Food-holding and -biting Behavior in Human Subjects Lacking Periodontal Receptors

M. Trulsson and H.S.J. Gunne

J DENT RES 1998 77: 574
DOI: 10.1177/00220345980770041001

J Dent Res 77(4): 574-582, April, 1998

Food-holding and -biting Behavior in Human Subjects Lacking Periodontal Receptors

M. Trulsson[1]* and H.S.J. Gunne[2]

Departments of Physiology[1] and Prosthetic Dentistry[2], Umeå University, S-901 87 Umeå, Sweden; *corresponding author

Abstract. Previous studies have suggested that information provided by periodontal mechanoreceptors is particularly important for the fine motor control of the mandible, *i.e.*, when humans hold and carefully manipulate food particles between the teeth with low biting forces. In the present study, we further evaluated this hypothesis by comparing the performance of three age- and gender-matched groups of subjects for which the integrity of the periodontal sensory apparatus differed. Specifically, the subjects had either natural teeth (natural group), dental prostheses supported by oral mucosa (denture group), or dental prostheses supported by osseointegrated implants (implant group). Each subject was instructed to hold half a peanut between the upper and lower central incisors for *ca.* 3 sec, and then to split it. The force applied by the anterior teeth was continuously monitored by a transducer-equipped bar on which the morsel rested. While the peanut was held, the force generated by subjects in the denture and implant groups was more variable and averaged four times that generated by subjects in the natural group. The peanut was split by a distinct, rapid ramp-increase in force that was similar for all three groups. In subjects lacking periodontal receptors, the morsel frequently escaped from the incisal edges during both phases of the task. The results demonstrate a marked disturbance in the control of precisely directed, low biting forces in subjects lacking periodontal receptors and suggest that the receptors play a significant role in the specification of the level, direction, and point of attack of forces used to hold and manipulate food between the anterior teeth. Moreover, other types of mechanoreceptors can not fully compensate for the loss of periodontal receptors.

Key words: biting, mastication, dental implant, complete denture, sensori-motor control.

Received November 27, 1996; Last Revision August 25, 1997; Accepted August 27, 1997

Introduction

In a recent study on mechanoreceptive afferents innervating the periodontal ligament of the anterior teeth in man, it was found that most afferents exhibit highest sensitivity to force magnitudes and force changes at surprisingly low contact-force levels, < 1 N (Trulsson and Johansson, 1994). Moreover, a quantitative model of responses in periodontal receptors, based on these data, demonstrated that these receptors efficiently encode information about food contact during biting, continuously discharge while food is held between the incisors, and show only a moderate increase in discharge rate to the rapid and strong biting forces required to bite through food (Trulsson and Johansson, 1995). In contrast, only a minority of the periodontal receptors reliably encode the rapid force increase required to split food. These findings led us to propose that periodontal receptors provide information used to control the mandible, particularly when subjects come into contact with, manipulate, and hold food prior to jaw-power actions (Trulsson and Johansson, 1995, 1996b).

To evaluate this hypothesis, we developed a simple behavioral task involving holding and splitting a morsel between a pair of opposing incisors (the "hold-and-split task"; Trulsson and Johansson, 1996a). Interestingly, when subjects were asked to hold a morsel between the incisors, they spontaneously exerted low contact forces (< 1 N) that matched the sensitivity characteristics of the periodontal receptors. As such, subjects appeared to use hold forces large enough to achieve a stable contact with the morsel without compromising the sensitivity of most receptors to force changes. Moreover, when we blocked information from the periodontal receptors by anesthetizing the periodontal tissues, subjects generated considerably greater and more variable hold forces (Trulsson and Johansson, 1996a). It was concluded that the periodontal receptors play a decisive role in the specification of the hold-force levels used.

The purpose of the present study was to evaluate this hypothesis further. To assess the extent to which control of the "manipulative" and "power" elements of human biting behavior depends on periodontal receptors, we compared behavior on the hold-and-split task among subjects with natural teeth and subjects with prostheses supported only by the oral mucosa or by osseointegrated implants, *i.e.*, subjects who lacked periodontal receptors (Linden and Scott, 1989; Bonte *et al.*, 1993).

Materials and methods

Subjects

This study was approved by the local ethical committee at the Umeå University and was performed on three subject groups that were matched with regard to sex and age (Table). A total of 24 subjects, eight in each group, participated in the experiments after giving informed consent. The 'natural' group was comprised of subjects with natural teeth in both jaws and the 'denture' group of patients with removable complete dentures in both jaws. The 'implant' group consisted of patients rehabilitated with fixed full-arch prostheses supported by osseointegrated implants ad modum Brånemark (Nobel Biocare AB, Gothenburg, Sweden) in both the maxilla and the mandible. All subjects were in good general health with no history of neurological disorders. At the time of the experiment, they showed no clinical signs or symptoms of any oral problem or oro-facial malfunction. Neither did they report any functional problem regarding speaking or biting and chewing on food. The subjects in both the denture and the implant groups had used prostheses for more than one year (Table) and were satisfied with their dental treatments. The front teeth of the subjects in the natural group exhibited no periodontal breakdown, and had not been exposed to any endodontic or prosthetic treatment.

Apparatus and experimental procedure

All subjects were seated comfortably in an upright position in an office chair positioned in a quiet room. The force profiles applied to half a peanut (small to mid-sized; Estrella™, AB Estrella, Sweden) by a single pair of opposing upper and lower central incisors were recorded (Fig. 1; see also Trulsson and Johansson, 1996a). With the right thumb and two fingers, the subject held a 9-cm-long plastic bar connected to two duralumin blocks

Table. Characteristics of subjects in the three test groups

Test Group	Natural[a]	Denture[b]	Implant[c]
No. of subjects	8	8	8
Gender			
male	2	3	2
female	6	5	6
Age (years)			
mean (SD)	60.1 (8.3)	64.7 (12.0)	61.4 (10.6)
range	46-73	49-81	48-73
Years with current prosthesis			
mean (SD)		30.4 (20.1)	4.0 (3.3)
range		6-57	1-10

[a] Natural = Natural teeth.
[b] Denture = Removable complete dentures.
[c] Implant = Fixed full prosthesis on osseointegrated implants *ad modum* Brånemark.

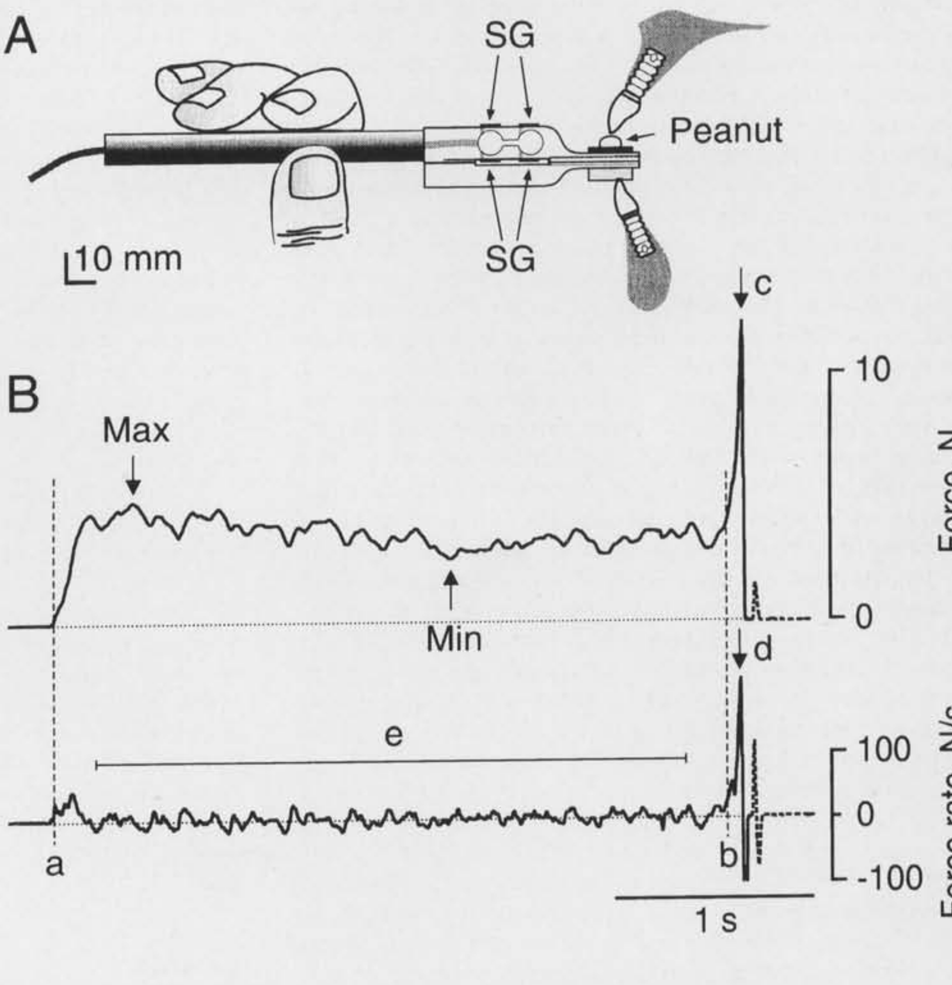

Figure 1. (A) Apparatus used to record the forces exerted on the morsel. The peanut rested on a thin piece of rubber affixed to a duralumin block equipped with strain gauges (SG) for force measurement. The strain gauges were covered with silicon (not shown), to protect them from the saliva. (B) Example of a force profile obtained from a subject in the implant group during the hold-and-split task (upper trace). Dashed part of the curves indicates a second force peak caused by the upper incisors gently hitting the support plate following the split. The lower trace illustrates the force rate. (a) Initial contact with the food; (b) onset of the split phase; (c) split force; (d) peak force rate during the split phase; and (e) interval beginning 0.2 sec after initial contact with the food and ending 0.2 sec prior to the onset of the split phase. The averaged hold force and the standard deviation of the hold force were measured during this interval.

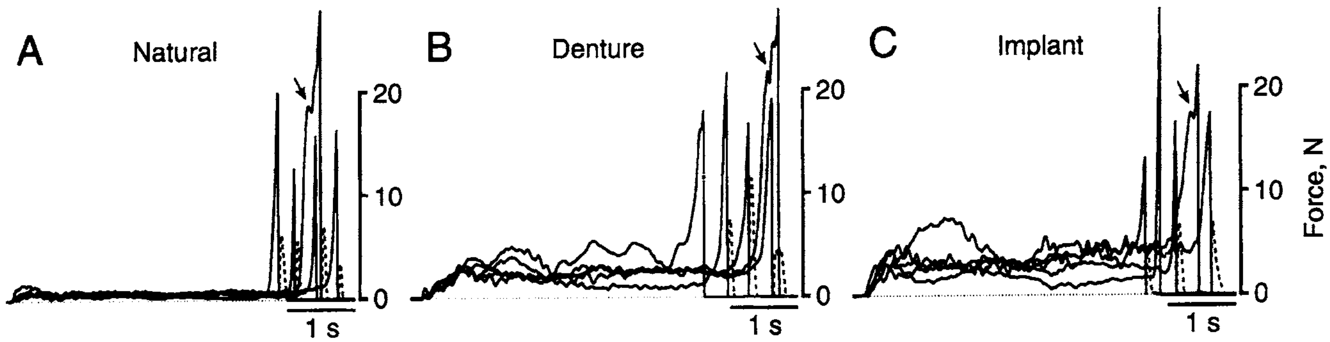

Figure 2. Examples of force profiles obtained from one subject in the natural (A), denture (B), and implant (C) groups, respectively. Five superimposed trials are shown for each subject. Arrows indicate trials during which the peanut was not split by the first force ramp (see text). For further details see legend to Fig. 1.

which terminated in two parallel, rectangular plates (total weight, 28 grams; stiffness between the plates, 50 N/mm). Strain-gauge force transducers were attached to the upper duralumin block for continuous measurement of the force applied normally to the surface of the upper plate (DC-200 Hz). The design of the apparatus (Fig. 1A) ensured that the force measurement would be insensitive to the point of force application on the plate (Lockery, 1971). To prevent damage to the teeth, we glued a thin piece of rubber and a piece of Plexiglas to the upper and lower plates, respectively.

For each trial, half a peanut was positioned on the upper plate. With the plate maintained in the horizontal plane, the subject positioned the transducer end of the bar in the mouth so that the morsel could be contacted and split by an upper central incisor (Fig. 1A). The instruction given to the subject was to "contact and hold the peanut with your teeth, but do not use more force than necessary". After the subject had held the peanut between the teeth for about 3 sec, the subject was instructed to "split the peanut in a natural manner". After five practice trials, each subject performed the "hold-and-split task" 20 times. Thus, in total, data were obtained from 480 trials.

Sometimes the peanut was lost prior to being split, *i.e.*, either the subject dropped it while positioning the transducer bar in the mouth or it escaped from the incisal edges of the teeth after contact. If the peanut was lost, a new one was provided and the trial was repeated. The number of trials on which the peanut escaped from the bite was recorded. After the experiment, all subjects were interviewed about their experiences during the task.

Analysis of force data

The temporal profiles of the forces developed between the incisors were collected and analyzed with a laboratory computer system (SC/ZOOM; Department of Physiology, Umeå University). Data were sampled with 12-bit resolution at 800 samples/sec. Force rates were obtained by symmetrical numerical time differentiation (± 5 points). Several force measurements were taken from individual trials (Fig. 1B). The *averaged hold force* was measured as the mean value of the force during the interval (e in Fig. 1B), beginning 0.2 sec after initial contact with the food (a in Fig. 1B) and ending 0.2 sec prior to the onset (b) of the split phase. The split phase was characterized by a distinct rapid ramp-increase in force (b to c) which split the peanut. The *standard deviation of the hold force* was determined for the individual trials during the same interval (e). Likewise, the *minimum hold force* ("Min" in Fig. 1B) was searched for by the computer during the same interval, whereas the *maximum hold force* ("Max") was searched for from the moment of food contact until the onset of the split phase. The moment of *initial contact* (a in Fig. 1B) and the *onset of the split phase* (b) were both reliably identified from the force-rate signal. The beginning of the split phase was detected at the point at which the force rate exceeded 25 N/sec, the minimum rate-of-force increase that could be reliably detected in single trial records. The *split force* (c) was defined as the peak force prior to the moment the morsel split, marked by a rapid force decline. This also indicated the *end of the split phase*. The peak rate of force recruitment (*peak split force rate*; d in Fig. 1B) during the split phase was searched for by the computer during the split phase.

Multivariate analysis of variance was used to confirm that at least one of the quantitative measures differed significantly among the three groups. The impact of the different groups on each quantitative measure was subsequently assessed by univariate analysis of variance. Logarithmic transformations were used as needed to ensure normality of residuals and equal variances. Linear trends in the measures were quantitatively assessed by regression techniques. All means and standard deviations were calculated arithmetically except for coefficients, for which geometric descriptive statistics were determined. The Fisher exact probability test was used to evaluate the impact of the different groups on the frequencies of behavioral events. A p-value < 0.05 was considered statistically significant for all tests.

Results

Subjects in the natural group produced low, relatively steady forces during the hold phase (Fig. 2A). During the subsequent split phase, the force rapidly increased until the split occurred and then fell sharply. A similar pattern was observed for subjects in the denture and implant groups (Figs. 2B and 2C). However, there were several differences indicating an impaired performance, most markedly expressed by exaggerated and unstable forces during the hold phase.

Hold phase

The subjects in the natural group used quite low averaged hold forces (0.59 ± 0.23 N, mean ± SD; Figs. 3 and 5A). Significantly higher averaged hold forces were used by the subjects in the denture and the implant groups (2.21 ± 1.02 N and 2.63 ± 1.05 N, respectively; P-values < 0.001; Figs. 3, 5B, 5C). A similar relationship among the three groups was seen in comparisons of the maximum (natural group, 1.39 ± 0.47 N; denture group, 4.03 ± 1.87 N; and implant group, 4.90 ± 1.90 N) and the minimum hold forces (natural group, 0.14 ± 0.11 N; denture group, 0.68 ± 0.32 N; and implant group, 0.88 ± 0.53 N). In all groups, the maximum hold force typically coincided with a pronounced force peak that occurred soon after tooth contact with the peanut (Figs. 1B and 2). In contrast, the occurrence of the minimum hold force was distributed uniformly across the hold phase.

It is evident, from the standard deviations listed above, that the among-subject variability in the averaged hold force was considerably greater for the denture and implant patients than for the subjects with natural teeth (see also the distributions of the individual mean values in Fig. 3). Likewise, the among-trial variability in the averaged hold force, measured as the trial-to-trial standard deviations of the averaged hold forces for each subject, was greater for the subjects in the denture and implant groups (1.01 and 1.25 N, respectively) compared with the natural group (0.35 N; P < 0.001; Fig. 4A). However, the among-trial coefficient of variation (standard deviation/mean) was similar for subjects in the three groups (on average, natural group, 0.58, denture group, 0.50, and implant group, 0.49; P > 0.6), due to the proportionally higher mean averaged hold forces for the denture and implant patients. Furthermore, the variability computed for each individual trial as the standard deviation of the hold force was significantly greater for the denture and implant groups (on average, 0.71 and 0.88 N, respectively) compared with the natural group (0.19 N; P < 0.001; Fig. 4B). However, similar to the among-trial coefficients, the intra-trial coefficients of variation did not differ among groups (on average, natural group, 0.38, denture group, 0.33, and implant group, 0.38; P > 0.6).

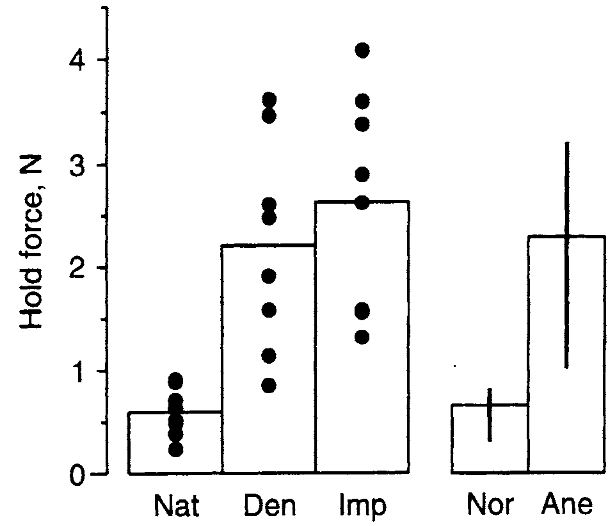

Figure 3. Bar histograms to the left summarize magnitude of averaged hold force used by subjects in the natural (Nat), denture (Den), and implant (Imp) groups. Height of bar indicates mean magnitude of the force exerted across all subjects in each group. Average values for individual subjects are indicated by filled circles (n = 20). For comparison, data obtained during a hold-and-split task with peanuts (Trulsson and Johansson, 1996a) are shown to the right. Bar histograms represent the averaged hold force used by subjects during normal conditions (Nor) and periodontal anesthesia (Ane). Heights of bars indicate mean values across all subjects and vertical lines the range of average values for individual subjects.

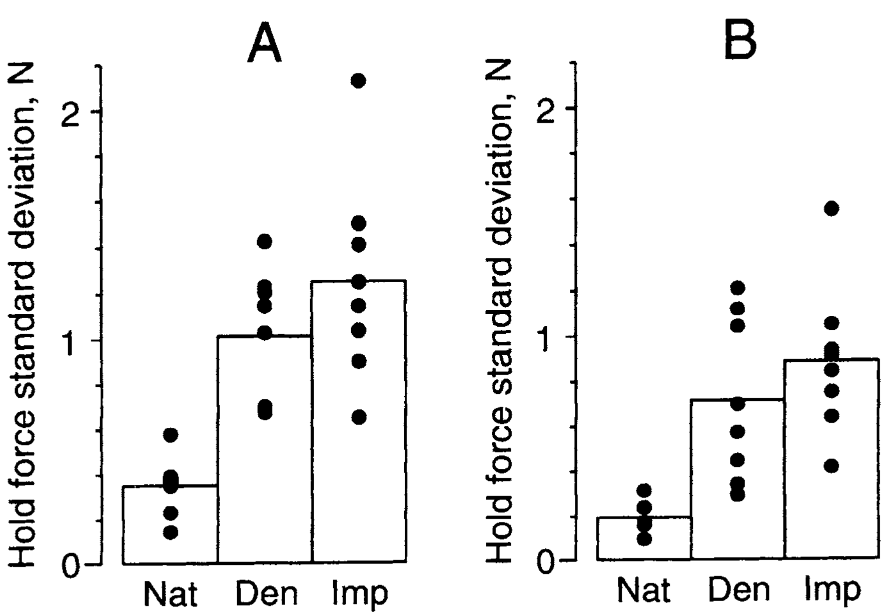

Figure 4. Bar histograms summarizing the among-trial (A) and intra-trial (B) variabilities in hold force for subjects in the natural (Nat), denture (Den), and implant (Imp) groups. Height of bar indicates mean of the hold force standard deviation (SD) across all subjects in each group. Average values for individual subjects are indicated by filled circles (A, n = 20; B, n > 100).

The magnitude and variability in the hold force are further illustrated for each of the 24 subjects in Fig. 5: Each plot illustrates the averaged hold force (solid curve) ± the standard deviation of the hold force (dashed curves) for consecutive trials for one subject. Thus, the vertical position and regularity of the solid curve reflect the amplitude and among-trial variability of the averaged hold forces, respectively, whereas the distance between the dashed curves reflects the subject's intra-trial variability. No obvious differences were seen among the three groups regarding trends for the subjects to exert greater or lesser averaged hold forces as the testing proceeded: A statistically significant

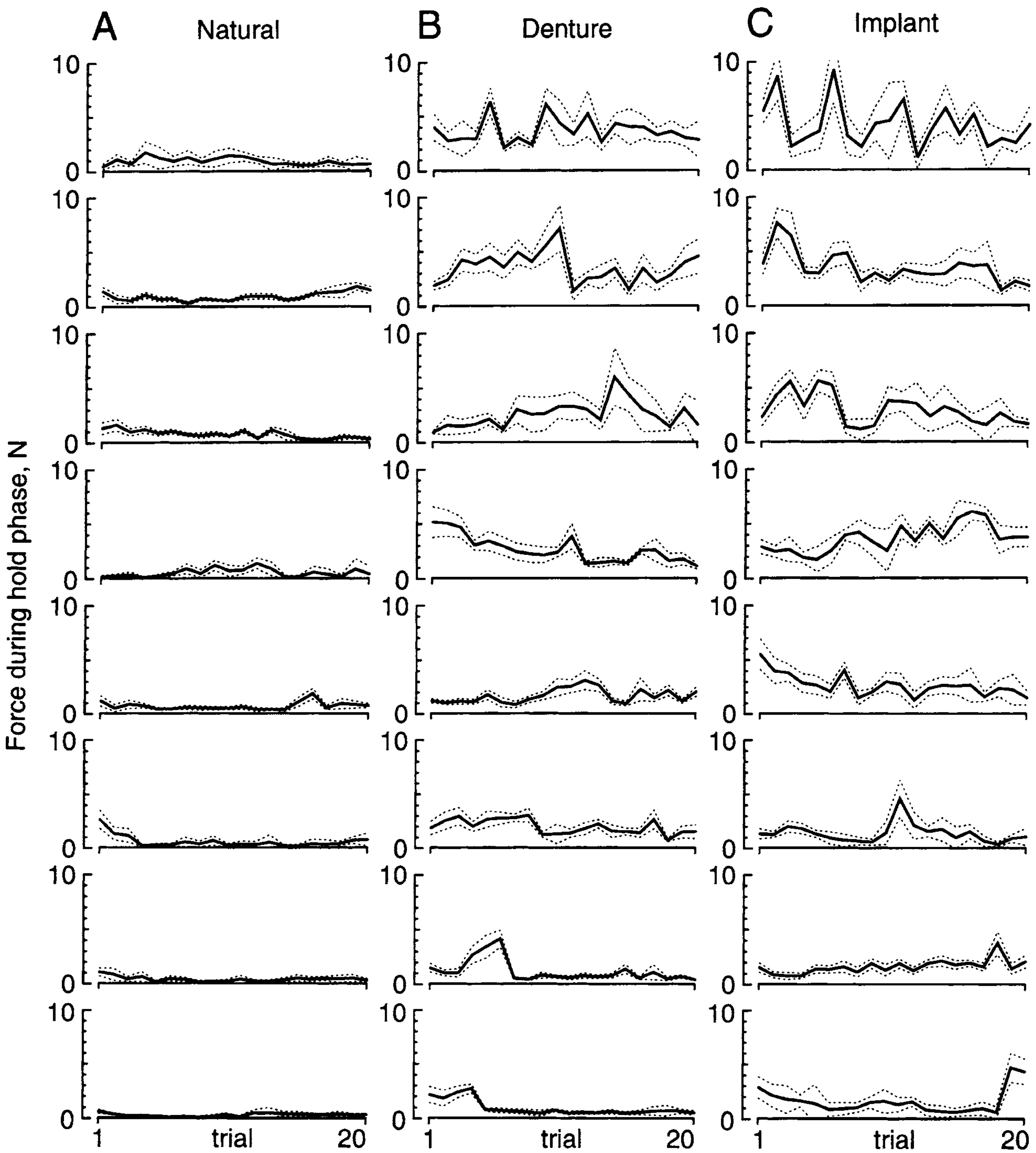

Figure 5. Averaged hold force (solid curve) ± 1 standard deviation of the hold force (dashed curves) for 20 consecutive trials (n > 100). Data from each of the eight subjects in the natural, denture, and implant groups are shown.

($p < 0.05$) proportion of the trial-to-trial variability could be attributed to systematic trends for three, three, and four of the subjects in the natural, denture, and implant groups, respectively (Fig. 5).

Split phase

During the split phase, all subjects rapidly increased the force until the peanut split, upon which the force fell to zero. In about 85% of the trials (data from all subjects pooled), the upper incisors came into contact with the metal plate on which the divided morsel rested, producing a small, second rise in force (dashed force profiles in Figs. 1B and 2). There were no obvious differences among the groups regarding the frequency of trials in which the upper incisors came into contact with the metal plate at split, the size of the related

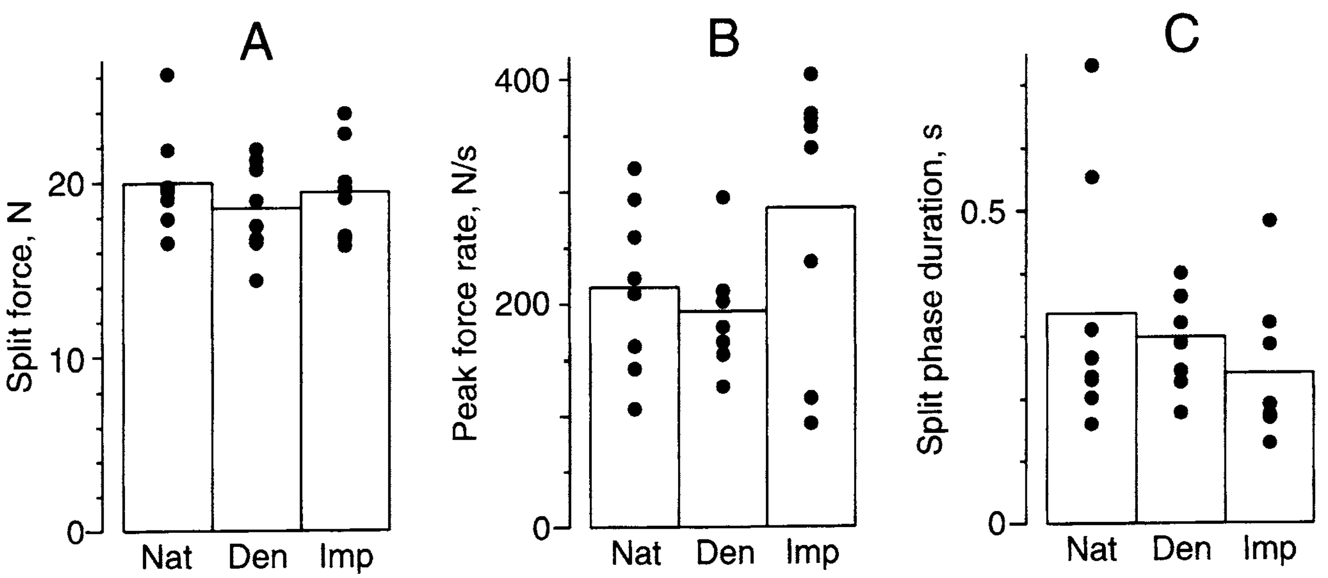

Figure 6. Bar histograms representing split force (A), peak force rate (B) during the split phase, and duration of the split phase (C) for subjects in the natural (Nat), denture (Den), and implant (Imp) groups. Height of bar indicates mean values across all subjects in each group, and average values for individual subjects are indicated by filled circles (n = 20).

rise in force, or its time course (Fig. 2).

The split force (force at the moment of split) was similar for the three groups (natural group, 20.0 ± 2.9 N; denture group, 18.5 ± 2.6 N; and implant group, 19.4 ± 2.8 N; $P > 0.5$; Fig. 6A). Neither the peak force rate (natural group, 214.5 ± 74.8 N/sec; denture group, 193.1 ± 50.7 N/sec; and implant group, 284.9 ± 121.4 N/sec), nor the duration of the split phase (natural group, 336 ± 199 ms; denture group, 298 ± 77 ms; and implant group, 242 ± 117 ms) differed significantly among the groups (Figs. 6B and 6C; $P > 0.1$ in both instances). The subjects in the implant group, however, showed a tendency for both higher values of the peak force rate and lower values of the split-phase duration—on average, 133% and 72% of those for the natural group, respectively.

In 23% of the trials (data from all subjects pooled), the split phase showed a bi- or multi-phasic increase in force. After an initial distinct ramp-increase in force, there was one or more short periods of force decay, followed by "compensatory" increases in force, eventually leading to splitting of the morsel (see trials with arrows in Fig. 2). Trials with "compensatory" force increases occurred in all groups of subjects, and the patterns of these were similar (Fig. 2).

Additional behavioral observations

In the natural group, all subjects reported that the task was easy. Indeed, they performed the task without any obvious problems; on average, the peanut was lost while being held or split in only 1.8% of the trials (range among subjects, 0 to 5%). Surprisingly, all subjects in the denture group also reported that the task was easy, despite the fact that some of them had considerable problems with retention of the prostheses (the prostheses often tilted when the greater force was applied to split the peanut). This was compensated for, however, by subjects' contracting the facial muscles to "hold" the prosthesis in a stable position during the task. When applying force to the peanut, the denture group lost it on 16% of the trials (range among subjects, 0 to 30%). All but two of the subjects in the implant group experienced the task as easy. These two subjects both complained that they could not feel the location of the peanut or where contact was made. One of them also showed apparent difficulties when positioning the hand-held bar in contact with the lower incisors. The subjects in the implant group lost the peanut while applying hold or split forces on 14% of the trials (range among subjects, 0 to 30%). Thus, for the subjects in the denture and implant groups, the peanut escaped from the bite at a significantly higher frequency than for the subjects in the natural group ($P < 0.001$, Fisher exact probability test).

Discussion

This study demonstrated striking disturbances in the control of certain jaw motor behaviors in subjects lacking periodontal receptors. Subjects with natural teeth, supported by an innervated periodontal ligament, performed in a very skillful manner when holding and manipulating food between the incisors (Trulsson and Johansson, 1996a). Typically, these subjects used quite stable and small hold forces (< 1 N). In contrast, subjects with dental prostheses supported only by the oral mucosa or osseointegrated implants showed more variable and greater hold forces—on average, four times greater. Furthermore, the morsel escaped from the bite more frequently in these patients, indicating an impaired control of the direction and/or point of attack of the action vectors.

Periodontal receptors are important for the control of the hold force level

In Trulsson and Johansson (1996a) (first describing the hold-and-split task), two lines of evidence were presented pointing to the decisive role played by periodontal receptors in the specification of hold forces. First, the hold-force levels for subjects with natural teeth were shown to correspond to the range of force intensities most efficiently encoded by the periodontal receptors; and second, the control of these forces was shown to be disrupted during periodontal anesthesia.

In the present study, the subjects with natural teeth produced hold forces with variability and amplitudes similar to those in Trulsson and Johansson (1996a): The hold forces averaged 0.59 N and 0.63 N, respectively (see Fig. 3 for comparison). The apparent difference in age for the subjects in the two studies (on average, 60 and 23 years, respectively) did not seem to have any major effect on subjects' performance. It should be noted, however, that the instructions to the subjects were slightly different. In the earlier study, the subjects were not given any instructions regarding the forces that they were to use. But in the present study, the subjects were told "not (to) use more force than necessary" when holding the peanut between the teeth. This instruction was given to ensure that the subjects would not voluntarily use excessive clenching forces during the hold phase. Such a misunderstanding was occasionally observed in a pilot study on elderly individuals.

Most interestingly, the averaged hold forces produced by the subjects with dental prostheses were remarkably similar to those generated by dentate subjects with periodontal anesthesia: The hold forces averaged 2.42 N and 2.29 N, respectively (see Fig. 3). Also, the variability in hold force (expressed as standard deviations) was about the same, both among trials (on average, 1.13 N and 0.96 N, respectively) and within trials (on average, 0.80 N and 0.67 N, respectively). Thus, the finding that subjects with a chronic loss of periodontal receptors behaved just like subjects with acute periodontal anesthesia supports the suggestion of Trulsson and Johansson (1996a) that the periodontal receptors play a significant role in the specification of hold-force levels. Moreover, the results demonstrate that the loss of periodontal receptors cannot be fully compensated for by other mechanoreceptors. Interestingly, a disturbed control of low force biting, similar to that observed in this study, has been observed in monkeys after lesions of the lateral precentral cortex (Luschei and Goodwin, 1975). This suggests that cortical processes are involved in the control of the low bite forces used during the hold phase in the present task.

Specification of the hold-force level without periodontal receptors

An interesting question is how the brain controls the hold-force level when information from periodontal receptors is absent. Several different hypothetical strategies may account for this control. Information about force magnitude may, for instance, be extracted from other, less sensitive, types of mechanoreceptors and used to specify the hold force used. Alternatively, instead of using a "force-control" mode, the subjects may switch to a "position-control" mode, *i.e.*, when a secure contact between the food and the dentition is identified, the subject may try to maintain the position of the jaw, instead of controlling the applied force. Importantly, both of these strategies require sensory information which may be gained from many different types of mechanoreceptors in and around the oral cavity. Possible candidates close to the teeth are mechanoreceptors located in the mucosa, periosteum, and bone sutures. In the complete-denture patient, the mechanoreceptors in the underlying mucosa may signal the pressure produced by the prosthesis (Sakada, 1983). For patients with bridges supported by implants, the tension produced in the bone structures during loading may activate receptors in the periosteum and bone sutures (Linden, 1978; Larson *et al.*, 1981; Sakada, 1983). However, for dentulous subjects with anesthesia of the periodontal ligament, signals from periodontal receptors and from many of the receptors in the surrounding tissues are blocked (Trulsson and Johansson, 1996a). This—together with the observation that subjects with anesthesia, complete dentures, and implant bridges behave similarly during the hold phase—suggests that more distant sensory channels may provide the critical information. Indeed, muscle spindles in the jaw muscles have been shown to respond strongly during voluntary biting in monkeys. The primary afferents, which are very active shortly after contact with the food, may be particularly capable of signaling contact information (Lund *et al.*, 1979; Larson *et al.*, 1981). Other interesting candidates are the mechanoreceptors in the temporomandibular joint. Unfortunately, little is known about their functional properties and even less about their activity during motor function. Recordings from the trigeminal ganglion in the rabbit show that they respond to passive movements of the jaw (Lund and Matthews, 1981). However, in a recent study on the human hand, joint receptors seemed to be more sensitive to small finger movements produced during a motor task than to larger passive joint rotations, suggesting that the primary stimulus for these receptors is the actively generated joint torque and not the joint rotation per se (Macefield and Johansson, 1996). Thus, it may be speculated that the counter-forces and torques that develop in the temporomandibular joints during biting may be encoded by mechanoreceptors inside the articular tissues. Auditory and visual signals may also play an important role in this regard. Acoustic receptors in the inner ear may provide sensory information about impact forces on the teeth, *e.g.*, during contact between the food and the teeth. Especially with implant-supported bridges, they may be directly activated through bone conduction. In addition, it cannot be excluded that, instead of using sensory information collected during the task, subjects may adjust the motor commands in advance of the movement, based on previous experiences. By seeing the peanut prior to putting it into the mouth, the subject may retrieve information relevant to object properties for anticipatory adjustment of the motor commands (*cf.* Gordon *et al.* 1993).

Periodontal receptors are not crucial for the split phase

After the instruction to split the peanut, all subjects rapidly increased the force until the peanut broke, causing a sharp fall in the force record. The patterns were similar for subjects in all three test groups, and when the peanut was not split by the first force ramp, "compensatory" increases in force occurred in all groups (see arrows in Fig. 2). Despite the fact that some of the subjects with complete dentures had obvious problems with retention of their prostheses, the quantitative measures extracted during the split phase were similar among the three groups. The force at the moment of split (split force) was related to factors reflecting the mechanical properties of the food and the cleaving effects of the incisal edges. The rate at which the force increased, however, was controlled by the nervous system. That the peak force rate and the split-phase duration were similar for subjects with and without periodontal receptors is consistent with the finding of Trulsson and Johansson (1996a) that periodontal anesthesia has no effect on the split phase. If the periodontal receptors had provided important "positive feedback" during biting, as suggested by Lund and Lamarre (1973), a lower peak force rate and a longer split-phase duration would have been observed for subjects lacking periodontal receptors. On the contrary, compared with the natural group, the implant group showed a tendency for higher peak force rates and shorter split-phase durations (see Figs. 6B and 6C). Thus, the present findings support the conclusion of Trulsson and Johansson (1996a) that the periodontal receptors are not necessary for the control of force development during the split phase. However, this does not exclude the possibility that periodontal receptors may be of importance during chewing (Lavigne *et al.*, 1987; Inoue *et al.*, 1989; Morimoto *et al.*, 1989; Ottenhoff *et al.*, 1992), which is a task fundamentally different from biting. It is well-documented that sensory information can be used differently, depending on the task (see Lund, 1991). Furthermore, chewing movements mainly activate molar and premolar periodontal receptors, which may have different sensitivity characteristics compared with the receptors involved in incisal biting (Trulsson and Johansson, 1996b).

Periodontal receptors and spatial control of jaw actions

A requirement for efficient biting behavior is that the three-dimensional, time-varying, jaw action vector is in accord with the spatial distribution of food in relation to the teeth. Given their capacity to furnish spatial information about the patterns of contacts across the dentition, periodontal receptors most likely play an important role in this spatial control (Trulsson *et al.*, 1992; Trulsson, 1993; Trulsson and Johansson, 1996a,b). The present study clearly demonstrates an impaired control of the jaw-action vector for subjects lacking periodontal receptors: The subjects in the denture and implant groups lost the peanut with a high frequency similar to that experienced by dentate subjects with periodontal anesthesia (Trulsson and Johansson, 1996a). Moreover, two subjects with implant-supported bridges reported that they could not feel the location of the peanut or where the contact was made. Similar comments were often reported by anesthetized subjects (Trulsson and Johansson, 1996a).

Comparison with earlier studies on edentulous patients

Numerous studies on edentulous patients with removable complete dentures report a substantial functional improvement following treatment with osseointegrated implants. This has been shown in terms of both occlusal tactile sensibility (*e.g.*, Lundqvist and Haraldson, 1984; Jacobs and van Steenberghe, 1991) and oral motor function (for references, see Karlsson and Carlsson, 1993). Furthermore, based on studies measuring various "functional" parameters—such as maximal bite force, chewing efficiency and muscle activity—it is concluded that "masticatory function following implant rehabilitation is equal to, or very close to, that found in subjects of the same age with a natural dentition" (Karlsson and Carlsson, 1993). From the results of the present study, it is obvious that subjects with implant-supported prostheses nevertheless demonstrate specific motor disturbances that can be attributed to the absence of periodontal receptors. Moreover, in our particular task, no difference was found in motor performance between subjects with implants and those with removable complete dentures.

Acknowledgments

This study was supported by the Swedish Medical Research Council (project no. 8667), the Swedish Dental Society, and the Umeå University. We thank Dr. G. Westling for designing and building the bite-force recorder and Dr. G. Essick for valuable comments on the manuscript.

References

Bonte B, Linden RW, Scott BJ, van Steenberghe D (1993). Role of periodontal mechanoreceptors in evoking reflexes in the jaw-closing muscles of the cat. *J Physiol* (Lond) 465:581-594.

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

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.

Jacobs R, van Steenberghe D (1991). Comparative evaluation of the oral tactile function by means of teeth or implant-supported prostheses. *Clin Oral Implant Res* 2:75-80.

Karlsson S, Carlsson GE (1993). Oral motor function and phonetics in patients with implant-supported prostheses. In: Osseointegration in oral rehabilitation. Naert I, van Steenberghe D, Worthington P, editors. London: Quintessence, pp. 123-132.

Larson CR, Smith A, Luschei ES (1981). Discharge characteristics and stretch sensitivity of jaw muscle afferents in the monkey during controlled isometric bites. *J Neurophysiol* 46:130-142.

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.

Linden RW (1978). Properties of intraoral mechanoreceptors represented in the mesencephalic nucleus of the fifth nerve in the cat. *J Physiol* (Lond) 279:395-408.

Linden RW, Scott BJ (1989). The effect of tooth extraction on periodontal ligament mechanoreceptors represented in the mesencephalic nucleus of the cat. *Arch Oral Biol* 34:937-941.

Lockery HE, inventor (1971). BLH Electronics, Inc., assignee. Half bridge moment desensitization of parallelogram-type beams. US patent 3,576,128. Apr 27.

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.

Lund JP, Matthews B (1981). Responses of temporo-mandibular joint afferents recorded in the Gasserian ganglion of the rabbit to passive movements of the mandible. In: Oral-facial sensory and motor functions. Kawamura Y, Dubner R, editors. Tokyo: Quintessence, pp. 153-160.

Lund JP, Smith AM, Sessle BJ, Murakami T (1979). Activity of trigeminal α- and γ-motoneurons and muscle afferents during performance of a biting task. *J Neurophysiol* 42:710-725.

Lundqvist S, Haraldson T (1984). Occlusal perception of thickness in patients with bridges on osseointegrated oral implants. *Scand J Dent Res* 92:88-92.

Luschei ES, Goodwin GM (1975). Role of monkey precentral cortex in control of voluntary jaw movements. *J Neurophysiol* 38:146-157.

Macefield VG, Johansson RS (1996). Control of grip force during restraint of an object held between finger and thumb: responses of muscle and joint afferents from the digits. *Exp Brain Res* 108:172-184.

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 FA, van der Bilt A, van der Glas HW, Bosman F (1992). Peripherally induced and anticipating elevator muscle-activity during simulated chewing in humans. *J Neurophysiol* 67:75-83.

Sakada S (1983). Physiology of mechanical senses of the oral structure. In: Frontiers of oral physiology. Vol. 4. Kawamura Y, editor. Basel: Karger, pp. 1-32.

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

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: Brain and oral functions. Morimoto T, Matsuya T, Takada K, editors. Amsterdam: Elsevier Science, pp. 155-163.

Trulsson M, Johansson RS (1996a). Forces applied by the incisor and roles of periodontal afferents during food-holding and -biting tasks. *Exp Brain Res* 107:486-496.

Trulsson M, Johansson RS (1996b). Encoding of tooth loads by human periodontal afferents and their role in jaw motor control. *Prog Neurobiol* 49:267-284.

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.