Exp Brain Res (1996) 107:486–496

RESEARCH ARTICLE

Mats Trulsson · Roland S. Johansson

Forces applied by the incisors and roles of periodontal afferents during food-holding and -biting tasks

Received: 15 November 1994 / Accepted: 28 August 1995

Abstract The force exerted by the central incisors while holding and splitting a food morsel was analyzed to characterize human biting behavior. The force was continuously sampled by a transducer-equipped plate upon which a small piece of dry biscuit or half a peanut rested. Subjects were instructed to position the plate between the incisor teeth and to split the morsel either immediately ("split task") or after holding it for a brief period ("hold-and-split task"). While holding either food substance between the incisors, subjects automatically exerted light contact forces of less than 1 N (0.36–0.76N range among subjects). Considering that the subjects had no instructions about what force levels to employ, the hold force was remarkably stable during individual trials and highly similar among trials. Even during the split task, subjects opted to "hold" the morsel momentarily on ca. 50% of the trials with a similar, low contact force. For both tasks, subjects split the morsel by exerting a distinct, rapidly executed ramp increase in force. The split occurred at 7.8–10.3 N (range among subjects) bite force for the biscuit and 16.0–19.0 N for the peanut. The magnitude of the forces used during the hold phase were within the range over which most periodontal afferents are optimally sensitive to changes in force, i.e., forces below about 1 N. This observation suggested that the subjects automatically adjusted the force to maximize the availability of information from periodontal afferents and avoided higher forces at which the sensitivity of most afferents was not optimal. We further confirmed that the periodontal receptors serve a role in controlling the hold force by anesthetizing the periodontal tissues: subjects employed considerably higher and more variable hold forces, but there was no effect on the split phase. In addition, the morsel frequently escaped from the incisal edges of the teeth while the subject attempted to maintain it in position. It was concluded that subjects rely on signals from periodontal afferents to regulate the jaw muscles, particularly when they first contact, manipulate, and hold food substances between the teeth.

Key words Periodontal afferent · Mechanoreceptor · Biting · Sensorimotor control · Human

M. Trulsson (✉) · R. S. Johansson
Department of Physiology, University of Umeå,
S-90187 Umeå, Sweden;
Fax: +46-90 16 66 83

Introduction

There are several investigations indicating that periodontal afferents, which are activated by forces applied to the crowns of the teeth, are involved in the control of the jaw muscles during biting and chewing (see Lund 1991 for review). Inhibitory reflex responses may be evoked in the jaw-closing muscles in humans when the periodontal receptors are stimulated by tapping briskly on the teeth (e.g., Sessle and Schmitt 1972; van der Glas et al. 1985; Brodin et al. 1993). This promotion of jaw opening is thought to be analogous to the automatic withdrawal movements of a limb that is triggered by unexpected touch or noxious stimuli. However, periodontal afferents may also excite the motoneurons of jaw-closing muscles in humans during powerful biting, since local anesthesia of the teeth greatly reduces maximum voluntary biting force (Lund and Lamarre 1973). The notion that periodontal receptors can provide a "positive feedback" during power phases of jaw-closing actions has been further supported in more recent animal experiments (Lavigne et al. 1987; Morimoto et al. 1989; see also Inoue et al. 1989) and human experiments (Amano and Yoneda 1980; Ottenhoff et al. 1992a, b; Brodin et al. 1993). Since the responses of most periodontal afferents saturate at these high tooth loads, they would not be expected to provide much information about the precise magnitude of the force. Typically, their discharge rates follow a "hyperbolic" stimulus-response relationship for which forces above about 1 N lead to no greater response (Pfaffmann 1939; Hannam 1969; Trulsson and Johansson 1994; see also Appenteng et al. 1982). Moreover, the dynamic and static sensitivities of human periodontal afferents decrease in parallel with increasing amplitude of tooth loading (Trulsson and Johansson 1994). Because of their pronounced sensitivity to force magnitude and change at very low contact forces, one would conclude that their input may be particularly important to orofacial function during the initial contact with food during the chewing cycle and during other manipulative actions involving the teeth, e.g., while food is positioned and held prior to biting.

The purpose of the present study was to analyze the role of periodontal afferent signals in controlling "manipulative" and "power" elements of human biting behavior. In addition to positioning a morsel of food in the mouth, the tasks involved holding and splitting the morsel between a pair of opposing incisors. We first recorded and analyzed the time-varying forces exerted by the teeth, since little is known about these forces. The force profiles were related to the force-encoding properties of human periodontal afferents. Second, by blocking the afferent input from the periodontal tissues and observing the effects on subjects' behavior, we assessed the extent to which control of the "manipulative" and "power" elements depended on the periodontal afferent input. An abstract of preliminary results has been published previously (Trulsson and Johansson 1993).

Materials and methods

Subjects

Two female and two male subjects (ages 18–31 years) were extensively studied. Each subject gave informed consent in accordance with the Declaration of Helsinki. The study was approved by the local ethical committee at Umeå University.

Apparatus

A simple device was fabricated by which the forces exerted on test food substances by the teeth could be measured (Fig. 1A). The thickness of one end of a 12-cm-long hard wooden bar (diameter 10 mm, weight 18 g) was reduced to accommodate a duralumin plate (stiffness 30 N/mm). The free-end portion of the plate provided support for the test morsel. Strain gauges were mounted to the proximal portion of the plate to continuously measure the force applied normally to its surface (d.c. –200 Hz). Force signals were sampled by a data collection/analysis system at 800 Hz with 12 bits of resolution (SC/ZOOM; Department of Physiology, Umeå University).

Behavioral task

For each trial, a morsel of the test food substance was positioned on the free-end portion of the duralumin plate, which was thereafter maintained in a horizontal position. The subject inserted the transducer end of the bar in their mouth until the mid-portion of the morsel could be contacted by an upper central incisor (Fig. 1A). If the food was lost prior to splitting (i.e., either the subject dropped the food while positioning the transducer bar in the mouth or the food escaped from the incisal edges of the teeth after contact), a new morsel was provided and the trial was resumed.

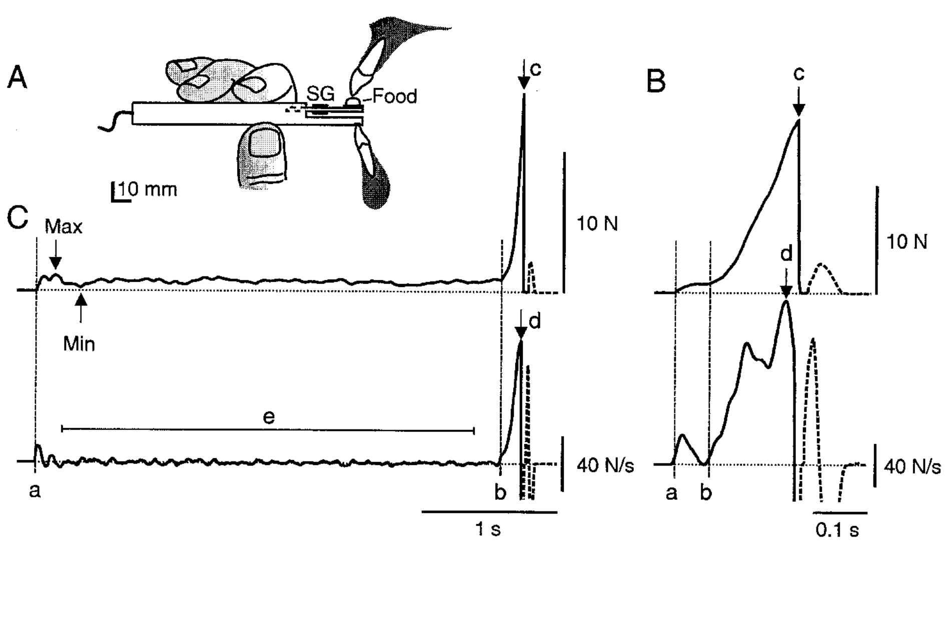
Two tasks were studied. For the "split task" the subject was instructed to split the food without delay. For the "hold-and-split task" the subject was instructed to hold the food for about 3 s between the teeth before splitting it. The subjects were not given any instructions regarding the forces that they were to use.

Two test foods that differed in consistency and texture were studied: half a peanut (Estrella; AB Estrella, Sweden) and a piece of a biscuit (McVities Digestive, United Biscuits, UK).

Experimental procedure

Each subject participated in four series of 40 trials (80 trials were delivered in the first series). Subjects were instructed on the split

Fig. 1 **A** Apparatus used to continuously record the force exerted on the test food substance. Subjects were instructed to position the bar so that the morsel (a peanut in this case) could be held and split by a pair of opposing central incisors. The food morsel rested on a horizontal plate of duralumin equipped with strain gauges (*SG*) for force measurement. **B, C** Examples of single-trial force profiles (*upper traces*) obtained during the split task (**B**) and the hold-and-split task (**C**). The *lower traces* illustrate the force rate. *Dashed* components of the curves indicate additional force peaks caused by the upper incisors gently hitting the support plate following the split. Events of interest include: *a* initial contact with the food; *b* onset of the split phase; *c* point at which maximum split force was attained; *d* point at which maximum or peak split force rate was attained; *e* interval in **C** beginning 0.2 s after initial contact with the food and ending 0.2 s prior to the onset of the split phase. Note the slower time base in **C** than in **B**



task prior to the first and third series and the hold-and-split task prior to the second and fourth series. The first half of the trials in each series employed a biscuit morsel; and the second half, a peanut morsel. The third and fourth series of trials were administered 24 h after the first and second series and after local anesthesia to the periodontal tissues.

Anesthesia of periodontal tissues

Anesthesia was accomplished by injection of a prilocaine solution (30 mg/ml) with felypressin (0.54 µg/ml; Citanest, Octapressin, Astra). The four maxillary incisors were anesthetized by local infiltration of about 1 ml in the buccal sulcus opposite each tooth combined with a nasopalatine block (ca. 0.1 ml). In the lower jaw, the anesthesia was accomplished by bilateral mental block (ca. 1.5 ml at each side) combined with lingual infiltrations (ca. 0.2 ml at each side).

Clinical anesthesia of the teeth was confirmed with an electrical "pulp tester" (Model 2006, Vitality Scanner; Analytic Technology, Redmond, Wash., USA), and of the adjacent gingiva by lack of response to touch and pinprick. Thus, afferent fibers from the pulp, periodontal ligaments, the gingiva, and lower and upper labial mucosa were presumed to have been blocked.

Extraction of quantitative estimates that characterize biting behavior

For each trial, the data collection/analysis software provided a profile of the force and a profile of its first derivative, the *force rate* (calculated within windows of ±6.25 ms), as a function of time (Fig. 1B, C). From the pair of profiles, the following events were identified:

A. The time of *contact* (*x*-value at point a in Fig. 1B, C), identified as the time of occurrence of the first increase in the force from baseline
B. The *onset of the split phase* (*x*-value at point b), identified as the time at which the force rate first exceeded 5 N/s during the force ramp that split the morsel (5 N/s was the minimum rate that could be reliably detected in single-trial records)
C. The *end of the split phase* (*x*-value at point c), identified as the time at which the morsel was split, indicated by the rapid decline in the force ramp

The following quantitative measures were subsequently extracted to characterize the subject's biting behavior during each trial:

1. The *split force* (*y*-value at point c in Fig. 1B, C), defined as the peak force attained at the moment that the morsel was split
2. The *peak split force rate* (*y*-value at point d in Fig. 1B, C), defined as the maximum value of the force rate that occurred during the *split phase* (i.e., the period between points b and c)
3. The *duration of the split phase*, defined as the time interval between the events that delimited the split phase, b and c
4. The *averaged hold force*, defined as the mean value of the force during the central "stationary" portion of the *hold phase*, indicated as "e" in Fig. 1C. This portion of the hold phase was defined as the period that began 0.2 s after initial contact with the food ("a") and ended 0.2 s prior to the onset of the split phase ("b")
5. The *standard deviation of the hold force*, calculated over the central stationary portion of the hold phase to assess the stability at which the subject held the morsel during the individual trial.

Statistical analyses

The impact of the two different tasks, the two different food substances, and presence (vs absence) of anesthesia on each of the five quantitative measures described above was assessed by repeated-measures analysis of variance. Linear trends in the measures were quantitatively assessed using regression techniques. Logarithmic transformations were used as needed to assure normality of residuals and equal variances for subgroups of observations. All means and standard deviations were calculated arithmetically except for proportions, percentages, and coefficients, for which geometric descriptive statistics were determined. The generalized Wilcoxon test was used to evaluate the impact of the different tasks, food substances, and anesthesia on the frequencies of behavioral events that were not anticipated prior to data collection. A *P*-value of less than 0.05 was considered statistically significant for all tests.

Results

Split phase

Normal periodontal sensibility

There was no observable difference in the force profiles for the two different behavioral tasks during the split phase (e.g., compare the profiles in Fig. 2B with those in Fig. 2C). The split phase, however, appeared to differ for trials employing the two different food substances. For example, more force was typically required to split the peanut than the biscuit (compare the profiles shown in Fig. 2B with those shown in Fig. 2A). Moreover, the force profiles for the biscuit often exhibited small superimposed irregularities that reflected small breakages in the surface before the split (Fig. 2A). Thus, the differences can be attributed to differences in the physical properties of the biscuit and peanut morsels.

Quantitative analyses confirmed the differences that were suggested by visual inspection. The split force, peak split force rate, and duration of the split phase did not differ significantly for the split, and the hold-and-split tasks (*P*-values >0.08, 0.57, and 0.61, respectively). Second, the force required to split the peanut (mean 17.6 N) was 95% greater (range of means among subjects 70–136% greater; $P<0.002$) than that required to split the biscuit (9.0 N). Third, the duration of the split phase required for the peanut (mean 225 ms) was 81% greater (range 67–110% greater; $P<0.002$) than that required to split the biscuit (125 ms). Fourth, the peak split force rate for the peanut morsel (mean 196.3 N/s) was 25% greater than that for the biscuit (157.6 N/s), however this difference was not statistically significant ($P>0.12$). That the peanut required greater forces over a longer period of time is further illustrated for the individual subjects in Fig. 3. The values shown in Fig. 3 also substantiate a remarkable consistency among subjects in splitting the morsels in the absence of anesthesia. The mean split force varied among subjects by only 2.5 N and 3 N for the biscuit and peanut, respectively. The mean peak split force rate differed less than 46% and the mean duration of the split phase differed no more than 60 ms.

In addition to a high degree of consistency among subjects in splitting the morsels, each subject performed the task in a reliable manner from trial to trial. Accounting for differences among tasks and morsels, the coefficients of variation for the four subjects approximated 0.27, 0.28, 0.35, and 0.25 (subjects A, B, C, and D, re-

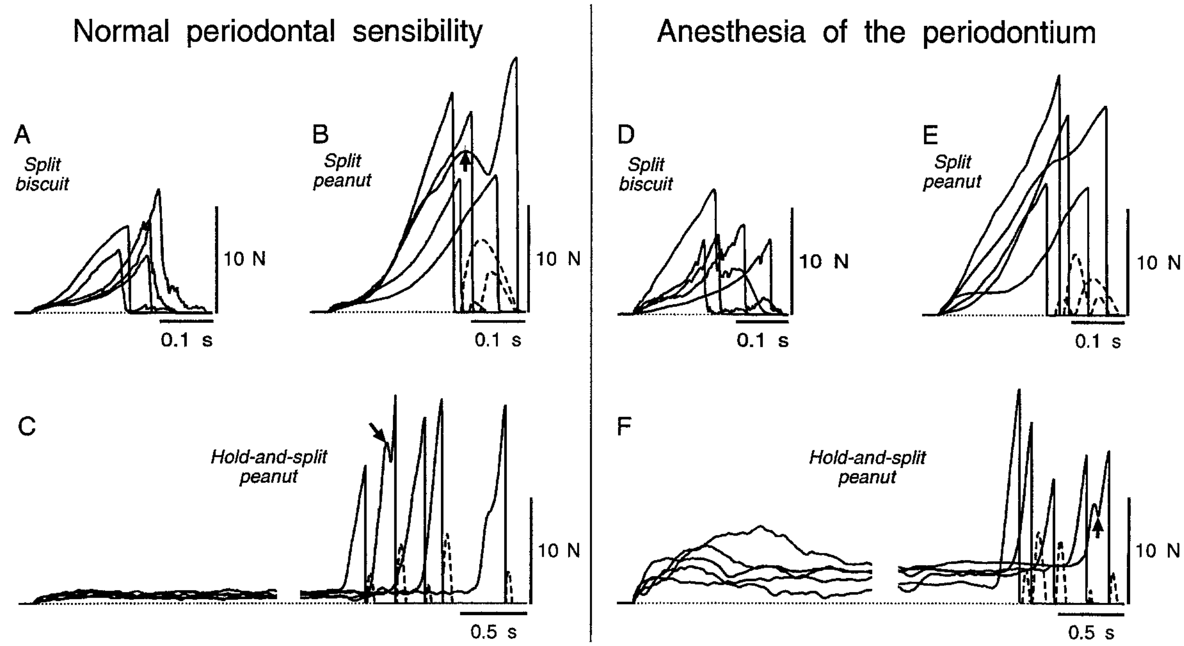


Fig. 2 Examples of force profiles (*solid curves*) obtained during the split task (**A, D** biscuit morsel; **B, E** peanut morsel) and the hold-and-split task (**C, F**). Five superimposed trials are shown in each set. *Arrows* indicate trials during which the peanut was not split by the first force ramp (see text). **A-C** Normal periodontal sensibility; **D-F** anesthesia of the periodontium. Note the slower time base in **C** and **F** than in **A**, **B**, **D**, and **E**. For further details see legend to Fig. 1

spectively) for the split force; 0.31, 0.40, 0.39, and 0.36 for the peak split force rate; and 0.41, 0.54, 0.39, and 0.42 for the duration of the split phase. Thus, the trial-to-trial variability (in terms of the standard deviation) of the three measures averaged only 29%, 36%, and 44%, respectively, of the means. The variability in the split force can be attributed in part to variation in the physical properties of different peanuts and of different biscuits.

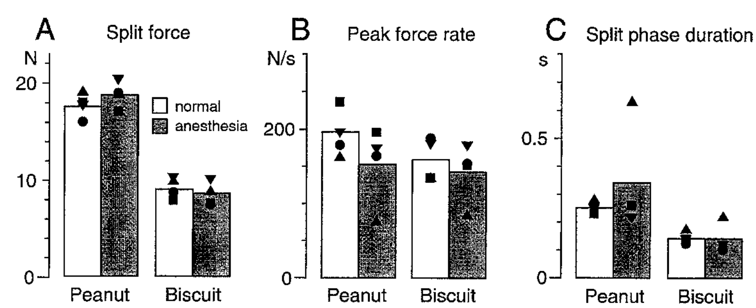
In a small percentage of trials (ca. 21%, mostly with the peanut morsel), the split phase was characterized by a biphasic increase in force. After an initial, distinct ramp increase in force, a second increase was observed that attained a higher force level (see trials with arrows in Figs. 2B, C). The second ramp began after a 25- to 50-ms-long decay in the maximum force attained during the first ramp and succeeded in splitting the morsel. The peak split force rate was typically attained during the second ramp. Interestingly, the duration of the split phase for the two-ramp trials was not necessarily longer than that on trials during which the morsel was split by the first and only ramp (e.g., see trial with arrow in Fig. 2C; but see trial with arrow in Fig. 2B).

For both food substances the force fell rapidly to zero once the morsel had been split. In about 80% of the trials with the peanut morsel, however, the upper incisor lightly contacted the metal plate upon which the divided morsel rested. This action produced an additional small rise in force (see dashed components of profiles in Figs. 1 and 2).

Fig. 3A-C Bar histograms summarizing effect of anesthesia on split phase. Height of bar indicates mean split force (**A**), mean peak split force rate (**B**), and mean duration of split phase (**C**). Mean values for individual subjects are indicated by *symbols*. Subjects A, B, C, and D are represented by an *upward-pointing triangle*, a *downward-pointing triangle*, a *circle*, and a *square*, respectively. Data from both behavioral tasks have been pooled. *Open* and *filled bars* indicate normal periodontal sensibility and anesthesia of the periodontium, respectively

Anesthesia of the periodontium

The split phase after anesthesia of the periodontium appeared remarkably similar to that observed prior to anesthesia (compare profiles in Fig. 2D-F with those shown in Fig. 2A-C). Repeated-measures analyses of variance con-



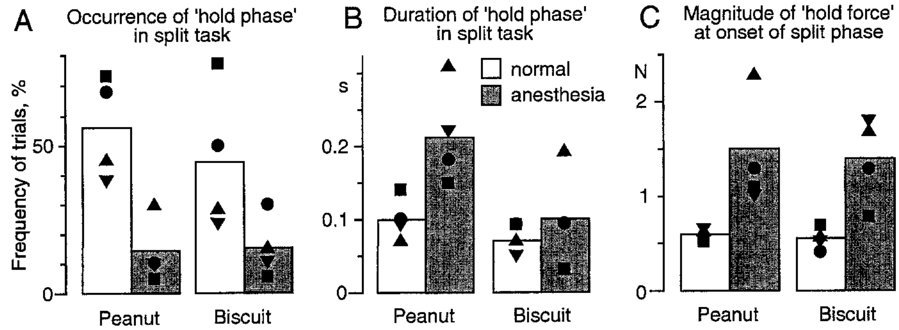


Fig. 4A-C Bar histograms summarizing trials of the split task in which subjects spontaneously opted to "hold" the food substance momentarily before biting. Height of bar indicates mean frequency of this phenomenon (**A**), its mean duration (**B**), and the mean magnitude of the force exerted (**C**). Mean values for individual subjects are indicated by *symbols*. *Open* and *filled bars* indicate normal periodontal sensibility and anesthesia of the periodontium, respectively

firmed that neither the split force, the peak split force rate, nor the duration of the split phase differed for the two conditions (P>0.48, 0.10, and 0.61, respectively; cf. Fig. 3).

The differences in splitting the biscuit and peanut that were observed in the absence of anesthesia were observed in its presence. The force required to split the peanut was again found greater than that required for the biscuit (118% greater, on the average). The duration of the split phase required for the peanut exceeded that required to split the biscuit (121% greater, on the average). And, as for the absence of anesthesia, the peak split force rate recruited to split the biscuit approximated that recruited to split the peanut.

In the presence of anesthesia, the subjects varied to a greater extent in the manner in which they split the morsels than in the absence of anesthesia. This was due solely, however, to the data provided by only one of the four subjects (see Fig. 3). Moreover, each subject split the morsel with the reliability observed in the absence of anesthesia. Specifically, the coefficients of variation for the four subjects approximated 0.27, 0.23, 0.24, and 0.30 for the split force; 0.37, 0.32, 0.34, and 0.38 for the peak split force rate; and 0.40, 0.44, 0.42, and 0.52 for the duration of the split phase. Thus, the trial-to-trial variability (in terms of the standard deviation) of the three measures averaged only 26%, 35%, and 44%, respectively, of the means. The percentages are almost identical to those observed in the absence of anesthesia (29%, 36%, and 44%, respectively).

Moreover, the anesthesia did not influence the incidence at which the upper incisor contacted the metal plate after the split or the manner in which it did so (cf. Fig. 2E, F). Likewise, trials with second, compensatory ramp increases in force occurred during anesthesia (cf. Fig. 2F), and the frequency and pattern of these were similar to that observed with normal sensibility.

Hold phase

Normal periodontal sensibility – split task

In this study subjects were first tested with the split task (they were instructed to split the food without delay).

Table 1 Mean (and standard deviation) of estimates from the hold-and-split trials

	Normal sensibility				Anesthesia of periodontium			
	Biscuit		Peanut		Biscuit		Peanut	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Averaged hold force (N)								
Subject A	0.40	0.16	0.32	0.16	0.85	0.23	1.03	0.57
	0.51[a]	0.24[a]	0.38[a]	0.14[a]				
Subject B	0.81	0.24	0.71	0.30	2.76	0.59	2.54	0.65
	0.87	0.18[a]	1.07	0.28[a]				
Subject C	0.55	0.21	0.80	0.37	1.79	0.81	2.39	1.21
Subject D	0.62	0.12	0.80	0.25	1.13	0.36	3.19	1.41
SD of hold force (N)								
Subject A	0.15	0.05	0.14	0.06	0.34	0.13	0.74	0.33
	0.25	0.07[a]	0.23	0.07[a]				
Subject B	0.17	0.07	0.15	0.06	0.50	0.19	0.51	0.18
	0.17	0.06[a]	0.16	0.05[a]				
Subject C	0.18	0.08	0.22	0.10	0.25	0.11	0.40	1.14
Subject D	0.19	0.05	0.23	0.10	0.35	0.11	1.03	1.57

[a] Data obtained 12 months earlier from subjects A and B were available. Note remarkable consistency in estimates over time

Yet, on about half of the trials, the profiles exhibited an initial period during which the force increased slowly or remained the same prior to the split phase. This initial period was identified as an inflection in the force record prior to the split phase and was interpreted to constitute a brief "voluntary hold phase" (Fig. 1B, see also Fig. 2A, B). As such, its presence could be most easily confirmed by inspection of the force rate signal. There were no notable differences in the incidence of this uninstructed behavior for the two different food substances (P>0.1; mean 50% of the trials; 30–75%, range of means among subjects), in its duration (P>0.07; mean 86 ms; 66–115 ms, range among subjects) or in its magnitude (P>0.7; mean 0.58 N; 0.50–0.62 N, range among subjects; see Fig. 4). The magnitude value was sampled immediately prior to the onset of the split phase (i.e., at event b; cf. Fig. 1B). The duration was defined as the length of the interval between initial contact "a" and the onset of the split phase "b."

Normal periodontal sensibility – hold-and-split task

Prior to the second series of trials, the subject was first instructed to hold the morsel between the teeth for a brief period of about 3 s before biting. Consistent with the instruction, subjects held the food for 2.1–3.7 s (range of mean hold durations among subjects).

Quantitative analyses revealed that the averaged hold force used with the peanut morsel did not differ from that used with the biscuit morsel (P>0.4; see Fig. 6A and Table 1). Over subjects and morsels, the mean averaged hold force was 0.63 N.

Three estimates of the variability in the hold force are required to appreciate the consistency of the subjects' behavior. The first assesses the degree to which the subjects differed, on average. The second assesses the degree to which each subject employed the same force from trial to trial. The third assesses the degree to which each subject maintained the force constantly during the hold phase of the individual trials. These will be considered in turn.

First, the mean averaged hold forces differed little among subjects (cf. means reported in Table 1, top left). Averaged over morsels, the mean estimates for the four subjects approximated 0.36, 0.76, 0.67, and 0.71 N, confirming that the among-subject variability was quite low. In fact, three of the subjects showed nearly identical mean values.

Second, the standard deviations of the averaged hold forces were modest (cf. standard deviations reported in Table 1, top left). The among-trial coefficients of variation for the four subjects approximated 0.44, 0.35, 0.42, and 0.25, confirming that each subject used about the same averaged hold force from trial to trial. Thus, the trial-to-trial variability (standard deviation) of the averaged hold force approximated 36% of each subject's mean. That each subject used about the same averaged hold force from trial to trial is further demonstrated in Fig. 5. The left positioned plot(s) for each subject illustrate the averaged hold force (thick black curve) and the intratrial standard deviation of the hold force (shading) for consecutive trials with the peanut morsel. Inspection of these plots, for example, suggests that subject A employed the lowest and least variable averaged hold forces as indicated by the vertical position and regularity, respectively, of the curve that represents the data. In addition, she applied the hold force steadily during the individual trials, as indicated by the narrow window of shading.

Third, the standard deviations of the hold forces were small (cf. means reported in Table 1, bottom left). Averaged over morsels and trials, the within-trial coefficients

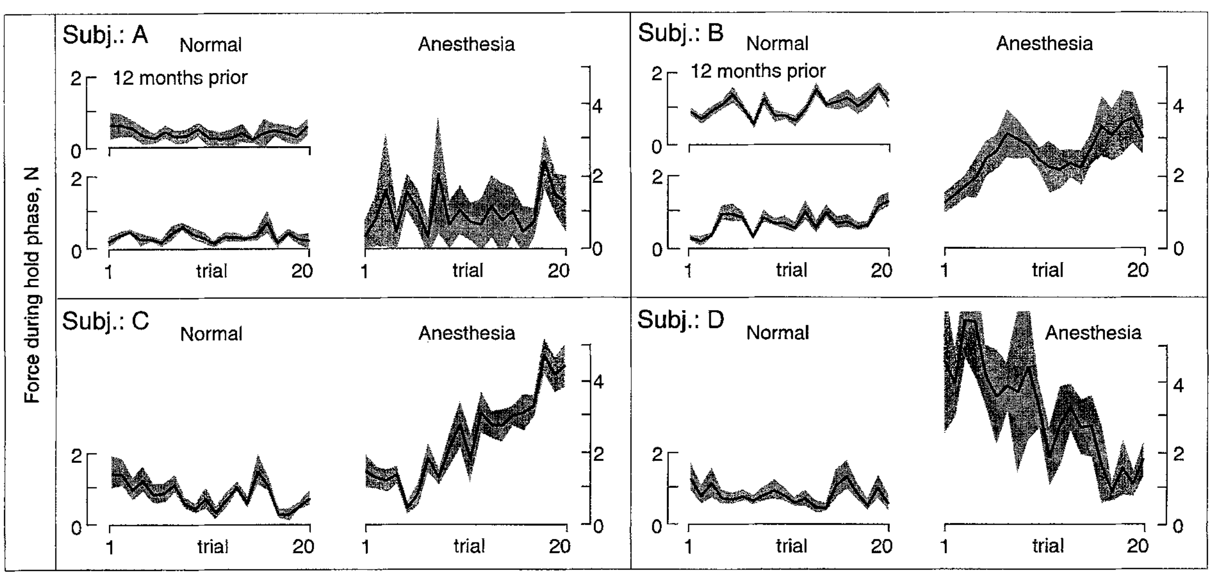


Fig. 5 Averaged hold force (*dark solid curve*) ±1 SD of the hold force (*shading*) for 20 consecutive trials with the peanut morsel during normal sensibility and during anesthesia of the periodontium. Data from each of the four subjects are shown. For subjects A and B, data collected 12 months earlier in the absence of anesthesia are also shown

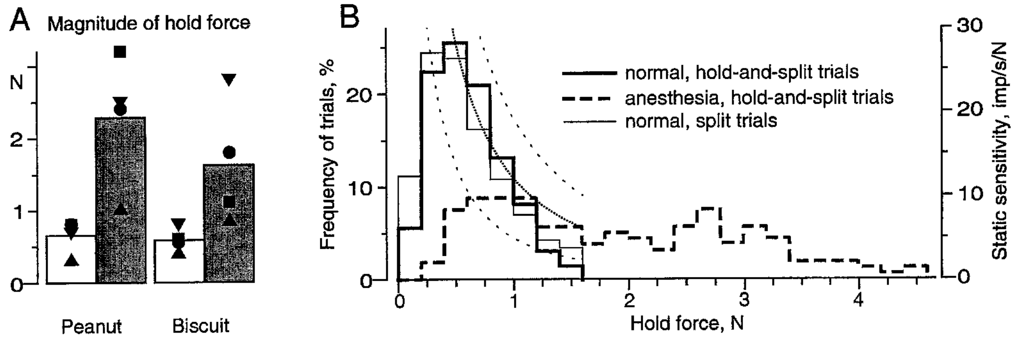


Fig. 6 **A** Bar histograms summarizing magnitude of averaged hold force employed by subjects during the hold-and-split task. Height of bar indicates mean magnitude of the force exerted. Mean values for individual subjects are indicated by *symbols*. *Open* and *filled bars* indicate normal periodontal sensibility and anesthesia of the periodontium, respectively. **B** Frequency distributions of hold forces pooled over subjects and food substances. *Solid* and *dashed thick-line histograms* refer to trials with normal periodontal sensibility and trials with anesthesia of the periodontium, respectively. The *solid thin-line histogram* represents the corresponding "hold forces" during the split task for trials in which subjects spontaneously opted to "hold" the food substance momentarily before biting. The *superimposed curves* represent the sensitivity to changes in steady state force stimulation of a population of human periodontal afferents. The *three dotted curves* refer to the mean ±1 SD of the first force differential averaged across the 19 periodontal afferents in Trulsson and Johansson 1994

of variation for the four subjects approximated 0.42, 0.21, 0.30, and 0.29 confirming that each subject maintained the force relatively constant throughout the hold phase. Thus, the within-trial variability (standard deviation) of the hold force approximated only 30% of the averaged hold force for each individual trial. Interestingly, the maximum value of the hold force during the individual trial often occurred very early in the hold phase, viz., within a few hundred milliseconds after initial contact with the morsel (e.g., see Figs. 1C and 2C). In contrast, the minimum value of the hold force occurred randomly within the hold phase.

Anesthesia of the periodontium – split task

After anesthesia of the periodontium, each subject was first tested with the split task (third series of trials; see Methods). Similar to the first series of trials, the force profiles of the third series exhibited brief uninstructed hold phases (e.g., see Fig. 2D-E). The incidence was surprisingly less, however, only 14% on average (P<0.01; 5–22%, range among subjects) with no notable difference for the two different food substances (P>0.1; see Fig. 4). Compared to the absence of anesthesia, the duration of this uninstructed behavior was greater for the peanut morsel, but not for the biscuit morsel (P<0.02 and P>0.5, respectively). Most importantly, the magnitude of the force prior to the onset of the split phase (i.e., at event "b"; see Fig. 1B) was significantly greater in the presence of anesthesia (P<0.04) with no notable difference for the two different food substances (P>0.7; mean 1.43 N; 0.94–2.01 N, range of means among subjects).

Anesthesia of the periodontium – hold-and-split task

The subjects were finally tested with the hold-and-split task (fourth series of trials). Quantitative analyses revealed that the averaged hold force used with the peanut morsel did not differ from that used with the biscuit morsel (P>0.2; see Fig. 6A and Table 1, top right). Over subjects and morsels the mean averaged hold force was 1.96 N. Importantly, this was three times greater than that observed in the absence of anesthesia (P<0.001). The mean averaged hold forces differed appreciable among subjects (cf. means in Table 1, top right) and approximated 0.94, 2.65, 2.09, and 2.16 N, spanning a range 5 times greater than that observed in the absence of anesthesia.

The standard deviations of the averaged hold forces were also three times greater than those observed in the absence of anesthesia (cf. standard deviations in Table 1, top right). However, in relative terms, the among-trial coefficients of variation for the four subjects approximated 0.39, 0.24, 0.48, and 0.38 due to the proportionally higher mean averaged hold forces. Thus, the trial-to-trial variability (standard deviation) of the averaged hold force approximated only 36% of each subject's mean, which is identical to the value obtained in the absence of anesthesia. That this variability represents both a random and non-random component is suggested by Fig. 5. The right positioned plot for each subject illustrates the averaged hold force (thick black curve) ± the standard deviation of the hold force (shading) after anesthesia. Trends for the subject to exert greater averaged hold forces (subjects B and C) or lesser averaged hold forces (subject D) as the testing proceeded were observed after the anesthesia. Table 2 shows the percentage of the variability in the averaged hold force reported in Table 1 that can be attributed to a linear trend upon repetitive testing with the same morsel.

Inspection of Table 2 reveals that in 5 of the 8 cases after anesthesia (4 subjects×2 morsels), a statistically significant proportion of the trial-to-trial variability in the averaged hold force can be attributed to systematic trends (increases or decreases) in the averaged hold force upon repetitive testing. In contrast, in only 3 of the 8

Table 2 Percentage of trial-to-trial variance in averaged hold force (cf. Table 1) attributable to a linear trend upon repetitive testing

	Normal sensibility (%)		Anesthesia of periodontium (%)	
	Biscuit	Peanut	Biscuit	Peanut
Subject A	0	0	7	6
Subject B	31*	28*	46**	55**
Subject C	10	26*	64**	82**
Subject D	26	4	6	77**

* Significant at: $P<0.05$; $^{**}P<0.001$

cases prior to anesthesia can a statistically significant proportion be attributed to similar trends. Moreover, the percentage geometrically averaged only 4%, compared to 27% after administration of the anesthesia.

Similar to the among-trial variability, the within-trial variability was about three times greater in the presence of anesthesia (cf. means reported in Table 1, bottom right). Averaged over morsels, the coefficients of variation for the four subjects approximated 0.55, 0.18, 0.16, and 0.31. Thus, after anesthesia the within-trial variability (standard deviation) of the hold force approximated 27% of averaged hold force for each individual trial, which is almost identical to the value obtained in absence of anesthesia. In four of the eight cases for which systematic trends in the averaged hold force were identified , trends in the within-trial variability were also observed. That is, as the averaged hold force systematically increased or decreased from trial to trial, so did the extent to which the morsel was held steadily during the trial.

Additional behavioral observations

After the experiments, all subjects were asked about their experiences during the tasks. With normal sensibility, they all reported that the task was easy and felt natural. In contrast, the task was considered more difficult during anesthesia. The subjects reported devoting considerable attention to positioning the hand-held bar with the morsel and were uncertain about the "position of the lower jaw." They also repeatedly reported the lack of distinct sensations of contact with the morsel and that they could not feel where the contact was made. Consequently, with anesthesia, the food escaped from the bite while the subject applied force on it at a significantly higher frequency (14% of the trials) than with normal sensibility (<2%; $P<0.02$, generalized Wilcoxon test). This happened more frequently with peanuts (18%) than with biscuits (10%). We interpreted this to reflect a lack of adequate contact information required for precise spatial control of the action forces with reference to the shape and location of the morsel. Interestingly, with the biscuits the subjects sometimes could hear that they were in contact with the food, i.e., to confirm contact they apparently used sound cues caused by slight cracking of the surface.

Discussion

The forces employed by our subjects splitting natural foods were by an order of magnitude smaller than the maximum biting force that can be exerted by the incisors (cf. Rugh and Solberg 1972). Moreover, the forces applied while the subjects just held the food between the incisors were smaller than the split forces, again by an order of magnitude, and were typically less than 1 N. Considering that the subject had no instructions about what force levels to exert, the hold force was remarkably stable during the individual trials and across trials. Moreover, during the split task, in about half of the trials, the subjects spontaneously opted to hold the morsel momentarily with the same low force (viz., 0.58 N compared with 0.63 N, on average) before biting. Anesthesia of the periodontal ligament drastically reduced the incidence of this uninstructed hold phase. And, when present, the amplitude was increased similarly to the hold force in the hold-and-split task after anesthesia (viz., 1.43 N compared with 1.96 N, on average).

Periodontal afferents played a key role in specifying the employed hold forces

A striking correspondence was observed between the magnitude of the forces used during the hold phase and the force range over which the large majority of human periodontal afferents exhibit the highest static and dynamic sensitivity, i.e., forces below ca. 1 N (Trulsson and Johansson 1994). This suggests that the subjects automatically adjusted their bite force during the hold phase to maximize the availability of information from periodontal afferents. As shown in Fig. 6B, with normal periodontal sensibility the distribution of hold forces is skewed to coincide with the range over which periodontal afferents are most sensitive to changes in force. The sensitivity curves in Fig. 6B illustrate the first force differential of the steady state discharge rate (mean ±1 SD) as a function of force amplitude (data obtained from the 19 periodontal afferents analyzed in Trulsson and Johansson 1994). Thus, the subjects chose to use hold forces great enough to achieve a stable clasp, but they avoided higher forces at which the sensitivity of most afferents was lower. (Note that, for forces above ca. 0.5 N, the diminishing probability of using a given force paralleled the decreasing sensitivity of the afferents.)

The hypothesis that the periodontal afferent signals played a decisive role in the specification of the force by which the morsel was held is also supported by the experiments with periodontal anesthesia: greater and more variable hold forces were employed by all subjects. However, the relative precision of this manipulative motor act was not compromised, i.e., the coefficients of variation for the hold forces were similar before and after anesthesia, both between and within trials. Although other interpretations are certainly possible, the motor system appears to specify and maintain a hold force in a manner to optimally extract information during this preparatory phase. Since higher and more variable forces (in absolute terms) are employed in the presence of anesthesia, we conclude that no other receptor mechanism is better in this regard than that of the periodontal ligament. That the relative precision is not compromised suggests that the variability is neither generated by noise in sensory signals nor reflects a limitation of motor control. Rather, it may reflect the action of a purposeful mechanism by which information is extracted as a result of the dynamic sensitivity of available receptor systems.

During anesthesia, the subjects often showed linear trends to exert greater or lesser averaged hold forces as the testing proceeded (see Fig. 5). Since the level of anesthesia was confirmed by clinical testing before the first trial, we do not believe that these trends simply reflect differences in the level of anesthesia. Rather, they may reflect a search strategy adopted by the subjects for a more sensitive receptor system. That is, in the absence of periodontal afferent input, other channels (e.g., muscle or joint receptors) were sought to provide sensory cues. Auditory and visual signals may also have assumed an important sensory role in this regard. For example, with the biscuits the sound related to the initial cracking of the surface could have provided a contact cue. This might explain the tendency of subjects to use lower hold forces with biscuits than with peanuts during anesthesia (Fig. 6A) and the shorter duration of the hold phases during the split task (Fig. 4B). That acoustic receptors may be involved in audiomotor reflexes in the masticatory system has been shown by van der Glas and van Steenberghe (1988). Another explanation may be that the subjects adjusted the motor commands in advance of the movement based on previous experience, i.e., by seeing the morsel prior to putting it into the mouth, the subject may have retrieved relevant object properties for anticipatory adjustment of the motor commands (cf. Gordon et al. 1993).

Both during normal sensibility and during anesthesia of the periodontium, the only sites of contact with the food (and the hand-held bar) were at the edges of a pair of opposing incisors. Therefore, it seems reasonable to assume that the effects of the anesthesia were essentially due to the blocking of the periodontal afferents of the incisors. Furthermore, recordings in man from afferents that respond to light mechanical stimulation of cutaneous, transitional, or mucosal zone of the lip or the gingiva indicate that these are not sensitive to weak loading of the teeth (cf. Trulsson et al. 1992).

Taken together, we have provided two independent lines of evidence pointing to the decisive role played by periodontal afferents in specifying the employed hold forces: (1) the hold force amplitudes correspond with the range of force intensities most efficiently encoded by the periodontal afferents, and (2) the control of these forces is disrupted during periodontal anesthesia.

Periodontal afferent input was not necessary for the execution of the split phase

During the split phase, the force rapidly increased until the split occurred and then fell sharply. These tooth loads quickly reach magnitudes at which the force-encoding capacities of most human periodontal afferents saturate, i.e., they would not provide much information about the forces during the split phase (Trulsson and Johansson 1994, 1995). However, there are periodontal afferents that would represent the force profile during the split phase rather well (four out of 19 afferents analyzed in Trulsson and Johansson 1994). These afferent signals might play a role in providing a positive feedback to the jaw-closing muscles during maximal voluntary biting (Lund and Lamarre 1973) and in the slow, closing power phase of the chewing cycle (Lavigne et al. 1987; Inoue et al. 1989; Morimoto et al. 1989). Likewise, they might govern the "additional muscle activity" by means of a "restricted closed-loop control during chewing," as proposed by Ottenhoff et al. (1992b). Accordingly, we hypothesized that the blocking of the afferent input during anesthesia of the periodontium would profoundly disturb the execution of the power phase of our tasks, i.e., the split phase. Specifically, we expected to see changes in the peak force rate (Fig. 3B) and the split phase duration (Fig. 3C). However, no significant effects were observed. The peak force at the moment of split, i.e., the split force (Fig. 3A), was not expected to change, since it is governed mainly by the resistance of the food.

Assuming that the periodontal afferents play an important role in positive feedback to the jaw-closing muscles during biting, we expected that the anesthesia of the periodontium would disrupt the pattern of jaw closure following a successful split (cf. Hannam et al. 1968; Lamarre and Lund 1975). That is, there would have been no withdrawal of an excitatory input to the jaw-closing motoneurons related to the rapid unloading of the teeth during periodontal anesthesia. However, our data failed to support this prediction, since there was an almost instantaneous arrest of jaw closure following split during both normal sensibility and periodontal anesthesia. Rather than ruling out that the periodontal afferents mediate the jaw unloading reflex (Hannam et al. 1968), it is unlikely that any reflex mechanism could have played a role in mediating this fast arrest owing to the neuromuscular delays necessarily involved. Instead, "preparatory" cocontractions of the jaw-opening and -closing muscles could have been responsible, providing an equilibrium jaw position at a point before the teeth came together (Miles and Wilkinson 1982). Also, the force exerted during the split phase in the present experiments may have been governed largely by predictive control mechanisms based on anticipation of the split force. However, the findings of "compensatory" increases in force output if the morsel was not split by the first force ramp, also during periodontal anesthesia (see Fig. 2; trials indicated by arrows), indicate that the periodontal afferents did not play a decisive role in their control.

Taken together, these observations suggest that periodontal afferent input was not necessary for the control of the split phase, which represents a power phase in mastication.

Periodontal afferent information contributed to the spatial control of jaw actions

During anesthesia of the periodontium, the subjects had difficulty in spatially controlling the jaw action: The application of hold and/or bite forces often caused the morsel (particularly if a peanut) to elude the grasp. Necessary spatial information about the pattern of contacts across the dentition was not available for precise control of the directions and/or points of attack of the hold and bite forces. The lack of periodontal afferent information may have been the reason for this. Indeed, populations of such afferents possess the capacity to furnish spatial information about the pattern of contacts across the dentition when a bolus of food is first engaged, e.g., while food is being positioned for biting (cf. Trulsson et al. 1992; Trulsson 1993). In this respect the masticatory system may be analogous to the digit control mechanisms involved in precision manipulation of small objects. Responses occurring in tactile afferents very near to the moment of contact with an object provide spatiotemporal information about the contact condition necessary for an appropriate application of manipulative forces (Westling and Johansson 1987). Indeed, during finger numbness manipulative forces are erroneously applied and small items escape the grip, making manipulation impossible, e.g., during buttoning attempts. Hence, it seems likely that the early afferent information about the contact pattern across the dentition would contribute to the regulation of the three-dimensional, time-varying action vector brought about by the jaw at each closure. Our observation that subjects often opted to hold the food momentarily with a low, relatively steady force before biting in the "split" task also supports the concept of operation of a strategy aimed at gathering early, state-related information.

Limitations of study

The results are based on multiple tests performed on four extensively studied subjects. It may be argued that the small number of subjects and large number of tests limit the impact of the arguments that we make. However, the subjects performed the tasks in a remarkably consistent manner, and the very same effects of anesthesia on the behavior, particularly during the hold phase, were observed in all subjects. Thus, it is not likely that the results of primary interest to the authors would have differed greatly if more subjects had been tested or if more stringent statistical criteria for significance had been employed.

Although the nonrandom experimental sequence might be viewed as a limitation by some investigators, it proved a posteriori to be most fortuitous. To summarize, the subjects were first tested without anesthesia, and then with anesthesia. For both, subjects were first instructed and tested with the split task, and then with the hold-and-split task. Thus, the lack of effect of anesthesia (day 2) on the split phase might be attributed to learning acquired during the 1st day of testing. This, however, is unlikely, since the subjects had experienced ample alternative biting during the 24-h interlude. Moreover, that specific task parameters (forces, durations, and rates) were not learned is suggested by the greatly different and impaired behavior exhibited during the hold phase after anesthesia. In contrast to a limitation, the utility of the nonrandom sequence can be appreciated by the observation that the subjects exhibited a short "hold-like phase" on half of the first series of trials even though they had not practiced or been instructed on the hold-and-split task. The implications of this important finding to the role of periodontal input in motor control would not have been so convincing if any other experimental sequence had been employed. Moreover, the uninstructed behavior was observed on only 14% of the trials following anesthesia, suggesting that it had not been learned during experience with the hold-and-split task. More likely, information about the location and consistency of the morsel and the attack of the teeth (i.e., the incisal edge-morsel relationship) were no longer signaled by the periodontal afferents when low forces were applied by the teeth. As a result, the uninstructed hold behaviors became less frequent and alternative motor strategies were sought, not using this type of information.

Acknowledgements This study was supported by the Swedish Medical Research Council (project 8667), Office of Naval Research, Arlington, VA (grant N00014-92-J-1919), and the University of Umeå. Valuable comments on the manuscript by Dr. G. Essick are gratefully acknowledged.

References

Amano N, Yoneda M (1980) Tonic periodontal-masseteric reflex in man. In: Kubota K, Nakamura Y, Schumacher G-H (eds) Jaw position and jaw movement. VEB Verlag Volk und Gesundheit., Berlin, pp 273–292

Appenteng K, Lund JP, Seguin JJ (1982) Intraoral mechanoreceptor activity during jaw movement in the anesthetized rabbit. J Neurophysiol 48: 27–37

Brodin P, Türker KS, Miles TS (1993) Mechanoreceptors around the teeth evoke inhibitory and excitatory reflexes in the human masseter muscles. J Physiol (Lond) 464: 711–723

Glas HW van der, Steenberghe D van(1988) Bilateral post-stimulus electromyographic complexes in human masseter muscles after stimulation of periodontal mechanoreceptors of bi- and unilaterally innervated teeth. Arch Oral Biol 33: 41–49

Glas HW van der, Laat A de, Steenberghe D van(1985) Oral pressure receptors mediate a series of inhibitory and excitatory periods in the masseteric poststimulus EMG complex following tapping of a tooth in man. Brain Res 337: 117–125

Gordon AM, Westling G, Cole K, Johansson RS (1993) Memory representations underlying motor commands used during manipulation of common and novel objects. J Neurophysiol 69: 1789–1796

Hannam AG (1969) The response of periodontal mechanoreceptors in the dog to controlled loading of the teeth. Arch Oral Biol 14: 781–791

Hannam AG, Matthews B, Yemm R (1968) The unloading reflex in masticatory muscles of man. Arch Oral Biol 13: 361–364

Inoue T, Kato T, Masuda Y, Nakamura T, Kawamura Y, Morimoto T (1989) Modifications of masticatory behavior after trigeminal deafferentation in the rabbit. Exp Brain Res 74: 579–591

Lamarre Y, Lund JP (1975) Load compensation in human masseter muscles. J Physiol (Lond) 253: 21–35

Lavigne G, Kim JS, Valiquette C, Lund JP (1987) Evidence that periodontal pressoreceptors provide positive feedback to jaw closing muscles during mastication. J Neurophysiol 58: 342–358

Lund JP (1991) Mastication and its control by the brain stem. Crit Rev Oral Biol Med 2: 33–64

Lund JP, Lamarre Y (1973) The importance of positive feedback from periodontal pressoreceptors during voluntary isometric contraction of jaw-closing muscles in man. J Biol Buccale 1: 345–351

Miles TS, Wilkinson TM (1982) Limitation of jaw movement by antagonist muscle stiffness during unloading of human jaw closing muscles. Exp Brain Res 46: 305–310

Morimoto T, Inoue T, Masuda, Y, Nagashima T (1989) Sensory components facilitating jaw-closing muscle activities in the rabbit. Exp Brain Res 76: 424–440

Ottenhoff FAM, Vanderbilt A, Vanderglas HW, Bosman F (1992a) Peripherally induced and anticipating elevator muscle-activity during simulated chewing in humans. J Neurophysiol 67: 75–83

Ottenhoff FAM, Vanderbilt A, Vanderglas HW, Bosman F (1992b) Control of elevator muscle activity during simulated chewing with varying food resistance in humans. J Neurophysiol 68: 933–944

Pfaffmann C (1939) Afferent impulses from the teeth due to pressure and noxious stimulation. J Physiol (Lond) 97: 207–219

Rugh JD, Solberg WK (1972) Measurement of human oral forces. Behav Res Methods Instrum 4: 125–128

Sessle BJ, Schmitt A (1972) Effects of controlled tooth stimulation on jaw muscle activity in man. Arch Oral Biol 17: 1597–1607

Trulsson M (1993) Multiple-tooth receptive fields of single human periodontal mechanoreceptive afferents. J Neurophysiol 69: 474–481

Trulsson M, Johansson RS (1993) Encoding of biting forces by human periodontal mechanoreceptors. IUPS Abstr 322:25

Trulsson M, Johansson RS (1994) Encoding of amplitude and rate of forces applied to the teeth by human periodontal mechanoreceptive afferents. J Neurophysiol 72: 1734–1744

Trulsson M, Johansson RS (1995) Human periodontal afferents: encoding of force and role in control of jaw actions. In: Morimoto T (ed) Brain and oral function. Elsevier Science, Amsterdam (in press)

Trulsson M, Johansson RS, Olsson KÅ (1992) Directional sensitivity of human periodontal mechanoreceptive afferents to forces applied to the teeth. J Physiol (Lond) 447: 373–389

Westling G, Johansson RS (1987) Responses in glabrous skin mechanoreceptors during precision grip in humans. Exp Brain Res 66: 128–140