Jaw Reflexes Evoked by Mechanical Stimulation of Teeth in Humans

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Yang, J. and K. S. Türker. Jaw reflexes evoked by mechanical stimulation of teeth in humans. *J. Neurophysiol.* 81: 2156–2163, 1999. The reflex response of jaw muscles to mechanical stimulation of an upper incisor tooth was investigated using the surface electromyogram (SEMG) of the masseter muscle and the bite force. With a slowly rising stimulus, the reflex response obtained on the masseter SEMG showed three different patterns of reflex responses; sole excitation, sole inhibition, and inhibition followed by excitation. Simultaneously recorded bite force, however, exhibited mainly one reflex response pattern, a decrease followed by an increase in the net closing force. A rapidly rising stimulus also induced several different patterns of reflex responses in the masseter SEMG. When the simultaneously recorded bite force was analyzed, however, there was only one reflex response pattern, a decrease in the net closing force. Therefore, the reflex change in the masseter muscle is not a good representative of the net reflex response of all jaw muscles to mechanical tooth stimulation. The net response is best expressed by the averaged bite force. The averaged bite force records showed that when the stimulus force was developing rapidly, the periodontal reflex could reduce the bite force and hence protect the teeth and supporting tissues from damaging forces. It also can increase the bite force; this might help keep food between the teeth if the change in force rate is slow, especially when the initial bite force is low.

INTRODUCTION

The reflex connection between the periodontal mechanoreceptors and the jaw-closing muscles has been subject to much study. Some of these studies suggested that the reflex responses from these receptors are principally inhibitory (Bonte et al. 1993; Dessem et al. 1988; Louca et al. 1996; Sessle and Schmitt 1972; Van der Glas et al. 1985). In contrast, other researchers have demonstrated evidence for an excitatory connection to the jaw-closing muscles from periodontal receptors (Amano and Yoneda 1980; Funakoshi 1981; Lavigne et al. 1987; Lund and Lamarre 1973). Recently we have stressed the importance of the rate of rise of the stimulus force in eliciting excitatory or inhibitory responses from the masseter. The slowly rising stimulus mainly induced an excitatory reflex, whereas the rapidly rising stimulus usually induced inhibition (Brodin et al. 1993b; Türker et al. 1994). There were also other variables that affected the success of the stimulus in inducing a certain type of reflex response, such as the presence of a preload and the exact stimulus force profile (Türker et al. 1997a).

In each of these studies, the reflex response was determined using the surface electromyogram (SEMG) of jaw muscles; usually only one muscle, the ipsilateral masseter. In contrast to the large number of studies using the SEMG, the reflex changes in the bite force induced by a tooth stimulus have never been studied systematically (Yamamura et al. 1993). It is possible that the much-studied masseter muscle may not represent effective changes in bite force in response to a tooth stimulus. This is because the bite force can be developed using a large number of combinations of activation of jaw muscles or sections of jaw muscles (Hannam and McMillan 1994; Van Eijden et al. 1990). Hence the theories regarding the changes in the masticatory forces that originated from reflex studies in only one jaw muscle may be misleading (e.g., Brodin et al. 1993b; Hannam et al. 1970).

Furthermore there are some difficulties in interpreting the SEMG data. For example, an increase in the poststimulus SEMG, preceding an inhibitory phase, may be an artifact of the averaging process (Widmer and Lund 1989). Similarly, an increase after a decrease in SEMG records can be simply a cluster of delayed action potentials by the preceding inhibition (Miles et al. 1987). Any such clusters of action potentials related to the stimulus will fire again at about one interspike interval and hence induce several peaks and troughs. These changes in the SEMG may be described wrongly as an excitatory or an inhibitory connection of the stimulated afferent to the motoneurons (Awiszus et al. 1991; Türker and Cheng 1994). This is termed the ''synchronization-related error'' for the averaged SEMG records. SEMG also have one other major pitfall, ''number related error,'' where a large postsynaptic potential (PSP) shadows a later PSP because many of the active motoneurons discharge in response to the earlier PSP can no longer fire for a further one interspike interval. This period resembles a ''silent period'' or a period with reduced activity on the averaged graph, and the PSP underlying this period may only be examined by the discharge rate of the single motor units in the muscle (Türker et al. 1997b).

The bite force is not affected by the aforementioned artifacts and represents the net response of the masticatory system to mechanical tooth stimulation. Therefore the present experiments were designed to study the reflex changes in the bite force in response to a mechanical stimulation of an upper incisor tooth in man. The other aim of this study was to compare the reflex response of the bite force with the much-studied SEMG of the masseter. Preliminary results of this study were published in abstract form (Yang and Türker 1997).

METHODS

Fourteen experiments were carried out on nine young, healthy, and consenting subjects, aged from 19 to 26 yr (5 males and 4 females). All subjects had normal dentition and no history of orofacial neuromuscular dysfunction or orthodontic treatment. These experiments were approved by the Human Ethics Committee of The University of Adelaide.
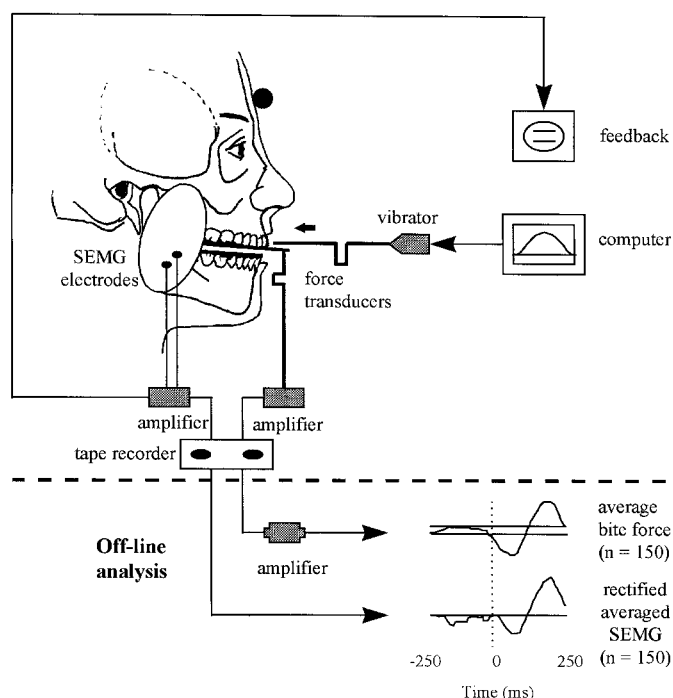
FIG. 1. Diagrammatic illustration of the methods. Shape of the stimulus profile was determined on a computer, which sent this wave to a vibrator to activate the tooth. Strength and the profile of the stimulus were measured by a force transducer placed in series. Bite force was measured with a force transducer mounted under the upper bar, which carried the impression of the upper teeth. Lower bar that carried the impression of the lower teeth was fixed to the rigid frame to ensure that the vertical distance (5 mm) between the bite bars was kept constant. Position of the subject's head was secured further by asking the subject to rest his/her forehead on a horizontal bar/headrest. Subject controlled the level of muscle activity with the help of feedback from the ipsilateral masseter. Surface electromyogram (SEMG) of bilateral masseter and the isometric bite force were recorded simultaneously. During the off-line analysis, the bite force was amplified, filtered, and averaged in 150 trials. SEMG was rectified and averaged (150 trials) around the time of the stimulus.

Details of the experimental set-up have been given elsewhere (Brodin et al. 1993b; Türker et al. 1997a) and are summarized here. The subject was seated comfortably with his/her upper teeth held in a fixed relation to a Teflon probe mounted on the moving coil of an electromechanical vibrator. The subject bit into the impression of his/her teeth that was attached to a rigid frame. The relationship of the jaws to the bite bars was kept constant by means of the dental impression (Formasil II) of the subject's teeth. The position of the head was secured further by a headrest that gently touched the forehead. The dental impression material was cut away from around the upper left lateral incisor so that the tooth could be contacted and stimulated by the probe (Fig. 1).

Periodontal mechanical stimulation

The periodontal mechanoreceptors of the upper left lateral incisor were stimulated with 2.5 N slowly rising force (25 N/s) or rapidly rising force (1,250 N/s). The stimulus was delivered orthogonally to the labial surface of the tooth with the interstimulus interval varying randomly between 2 and 5 s. The shape of the force profile was a slowly rising half sinusoid wave (time to peak = 100 ms) (type-SSR force profile in Türker et al. 1997a). The probe applied a background load (0.2–0.5 N) to the tooth preceding the stimulus, and the incisal edge rather than the center of the tooth was stimulated. To make sure that the probe did not slip and that the effective stimulus profile was smooth, the high-pass filtered force (at 50 Hz) record was monitored carefully throughout the experiment.

SEMG

Bipolar surface electrodes were placed over the masseter on both sides of the face. The SEMG signal was filtered (20–1,000 Hz), amplified (2,000 times), and recorded on a video recorder (Vetter 400) for off-line analysis.

During off-line analyses, the SEMG was filtered (20–500 Hz), sampled at 1 kHz, full-wave rectified and averaged (12 bits resolution) around the time of the stimulus. The cumulative sum (CUSUM) (Ellaway 1978) of the averaged SEMG record was constructed (1-ms binwidth). The procedure performed to obtain reflex response from the CUSUM is described fully in Türker et al. (1997a) and is summarized here. From the prestimulus period of the CUSUM records of SEMG, the maximal positive and negative deflections indicating the variance levels of SEMG in the prestimulus period, were obtained. The larger of the two values then was used to make a symmetrical "error box" (Fig. 2, ■ and □). From the CUSUM records, the existence of a reflex response was determined by comparing the size of the error box with the deflections in the poststimulus CUSUM, within the reaction time to this stimulus. The reaction time for the masseter SEMG for slowly and rapidly rising stimuli has been reported to be 140 and 80 ms, respectively (Brodin et al. 1993a). Any response above or below the limits of the error box occurring before the reaction time was considered as a significant increase or decrease in SEMG, respectively (Fig. 2).

Force

The isometric bite force was measured by a strain gauge (Load Cell, A&D Company, LC1205-K100; sensitivity: 0.005–100 kg) mounted on the upper bite bar. The minimum bite force that can be measured reliably was 50 mN. This limitation is not expected to affect the bite force values in this study because the steps of bite force we report here are in 100 mN. The bite force was recorded on a video recorder for off-line analysis.

During the off-line analyses, the bite force signal was amplified, filtered (DC, 50 Hz), and averaged in 150 trials. The net reflex change in the closing force in response to the tooth stimulation was determined by using the bite force as the source and the timing of the stimulus as the trigger. From the averaged records of the bite force, the maximal variation of the prestimulus (−250–0 ms) force was measured and extrapolated to the poststimulus period (0–250 ms). An increase of the bite force that was above, or a decrease of the bite force
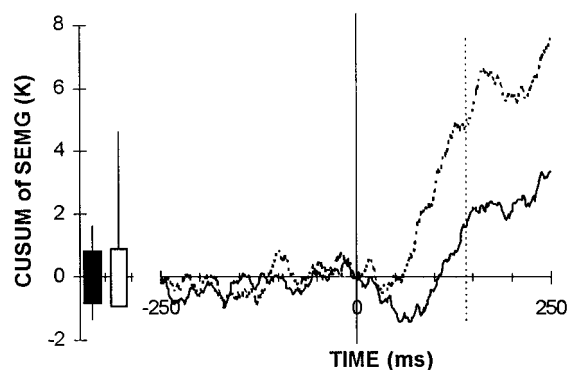

FIG. 2. Cumulative sum (CUSUM) of the SEMG from bilateral masseter to slowly rising stimulation. ■, maximal prestimulus variability in the ipsilateral masseter SEMG. □, maximal prestimulus variability for the contralateral masseter SEMG. Reflex response was determined by comparing the size of error box with the deflections in the poststimulus CUSUM within 140 ms of the stimulus (the SEMG reaction time to this stimulus). Bars on the error boxes represent the maximal reflex change. —, ipsilateral CUSUM, which shows a decrease followed by an increase. - - -, reflex response from the contralateral side, which shows only an increase. · · ·, reaction time (140 ms). Stimulus was given at *time 0*.
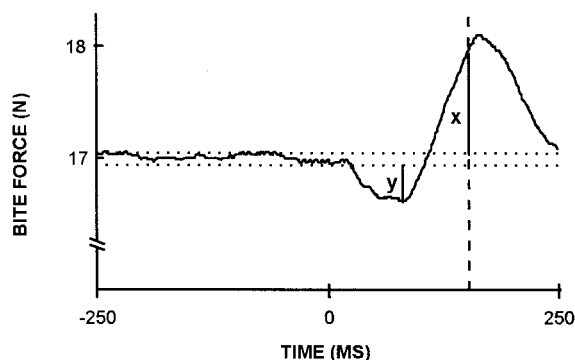
FIG. 3. Reflex change of the bite force in response to slowly rising stimulus. · · ·, maximal variability in the averaged prestimulus bite force. Changes in the bite force, which was *above* or *below* these lines and occurring before the reaction time, were determined as a reflex response. Ratio of the maximum to minimum reflex response in bite force was calculated. Ratio = x/y where x is the maximal increase and y is the maximal decrease in the poststimulus period before the reaction time (- - - at time 155 ms).

that was below the maximal prestimulus force variation, was determined (Fig. 3). We have reported earlier (Brodin et al. 1993a) that the fastest reaction time to slowly and rapidly rising mechanical stimuli to teeth as expressed on the masseter surface EMG were 140 and 80 ms, respectively. However, due to the time taken for the electrical events to induce measurable force changes, the reaction time for the force record needed to be corrected accordingly with the SEMG-force relationship observed for the masseter muscle in human subjects. The SEMG-force delay was found to be 15 ms in this study, which is similar to the findings of others in hand muscles (Johansson and Westing 1984). Therefore the corrected reaction time for the force record was 15 ms longer than the reaction time for the SEMG, that is, 155 ms for the slowly rising and 95 ms for the rapidly rising stimuli.

With slowly rising stimuli, the ratio of the maximal increase to the maximal decrease in the bite force was calculated thus: ratio = x/y, where x is the maximal increase and y is the maximal decrease in the bite force preceding the reaction time (Fig. 3).

Experimental protocol

Subjects were divided into two groups (*A* and *B*). In *group A*, eight experiments were carried out on six subjects. In each experiment, the subject bit into bite bars on which a strain gauge was mounted to measure the bite force and the interincisal separation was 5 mm. The subject was asked to control the activity of the ipsilateral masseter muscle using the discharge frequency of one of its motor units (Miles and Türker 1986). Details of recording and discriminating motor unit action potentials have been given elsewhere (Miles et al. 1987). Briefly, a fine bipolar electrode (Teflon-insulated, 0.07-mm-diam silver wire) was inserted to record motor unit potentials from the left masseter muscle. The shapes of motor unit potentials were recognized using a computer-based template-matching algorithm (SPS-8701). Using the discharge frequency of a selected unit as feedback, the subject was asked to maintain a contraction level that discharged the unit at [~12 Hz]. The slowly rising stimuli were applied when the unit was discharging regularly. To avoid muscle fatigue, each run consisted of 50 stimuli. The subject was asked to rest on the bars for 30 s between each run, and then repeat the biting for the other two runs. The purpose of the other two repeat runs was to increase the reliability of the data for individual units. After 150 stimuli (3 runs), the subject was asked to come off the bite bars and rest for 10 min, thus completing one experimental session. In each experiment, four to six experimental sessions of 150 stimuli were performed. Therefore, 35 experimental records were achieved in six subjects in eight separate experiments. Each experimental session used a different motor unit as the feedback.

In *group B,* six subjects participated in six experiments in which the reflex response of bite force was studied by using slowly rising and rapidly rising stimulus. Using 5 and 10% of the maximal SEMG activity as the feedback, 2.5 N slowly rising or rapidly rising stimuli were applied to the tooth. In each experiment, four experimental sessions, two for slowly rising and 2 for rapidly rising stimulus, of 150 stimuli were achieved.

Statistical analysis

Comparisons of the reflex response patterns to different stimuli (slowly rising and rapidly rising) and to different methods (SEMG and bite force) were determined using contingency table analysis (Everitt 1993). The Spearman rank order correlation coefficient rho (Pagano 1994) was calculated from the bite force ratio against the background bite force level. A *P* value of < 0.05 was considered statistically significant for all tests.

RESULTS

Reflex response patterns produced by slowly-rising stimulation (Group A)

The reflex response pattern, determined by the CUSUM of the SEMG, is illustrated in Table 1. Because the ipsi- and contralateral masseter demonstrated very similar reflex responses in the SEMG (Bonte et al. 1993; Türker et al. 1997a), the SEMG results described in the following section came from the ipsilateral side only.

Using the SEMG analysis method, 18 of 35 experimental session records, each using a different single motor unit as feedback, showed a sole excitatory reflex response (E); 6/35 sole inhibition (I); 8/35 inhibition followed by excitation (I/E), and 3/35 no reflex (that is, poststimulus CUSUM deflection did not go above or below the limits of the error box). The main pattern in the SEMG was E. Conversely, in the averaged bite force records, the dominant reflex pattern was I/E, which is a decrease followed by an increase in the net bite force (Fig. 4).

The reflex response pattern and the average bite force for each trial, is illustrated in Table 2.

In the poststimulus period, the CUSUM of the SEMG, going beyond the error box size was extrapolated back to the baseline, and the timing of the first deflection in the same direction was noted as the latency of the reflex response (Türker et al. 1997a). The average latency for the inhibitory reflex response in the SEMG was 20 ms (ranging from 8 to 33 ms), and the bite force decreased with an onset latency of ~35 ms (ranging from 23 to 74 ms). For the bite force records, the latency of the reflex response was measured from the point of deflection below or above the prestimulus variability limits. The average onset latency difference between the SEMG and the bite force was

TABLE 1. *SEMG and bite force with the slowly rising stimulus*

	E	I	I/E	No Reflex	Total
SEMG	18	6	8	3	35
Bite force	0	4	31	0	35

With slowly rising stimulation, the incidence of reflex response patterns in the surface electromyogram (SEMG) of ipsilateral masseter and the bite force in 35 experimental records are shown. E, sole excitation or a net bite force increase; I, sole inhibition or a net bite force decrease; I/E, inhibition followed by excitation or a bite force decrease followed by an increase. The reflex response pattern in the SEMG is compared with the reflex response pattern in the bite force. The patterns were significantly different ($P < 0.001$).
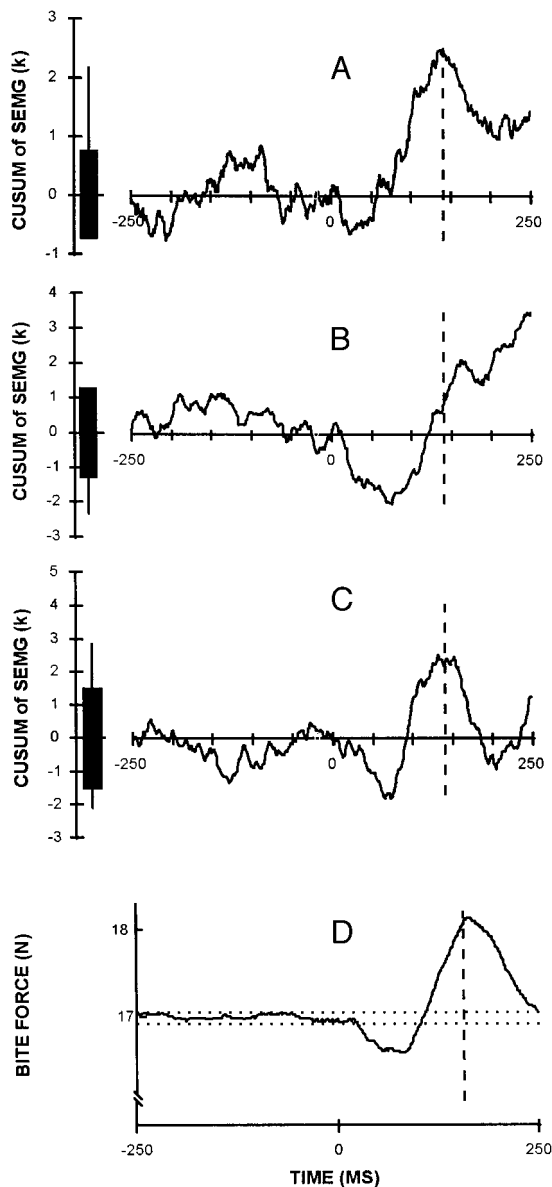
FIG. 4. Reflex patterns in the CUSUM of the SEMG and the bite force to slowly rising stimulus. CUSUM of the SEMG records displayed 3 different reflex patterns in response to slowly rising stimulation: sole excitation (*A*), sole inhibition (*B*), and inhibition followed by excitation (*C*). There was mainly 1 reflex response pattern for the bite force, a bite force decrease followed by an increase (*D*). CUSUM in *A* and the bite force in *D* were recorded simultaneously from 1 subject. *B* and *C* came from 2 other subjects. Stimulation was given at *time 0*. - - -, reaction time of the subject to this stimulus (140 ms in CUSUM, 155 ms in bite force). Any change in the records that occurred before the reaction time and was larger than the prestimulus limits was considered a reflex response.

15 ms. This delay between the muscle's electrical activity and the resultant force change was similar to that found in hand muscles (8–12 ms) (Johansson and Westling 1984).

To find out how background clenching levels affected the reflex response of the bite force, the ratios of the increase/reduction of the bite force were calculated (Fig. 3). The ratio data from six subjects then were plotted against the background bite force (Fig. 5). There was a significant negative relationship between the ratio and the background bite force (rho = -0.3825, $P < 0.05$). When the background bite force was low,

the ratio was high. Conversely, when the background bite force was high, the ratio was low, almost reaching zero.

Reflex response patterns evoked by slowly and rapidly rising stimuli (Group B)

Six subjects participated in six experiments at two different bite force levels (5 and 10% MVC) using rapidly and slowly rising stimuli (Fig. 6). The SEMG and bite force reflex patterns in response to rapidly rising stimulation are summarized in Table 3. In the SEMG records, the rapidly rising stimulus induced three different reflex response patterns. However, in the bite force records, there was only one reflex response pattern; a net reduction in the closing force (I). The reflex response patterns for the SEMG and those for the bite force, were significantly different.

The incidence of reflex patterns in bite force, in response to slowly or rapidly rising stimulation, is shown in Table 4. For the slowly rising force, the reflex response patterns in the bite force were: E, I, and I/E, but mainly I/E as observed in *group A*. With the rapidly rising stimulus, however, the reflex response in the bite force was only a net force decrease (I). The difference between the reflex response patterns in the bite force evoked by slowly and rapidly rising stimulation was significantly different.

DISCUSSION

This study showed, for the first time, that the net response of all jaw muscles to a mechanical tooth stimulus depends on the rate of rise of the stimulus force. Although the rapidly rising stimuli always induced a net decrease in the bite force, slowly rising stimuli mainly induced a decrease followed by an increase. The simultaneously recorded SEMG of the ipsilateral masseter muscle, on the other hand, displayed three different combinations of reflex responses. Therefore the reflex change in the masseter muscle does not represent the net reflex responses of all jaw muscles in response to a mechanical tooth stimulus.

Reflex responses as obtained from the SEMG of the masseter and the bite force

Although the masseteric EMG may represent the closing force in the anesthetized rabbit (Hidaka et al. 1997), human studies do not indicate such close relationship between the masseteric SEMG and the bite force (Mackenna and Türker 1983). Despite that, the reflex response in the masseter SEMG often has been taken to represent the bite force, and speculations have been made regarding changes in bite force during chewing (e.g., Brodin et al. 1993b; Hannam et al. 1970).

It is well known that bite force is developed by at least three pairs of major jaw-closers and also opposed by several jaw-openers. Not only do individual jaw muscles have preferred functions, but they also even have functional compartments, which are activated preferentially in certain tasks (Hannam and McMillan 1994; Van Eijden et al. 1990). The complexity of jaw muscles is displayed further by their histochemical and neurological differences from the limb muscles (Lund 1991). The openers lack muscle spindles and do not show much of a reflex response in human subjects (Matthews 1975). However, they still affect the bite force by stiffening the jaw especially

TABLE 2. *Reflex response and average bite force values for each trial*

	Trials					
Subjects	1	2	3	4	5	6
Se	I/E (8.0)	E (8.0)	I (8.0)	E (24.0)		
C	E (3.2)	E (4.0)	E (15.0)	I/E (32.0)		
T	E (5.4)	E (6.4)	I/E (6.4)	E (17.2)		
M	I (10.0)	I (13.0)	I (18.0)	I (24.0)		
Si	E (16.0)	E (16.0)	I/E (20.0)	E (32.0)		
C	E (13.0)	E (16.0)	E (16.0)	0 (27.0)	0 (36.0)	
H	I (10.0)	0 (12.0)	E (12.0)	E (24.0)		
T	I/E (14.0)	I/E (14.0)	E (15.0)	E (19.0)	I/E (20.0)	I/E (21.0)

At least four trials were completed for each subject. Two of the subjects (*T* and *C*) participated on two experimental days. The reflex responses are indicated for each trial in each subject. The average force level (in Newtons) for each trial is shown in parentheses. There was no significant relationship between the average force level for each trial and the outcome of the trial (Polychotomous Logistic Regression, BMDP Statistical Software).

during difficult or novel tasks (Miles and Madigan 1983). Therefore both the jaw-openers and jaw-closers may take part in determining the net output of the masticatory system to a mechanical tooth stimulus.

Before the present study, the net reflex response of all jaw muscles rarely was studied (Türker and Miles 1985; Yamamura et al. 1993; Yemm 1972a,b). In the only similar study, the reflex response was assumed to continue for 3 s after the application of the stimulus (Yamamura et al. 1993). This is >20 times the reaction time that we have measured in response to a similar stimulus to a tooth (Brodin et al. 1993a). Therefore we cannot include Yamamura's work as a comparable study to the reflex results described here.

A comparison of the reflex response of the SEMG of masseter and the bite force in response to the slowly rising stimulation (Table 1) shows that the main pattern in the bite force was I/E, a net bite force decrease followed by an increase. However, sole excitation (E) was the dominant pattern observed in the SEMG of the masseter recorded simultaneously (Fig. 4). One possible explanation for these somewhat conflicting results could be our method of analysis (Türker et al. 1997a). In our SEMG analysis method, short-lasting reflex responses can be masked by the size of the error box. Therefore the existence of such reflex responses can be underestimated. Alternatively, the differences in the reflex patterns between the masseteric SEMG and the bite force may indicate that the reflex response pattern of masseter does not represent the net response of all jaw muscles.
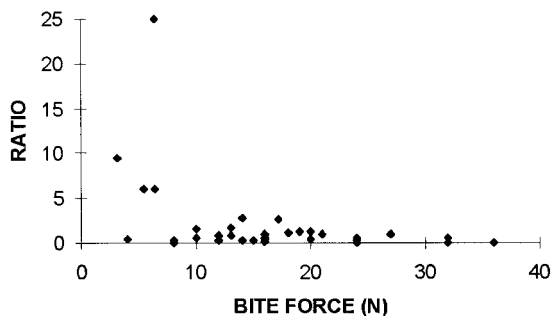

FIG. 5. Force increase and force decrease, Ratios of reflex bite force changes to slowly rising stimulation against the background clenching levels in Newtons (N) are shown. Data came from 35 experimental records in 8 separate experiments, which were performed on 6 subjects. When the background bite force increased, the ratio decreased (rho = −0.3825, $P < 0.05$).

Receptors and pathways

In reduced animal preparations, it is possible to induce activity in two different pathways in response to tooth stimulation. One is presumably the disynaptic inhibitory pathway that responds to rapidly applied mechanical stimuli, and the other is the longer-latency excitatory response, when the rate of application of the stimulus is low (Appenteng et al. 1989; Dessem et al. 1988; Kidokoro et al. 1968a,b; Linden 1990).

In human subjects, the majority of periodontal mechanoreceptors can be activated by forces applied in many directions (Trulsson et al. 1992). Therefore the direction of stimulation used in the present experiments must have activated a large number of periodontal mechanoreceptors. The majority of the receptors belong to the ''hyperbolic'' group, the members of which reach their maximal firing rate <3 N and lose their dynamic sensitivities when the preload is >0.5 N. The second group of receptors known as ''nearly linear'' receptors is observed less often. These receptors display a nearly linear response to force increases of up to ~22 N. Unlike the hyperbolic receptors, the nearly linear receptors do not lose their dynamic sensitivities in the presence of preload (Trulsson and Johansson 1994, 1995). We propose that these two different receptors with varying thresholds and sensitivities to the rate of force application (see Linden 1990 for similar classification in periodontal mechanoreceptors in animals) may underlie the reflexes observed in the present study.

However, it is possible that no matter how carefully the stimulus force is applied on the tooth, it can activate both of these reflex pathways simultaneously. If the force is applied slowly, the excitation may dominate inhibition. However, if the force is applied rapidly and the fast component of the force is very large, a large group of rapidly adapting receptors will be activated (Trulsson and Johansson 1994) and an inhibitory reflex response would be dominant.

It could be argued that the initial reduction of the bite force causes sudden jaw opening by releasing the constant pressure from the bite bars and allows the bars to recoil. This opening ''stimulus'' may stretch the muscle spindles in the jaw-closers, which then may result in a reflex increase of the bite force (Mitchell et al. 1992; Yemm 1972a,b). This increase in bite force was observed only in response to the slowly rising stimuli. If the initial reduction of bite force was the stimulus for the late increase in force, then there should have been a larger increase in bite force in response to the rapidly rising stimuli,
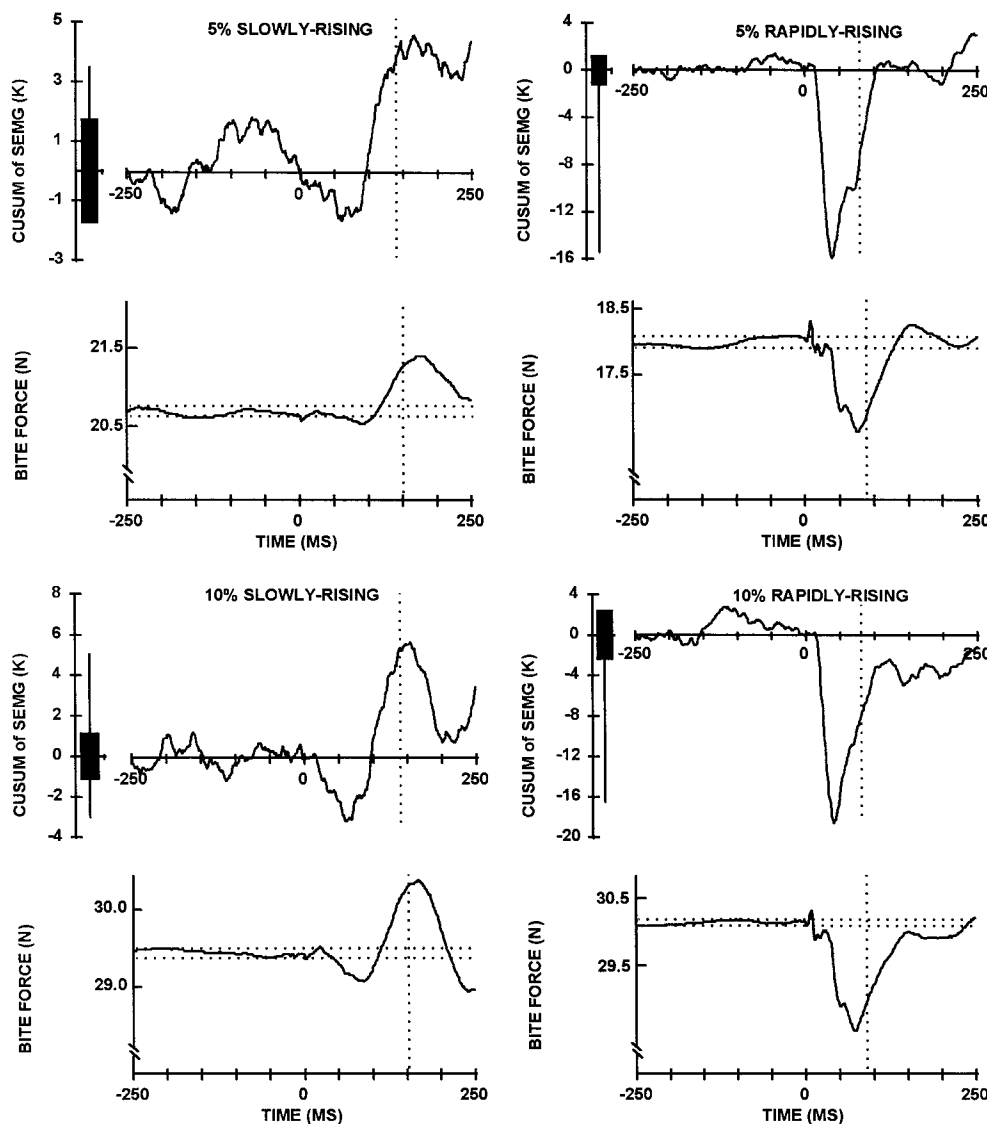
FIG. 6. Different reflex response produced by slowly and rapidly rising stimulus. This figure shows a sample of different reflex responses in the bite force produced by slowly and rapidly rising stimuli. *Left*: reflex responses in the CUSUM of the SEMG and the bite force evoked by slowly rising stimulus. *Right*: reflex changes in the CUSUM of the SEMG and the bite force that were elicited by rapidly rising stimuli. Background clenching level of *top 2 records* were 5% of the maximum activity of ipsilateral masseter SEMG and *bottom 2* were 10% of the maximum SEMG activity. ···, reaction time (140 ms for CUSUM and 155 ms for bite force with slowly rising stimulation; 80 ms for CUSUM and 95 ms for bite force with rapidly rising stimuli).

which induced a much larger reduction in bite force than did the slowly rising stimuli. We are tempted to conclude therefore that the muscle spindles may not contribute to this increase in the bite force in response to slowly rising stimuli.

Reflex pattern of the bite force and the background clenching level

In the present study, it became clear that when using slowly rising stimulus, the reflex response varied depending on the

background bite force level. In the low bite force level, there was a small reduction, followed by a relatively large increase in the bite force. On the other hand, when the background bite force level was high, the reflex reduction became dominant. There are at least two possible explanations for this phenomenon.

First, the differences in reflex response may be due to the recruitment of different types of motor units by the same periodontal stimulus. For example, it has been reported that,

TABLE 3. *SEMG and bite force with the rapidly rising stimulus*

	E	I	I/E	No Reflex	Total
SEMG	1	4	7	0	12
Bite force	0	12	0	0	12

The reflex pattern of the SEMG and the bite force in response to rapidly rising stimulation is illustrated in 12 experimental records on six subjects. There were three different reflex response patterns in the SEMG records and only one reflex response pattern in the bite force records. The patterns in the two rows were significantly different.

TABLE 4. *Reflex changes in the bite force using slowly and rapidly rising stimuli*

	E	I	I/E	No Reflex	Total
Slowly rising	2	2	8	0	12
Rapidly rising	0	12	0	0	12

The reflex response patterns in the averaged bite force in response to slowly and rapidly rising stimuli are shown. For the slowly rising stimulus, the dominant reflex response pattern was I/E. With the rapidly rising stimulus, there was only one reflex response pattern (I). The patterns of reflex responses elicited by the two stimulus types were significantly different.

in the masseter of the lightly anesthetized rat, small and large motor units receive excitatory and inhibitory reflex responses from the periodontal mechanoreceptors, respectively (Yamamura and Shimada 1992). Therefore, in a low bite force level, the reflex excitation of the small-sized motor units would be relatively large and help to hold food firmly and manipulate it between the teeth (Trulsson and Johansson 1995). However, when the background bite force level is already high, the same periodontal input may inhibit the larger motor units that are operating at that level of bite force, thereby limiting further increase in bite force to protect the teeth and supporting tissues from damaging forces. This would mean that large forces cannot be developed reflexly and that the reflex increase in the bite force is somewhat limited to the forces encountered in the preceding chewing cycle (van der Bilt et al. 1995).

This system would work quite well in that each time a large force is required to overcome an unexpected resistance, the force increase would involve the higher centers and control its damaging effects (Ottenhoff et al. 1992). Conscious interference in bite force also can increase the flow of information from the receptors to the cortex, which is reduced during normal chewing (Lund 1991; Olsson et al. 1986), giving the cortex precise information about bite performance.

Second, it is possible that the presynaptic effect can modify the efficacy of the synaptic input of the periodontal mechanoreceptors to the motoneurons of jaw muscles. Such presynaptic modulation on the primary afferent input has been well recognized during mastication (Lund and Olsson 1983; Olsson et al. 1986; van der Bilt et al. 1997). This modulation is geared to limit the forces developed by reflex connections of the primary afferents to the motoneurons. In this case, at higher bite force levels, the peripheral and central input to the interneuronal system that control the efficacy of the synaptic input on the motoneurons also would be high. This extra input then could induce presynaptic modulation on the periodontal mechanoreceptive input on the motoneurons.

Furthermore the effective reflex mechanism of the masticatory muscles, as indicated by the averaged bite force records, shows that it might protect the teeth and supporting tissues from damaging forces when the applied stimulus is developing rapidly, such as biting on a small stone in food. After a brief inhibitory period, it also might help increase the bite force to hold the food between the teeth if the change in stimulus rate is slow, such as biting on a piece of meat, especially at low bite force levels.

It is not possible to deduce that these reflexes will work in exactly the same way during natural mastication. It is well known that the effectiveness of the primary afferent input is under presynaptic and postsynaptic modulation during mastication (Olsson et al. 1986; van der Bilt et al. 1997). However, some circumstantial evidence from key publications in this field indicates that the reflex mechanism, as described in this study, may be functioning under cortically induced chewing in the anesthetized rabbit (Lavigne et al. 1987; Morimoto et al. 1989). Chewing on steel balls caused a jaw-opening reflex as an initial response (Fig. 8 of Lavigne et al. 1987). The jaw-opening reflex did not occur in subsequent cycles, instead, the periodontal input induced excitation rather than inhibition in the jaw-closers. This adaptation may have occurred by reducing the effectiveness of the periodontal input and increasing the effectiveness of the muscle spindle input to the motoneuron

pool (van der Bilt et al. 1997). This initial jaw-opening reflex response was not observed when the obstruction was a foam strip (Fig. 3 of Morimoto et al. 1989). In these experiments, a steel ball between the teeth may be compared with our rapidly rising stimulus and the foam with our slowly rising stimulus.

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