. 1A). The tolerance limit of the transducer, made of high-speed steel, was 100 N. The performance of this type of transducer and the recording methods are described elsewhere (Ogata et al. 1993). To fix the transducer at the lower molar region, the facial skin was excised from the corner of the mouth to the molar region. After the crowns of the lower first and second molars were ground, the transducer was fixed to the ground surface with self-curing resin so that the upper surface of the transducer aligned with the occlusal surface of the remaining molars (Fig. 1B). All wound margins were anesthetized by small injections of xylocaine hydrochloride.

**Cortical stimulation**

Glass-coated metal electrodes with an impedance of 1–2 MΩ at 1 kHz were used for the intracortical microstimulation. The reference electrode was placed on the cranium at the bregma. Square pulses (30 Hz, duration 0.2 ms, 80 μA) were used for evoking CRJMs. Because various types of CRJMs are induced by CMA stimulation, cortical stimulation sites were selected to induce a certain type of movement with reference to the distribution map of the rabbit CMA presented by Liu et al. (1993).

**Intraoral stimulation**

A thin strip of polyurethane foam held by an experimenter with the use of forceps was placed during CRJMs between the upper first molar and the upper surface of the transducer mounted on the lower molars. Five test strips of the same size (2 mm thick, 5 mm wide, 15 mm long) but of different hardness (Hs: 27, 47, 67, 84, and 91; Japanese Industrial Standard, K 6301) were prepared. They were numbered from 1 to 5 in increasing order of hardness (1 = least hard, 5 = hardest).

**Section of trigeminal sensory branches**

The maxillary nerve was exposed at the bottom of the orbit after incision of the skin along the upper border of the zygomatic arch, and then cut close to the foramen rotundum. The inferior alveolar nerve was exposed in the mandibular canal after grinding of the overlying bone and then cut close to the foramen mandibulare. By this procedure, intraoral sensations except those in the tongue and posterior part of the palate were blocked.

**Data analysis**

The jaw movements, EMG activity, and masticatory force were simultaneously recorded on an eight-channel digital audio tape data recorder (PC-208 M, Sony-Magnescale, Tokyo, Japan). The data were replayed on paper with a recorder (Rectocorder, Nihon-denki Sanei). Selected data were digitized at 2 kHz and fed into a personal computer (Macintosh Quadra 800, Apple). The data were analyzed by the use of Super Scope II (GW Instruments) and WinJ 1.2f (Informix Software). EMG data were software rectified and smoothed by a nine-point moving average. The moving average was also performed on the data concerning jaw movements and masticatory force. Then, the sampling rate of all data was halved from 2 to 1 kHz to reduce the data volume.

CRJMs before and after strip application were designated as control cycles and experimental cycles, respectively. The following three variables were analyzed.

1) Jaw movement: minimum gape (or intermaxillary distance), maximum gape, net gape (i.e., difference between the maximum and minimum gaps), and horizontal jaw movements were analyzed. The interval between two consecutive maximum jaw openings was determined as a total cycle length (TCL). The rhythm of the jaw movement cycles was represented as TCL.
2) Masticatory force: The peak force, impulse (\( \int F \text{dt} \)), duration, and build-up speed of force (Fig. 1C) were analyzed. The beginning and end of the force change were determined automatically by the use of the computer. The points of maximum jaw opening were first identified. The mean and SD of the baseline masticatory force during 1/10 of the TCL from the maximum jaw opening were calculated. Force onset was identified when the force level exceeded the mean level by 2 SD.

3) EMG: the integrated EMG activity (IEMG) and burst duration were analyzed. The beginning and end of EMG bursts were also determined automatically. For the masseteric EMG, the mean and SD of the digitized EMG data during 1/10 of the TCL immediately before the point of maximum opening were first calculated. For the diaphragmatic EMG, those of the digitized EMG data during 1/10 of the TCL from the onset of the power phase were calculated. The bursts were identified when the muscle activity exceeded individual mean levels by 3 SD.

Furthermore, after smoothing the rectified EMG data with a low-pass finite impulse response filter at a cutoff frequency of 50 Hz, we evaluated 1) the temporal relations of EMG and masticatory force to a jaw movement cycle and 2) the latency of the masseteric EMG response to strip application. The latter was measured as the time between the tooth contact with a strip (the onset of the force) and the change in the EMG activity between control and experimental cycles. For this purpose, five control and five experimental cycles in a trial were averaged, respectively, triggered at the maximal jaw opening. The SD of the waveforms from the control cycles was then calculated. To take account of the fluctuation of EMG among control cycles, a threshold for a difference between the averaged EMG waveforms from control and experimental cycles was defined as twice the largest SD calculated for the control waveforms between the trigger point and the point that corresponded to 10 ms after the force onset in the experimental cycles. The moment when the averaged waveform of the experimental cycles first exceeded that of the control cycles by the threshold was taken as the onset of an EMG response to strip application. A total of 40 trials was performed in the eight animals.

**Statistical analysis**

In multiple groups classified by two factors (the hardness of the test strips, and before and after denervation), a null hypothesis that each variable had a normal distribution was initially tested by a \( \chi^2 \) test. Then, a null hypothesis that the variance had homogeneity was tested by the Bartlett test or the \( F \)-test. If the two null hypotheses were accepted, the difference between groups and interaction between the two factors were tested by two-way analysis of variance for repeated measures of two factors. When the difference among groups classified by the hardness of the test strips was recognized as significant and no significant interaction was found between the two factors, the difference was further tested by the Fisher’s protected least significant difference (multiple comparisons). Similarly, when the difference between groups before and after denervation was recognized as significant and no significant interaction was found between the two factors, we considered that the effect of denervation was significant.

When either or none of the above two null hypotheses were accepted, the difference was tested by the Friedman test or the Wilcoxon signed-rank test according to the number of the groups compared. Pearson’s correlation coefficient was calculated between the masseteric IEMG and peak force and between the IEMG and \( \int F \text{dt} \). Regression lines were drawn by the method of least squares, and the slopes before and after denervation were compared by analysis of covariance.

The level of \( P < 0.05 \) was assumed as significant.

**RESULTS**

Crescent-shaped jaw movements were composed of three phases: jaw-opening, jaw-closing, and power phases (Fig. 2, bottom left). The jaw-opening phase is the phase from the most closed position to the most opened position, the jaw-closing phase is the most opened position to the lateralmost position, and the power phase is the phase between the above two phases. We observed that the jaw-opening phase could often be divided into two subphases; the first phase, accompanied by a slight horizontal shift toward the midline, and the second phase, more or less straight. The crescent-shaped jaw movements were also evoked when the same cortical sites were stimulated after denervation.

An example of the effects of strip application before denervation is shown in Fig. 2. A small force was recorded during control cycles, indicating that the transducer was in contact with the upper molars at the power phase (Fig. 2A).
In experimental cycles, the force increased simultaneously with an increase in the masseteric EMG activity and its duration (Fig. 2B). The effects on the digastric EMG bursts were relatively minor. Jaw movement patterns in the frontal plane before, during, and after strip application are shown in Fig. 2, bottom. Dotted lines indicate the uppermost position where the transducer contacts with the upper molars. During strip application, the jaw did not reach this line because of the intercalated strip. Although the minimum gape increased with strip application, the maximum gapes did not change remarkably. After the strip was removed, the above changes in the force, EMG bursts, and jaw movements disappeared immediately (Fig. 2C).

Changes in masticatory force, EMG activity, and jaw movement pattern according to strip hardness

Figure 3A presents the effects of chewing strips of various hardness on the masticatory force, EMG activity, and jaw movements recorded in an animal before denervation. The left record is the control cycle, and the other records are the experimental cycles arranged in increasing order of strip hardness. The masticatory force increased in proportion to the hardness, reaching >80 N when the hardest strip (No. 5) was applied. The masseteric EMGs also increased in a hardness-dependent manner, whereas the digastraic EMGs did not change appreciably. A characteristic change in the jaw movement traces was an increase in the minimum gape with the increase in strip hardness. In contrast, both the maximum gape and the horizontal excursion were not greatly affected by the change in strip hardness. An example observed after denervation in the same animal is shown in Fig. 3B.

The data obtained from eight animals (mean ± SD) are shown in Figs. 4–6, and the results of statistical analyses of the parameters are summarized in Table 1.

The effects of changing strip hardness on the four parameters of masticatory force were statistically analyzed. The peak force increased significantly according to the increase in strip hardness both before and after denervation (P < 0.001) (Fig. 4A). Irrespective of denervation, there is no significant difference between the slopes of regression lines relating hardness to the parameter (Table 1). The multiple comparison test demonstrated that the differences in the peak force made by the change in strip hardness were significant between all pairs. After denervation, marginal significance was detected in the decrease in peak force values (on average 6 N, P = 0.07). In contrast, the duration of the force was not significantly affected by the change in strip hardness either before or after denervation (Fig. 4B). \( \int F dt \) also increased significantly with the increase in strip hardness both before and after denervation (P < 0.001) (Fig. 4C). This effect is mainly ascribed to the hardness-dependent increase of peak force. The buildup speed of force was slowed down after denervation (P < 0.001). This effect resulted mainly from the elongation of the force duration (Fig. 4B) and partly from the reduction of the peak force. The buildup speed of force significantly increased according to strip hardness (P < 0.001) (Fig. 4D). The multiple comparison test showed that the differences were significant between all pairs (P < 0.05) except the pairs of Nos. 1 and 2, Nos. 2 and 3, and also Nos. 4 and 5.

The relationship between strip hardness and IEMG of the masseteric bursts is shown in Fig. 5A. The ordinate indicates the difference in the values between the control and experimental cycles, represented as the percentage of the control value (IEMG of the control cycle). The mean increment was ~80% for the hardest strip (No. 5) and ~30% for the softest strip (No. 1). The masseteric IEMG increased significantly in a hardness-dependent manner (P < 0.001). The duration of the masseteric EMG bursts also changed significantly with the increase of strip hardness (Fig. 5B). The mean duration before and after denervation, which elongated significantly after denervation.
FIG. 3. Modification of masticatory force, EMG activities, and jaw movements according to strip hardness. A: before denervation. B: after denervation. A and B, leftmost records: data of control cycles (without strip). No. 1—No. 5: hardness of test strips (No. 1, least hard; No. 5, hardest). Note that both masticatory force and masseteric EMGs increased with increase in strip hardness.

(\(P < 0.05\)), ranged between \(-130\) and \(150\) ms and between \(-140\) and \(170\) ms, respectively. The multiple comparison test indicated that there was a significant difference in the duration between control and experimental cycles. The digastric IEMG also increased significantly with the increase of strip hardness (\(P < 0.05\)), but the effect seemed to be relatively minor (Fig. 5C). The mean duration of the digastric EMG bursts ranged between \(-145\) and \(160\) ms, but did not vary significantly with strip hardness (Fig. 5D).

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<th>TABLE 1. Summarized results of statistical analysis of the masticatory force, EMG activity, and jaw movements</th>
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Numerals in the columns indicate the strip hardness number inducing significant difference after denervation. Slope of the regression line: relationship between strip hardness and each parameter. The slopes of the regression lines were calculated on the variables for which significant differences were recognized among groups classified by strip hardness. Before vs. After: difference between 2 regression groups. When there was no significant interaction between 2 factors (the strip hardness and before and after denervation) as a result of a 2-way ANOVA, the data obtained both before and after denervation were treated as a group. For further explanation, see Statistical analysis in the text. EMG, electromyogram; 2ANOVA, 2-way analysis of variance; ns, not significant; TCL, total cycle length. * \(P < 0.001\). † \(P < 0.05\). ‡ \(P < 0.01\).
The effects of varying strip hardness on the four parameters of jaw movement are shown in Fig. 6. The minimum gape increased significantly with the increase of strip hardness (Fig. 6A), whereas the maximum gape did not (Fig. 6B). The net gape thus decreased significantly ($P < 0.001$; Fig. 6C). The horizontal excursion at the power phase was exaggerated by strip application, but it did not vary significantly with strip hardness (Fig. 6D). The maximum gape, net gape, and horizontal excursion were reduced significantly by the denervation (Table 1). The cycle time (TCL) was $\sim 330$ ms ($\sim 3$ Hz), which was not significantly affected by strip hardness.
Pattern of masticatory force in a jaw movement cycle

The force was produced by a tooth-strip-transducer contact in experimental cycles, whereas it was produced by a tooth-transducer contact in control cycles. The periods of force exertion are shown by the thick lines on the jaw movement traces in Fig. 7. After denervation, although the jaw movements of the experimental cycles decreased both in the vertical and horizontal directions, the phase relation of the force to a jaw movement cycle was similar to that observed before denervation. In experimental cycles, the force appeared just before the start of the power phase and disappeared at approximately the start of the second opening phase. The mean force duration before denervation was \( \sim 210 \text{ ms} \) (\( \sim 65\% \) of the TCL) irrespective of strip hardness. In control cycles, the force appeared after the start of the power phase and disappeared just before the end of the first jaw-opening phase, in which the mean duration of the force exertion was \( \sim 135 \text{ ms} \), occupying 42\% of the TCL. As indicated by the filled triangles on the jaw movement traces before denervation. In experimental cycles, the force appeared just before the start of the power phase and disappeared at approximately the start of the second opening phase. The mean force duration before denervation was \( \sim 210 \text{ ms} \) (\( \sim 65\% \) of the TCL) irrespective of strip hardness. In control cycles, the force appeared after the start of the power phase and disappeared just before the end of the first jaw-opening phase, in which the mean duration of the force exertion was \( \sim 135 \text{ ms} \), occupying 42\% of the TCL. As indicated by the filled triangles on the jaw movement traces...
The latency of the EMG response to strip application was measured in 40 trials. In Fig. 9, A and B, two examples are shown, in which waveforms, aligned at maximum jaw opening and averaged, from the control and experimental cycles are superposed. The thick and thin lines represent the experimental and control cycles, respectively. The solid and dotted vertical lines indicate the force onset in experimental cycles and the onset of the difference between the EMG signals, respectively. Figure 9, C and D, are the same records as A and B, respectively, but with expanded scale. In the case shown in Fig. 9, A and C, the solid line preceded the dotted line by 13 ms. This result indicated that the latency of the EMG response to strip application was longer than the shortest latency for the jaw-stretch reflex, determined to be 6 ms in our preliminary study. In contrast, the dotted line preceded the solid line by 2 ms in the case shown in Fig. 9, B and D, implying that the latency of the EMG response was shorter than the shortest latency of the jaw-stretch reflex. In this case, therefore, the response would have been induced by a reflex that produce response beyond a chewing cycle. The latency was >6 ms in 29 of 40 trials but shorter in the remaining 11 trials before denervation, in which the mean latency was 20 ± 17 ms. After denervation, the latency was >6 ms in 28 of 40 trials, but was shorter in the remaining 12 trials. These ratios are almost the same as those obtained before denervation. The mean latency was 26 ± 29 ms, which is not significantly different from that obtained before denervation.

TABLE 2. Correlation coefficients* between Ma-IEMG and peak force and between Ma-IEMG and impulse

| Animal | Ma-IEMG vs. Peak Force | | Ma-IEMG vs. Impulse | |
|--------|------------------------|------------------------|------------------------|
|        | Before denervation | After denervation | Before denervation | After denervation |
| 1      | 0.52 | 0.89 | 0.55 | 0.88 |
| 2      | 0.66 | 0.64 | 0.75 | 0.69 |
| 3      | 0.80 | 0.85 | 0.79 | 0.85 |
| 4      | 0.70 | 0.84 | 0.81 | 0.87 |
| 5      | 0.78 | 0.63 | 0.85 | 0.68 |
| 6      | 0.55 | 0.66 | 0.71 | 0.71 |
| 7      | 0.62 | 0.68 | 0.68 | 0.74 |
| 8      | 0.55 | 0.62 | 0.81 | 0.76 |

Ma-IEMG, integrated activity of the masseteric EMG bursts.
* Pearson’s correlation coefficients.

**DISCUSSION**

**Masticatory force recording**

The present study may be the first to record masticatory force directly in the mouths of animals other than humans, although only the vertical force was measured. Several methods have been developed for recording masticatory force in humans (Ahlgren and Owall 1970; Anderson 1953, 1956; Atkinson and Shepherd 1967; Graf et al. 1974; Lundgren and Laurell 1986; McCall et al. 1978), but they are difficult to apply to small animals like rabbits. As an indicator for the estimation of masticatory force, mandibular bone strain has been recorded in some mammals (e.g., dog: Kakudo...
and Amano 1970; rabbit: Weijs and Dantuma 1981; Weijs and de Jongh 1977; macaque: Hylander 1986; Hylander et al. 1987). Mounting a three-element rosette strain gauge to the lateral surface of the mandibular alveolar bone in conscious rabbits, Weijs and de Jongh (1977) measured the bone strain during the feeding of a pellet, a carrot, and hay. They found that the strain reached its maximum at nearly the most closed position of the mandible during the power phase of a masticatory cycle (their Fig. 3) and that the duration of the strain occupied 50–55% of the TCL. These results are well in accord with the present findings. The direction of the peak compressive strain was ~33° from the occlusal plane, indicating the masticatory force directed more backward and downward than the tooth axis. Weijs and Dantuma (1981) estimated the forces exerted by simultaneous contractions of a number of muscles and showed that the vertical forces are larger than the horizontal ones. Accordingly, it is probable that the axial force represents a dominant part of the exerted force during chewing in the rabbit, even if it does not represent the whole masticatory force.

**Hardness-dependent change in masticatory force**

The peak and $\int F \, dt$ of the masticatory force measured at the anterior molar region changed in proportion to strip hardness. In the study by Weijs and de Jongh (1977), the compressive strain during the feeding of pellets and hay was about double that recorded during the feeding of carrots. In a human study, Anderson (1956) reported that the load on the tooth during chewing was greater for biscuit or raw carrot than for cooked meat. Similar findings have been reported on subjects with normal dentition (DeBoever et al. 1978; Gibbs et al. 1981) and on complete denture wearers (Michael et al. 1990). The masticatory force is thus greater for hard or tough foods than for soft foods in both humans and rabbits. In the above studies, however, the relationship between food consistency and masticatory force was estimated only qualitatively; the consistency of the test foods was not quantitatively analyzed. With the use of quantitatively evaluated test substances, the present study proves that the masticatory force is basically regulated in proportion to the hardness of chewing substances. In contrast, force duration was insensitive to the change in strip hardness. The buildup speed of force, obtained by dividing the peak amplitude by the duration, thus changed in a hardness-dependent manner, i.e., the harder the strip, the faster the buildup speed of force. This finding also accords with the results of bone strain measurement during chewing in the conscious rabbit (Weijs and Dantuma 1981). Furthermore, the present results suggest that the magnitude of the force is more susceptible to the consistency of the chewing substance than is the time factor (i.e., the duration) of the force.

**Hardness-dependent change in EMGs of masticatory muscles**

It has been reported in various animals including humans that EMG activity of the jaw-closing muscles is greater when hard food is chewed than when soft food is chewed (Horio and Kawamura 1989; Inoue et al. 1989; Luschei and Goodwin 1974; Plesh et al. 1986; Takada et al. 1994; Weijs and Dantuma 1981; Weijs and de Jongh 1977; Yamada and Haraguchi 1995). In most of these reports, however, the relationship between muscle activity and food properties was not quantitatively evaluated.

Previous studies in which anesthetized rabbits were used showed that masseteric EMG bursts were facilitated during...
the jaw-closing and power phases when a test substance was applied between the upper and lower molars during CRJMs (Lavigne et al. 1987; Morimoto et al. 1989). This facilitation was enhanced when strip hardness was increased (Liu et al. 1993). The present study confirms this finding and further reveals a linear relationship between strip hardness and the degree of change in masseteric IEMG. The IEMG increased by ~80% of the control value when the hardest strip (No. 5) was chewed, which is comparable with the results of Lavigne et al. (1987) but is relatively small in comparison with our previous results (Morimoto et al. 1989). This is because the facilitative response of the masseteric IEMG to strip application varies with the type of CRJMs, i.e., the CRJMs with high masseteric activity in the control cycles, which have been used in this study, show smaller facilitative responses in the experimental cycles than those with low masseteric activity (Liu et al. 1993; Morimoto et al. 1989).

This is also most likely an explanation for a different effect of denervation on the masseteric IEMG between this study and our previous study (Morimoto et al. 1989): in the previous study the masseteric IEMG decreased after denervation.

**Temporal relationship between EMG activity and masticatory force**

The peak of the masseteric EMG activity preceded that of the masticatory force by 31 ms in the experimental cycles before denervation. This interval is shorter than those measured in humans: 41 ms (Ahlgren and Owall 1970), 43 ms (Gibbs et al. 1981), and 73 ms (Hannam et al. 1975), but larger than that of monkeys: 22 ms (Hylander and Johnson 1989). The species differences in the interval may be partly related to the difference in the nature of muscle fibers and partly to the difference in the force recording method. The jaw-closing muscles can contract faster during chewing in the monkey than in the rabbit or human (Rowlerson 1990).

In the present study, the force attained its peak approximately when the jaw reached the minimum gape, which was ~100 ms after the onset of the force. A similar finding was reported in conscious rabbits (Weijs and de Jongh 1977). Because the peak of jaw-closing muscle activity preceded that of the masticatory force by ~30 ms as described above, control of the masseter muscle activity according to food properties is thus completed within <70 ms after the onset of the masticatory force.

In the experimental cycles before denervation, the force onset preceded the onset of masseter EMG response to strip application by 20 ± 17 ms. This result is well in accord with the finding reported by Lavigne et al. (1987) that the jaw-closing EMGs began to increase by ~12 ms after the teeth contacted a steel ball. In about one-third of the trials in the present study, however, the interval was shorter than the shortest latency for the jaw-stretch reflex (6 ms), and sometimes earlier than the force onset. These findings indicate that the masseteric EMG response precedes the moment, at which a strip contacts the transducer. Similar findings are reported in human studies (Ottenhoff et al. 1992a,b, 1993; van der Bilt et al. 1995), in which a small component of the additional muscle activity was induced to overcome the resistance at a short latency when an external force simulating food resistance was introduced while subjects were making rhythmic open-close jaw movements. The present study further showed that a similar masseteric response was produced even after section of the maxillary and inferior alveolar nerves. Thus periodontal sensation may not be essential for producing this response. Further studies are needed to elucidate the neuronal mechanisms of the reflex components in the load compensation during chewing.

**Hardness-dependent changes in jaw movement**

The minimum gape changed with strip hardness; the harder the strip, the wider the minimum gape. Such a hardness-dependent change in the minimum gape may be closely related to the change in masticatory force, as will be discussed below. The maximum gape did not vary significantly with strip hardness. This may be because the digastric activity did not change markedly with strip hardness. As a result of these effects on the minimum and maximum gapes, the net gape decreased significantly according to strip hardness.

The horizontal excursion at the power phase was exaggerated by strip application but decreased after denervation in both control and experimental cycles. This result agrees with the finding of Lund et al. (1971) that the tooth press produced lateral deviation of the mandible simultaneously with activation of the masseter, anterior temporal, and lateral pterygoid muscles in the rabbit. Sessle and Gurza (1982) found that tooth stimulation produced excitation of the upper and lower heads of the lateral pterygoid muscle in the monkey. The decrease in the horizontal excursions after denervation may be explained by the loss of excitatory periodontal inputs to the lateral pterygoid muscles.

**Different functions of intraoral and extraoral sensory receptors in the regulation of masticatory force during chewing**

After denervation of the maxillary and inferior alveolar nerves, the masticatory force was found to build up more slowly. This finding may well be accounted for by the loss of periodontal sensation. The threshold force required to elicit a response from periodontal mechanoreceptors was reported in conscious rabbits (Appenteng et al. 1982; Linden 1990). Recording single periodontal afferents in the inferior alveolar nerve of humans has revealed that most of the afferents showed the highest sensitivity to changes in static force at very low load (<1 N) and the sensitivity gradually decreased at higher forces, whereas a few receptor afferents increased the response linearly with an increment of the load >1 N (Trulsson and Johansson 1995). Similar responses of periodontal afferents are also reported in other animals (Hannam 1969). The low-threshold periodontal receptors are excited immediately when the teeth touch a chewing substance, and most of the molar periodontal receptors in the rabbit are fast adaptive (Appenteng et al. 1982). These properties of periodontal afferents could contribute to a quick buildup of the masticatory force in the beginning of tooth loading, probably via the periodontal-masseteric reflex path (Funakoshi and Amano 1974; Lund et al. 1971; Sessle and Greenwood 1976; Yamamura and Shimada 1992). On the other hand, periodontal afferents may not have much effect
on the peak force during chewing because of their properties described above.

Trulsson and Johansson (1995) have suggested that the periodontal afferent signals are used to control jaw movements, particularly when subjects contact, manipulate, and hold food before jaw power actions. This study focuses on a role of periodontal afferent on jaw power actions by the use of CRJMs of crescent-shaped pattern. In our previous study with conscious rabbits, the masseteric IEMG during chewing of pellets decreased after deprivation of periodontal afferents, which is different from the result in the present study, but 2 wk after the denervation no significant difference was detected in the IEMG (Inoue et al. 1989). In that case, the periodontal afferents would have also been involved in food manipulation to be needed before jaw power actions, which may explain the disparity between the two results.

The present study also shows that masticatory force could be regulated in a hardness-dependent manner even after deprivation of periodontal sensation. In human studies also, Michael et al. (1990) reported that the masticatory force could be regulated according to the hardness of the chewing substance under edentulous conditions. Spindle afferents from the jaw-closing muscles are likely to contribute this regulation, because it has been shown that the masseteric EMG activity could hardly respond to strip application during CRJMs after a lesioning of the trigeminal mesencephalic nucleus in addition to denervation of the trigeminal sensory branches (Morimoto et al. 1989). On the other hand, it has been reported that the lesion of the trigeminal mesencephalic nucleus tract in monkeys does not change the chewing pattern or the normal response to variations in food hardness (Goodwin and Luschel 1974). Taking these findings into consideration, it could be that both periodontal afferents and muscle spindles are responsible for this hardness-dependent change, and that removing only one of them does not have much effect alone.

The discharges of spindle afferents increase with an increase in EMG activity of the jaw-closing muscles during chewing or a biting task (Larson et al. 1981, 1983; Matsunami and Kubota 1972; Taylor 1981). Lund et al. (1979) also found that trigeminal fusimotor neurons of the alert monkey were activated vigorously before and during contraction of the jaw-closing muscles in a biting task. Furthermore, it has been reported that spindle discharges, recorded in rhythmic jaw movements, increase during the slowed shortening (Cody et al. 1975; Goodwin and Luschel 1975; Morimoto et al. 1995b; Taylor and Cody 1974; Taylor et al. 1981). The velocity of jaw closing in the power phase is obviously lowered coincident with the increased minimum gape as strip hardness is increased (Fig. 3). These findings prompt us to suppose that the coactivated spindles could fire faster. At least during CRJMs, the spindle discharges probably contribute to the hardness-dependent change in the masticatory force.

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Masticatory Force Regulation in Rabbits


