Reflex Responses Induced by Tooth Unloading

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Türker, Kemal S. and Melissa Jenkins. Reflex responses induced by tooth unloading. *J Neurophysiol* 84: 1088–1092, 2000. The reflex response of the masseter muscle to the rapid unloading of a single maxillary incisor tooth was studied. Unloading of a static force of 2 N in the horizontal direction resulted in a short-latency excitation, inhibition, and long-latency excitation of masseter muscle activity occurring at latencies of approximately 13, 20, and 40 ms, respectively, with a corresponding change in bite force occurring slightly later in each case. Following the blocking of periodontal input by the injection of local anesthetic around the stimulated tooth, inhibitory responses were abolished. Therefore, it is concluded that the observed masseteric inhibition was caused by the unloading of periodontal mechanoreceptors and thus that these receptors may contribute to the jaw unloading reflex.

INTRODUCTION

The periodontal mechanoreceptors are pressure receptors found in the connective tissue supporting the roots of the teeth in the jaw. These receptors respond to forces applied to the crowns of the teeth (Hannam 1970), and as a result of this activation, reflex changes in the activity of the jaw musculature can occur (reviewed by Linden 1990). Most of the studies investigating the reflex control of the jaw musculature by these receptors have looked at the response to tooth loading. However, it is evident that these receptors will also change their activity, and hence, potentially alter jaw muscle activity when a tooth is unloaded.

The unloading of periodontal mechanoreceptors occurs when an object breaks between the teeth during biting. The reflex changes in muscle activity elicited by the unloading stimulus on these receptors may contribute to the "unloading reflex," which occurs when the whole jaw is unloaded and helps stop the jaws from forcefully coming together. The periodontal mechanoreceptors have largely been dismissed as contributors to the stopping of the jaw during an unloading event since the removal of input from these receptors does not alter the unloading reflex response (Lamarre and Lund 1975; Poliakov and Miles 1994). Similarly, removal of muscle spindle input in monkeys failed to eliminate the observed unloading response (Goodwin and Luschei 1974). However, in none of the previous studies has the contribution of a particular receptor system been studied in isolation from stimulation of other receptors. It is possible that the removal of the input from one system is compensated for by the others, thus explaining the failure of previous studies to observe any change in the jaw unloading reflex with the removal of one particular receptor system.

The aim of the present study was to isolate the periodontal component of the jaw unloading reflex and thus determine if these receptors can contribute to the reflex. To achieve this aim, a method has been used in which periodontal mechanoreceptors are unloaded and the stimulation of other receptor systems is kept to a minimum. Preliminary results have appeared in abstract form (Jenkins and Türker 1997).

METHODS

These experiments were approved by the Human Ethics Committee of the University of Adelaide. Participants were 10 consenting adult volunteers (7 females, 3 males) aged 19 to 25 yr. All were neurologically normal with healthy dentitions and no history of masticatory dysfunction.

Subjects were seated comfortably with their teeth held fixed in relation to a rubber-tipped Perspex stimulating probe. This was achieved by having subjects bite into an impression of their upper and lower teeth attached to a pair of bite bars. The impression material was cut away from around the upper left central incisor to allow stimulation and "movement" of this tooth (details in Yang and Türker 1999).

Stimuli

An electromechanical vibrator delivered stimuli via a probe aligned orthogonally to the labial surface of the tooth. The unloading stimulus utilized was the withdrawal of a static 2 N load from the tooth. The waveform of the unloading stimulus was half sinusoidal and was 5 ms in duration (400 N/s). The tooth remained unloaded for 200 ms, then was reloaded to the same 2 N level slowly over a 500-ms period (Fig. 1). Stimuli were delivered with a random interstimulus interval of 2–5 s.

Recording

Bipolar electrodes were placed over the ipsilateral (left) masseter muscle and the ipsilateral anterior digastric muscle to record the surface electromyogram (SEMG; bandwidth 20–1000 Hz). Bite force was recorded by a force transducer mounted on the upper bite bar. Both SEMG and force data were recorded on a digital tape recorder for off-line analysis. The SEMG from the masseter was amplified, rectified, low-pass filtered (DC, 0.1 Hz), and displayed on an oscilloscope to provide feedback to the subject to enable a constant level of muscle activity to be maintained throughout the trials.

Protocol

Throughout the experimental trials, the subjects bit so as to maintain ipsilateral masseter SEMG at a predetermined level correspond-

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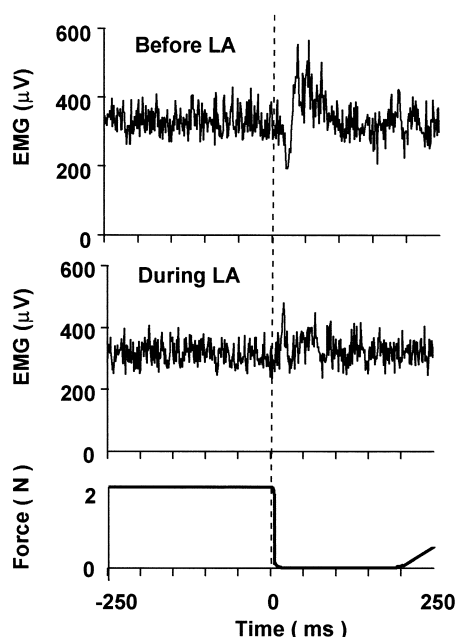
FIG. 1. The relationship between averaged (100 trials) surface electromyogram (EMG) from the ipsilateral masseter and the unloading force in one subject. The top trace is the averaged EMG response before local anesthetic block (LA) and the middle trace is the average EMG response during LA. The bottom trace illustrates the unloading stimulus. The time of stimulus delivery is shown with a vertical dashed line at *time 0*. Note that the inhibitory response disappears during LA.

ing to 10% of their maximum voluntary contraction (MVC). Subjects also wore earphones, through which white noise was played at 90 dB, to mask any sound made by the stimulating apparatus which may have stimulated acoustic receptors and initiated masseteric reflex responses (Sato et al. 1994; van der Glas et al. 1988).

Fifty identical stimuli were delivered in each experimental trial. At least two trials were delivered both before and during local anesthesia. Local anesthetic (3.5 ml of Xylocaine) was infiltrated buccally (canine to canine) and palatally (in the vicinity of the incisive fossa) around the stimulated tooth to block periodontal input. Ten to fifteen minutes were allowed for the anesthetic to take effect, and further stimuli were delivered only after subjects reported no tactile sensation to stimulation of the tooth. Although sensation around the tooth was blocked, subjects sometimes reported a sensation of nonlocalized vibration in the maxilla in response to unloading stimuli.

SEMG and force analysis

For each trial, the SEMG was filtered (20–500 Hz), full-wave rectified, and sampled at 1 kHz (12-bits resolution) before averaging ±250 ms around the time of stimulation (1-ms binwidth). A cumulative sum (CUSUM) (Ellaway 1978) of the averaged SEMG record was then constructed. This process of normalization expresses each CUSUM record in k units, with k being the prestimulus level of SEMG activity for that trial. The CUSUMs of pairs of trials using the same stimulus in the same subject were combined so that averaged responses to 100 stimuli were obtained.

For each subject, postlocal anesthetic records were subtracted from prelocal anesthetic records to estimate the periodontal contribution to the reflex response.

From the prestimulus period (−250 to 0 ms) of the CUSUM records, the maximal positive and negative deflections were obtained, and the larger of the two values were used to make a symmetrical "error box" (Yang and Türker 1999). A reflex response was deemed present if the CUSUM exceeded the size of the error box and occurred

within 150 ms of stimulus delivery (the minimum reaction time to the unloading stimulus as measured in preliminary trials).

The latency of a response was taken as the time between the initiation of stimulus delivery and the point at which the CUSUM record first began to clearly move in the direction of the reflex response. If the deflection was not clear, the CUSUM record was differentiated and the reflex initiation point was identified as the peak in the first derivative immediately preceding the reflex response. The size of a reflex response was taken as the maximal point of deflection.

Bite force was filtered (DC, 50 Hz) and averaged and the absolute limits of the prestimulus force variation (within 250 ms preceding the stimulus) for each record was used to construct an error box. As with the CUSUM data, poststimulus responses which exceeded the limits of the error box and which occurred within 150 ms of stimulus delivery were accepted as reflex responses.

The latency of a reflex response was measured as the point at which the bite-force record first began to clearly move in the direction of the reflex response. As with the latency measurements on the CUSUM records, if the deflection was not clear, the record was differentiated
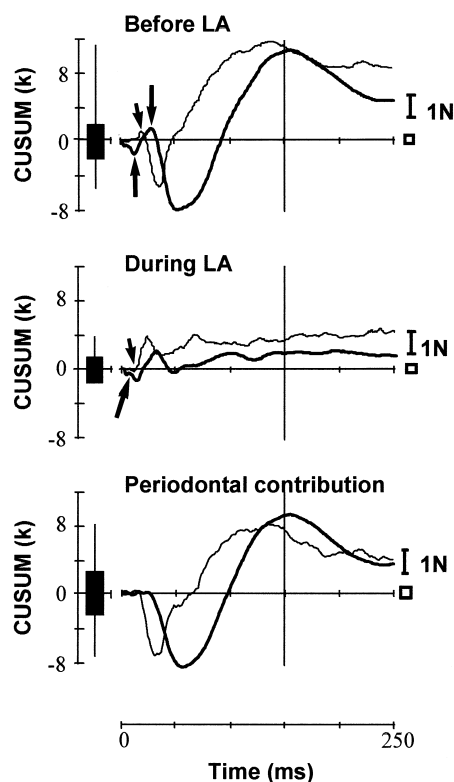
FIG. 2. The relationship between the CUSUM of the averaged ipsilateral masseter surface EMG (lighter line) and averaged bite force (darker line) in one subject. Stimulus delivery is at 0 ms. Scales and error boxes for the CUSUM records are shown at the left of each record; calibration bars and error boxes for force records are shown at the right. The reaction time cutoff is shown at 150 ms by a vertical dotted line. Large arrows indicate the latency measurements in the force records and small arrows indicate the latency measurements in the EMG CUSUM record. *Top graph*: the large upward arrow indicates the latency of the early excitatory response on the bite-force record. The large downward arrow indicates the latency of the inhibitory reflex response in bite-force record. Small downward arrow indicates the latency of inhibitory reflex in the CUSUM trace. *Middle graph*: the large upward arrow indicates the latency of the small decrease in the bite-force record (an artifact of the unloading stimulus). The small downward arrow indicates the latency of the early excitatory reflex response in the CUSUM record. *Bottom graph*: this graph was obtained by subtracting the During LA records from the Before LA records. This in effect gave us the contribution made by the periodontal mechanoreceptors to the reflex obtained by the unloading of 2 N force from one tooth.

TABLE 1. *Summary of reflex responses to tooth unloading*

	Excitation		Inhibition	
	Before local anesthesia	During local anesthesia	Before local anesthesia	During local anesthesia
CUSUM				
size (k)	1.37 ± 1.35 (4)	3.17 ± 2.82 (6)	−4.94 ± 2.14 (10)	−0.91 (1)
latency (ms)	13.0 ± 1.2 (4)	12.5 ± 1.1 (6)	19.5 ± 1.4 (10)	19.1 (1)
Bite force				
size (N)	0.89 ± 0.19 (9)	1.12 ± 0.18 (10)	−1.74 ± 0.90 (10)	−0.04 (1)
latency (ms)	11.9 ± 0.6 (9)	11.9 ± 0.9 (10)	28.0 ± 1.8 (10)	29.0 (1)

Values are means ± SD; number of subjects in parentheses.

and the reflex initiation point was identified as the peak in the first derivative immediately preceding the reflex response. The size of a response was measured as the net deflection of the bite-force record from the reflex latency to the point where the change in force terminates.

Statistical analyses

The size of responses before and during local anesthesia were compared using a paired *t*-test. The incidence of the reflex response before and during local anesthesia was compared using the Sign test. In all cases, alpha was set at 0.05.

RESULTS

Reflex response of the masseter muscle to tooth unloading

Three identifiable reflex components were observed in the CUSUMs of the masseteric SEMGs in response to tooth unloading. The first component was a weak short-latency excitation; the second was a prominent inhibition and the final reflex response was a long-latency excitation (Figs. 1 and 2).

The size of the short-latency excitatory reflex was barely above the prestimulus variations. In only four cases, this early deflection in CUSUM met the criteria used for reflex response (see METHODS). During local anesthesia, the incidence of this reflex increased to six and the size of the response increased significantly ($P < 0.05$; Table 1). The latency of excitation was 13 ± 1.2 ms and did not change significantly after the local anesthetic block (12.5 ± 1.1 ms).

A large inhibitory reflex response was observed in all 10 subjects preceding anesthesia. The latency for this response was 19.5 ± 1.4 ms. During local anesthetic block, the inhibitory reflex disappeared in all but one subject (Sign test; $P < 0.01$). In the subject who displayed an inhibitory reflex response during local anesthesia, the response size was substantially reduced (Table 1).

The longer latency increase in CUSUM was observed less consistently than the other two responses. This response was not analyzed in the present study since it has recently been shown that such long-latency responses following inhibitory reflex responses may in fact represent the tail end of the inhibitory postsynaptic potential (IPSP) rather than an excitatory postsynaptic potential (EPSP) (Türker and Powers 1999). Since our evidence does not include single-motor unit work, it was not possible for us to determine the true identity of this late response.

Response of the anterior digastric muscles

There was no measurable pattern in the poststimulus changes in the SEMG of the anterior digastric muscle in response to tooth unloading.

Bite-force changes in response to tooth unloading

An example of the relationship between the components of the CUSUM of the SEMG and bite force is shown in Fig. 2. The change in bite force in response to tooth unloading in one subject may be observed in this figure. In the "Before LA" and "During LA" records in Fig. 2, a small decrease is consistently observed that occurs prior to any change in CUSUM at a latency of about 5 ms (large upward arrow in During LA force record). Following this decrease was an increase occurring at about 12 ms (large upward arrow in Before LA force record). This increase in bite force was larger during anesthesia than before. Following this increase in bite force, a subsequent decrease was observed in all subjects before anesthesia, but in only one during anesthetic block (Sign test; $P < 0.01$; Table 1). A final increase in bite force was seen in the instances in which a corresponding late increase in the SEMG was observed.

DISCUSSION

Direction of unloading and receptors stimulated

During mastication, loading and unloading of forces on teeth mostly occur in the axial direction, and as such a technique that delivers axial forces to the teeth would be used to study jaw reflexes. We did not, however, use an axial unloading technique since this stimulus moves the jaws substantially and alters the activity of many receptor systems (temporomandibular joint receptors, muscle spindles, skin and mucosal receptors) including the periodontal mechanoreceptors (reviewed in Lund 1991). In the present study, we wished to isolate the periodontal component of the jaw unloading reflex. Unloading of force in the horizontal direction achieved this goal quite successfully since locally anaesthetizing the teeth altered the reflex significantly and isolated the contribution of the periodontal mechanoreceptors.

One may also argue that axial unloading and horizontal unloading stimuli may activate different receptors and hence the reflex response may be substantially different. However, there is evidence that individual human periodontal mechanoreceptor afferents are activated by forces applied to the teeth in almost all directions. Using microneurography, Trulsson and colleagues (1992) have shown that most periodontal mechanoreceptor afferents could be activated by static forces in two or

three of the four horizontal directions and in one or both of the axial directions. This finding suggests that receptive fields within the periodontal space are diffuse and can be activated by forces applied in many directions. This is not surprising since most human periodontal mechanoreceptors are of Ruffini type (Lambrichts et al. 1992) and that these receptors have very large receptive fields (slowly-adapting Type II; Johansson and Vallbo 1983). Therefore, the direction of unloading used in the current study must have activated a large number of them.

One has to be cautious, however, that the information regarding directional sensitivity of these receptors comes from one study and that it was performed on the receptors originating from mandibular teeth (Trulsson et al. 1992). Exact difference of the reflex responses of axial versus horizontal stimulation on the periodontally induced jaw reflexes needs to be studied further before any definite conclusions are drawn.

The early excitation

The failure of anesthesia to remove the early excitation indicates that this response is not of periodontal origin. The latency of this response suggests muscle spindle origin (Orchardson and Sime 1981). This response may have been initiated by the stimulation of spindles by vibration set up by sudden unloading. Another possible source of spindle stimulation may be the small decrease in bite force immediately following the unloading stimulus. This decrease occurred in all subjects at the same latency and magnitude and both before and during local anesthesia. Therefore, it is likely that this small decrease in the bite force was a mechanical artifact produced by the method of stimulation used in the present study. In effect, the unloading of the tooth allowed a slight opening of the jaws which constituted a stretch stimulus to the jaw muscle spindles which are known to be exquisitely sensitive to stretch (Appenteng 1990; Poliakov and Miles 1994). It is also possible that the receptors that are not anesthetized and that are sensitive to mechanical stimuli (such as the ones situated in the sutural tissues; Linden 1978) may also contribute to this reflex.

Inhibition

Unloading of the tooth resulted in a reflex reduction in the SEMG of the ipsilateral masseter muscles. Since the reflex response disappeared with anesthesia in 9 out of 10 subjects and dramatically reduced in size in the one remaining subject, it can be suggested that it is of periodontal origin.

There is evidence suggesting that periodontal input is subserved by both inhibitory and excitatory pathways (Appenteng et al. 1982; Türker et al. 1994, 1997). Changes in activity in both of these pathways may explain the masseteric inhibition with unloading. First, the reduction in muscle activity may be due to the stimulation of an inhibitory pathway by the sudden unloading (OFF) stimulus. A proportion of periodontal mechanoreceptors have been shown to exhibit an OFF response; that is, they are stimulated when a force is removed from a tooth (Hannam 1970; Loescher and Robinson 1989; Lund et al. 1983; Ness 1954). Receptors displaying this response most likely are the "rapidly adapting" receptors that are highly sensitive to changes in the rate of force application (Linden 1990; Trulsson and Johansson 1994). Second, the masseteric inhibition may in fact be a disfacilitation due to the removal of

a tonic excitatory input. The results of several studies (Lavigne et al. 1987; Morimoto et al. 1989; Ottenhoff et al. 1992a,b) indicate that, during chewing, periodontal mechanoreceptors are predominantly responsible for eliciting the additional muscle activity required to overcome the resistance encountered between the teeth. If this excitatory pathway is stimulated by pressure on the teeth during biting, then the removal of this pressure that would occur with tooth unloading would result in the removal of the excitatory input, and hence a reduction in jaw-closer muscle activity. Thus the inhibition seen with periodontal unloading could be due to both an activation of the inhibitory pathway and a removal or reduction of activity in the excitatory pathway.

Furthermore, the size of the inhibitory responses seen in the present tooth unload experiments is likely to be an underestimation of the periodontal inhibition that would occur in a natural jaw unloading situation. In the present study, only a single tooth was unloaded, whereas the fracturing of an object between the teeth would unload several teeth in the upper and lower jaw, thus involving many more receptors which would result in a greater inhibitory response.

It is likely that many other receptors contribute to the jaw unloading reflex. Disfacilitation of muscle spindles is probably the other main contributor to this reflex since these afferents are very active during conscious biting and any change in the muscle length is known to affect their output (Appenteng 1990). Together with the disfacilitation of muscle spindle contribution to the jaw closers and the active inhibition and disfacilitatory effect of periodontal afferents on the jaw closer, motoneurons are likely to induce powerful jaw unloading reflex which may help stop the jaw under normal conditions.

It has been suggested that the unloading reflex is not important in stopping the jaw, as the impact of the reflex on force development in the masseter muscles is too slow (Miles and Wilkinson 1982; van Willigen et al. 1997). Instead, mechanical factors such as the stiffening of the antagonist muscles (Miles and Madigan 1983; Miles and Wilkinson 1982) and the force-velocity properties of the jaw muscles (van Willigen et al. 1997) have been proposed as the principal factors responsible for halting jaw closure. If, however, masseteric inhibition did not occur following unloading, it is likely that the level of contraction that was present prior to unloading would rapidly be re-established and the jaw closing movement would resume. The masseteric unloading reflex and hence periodontal inhibition are thus more likely to have an important role in preventing further jaw closing from occurring after the initial slowing of the jaw.

Late excitation

The source of the long-latency excitation and the reason why it is not consistently observed is unclear and can only be speculated. This response was elicited equally both before and during local anesthesia and thus is not due to any reflex activity of the periodontal mechanoreceptors around the stimulated tooth. One possible source of this late excitation is the long-latency component of the stretch reflex (Poliakov and Miles 1994). This response must be regarded cautiously, however, as late responses in the SEMG and their CUSUMs can be contaminated by aftereffects of an earlier response (Türker and Powers 1999).

Conclusion

This study has suggested that, in contrast to the conclusions of previous studies, periodontal mechanoreceptors can contribute to the unloading reflex by inducing a reflex inhibition of the masseter muscles and by reducing the bite force. Therefore, these receptors, in conjunction with additional receptors involved in the unloading reflex and the mechanical properties of the jaw muscles, may help stop the jaw when an object breaks between the teeth.

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