

## RESEARCH ARTICLE

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## Phasic and tonic stretch reflexes in muscles with few muscle spindles: human jaw-opener muscles

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**Abstract** We investigated phasic and tonic stretch reflexes in human jaw-opener muscles, which have few, if any, muscle spindles. Jaw-unloading reflexes were recorded for both opener and closer muscles. Surface electromyographic (*EMG*) activity was obtained from left and right digastric and superficial masseter muscles, and jaw orientation and torques were recorded. Unloading of jaw-opener muscles elicited a short-latency decrease in *EMG* activity (averaging 20 ms) followed by a short-duration silent period in these muscles and sometimes a short burst of activity in their antagonists. Similar behavior in response to unloading was observed for spindle-rich jaw-closer muscles, although the latency of the silent period was statistically shorter than that observed for jaw-opener muscles (averaging 13 ms). Control studies suggest that the jaw-opener reflex was not due to inputs from either cutaneous or periodontal mechanoreceptors. In the unloading response of the jaw openers, the tonic level of *EMG* activity observed after transition to the new jaw orientation was monotonically related to the residual torque and orientation. This is consistent with the idea that the tonic stretch reflex might mediate the change in muscle activation. In addition, the values of the static net joint torque and jaw orientation after the dynamic phase of unloading were related by a monotonic function resembling the invariant characteristic recorded in human limb joints. The torque-angle characteristics associated with different initial jaw orientations were similar in shape but spatially shifted, consistent with the idea that voluntary changes in jaw orientation might be associated with a change in a single parameter, which might be identified as the threshold of the tonic stretch reflex. It is suggested that functionally significant phasic and tonic stretch reflexes might not be mediated exclusively

by muscle spindle afferents. Thus, the hypothesis that central modifications in the threshold of the tonic stretch reflex underlie the control of movement may be applied to the jaw system.

**Key words** Jaw movement · *EMG* · Stretch reflex · Muscle spindle · Human

### Introduction

Proprioception probably plays a fundamental role in kinesthesia, in the organization of spatial frames of reference for movement production and in the position- and velocity-dependent regulation of muscle activity essential for the stability of posture and movement (Feldman and Levin 1995). It is usually assumed that this regulation (termed the stretch reflex) is produced mainly by muscle spindle afferents under the control of fusimotor innervation (Matthews 1981). Muscle spindles are found in most skeletal muscles, but there are notable exceptions. In humans, this includes a number of orofacial muscles, in particular, the lip muscle orbicularis oris and the jaw protruder lateral pterygoid, where, in each case, few muscle spindles have been reported. Similarly, the number of muscle spindles in the jaw-opener anterior digastric are few in comparison with the jaw-closer muscles (Lennartsson 1979; see Rowleson 1990 for review).

The stretch reflex plays a significant role in the regulation of activity of jaw-closer muscles (see Hannam and McMillan 1994; Lund et al. 1983; Luschei and Goldberg 1981; Smith 1992 for reviews). However, even though an unloading and tonic stretch response and tonic vibration reflexes have been observed in jaw-opener muscles (Hannam et al. 1968; Hellsing 1977; Lamarre and Lund 1975; Neilson et al. 1979), it has been suggested that the stretch reflex plays a minimal role in the regulation of activity in these muscles (see Luschei and Goldberg 1981 for summary).

In the present paper, we hypothesize that, even in jaw-opener muscles that have few muscle spindles, function-

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ally significant stretch reflexes can be observed. To test this hypothesis, we investigated jaw-opener reflexes using both stretch and unloading procedures. The role of the tonic stretch reflex in the regulation of electromyographic (*EMG*) activity in jaw-opener muscles was assessed by examining the torque-angle and static torque-*EMG* relationships in the unloading procedure.

## Materials and methods

The experimental procedures used in these studies have been approved by the ethics committees of the Department of Psychology, McGill University, and the Rehabilitation Institute of Montreal.

### Procedure

Jaw motion, torque and the *EMG* activity of jaw-opener and -closer muscles were recorded during opener and closer unloading trials, which involved sudden decreases in external torque.

On trials involving jaw-opener unloading, torques were applied by positioning the handle of a torque motor (Mavilor Motors; MT 2000) below the chin at the anterior end of the mandible (see Fig. 1). On each trial, the subject assumed a specified initial jaw orientation while resisting a constant net torque (the torque created by the motor minus the gravitational torque of the handle) that opposed jaw opening. The initial jaw orientation was established by asking the subject to raise or lower the jaw until a graphical display of the jaw orientation, which was out of view of the subject, reached a designated zone on a computer monitor. An abrupt decrease in load (10 ms duration) caused the jaw to move downward to assume a new orientation, at which the jaw-opening torque balanced the final upward load.

The jaw-opener unloading trials were repeated using two different initial jaw angles and the same initial load (see Fig. 4). On

each trial, the initial load was either partially or completely removed to one of four (and in one case five) different final levels. For each final level, 15 trials were recorded. The smallest final load was the torque necessary to just support the torque motor handle against gravity. The timing and the magnitude of the unloading were varied randomly. Subjects were instructed to resist the upward load by maintaining the initial jaw orientation as directed by the experimenter and to not correct for the movement of the jaw that resulted from the unloading ("do not intervene"). The final torque was maintained for approximately 0.5 s, after which the residual load was removed, allowing the subject to relax. Four subjects were tested for jaw-opener unloading (subjects S1 and S4 were authors of this report). A small number of trials in which a continuous drift was observed in the final orientation following unloading were excluded from analysis.

For unloading of jaw-closer muscles, a load opposing jaw closing was applied via a dental appliance attached to the torque motor handle. Complete unloading from a single initial jaw angle was tested and ten trials were recorded. Data were obtained for three subjects for jaw-closer unloading.

### Movement and torque recording

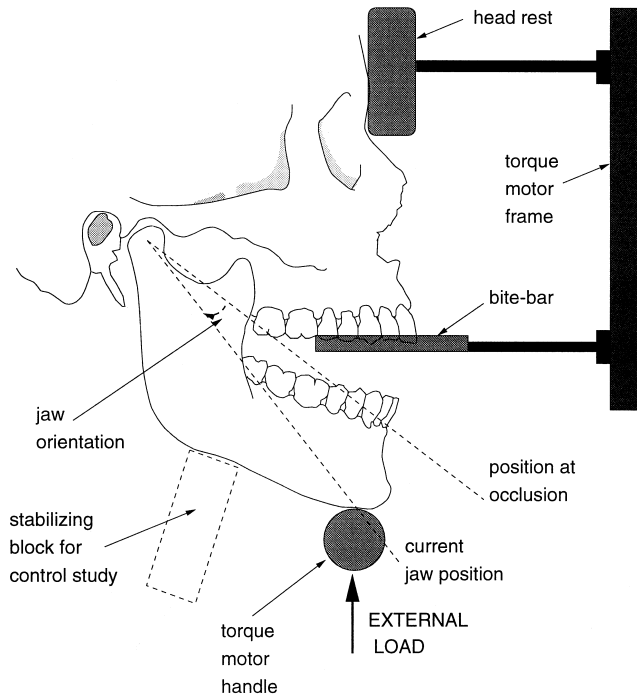
Jaw orientation and torque were recorded for 1 s at 1000 Hz. In all experiments, the head position was stabilized by using a custom-molded dental impression (Mizzy, N.J., USA), which was attached to a bite-bar and in turn firmly fastened to the torque motor frame. A separate, padded head rest was used to further restrict head motion. The position of the handle of the torque motor was recorded throughout the trial and was used to calculate the jaw orientation angle with respect to the position of the condyle center at occlusion. The coordinates of the condyle center were obtained by palpation to locate the condyle center and then by measuring the horizontal and vertical distances from that point to a known reference location (point of contact of the torque motor handle). Jaw muscle torque was calculated from the torque measured by strain gauges on the shaft of the torque motor and by taking into account the moment arm between the center of rotation of the jaw and the point of contact of the jaw with the torque motor handle.

### Muscle-activity recording

Jaw muscle activity patterns were recorded bilaterally from superficial masseter and anterior belly of the digastric using bipolar surface electrodes (two 1-mm silver bars separated by 10 mm; Neuromuscular Research Center). Both anterior digastric and masseter could be readily located by palpation. The electrodes were positioned over the belly of each muscle and oriented to maximize the magnitude of the signal during test maneuvers such as repetitive jaw opening and closing and isometric contraction. *EMG* signals were sampled at 1000 Hz, band-pass filtered between 30 and 400 Hz, rectified, and averaged off-line.

### Data scoring and analysis

Unloading reflex latencies were scored as the interval between the onset of the unloading – obtained from the torque record – and the first visible decrease in the *EMG* level as judged by visual inspection of the data on a trial-by-trial basis. The final torque and jaw orientation were scored when jaw position stabilized following unloading. Mean values (and standard errors) for final torque, jaw orientation, and reflex latency were calculated for each experimental condition and each subject separately (based on 10–15 observations per condition). Statistical tests for differences in reflex latency between conditions were carried out for each subject using *t*-tests.



**Fig. 1** Schematic diagram showing experimental subject during jaw-opener unloading. The head is stabilized during unloading trials using a dental impression of the maxillary teeth

## Control studies

A number of control studies assessed the extent to which aspects of the experimental setup might have contributed to the reflex effects that we report below. We examined the possible involvement of cutaneous afferents, which might have been activated as a result of the external load to the skin beneath the chin. We also explored the possible role of periodontal mechanoreceptors, due to the use of a dental appliance to stabilize the head.

To assess the role of cutaneous afferents, three variants on the jaw-unloading procedure were tested. The first was basically identical to the principal study – the head was restrained but the jaw was free to move. Loads comparable with those used in original test conditions were applied below the chin by means of the torque motor handle. The second and third procedures prevented jaw motion, but in different ways. In the second procedure, jaw opening was restricted by using padded blocks placed between the clavicle and the inferior border of the mandible. As in the original experiment, subjects applied a net jaw opening torque while upward-directed loads were applied below the chin with the torque motor handle. Muscle activity in jaw-opener and -closer muscles was recorded in response to sudden removal of the torque motor load. Since jaw motion was limited, changes in jaw *EMG* activity following unloading might be attributed to changes in cutaneous in-

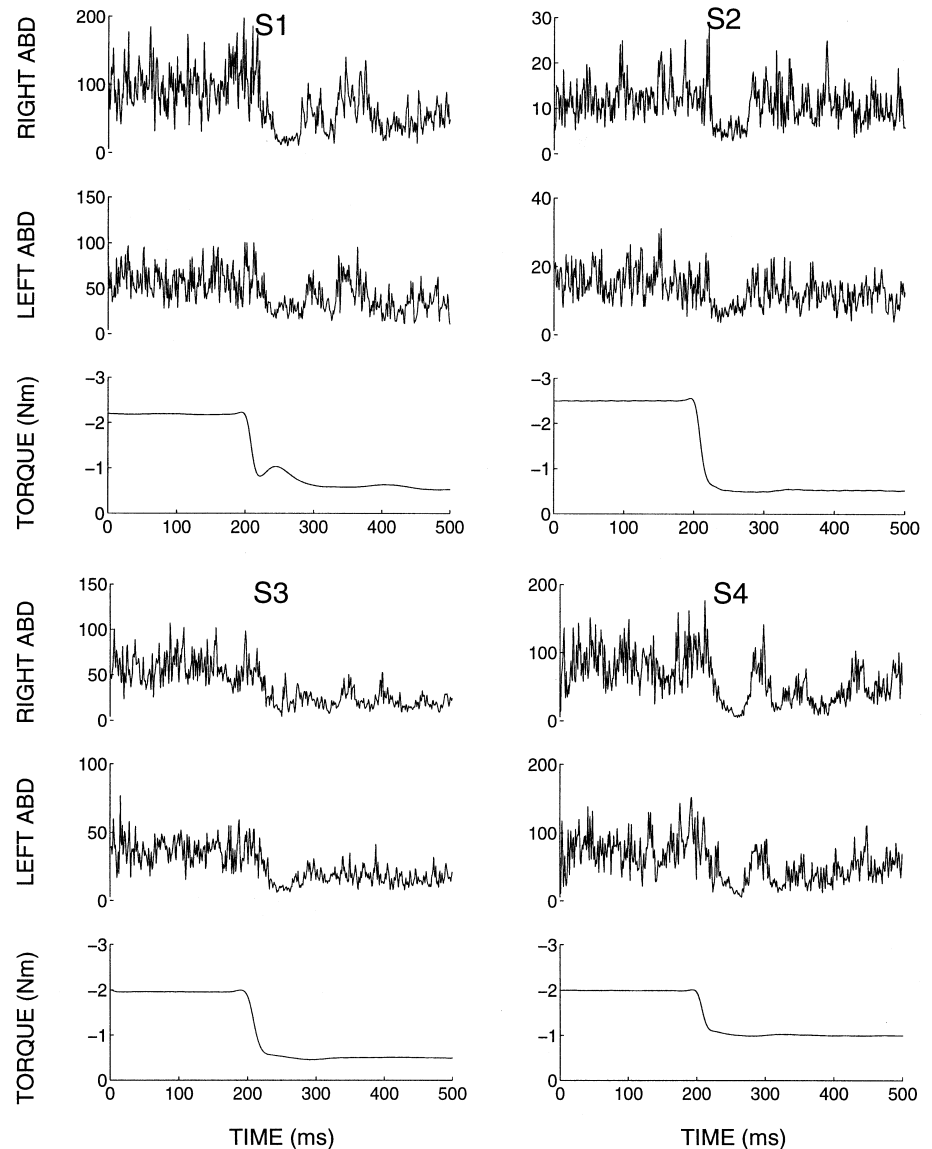
put rather than to changes in muscle length. In the third procedure, motion of the jaw was eliminated by having subjects cocontract opener and closer muscles while applying force to a custom-molded vinyl bite-bar placed between the teeth. Upward loads comparable in magnitude with those used during experimental trials were applied below the chin. The head was restrained as above. The rationale was similar to that of the second control condition. Jaw muscle *EMG* activity was recorded in response to changes in cutaneous load.

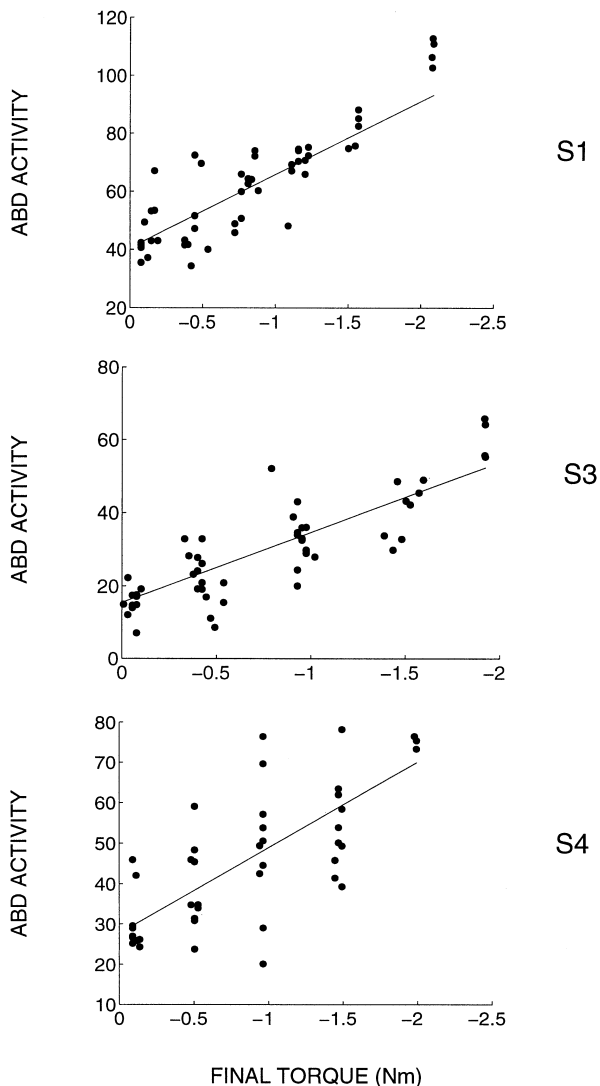
The possibility that the jaw-opener unloading reflex was attributable to periodontal mechanoreceptors was also assessed. This was accomplished by repeating the jaw-opener unloading procedure without the dental appliance, using only the padded head rest and velcro straps to stabilize the position of the head.

## Results

Following sudden unloading of the openers, the jaw moved downward to a new orientation, which stabilized within 100–200 ms. The maximum displacement of the jaw was in the range of 3–4°. The activity level in the

**Fig. 2** Mean *EMG* and torque during jaw-opener unloading. Means for large-amplitude (*S1*, *S2*) and small-amplitude unloading (*S3*, *S4*) are shown. *EMG* levels are in arbitrary units. (Note that the torque transient for *S1* after unloading was due to the velocity gain setting of the torque motor) *ABD* anterior belly of the digastric





**Fig. 3** Final levels of tonic *EMG* activity following jaw-opener unloading. Tonic *EMG* activity in anterior belly of the digastric is shown to increase progressively with the static torque level opposing jaw opening. (Jaw-closing torques are positive in all figures)

jaw-opener muscles likewise decreased abruptly and was followed by a short-duration silent-period and then by a period of tonic activity (Fig. 2). The silent period ranged in duration from an average of about 40–65 ms across subjects. The mean latency ( $\pm SE$ ) of the unloading response (the time between the onset of the unloading and the first visible decrease in the *EMG* level) was similar for all subjects: S1  $22 \pm 1$  ms; S2  $19 \pm 1$  ms, S3  $19 \pm 1$  ms; S4  $21 \pm 1$  ms.

The final tonic *EMG* level in jaw-opener muscles following unloading was found to vary as a function of the final torque opposing the jaw-opening movement (Fig. 3). The tonic *EMG* values were obtained by taking the mean rectified *EMG* level over a 400-ms period after the jaw position stabilized following unloading. A linear re-

gression function was fit to the individual observations. The Pearson product-moment correlation coefficient  $r$  between the tonic *EMG* level and static torque was 0.89, 0.83, and 0.74 for subjects S1, S3, and S4, respectively ( $P < 0.001$ , in all cases). For subject S2, the relationship between tonic *EMG* level and final torque level was not statistically reliable.

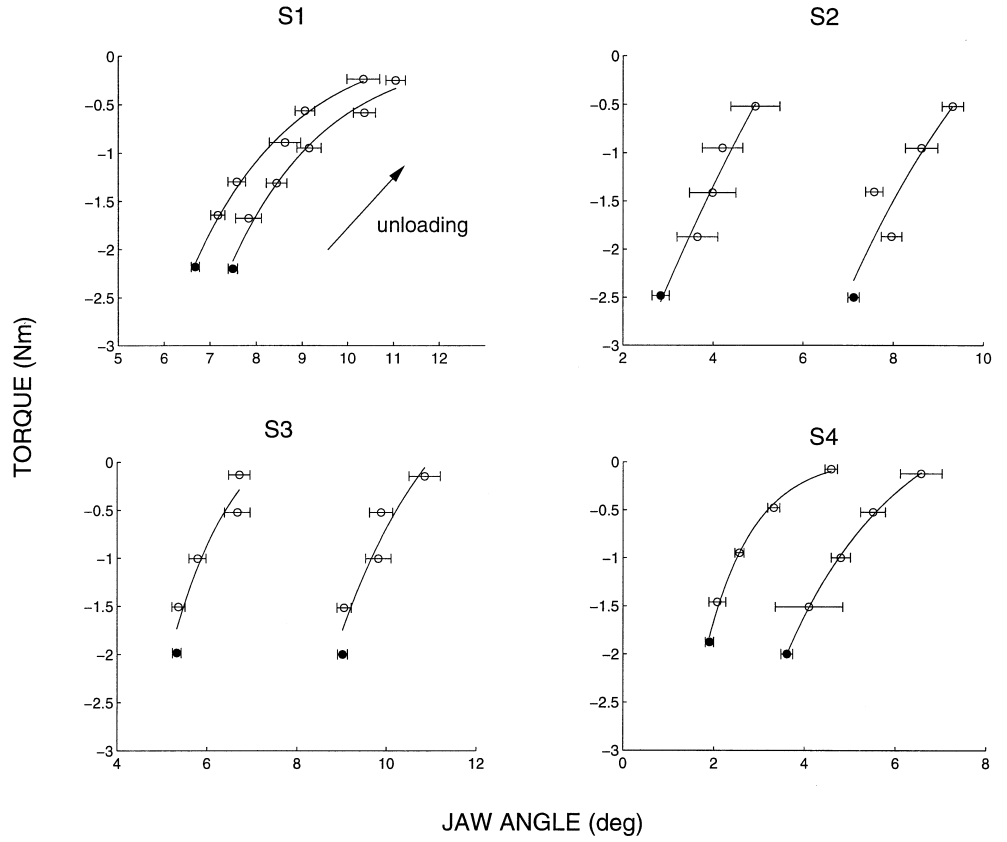
Subjects were instructed not to intervene voluntarily (e.g., Asatryan and Feldman 1965; Levin et al. 1992; see Latash 1993 for review). Since the unloading was rapid (less than 10 ms) and the magnitude and the timing of the unloading were unpredictable, there was little chance of voluntary intervention during unloading. Moreover, an examination of jaw orientation records following unloading suggests that, in most trials, subjects did not modify the final position following unloading despite its difference from the initial position (several degrees). The maximum change in jaw orientation over the final 500 ms of each trial was in the range of  $0.3$ – $0.5^\circ$  for different subjects.

The relationship between static joint torque and final jaw orientation is shown in Fig. 4 for jaw-opener unloading trials. The filled circles give the initial combinations of jaw orientation and torque; each of the open circles shows mean static torque-angle combinations following the dynamic phase of unloading. (It should be noted that torque levels following unloading are fixed by the experimental procedure, while joint angles are free to vary). Static joint torque was thus a monotonic function of jaw orientation, similar to that observed in the arm. An exponential function was used to fit the data. The curves for the two different initial jaw orientations were similar in shape but had different intercepts.

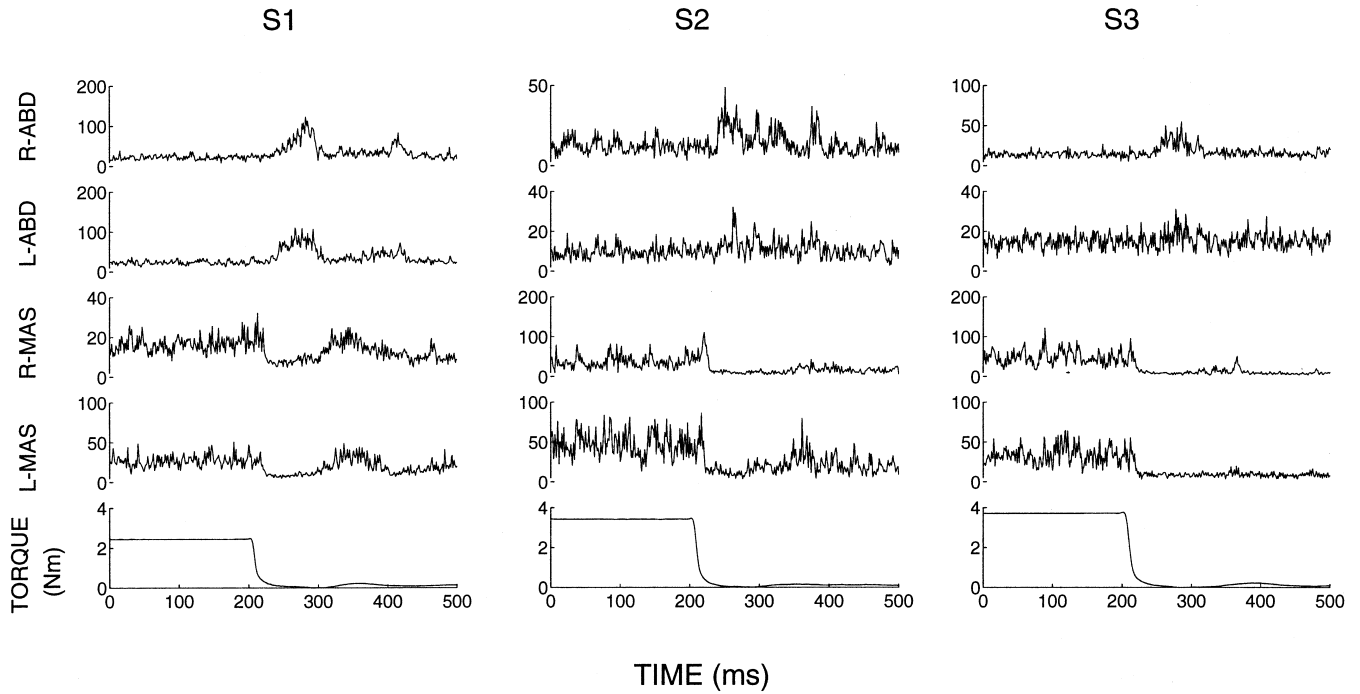
Mean torque and *EMG* activity during jaw-closer unloading are shown in Fig. 5. The jaw-closer unloading is associated with an abrupt decrease in *EMG* activity in the closer muscles and a somewhat later stretch response in the jaw openers. The mean latency of the silent period in the jaw closers was: S1  $13 \pm 1$  ms; S2  $16 \pm 1$  ms; S3  $9 \pm 1$  ms. For subjects S1 and S3, the mean latency of the silent period in jaw closers was shorter than observed in jaw openers ( $P < 0.01$  for both subjects). The latency of the silent period for jaw openers and closers did not differ significantly for subject S2. (Note that subject S4 was not tested in this condition).

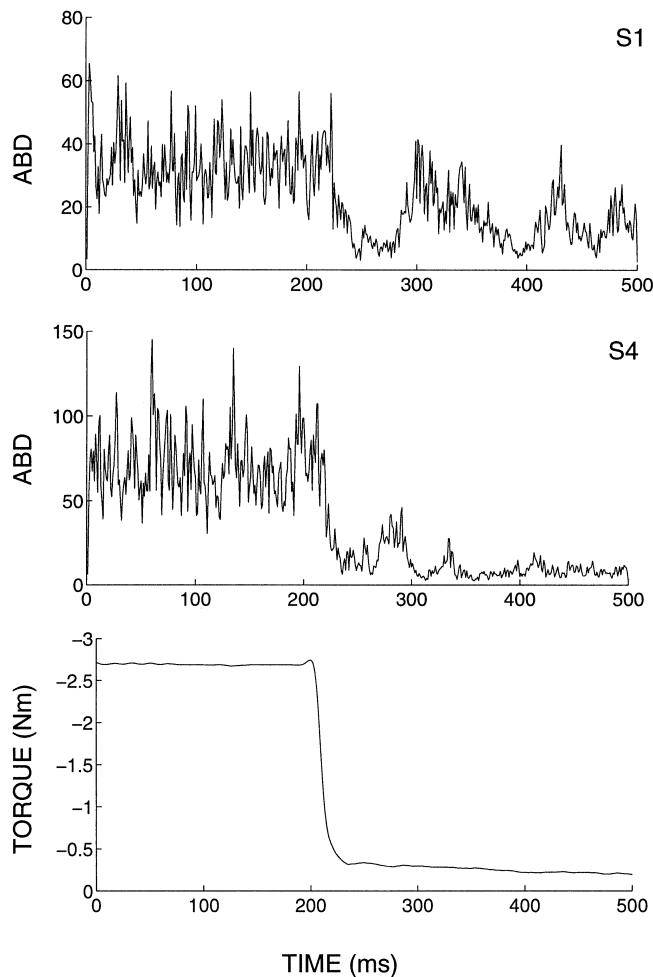
The unloading response in jaw-closer muscles was sometimes accompanied by a short burst of activity in their antagonists, the jaw openers (see Fig. 5). The mean latency of the jaw-opener stretch response – S1  $30 \pm 3$  ms, S2  $35 \pm 3$  ms; S3  $46 \pm 2$  ms – was significantly greater than the latency of the unloading response (latency of the silent period) in the same muscles ( $P < 0.01$  for all subjects).

**Fig. 4** Mean torque-jaw angle functions for jaw-opener unloading from two different initial gape angles. *Filled circles* show initial combinations of jaw orientation and torque. *Open circles* show mean torque-angle combinations following unloading. The torque-angle functions for jaw-opener unloading are almost parallel and differ primarily in terms of their intercepts



**Fig. 5** Mean EMG and torque records during jaw-closer unloading trials. *EMG* levels are in arbitrary units. *ABD* anterior belly of the digastric, *MAS* superficial masseter





**Fig. 6** Mean *EMG* and torque during jaw-opener unloading trials in which head position was stabilized without the use of a dental appliance. *EMG* levels are in arbitrary units *ABD* anterior digastric

#### Control studies

It has been shown previously that short-latency inhibition of jaw-opener muscles might arise as a consequence of loads applied to the periodontal mechanoreceptors of the maxillary teeth (Matthews 1975). As a control for this possibility – that forces applied to the dental appliance during the sudden unloading might have given rise to the reflex actions observed here – we repeated the jaw-opener unloading procedure for S1 and S4 without the dental appliance. The resulting pattern of activity in the jaw-opener muscles was similar to that observed in the trials recorded using the dental appliance (Fig. 6). The mean latency of the unloading response in these control trials was  $21 \pm 3$  ms and  $17 \pm 2$  ms for S1 and S4, respectively. The difference in latency between the two conditions, that is, jaw-opener unloading with and without the maxillary dental appliance, was not statistically significant for either subject, suggesting that the unloading response observed in the jaw-opener muscles was not

due to inhibition arising due to the mechanoreceptors of the maxillary teeth.

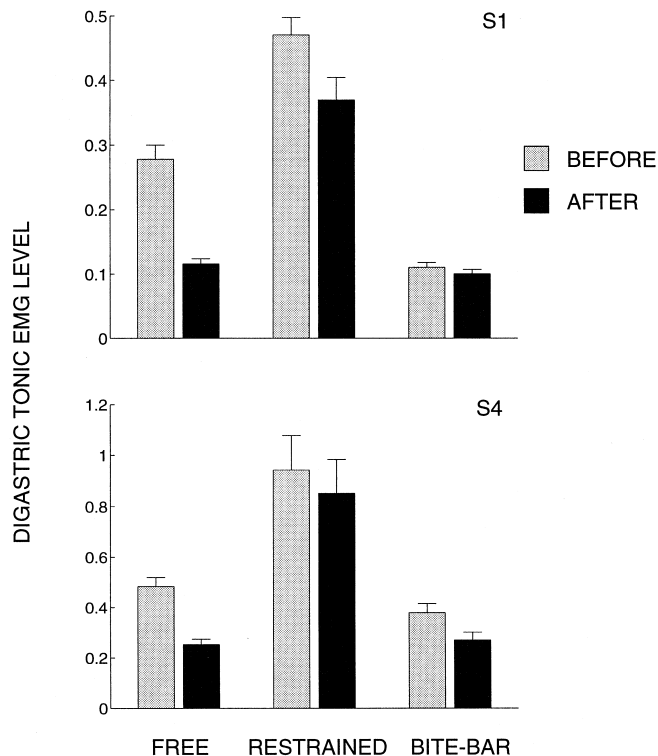
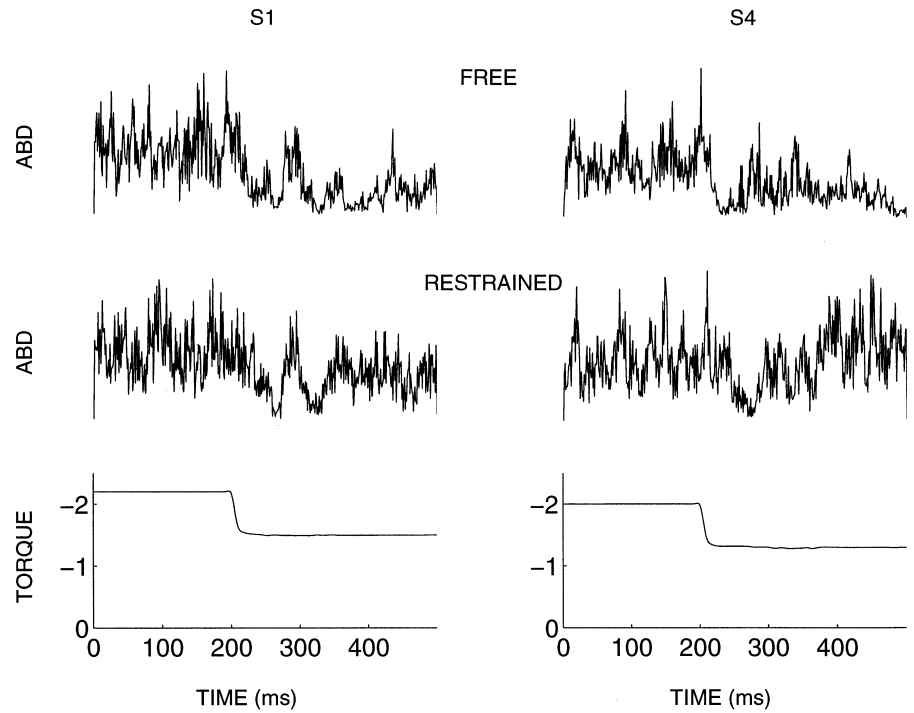
The stimulation of cutaneous afferents is known to result in short-latency changes to jaw-opener *EMG* activity (see Dubner et al. 1978 for review). Thus, a second control study tested for the possibility that inputs from cutaneous afferents, activated as a result of contact of the chin with the torque motor handle, might have given rise to the jaw opener unloading response. The basic jaw-opener unloading procedure was repeated, but motion of the jaw and hence shortening of the jaw-opener muscles was prevented. Under these conditions, afferent contributions from cutaneous inputs to jaw-opener muscles could be dissociated from activity in jaw-opener muscles arising from the motion of the jaw.

Figure 7 shows the mean activity level in the jaw-opener muscles both for trials in which the jaw was free to move following unloading and for trials in which movement was restrained by padded blocks. In both cases, a short-duration silent period was observed following unloading; however, the latency of the response differed in the two conditions. When the jaw was free to move, mean latencies of  $20 \pm 2$  ms and  $23 \pm 1$  ms were obtained for S1 and S4. These latencies were not statistically different from those for the same subjects in the initial experiment. When the jaw was restrained following unloading, significantly longer mean latencies of unloading responses ( $35 \pm 5$  ms and  $47 \pm 3$  ms) were obtained ( $P < 0.01$  for both subjects).

By comparing tonic *EMG* activity before and after unloading, the influence of cutaneous inputs on the level of tonic activity in jaw-opener muscles could be assessed. Tonic *EMG* levels were obtained by taking the mean rectified *EMG* level 200 ms prior to unloading and over a second 200-ms period after the unloading was complete. Figure 8 shows that mean tonic *EMG* levels before and after unloading differed depending on whether the jaw was free to move or restrained. When the jaw was free to move, tonic *EMG* levels decreased significantly following unloading ( $P < 0.01$  for both subjects). When the jaw was restrained with the blocks, *EMG* levels prior to and following unloading did not differ statistically for either subject.

The mean *EMG* activity is shown in Fig. 9 for the condition in which the subject cocontracted jaw-opener and -closer muscles while holding a vinyl bite-bar between the teeth. As in other conditions, there was a step-like decrease in the torque applied beneath the chin. In this case, we observed a short-latency silent period in masseter activity ( $19 \pm 1$  ms and  $25 \pm 2$  ms for S1 and S4, respectively) with no corresponding decrease in the activity level of jaw-opener muscles. As in the other cutaneous control test, no differences in tonic *EMG* levels following unloading were obtained in the bite-bar condition (see Fig. 8).

**Fig. 7** Mean *EMG* level and torque during jaw-opener unloading trials in which the jaw was either free to move or restrained using supporting blocks between the clavicle and the mandible. *EMG* levels are in arbitrary units. *ABD* anterior digastric



**Fig. 8** Tonic *EMG* level in anterior digastric prior to and following unloading in control trials involving free jaw movement, restrained movement, and unloading while subjects cocontracted jaw-opener and -closer muscles against a bite-bar between the teeth ( $\pm 1$  SE is shown). *EMG* levels are in arbitrary units

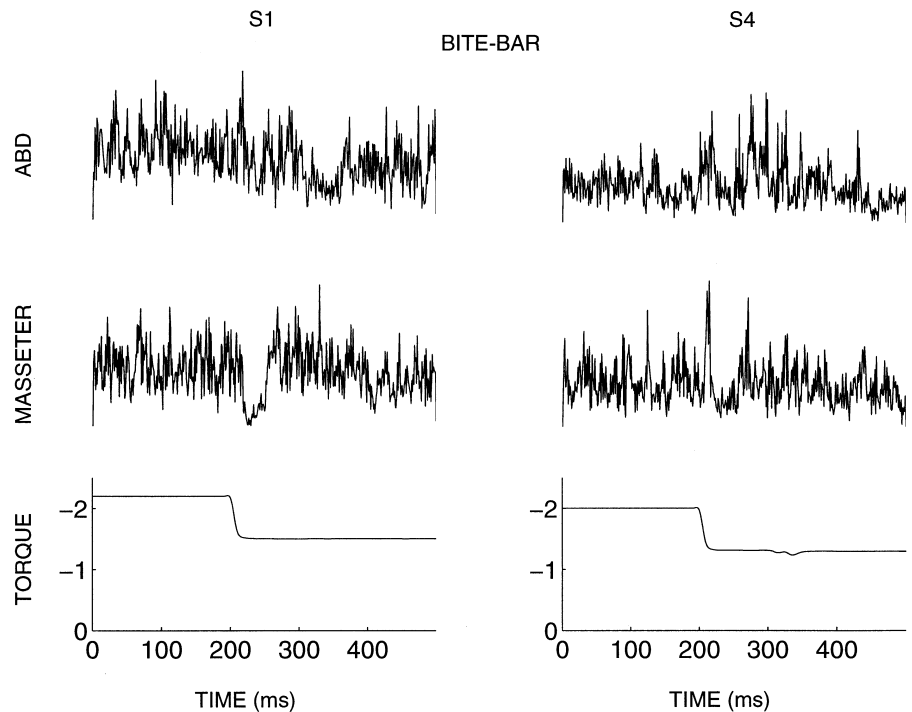
## Discussion

In the present paper, tonic and phasic reflexes were observed in jaw-opener muscles using both stretch and unloading procedures. The unloading responses observed in the jaw-opener muscles were characterized by short-latency decreases in opener *EMG* activity at intervals averaging about 20 ms following unloading. This latency is comparable with that reported for anterior digastric unloading (about 27 ms; Lamarre and Lund 1975).

The static joint torque following unloading was a monotonic function of the final jaw orientation. In addition, the tonic *EMG* levels in jaw openers following the achievement of final jaw position varied directly with final torque. Taken together, these findings are consistent with previous empirical and modeling studies of human arm movement that demonstrate the dependence of *EMG* level on joint angle. The present results are thus consistent with the idea that the tonic stretch reflex may play a functionally significant role in the regulation of jaw-opener *EMG* activity.

The torque-angle characteristics obtained during jaw-opener unloading were comparable in shape with those reported previously for unloading responses about the elbow and wrist (Asatryan and Feldman 1965). Characteristics that were initiated from different initial jaw orientations were similar in shape but were shifted spatially. The transition from one initial jaw orientation to the other is, therefore, presumably a voluntary action. These findings are in agreement with the hypothesis that voluntary changes in jaw orientation might be associated with changes to a single parameter,  $\lambda$ , resembling the threshold of the stretch reflex – in the present case, the thresh-

**Fig. 9** Mean *EMG* levels and torque during jaw-opener unloading while a subject held a bite-bar between the teeth



old corresponds to the jaw orientation at which tonic *EMG* activity and force development is initiated (see Figs. 3, 4). Thus, the  $\lambda$  model of motor control, initially formulated for limb skeletal muscles, may be applied to jaw muscles as well (Laboissière et al. 1996).

It has been demonstrated previously that low-threshold, nonnociceptive afferent inputs other than those arising in jaw-opener muscles might contribute to jaw-opener reflexes (see Dubner et al. 1978; Lund 1990; Luschei and Goldberg 1981; Matthews 1975; Sessle 1981 for reviews). This includes inputs originating in the periodontal ligament, oral mucosa, temporomandibular joint, facial skin, and muscle afferents. The results of our control studies suggest that at least some of these factors – inputs to jaw-opener motoneurons from mechanoreceptors in the periodontal ligament and from cutaneous receptors in the skin beneath the chin – can be ruled out as contributors to the unloading responses reported in the present study.

For example, the presence of an unloading response in the jaw openers in the absence of any load to the maxillary teeth suggests that the periodontal mechanoreceptors are unlikely to be the source of the observed reflex action. The pattern of the cutaneous reflexes that were evoked is likewise inconsistent with the pattern observed during jaw-opener unloading. In particular, when padded blocks were used to restrain jaw movements, the latency of the unloading response in jaw-opener muscles due to cutaneous inputs was significantly longer than the latency obtained when the jaw was free to move. Hence, cutaneous inputs are not likely to be involved in the initiation of the silent period which may be observed when the jaw is free. Cutaneous inputs to jaw-opener motoneurons might, nevertheless, play a role in determining the dura-

tion of the silent period. It should also be noted that cutaneous inputs to jaw-opener motoneurons cannot account for the changes in tonic level of activity in the openers when the jaw is free to move, since tonic *EMG* levels remained unchanged in trials in which unloading resulted in the removal of the cutaneous input alone.

The observation of tonic and phasic stretch responses in the jaw openers implies that proprioceptive inputs to motoneurons play an important role in regulating the activity of these muscles, even though they contain few muscle spindles. These inputs might arise from a number of sources. Spindle afferents in jaw-opener muscles might be sufficient in number to provide the observed patterns of responses (Lennartsson 1979). However, nonspindle afferents such as free nerve endings in the opener muscles might contribute as well (Alvarado-Mallart et al. 1975). Our data provide some support for this possibility. In spindle-rich masseter muscles, the latencies of unloading reflexes were shorter (averaging 13 ms) than latencies in jaw-opener muscles (mean value 20 ms). The difference is consistent with the possibility that unloading responses in jaw openers might have been mediated by smaller diameter afferent fibers and/or polysynaptic connections to motoneurons. Tendon organ afferents could likewise play a role. Tendon organs are present in reasonable numbers at least in jaw-closer muscles (Lund et al. 1978). However, they have yet to be identified in jaw openers. In addition, afferents from temporomandibular joint receptors and from closer muscles to jaw-opener motoneurons might possibly contribute to the reflex effects observed in the present study. The latter possibility is perhaps less likely, as there is no evidence of reciprocal inhibition – no Ia inhibitory interneuron – between closer or opener muscles that might



mediate this effect (see Luschei and Goldberg 1981 for summary).

The present findings might seem inconsistent with studies that suggest that proprioception plays a minimal role in the control of orofacial motion. For example, Goodwin and Luschei (1974) have shown that few changes occur in jaw movement patterns or *EMG* activity during mastication in monkeys following the elimination of proprioceptive input from muscle spindle afferents (also see Dellow and Lund 1971). However, the results of such experiments might not be appropriate to support the suggestion of a limited role for proprioception in the intact system if one takes into account the immediate and long-term consequences of deafferentation, such as changes in neuronal excitability, sprouting, and synaptic plasticity (Goldberger and Murray 1978; Hellgren and Kellerth 1989; Kaas 1991). Thus, deafferentation experiments might be inappropriate studies from which to draw conclusions regarding the role of muscle or skin afferents in intact systems. The observation of a silent period in response to unloading in jaw as well as in arm muscles (see Forget and Lamarre 1987; Gerilovsky et al. 1990) demonstrates that proprioception might play a fundamental role in the activation of motoneurons of normally innervated muscles.

The potential contribution of cutaneous stimuli to jaw-opener unloading was tested by varying the mechanical conditions rather than by deafferentation of the skin by anesthesia. As has been argued above, such deafferentation could interfere with the normal patterns of excitability of jaw muscles, making the interpretation of results equivocal. Instead, our control studies were based upon the intact system in which the motion of the jaw in response to unloading was restricted. We were thus able to specifically address the role of the cutaneous stimuli (pressure on the chin from the handle of the torque motor and then its sudden decrease) in jaw-opener muscle activity. In these conditions, the jaw-opener unloading response was either delayed or absent depending on experimental conditions, and no change in the tonic *EMG* level of opener muscles was observed. Our findings imply that, in trials in which the jaw was free to move, the cutaneous stimulus was not responsible for the initiation of the silent period, nor was it responsible for the position-dependent regulation of jaw-opener *EMG* activity.

Although the basic principles of sensorimotor integration are probably similar in the arm and the jaw, some differences should be emphasized. For example, in limb motor systems, influences of descending commands are usually mediated by interneurons of reflex loops. However, in the jaw, no Ia inhibitory interneuron has been identified between either closer or opener groups of muscles. There is, in addition, no evidence of recurrent inhibition of trigeminal motoneurons (see Luschei and Goldberg 1981; Olsson and Landgren 1990 for reviews). The central commands that underlie jaw motions might be produced by direct inputs to motoneurons from descending pathways or be mediated by the interneurons of other

jaw reflex pathways. This, however, does not rule out the applicability of the  $\lambda$  model to jaw muscles, since the model takes into account both direct and indirect control inputs to motoneurons.

A number of possible sources of experimental error should be taken into consideration. First, using surface *EMG* electrodes we could not separately investigate the reflex reactions of other jaw openers such as the mylohyoid and geniohyoid. Thus, although the recording electrode was oriented to measure activity in the digastric, and even though the fibers of the mylohyoid and anterior digastric lie in roughly orthogonal directions, contributions from other jaw-opener muscles cannot be completely ruled out. Second, the study has not examined separately the reflex contribution to the orientation of the jaw as opposed to its horizontal position (see Sessle 1981 for a summary of work on horizontal jaw reflexes). This information is relevant, since, at least in the case of human jaw motions in speech, the jaw orientation angle and the jaw position appear to be separately controlled (Ostry and Munhall 1994).

In summary, we have demonstrated phasic and tonic reflexes in jaw-opener muscles using both stretch and unloading procedures. Tonic *EMG* levels were shown to vary monotonically with final torque and jaw orientation. Jaw torque-angle functions obtained during jaw-opener unloading resemble the invariant characteristics of the human elbow joint (Feldman 1966). We conclude that phasic and tonic stretch reflexes are functionally significant not only in jaw closers but also in jaw-opener muscles and that the regulation of the thresholds of the tonic stretch reflex of muscles might, as in other musculoskeletal systems, underlie the control of jaw movements (see Laboissière et al. 1996).

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## References

- Alvarado-Mallart MR, Batini C, Buisseret-Delmas C, Corvisier J (1975) Trigeminal representations of the masticatory and extraocular proprioceptors as revealed by horseradish peroxidase retrograde transport. *Exp Brain Res* 23:167-179
- Asatryan DG, Feldman AG (1965) Functional tuning of the nervous system with control of movements or maintenance of a steady posture. I. mechanographic analysis of the work of the limb on execution of a postural task. *Biophysics* 10:925-935
- Dellow PG, Lund JP (1971) Evidence for central timing of rhythmic mastication. *J Physiol* 215:1-13
- Dubner R, Sessle, BJ, Storey AT (1978) The neural basis of oral and facial function. Plenum Press, New York
- Feldman A (1966) Functional tuning of the nervous system with control of movement or maintenance of a steady posture. II. Controllable parameters of the muscle. *Biophysics* 11:565-578
- Feldman AG, Levin MF (1995) The origin and use of positional frames of reference in motor control. *Behav Brain Sci* 18:723-806
- Forget R, Lamarre Y (1987) Rapid elbow flexion in the absence of proprioceptive and cutaneous feedback. *Hum Neurobiol* 6:27-37

- Gerilovsky L, Struppler A, Velho F, Niehage O (1990) Discharge pattern of tonically activated motor units during unloading. *Electromyogr Clin Neurophysiol* 30:459–467
- Goldberger ME, Murray M (1978) Axonal sprouting and recovery of function may obey the same laws. In: Cotman C (ed) *Neuronal plasticity*. Raven Press, New York, pp 73–96
- Goodwin GM, Luschei ES (1974) Effects of destroying spindle afferents from jaw muscles on mastication in monkeys. *J Neurophysiol* 37:967–981
- Hannam AG, McMillan AS (1994) Internal organization of human jaw muscles. *Crit Rev Oral Biol Med* 5:55–89
- Hannam AG, Matthews B, Yemm R (1968) The unloading reflex in masticatory muscle of man. *Arch Oral Biol* 13:361–364
- Hellgren J, Kellerth JO (1989) A physiological study of the monosynaptic reflex responses of cat spinal  $\alpha$  motoneurons after partial lumbosacral deafferentation. *Brain Res* 488:149–162
- Hellsing G (1977) A tonic vibration reflex evoked in the jaw opening muscles in man. *Arch Oral Biol* 22:175–180
- Kaas JH (1991) Plasticity of sensory and motor maps in adult mammals. *Ann Rev Neurosci* 14:137–167
- Laboissière R, Ostry DJ, Feldman AG (1996) Control of multi-muscle systems: human jaw and hyoid movements. *Biol Cybern* 74:373–384
- Lamarre Y, Lund JP (1975) Load compensation in human masseter muscles. *J Physiol (Lond)* 253:31–35
- Latash M (1993) Control of human movement. Human Kinetics, Urbana, Ill
- Lennartsson B (1979) Muscle spindles in the human anterior digastric muscle. *Acta Odontol Scand* 37:329–333
- Levin MF, Feldman AG, Milner TE, Lamarre Y (1992) Reciprocal and coactivation commands for fast wrist movements. *Exp Brain Res* 89:669–677
- Lund JP (1990) Specializations of the reflexes of the jaws. In: Taylor A (ed) *Neurophysiology of the jaws and teeth*. Macmillan, London, pp 142–161
- Lund JP, Richmond FJR, Touloumis C, Patry Y, Lamarre Y (1978) The distribution of golgi tendon organs and muscle spindles in masseter and temporalis muscles of the cat. *Neuroscience* 3:259–270
- Lund JP, Lamarre Y, Lavigne G, Duquet G (1983) Human jaw reflexes. In: Desmedt JE (ed) *Motor control mechanisms in health and disease*. Raven Press, New York, pp 739–755
- Luschei ES, Goldberg LJ (1981) Neural mechanisms of mandibular control: mastication and voluntary biting. In: Brooks VB (ed) *Motor control*. (Handbook of physiology, sect 1. The nervous system, vol II, part 2). American Physiological Society, Bethesda, Md, pp 1237–1274
- Matthews B (1975) Mastication. In: Lavelle CL (ed) *Applied physiology of the mouth*. Wright, Bristol, UK, pp 199–242
- Matthews PBC (1981) Muscle spindles: their messages and their fusimotor supply. In: Brooks VB (ed) *Motor control*. (Handbook of Physiology, sect 1. The nervous system, vol II, part 1) American Physiological Society, Bethesda, Md, pp 189–229
- Neilson PD, Andrews G, Guitart BE, Quinn PTG (1979) Tonic stretch reflexes in lip, tongue and jaw muscles. *Brain Res* 178:311–327
- Olsson KÅ, Landgren S (1990) Primary afferent and descending cortical convergence on the interneurons in the border zone of the trigeminal motor nucleus: a comparison between trigeminal and spinal interneurons. In: Taylor A (ed) *Neurophysiology of the jaws and teeth*. Macmillan, London, pp 162–191
- Ostry DJ, Munhall KG (1994) Control of jaw orientation and position in mastication and speech. *J Neurophysiol* 71:1515–1532
- Rowlerson AM (1990) Specialization of mammalian jaw muscles: fibre type compositions and the distribution of muscle spindles. In: Taylor A (ed) *Neurophysiology of the jaws and teeth*. Macmillan, London, pp 1–51
- Sessle BJ (1981) Initiation, regulation and significance of jaw muscle reflexes. In: Kawamura Y, Dubner R (eds) *Oral-facial sensory and motor functions*. Quintessence, Tokyo, pp 187–203
- Smith A (1992) The control of orofacial movements in speech. *Crit Rev Oral Biol Med* 3:233–267