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Sensory-motor regulation of human biting behavior

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Cover image: Schematic illustration of sensory input from the periodontal mechanoreceptors involved in the sensory-motor regulation of jaw muscle activity.

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Abstract

In order to control oral motor behavior, such as biting and chewing, we rely on information provided by a variety of sense organs, including periodontal mechanoreceptors (PMRs). The PMRs, located among the collagen fibers in the periodontal ligament that attaches the root of the tooth to the alveolar bone, send signals to the central nervous system when the surrounding collagen fibers are stretched by loading of the tooth. The information they provide is particularly important for sensorimotor regulation of the forces exerted during manipulative actions in mastication. Various types of dental status and treatment might affect the functioning of these receptors. For example, reduction of support by periodontal tissue is associated with a decrease in the number of PMRs, as well as enhanced mobility of the tooth. Connecting several teeth together with fixed bridges attenuates the mobility of each tooth and individuals with implant-supported bridges lack PMRs.

The general aim of the work presented here has been to improve our understanding of the role played by PMRs in regulation of normal jaw function and to elucidate how disturbance of the sensory information they provide, by disease or dental treatment, influences masticatory behavior. In this latter context special focus was directed towards prosthetic treatments, i.e., tooth- and implant-supported fixed bridges.

The subjects performed two motor behavioral tasks – a hold-and-split task (*Study I-IV*) and a novel manipulation-and-split task (*Study V*). In the first of these, holding and splitting morsels of food of differing hardness between the teeth was employed to examine the regulation of small holding forces and of the rate of increase in bite force during the split (the “split force rate”). The participants were instructed to hold the morsel (a piece of peanut or biscuit) between their teeth and not use more force than necessary to control it and then, approximately 3-4 seconds later, to split the morsel. In the latter task, motor behavior during food manipulation and the accuracy of the split were evaluated. These participants placed a spherical piece of candy in their mouth, moved it thereafter with their tongue to a position between their front teeth and finally attempted split it into two equal sized parts. Custom-made equipment was used to monitor changes in bite forces, jaw movements and muscle activity with time during these tasks.

The holding forces exerted by individuals with reduced support from periodontal tissue were almost 3-fold higher and more variable than those exerted by the healthy matched controls (*Study I).* In *Study II,* where different types of teeth were used to perform the same task, the holding force increased distally along the dental arch, being almost 3-fold higher for the molars than the incisors. Application of a local anesthetic to the teeth to block the sensory signals from the PMRs resulted in an approximately 2-3.5-fold elevation in holding forces (*Studies II* and *III*). In *Study IV* individuals with tooth- or implant-supported bridges were found to use holding forces approximately 2- and 2.5-fold higher, respectively, than the control subjects with natural teeth.

Although the splitting forces where the same for all of the groups, the rate at which this force was generated was higher when splitting harder food if periodontal sensibility was normal (*Studies III* and *IV*), an adaptation that was eliminated by periodontal anesthesia (*Study III*). This adaptation was also attenuated in periodontally affected individuals (*Study I*), as well as in the participants with tooth- or implant supported bridges (*Study IV*). In connection with the manipulation-and-split task the latter two groups demonstrated altered motor behavior, with a shorter contact phase prior to the split and a lower capacity than the dentated control group to split the candy into two equal parts (*Study V*).

The present findings demonstrate that sensory signals from PMRs play an important role in fine-tuning the amplitude and direction of bite forces during actions such as positioning and holding food between the teeth for biting. Furthermore, adjustment of the rate of increase in bite force to the hardness of food is carried out by individuals in whom this signaling is intact. In individuals with disturbed PMR signaling due to loss of support by periodontal tissue or bimaxillary full-arch splinting of the teeth (tooth-supported bridges) and in those lacking PMRs (i.e., with bimaxillary implant-supported bridges), regulation of these oral sensorimotor functions is impaired.

List of Publications

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

I. Impaired masticatory behavior in subjects with reduced periodontal tissue support.

   Johansson AS, **Svensson KG** and Trulsson M.

   J Periodontol. 2006; 77: 1491-1497

II. Forces applied by anterior and posterior teeth and roles of periodontal afferents during hold-and-split tasks in human subjects.

   Johnsen SE, **Svensson KG** and Trulsson M.

   Exp Brain Res. 2007; 178: 126-134

III. Regulation of bite force increase during splitting of food.

   Svensson KG and Trulsson M.

   Eur J Oral Sci. 2009; 117: 704–710

IV. Force control during food holding and biting in subjects with tooth- or implant-supported fixed prostheses.

   Svensson KG and Trulsson M.

   Manuscript

V. Intraoral manipulation and splitting of food in subjects with tooth- or implant-supported fixed prostheses.

   Svensson KG, Grigoriadis J and Trulsson M.

   Manuscript

Contents

List of abbreviations

ANOVA	Analysis of variance (a statistical term applied to models utilized to test whether the mean values for several groups are all equal)
BIC	Bayes information criterion (a statistical criterion for selecting a model from a set of parametric models consisting of different numbers of parameters)
CNS	Central nervous system (the brain and spinal cord)
CPG	Central pattern generator (a neural network in the CNS that produces rhythmic patterns of output, even in the absence of motor and sensory input)
EMG	Electromyography (a graphic recording of electrical currents associated with muscle contractions)
HSD	Honestly significant difference (a statistical term applied to a post-ANOVA pair-wise comparison test)
N	Newton (unit of force; 1 N is the force of Earth's gravity on an object with a mass of approximately 102 g (1⁄9.81 kg))
P-value	Probability value (a term used in statistical analysis)
PC	Personal computer
PMR	Periodontal mechanoreceptor (a sensory organ situated in the periodontal ligament surrounding the tooth that is stimulated by stretching of the ligament caused by application of a load to the tooth)
r.m.s.	Root mean squared (a mathematical procedure for determining the effective voltage or current of an alternating current (AC) wave)
SD	Standard deviation (a statistical measure of the variation in a set of measurements)
TMJ	Temporomandibular joint (the joint that hinges the lower jaw (mandible) to the skull)

Introduction

Obviously, one of the major aims of oral rehabilitation is to restore function. As the American Dental Association expressed in their definition of prosthetic dentistry, in 2003, “Prosthodontics is the dental specialty pertaining to the diagnosis, treatment planning, rehabilitation and maintenance of the oral function, comfort, appearance and health of patients with clinical conditions associated with missing or deficient teeth…” (http://www.ada.org/2555.aspx#prostho). While satisfactory assessment of the anatomical and esthetic outcomes can usually be achieved, objective evaluation of masticatory function is not yet possible (Woda et al 2006). The development of effective clinical routines for assessing this function requires a more detailed understanding of the regulation of the human masticatory system.

Accordingly, this thesis focuses on the regulation of the initial stage of human mastication, during which food is manipulated in the mouth, positioned between the teeth and bitten. Of particular interest is how prosthetic treatments with bridges supported by teeth or dental implants affect these behaviors.

Control of mastication

Mastication, the first stage of the digestive process, involves insertion and positioning of the food in the mouth for biting, crushing and grinding by the teeth. During the chewing process saliva is pressed into the food and after chewing, the bolus is transported further back in the mouth and subsequently swallowed.

Like locomotion and respiration, chewing involves the highly coordinated activities of several muscles, in this case those of the tongue, jaw and facial muscles, guided by rhythmic signals generated by a “central pattern generator” (CPG) within the central nervous system (CNS) (Dellow and Lund 1971). The output of the masticatory CPG located in the brainstem is modified by inputs from higher centers of the brain (e.g., the primary motor and somatosensory cortices), as well as by signals from peripheral sensory receptors, including muscle spindles in the jaw-closing muscles, receptors in the temporomandibular joints, mucosal receptors inside the oral cavity and skin receptors around the mouth in addition to mechanoreceptors in the periodontal ligaments surrounding the roots of the teeth (Lund 1991). Appropriate modification of the neural output from the CNS for regulation of biting and chewing is necessary for adequate adjustment of parameters such as the amplitude and rate of forces and jaw movements to the physical properties of the food being consumed (see Lund and Kolta 2006). For example, the delicate adaptation of jaw muscle activity to the hardness of food during chewing is strongly dependent on sensory signals from peripheral sensory receptors (Lund and Kolta 2006, Grigoriadis et al. 2010).

Sensors in the masticatory system

Muscle mechanoreceptors

The muscles of the human jaw contain so-called motor units each of whose component fibers are widely spread over a large area of the muscle, but innervated by one common motoneuron (α-motoneuron). Thus, the several motoneurons present can effectively adjust muscle activity to exert the force required. This is achieved either by increasing the frequency of firing of individual neurons in order to enhance contraction by the corresponding motor units and/or through activation of additional motoneurons and, thereby, recruitment of more motor units (see McComas 1998, Loeb and Ghez 2000, Miles 2004a). **Golgi tendon organs** are stretch-sensitive receptors located at the musculo-tendinous junction and situated in series with a small number of extrafusal muscle fibers. These receptors are activated by muscle contraction to signal the level of tension in the tendon, which provides information concerning the magnitude of the contractile force, thereby playing a role in regulating muscle contraction. Golgi tendon organs have been identified in the masseter and temporalis muscles of the cat (Lund et al 1978), but not in humans, so that information about their participation in the regulation of human jaw actions is lacking, to date. Jaw-closing muscles also contain stretch-sensitive receptors referred to as **muscle spindles** (Kubota and Masegi 1977). These are complex structures consisting of thick, myelinated afferent nerve fibers that surround intrafusal muscle fibers encapsulated in a thin, fusiform layer of connective tissue (see Hulliger 1984). Since these intrafusal muscle fibers are innervated by thin, myelinated efferent nerve fibers (γ-motoneurons), the muscle spindle contains both sensory and motor components.

When a muscle is stretched, the muscle spindles signal information about muscle length and changes in this length to the CNS, thereby playing an important role in regulating contraction of the muscle and also allowing the brain to determine the position and movement of the mandible (i.e., proprioceptive information) (Hulliger 1984, Hulliger et al 1985). At the same time, the γ-motoneurons modify the sensitivity of the sensory afferents of muscle spindles to stretch of the muscle. Thus, the α- and γ-motoneurons are often coordinately activated in such a manner as to maintain the sensitivity of spindle afferents, without saturation, over a wide range of muscle lengths (see Hulliger 1984, Pearson and Gordon 2000, Banks and Barker 2004, Miles 2004b). In contrast to the jaw-closing muscles, virtually no muscle spindles are present in the jaw-opening muscles of humans (Kubota and Masegi 1977).

The muscle spindles are proposeded to play an important part in sensory-mediated adaptation of chewing to food hardness. Indeed, in experimental animals the firing frequency of muscle spindles in jaw-closing muscles is dependent on the hardness of the object being chewed and, moreover, blockage of afferent input from these spindles reduces the activity of the jaw muscles (Morimoto et al. 1989, Hidaka et al. 1997, Hidaka et al 1999).

Temporormandibular joint mechanoreceptors

In general, receptors in the ligament and capsule of joints respond to extremes of joint rotation, indicating that these are involved in preventing overflexion. It has been proposed that temporomandibular joint (TMJ) receptors signal movements and positions of the jaw (see Klineberg 1980, Lund and Matthews 1981) and, indeed, a population of such receptors in rabbits have been classified as limited-range receptors, most of which are readily excitable by moderate TMJ movements (Lund and Matthews 1981). Although such receptors could therefore potentially provide detailed information concerning jaw position and movement, their role is thought to be quite limited in comparison to muscular and cutaneous receptors, only becoming significant in connection with extreme joint positions (see Sessle 2006).

Cutaneous and mucosal mechanoreceptors

The facial skin, lips and oral mucosa are characterized by rich mechanoreceptive innervation. Functionally, the mechanoreceptors in the soft tissues of the face and mouth resemble four types of receptors in the human hand: hair follicle afferents, slowly-adapting type I (Merkel's disk) and type II (Ruffini) afferents, and fast-adapting type I afferents (Meissner's corpuscle) (Johansson et al. 1988a, Edin et al. 1995, Trulsson and Essick 1997, Bukowska et al. 2010). These afferents respond not only to contact with objects, but also to contact between the lips, changes in air pressure generated in association with speech, and deformations in the facial skin and oral mucosa that accompany movements of the lips and jaws associated with chewing. Thus, in addition to exteroceptive information, these afferents provide proprioceptive information concerning jaw positions and movements (Johansson et al 1988b, Trulsson and Johansson 2002).

Periodontal mechanoreceptors

The root of a tooth is anchored to the alveolar bone by collagen fibers in the periodontal ligament that extend from the bone to the cementum on the surface of the root. Between these collagen fibers, lie nerve endings that respond to mechanical tension of the fibers produced by the application of force to the tooth (Cash and Linden 1982, Byers 1985). On the basis of their location and responsiveness to mechanical stimulation, these nerve endings are called periodontal mechanoreceptors (PMRs). The role of the PMRs in controlling jaw muscles during biting and chewing have been documented by several research groups (Lund 1991, Türker 2002, Lund and Kolta 2006, Trulsson 2006) and Trulsson and Johansson (1995, 1996b) have demonstrated their importance in connection with sensorimotor regulation of the forces exerted during manipulative actions involved in mastication, i.e., food positioning and holding for biting. Since PMRs are of special interest in the work discussed here, a more extensive description of their structure and function is provided below.

Histology

The PMRs are often referred to as "Ruffini-like", since they resemble the Ruffini-receptor (slowly-adapting type II receptor) in the skin. In both animals (Byers 1985, Byers et al 1986, Sato et al 1988, 1989, Byers and Dong 1989; Maeda et al 1989, Kannari 1990, Kannari et al 1991, Sato et al 1992) and man (Maeda et al 1990, Lambrichts et al 1992) their morphology varies extensively, from single, free nerve endings to more complex structures with finger-like extensions. The PMRs are innervated by myelinated afferent fibers with a large diameter (1-15 μm), conduction velocity ranging between 26-87 m/s, and cell bodies located in the trigeminal ganglion or in the mesencephalic nucleus of the brainstem (Beadreau and Jerge 1968, Gottlieb et al 1984, Heasman and Beynon 1986). Sensory neurons originating from these two different regions innervate different, but overlapping areas in the periodontal ligament. The ganglion fibers are distributed throughout the ligament, from the gingival margin to the apex of the root, with enrichment in the middle. On the other hand, mesencephalic nucleus fibers are located from the middle to the apex of the root, with enrichment near the apex (Byers and Dong 1989). These two groups of afferent fibers terminate at different sites in the brain stem, suggesting that their inputs serve different, currently unknown functions (Olsson and Westberg 1989).

Physiology and role in mastication

Along with other oro-facial receptors involved in the regulation of the jaw muscles the PMRs signal vital information to the nervous system concerning forces acting on the teeth, e.g., when they come into contact with food (see Trulsson and Johansson 1996a, Trulsson 2006). A number of animal studies have helped elucidate the involvement of PMRs in sensorimotor regulation of jaw muscles during chewing (Appenteng et al 1982, Lavigne et al 1987, Inoue et al 1989, Morimoto et al 1989). When placing an object between a pair of opposing molars during rhythmic chewing movements in the rabbit the EMG activity of the jaw-closing muscles rises, a phenomenon which can be attenuated by periodontal denervation (Lavigne et al 1987, Inoue et al 1989) or anesthesia (Morimoto et al 1989). Furthermore, blockage of the information provided by periodontal receptors in this same animal model significantly reduces the rate at which masticatory force is build up during chewing (Hidaka et al 1997).

Microneurographic recordings have revealed that human PMRs which provide temporal, spatial and intensive information about tooth loads (Johansson and Olsson 1976, Trulsson et al 1992, Trulsson 1993, Trulsson and Johansson 1994, Johnsen and Trulsson 2003, 2005, Trulsson and Essick 2010) all adapt slowly to such loads exhibiting responses similar to those of the slowly-adapting type II (Ruffini) receptors in the skin (Trulsson and Johansson 1996a). Even though each individual sensor is broadly sensitive to forces in certain directions and often responds to forces applied to more than one tooth (Trulsson et al 1992, Trulsson 1993, Johnsen and Trulsson 2003), PMRs do reliably encode information about the load and direction of forces applied to individual teeth. Significantly, approximately 80% of these afferents demonstrate most pronounced sensitivity to changes in force at surprisingly low levels, below 1 N for anterior teeth and 3 N for posterior teeth (Fig 1).

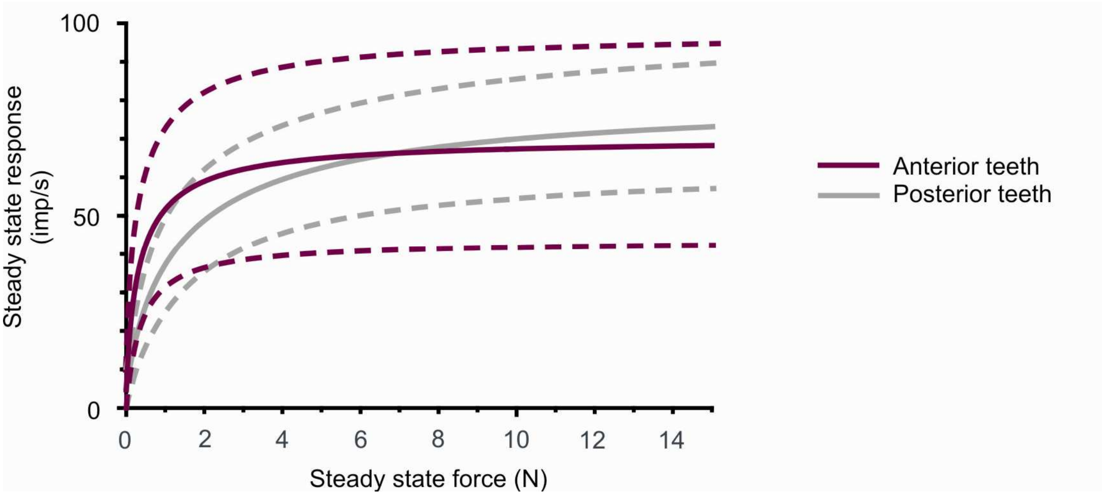

Figure 1. Mean value of all steady-state stimulus response functions for periodontal afferents at anterior (plum colored lines) and posterior (grey lines) teeth. The solid and dashed lines represent the mean ± 1 SD of the stimulus response functions (data obtained from 19 periodontal afferents of anterior teeth; Trulsson and Johansson 1994, and 20 periodontal afferents from posterior teeth; Johnsen and Trulsson 2005). From Johnsen and Trulsson (2005).

A quantitative model of the responses of periodontal afferents based on such data has been employed to assess signaling during holding and splitting food with the front teeth, as well as during chewing with the posterior teeth (Trulsson and Johansson 1996a, Johnsen and Trulsson 2005). This model indicates that most periodontal afferents from both anterior and posterior teeth characteristically respond strongly at the time of initial contact with food and encode the bite forces when food is held gently between the teeth. In contrast, these afferents provide little information about forces utilized to split or crush food during biting or chewing, since with such high forces their sensitivity is attenuated as a consequence of "saturation". Thus, PMRs are best able to convey information concerning contact with food and dentition at the low forces employed for holding and manipulation. In fact, when the periodontium is anesthetized force control is severely impaired and subjects exert considerably higher and more variable forces during such maneuvers (Trulsson and Johansson 1996b).

Furthermore, in connection with such tasks patients equipped with full dental prostheses supported either by the oral mucosa or by osseointegrated implants (and thereby lacking PMRs) behave as though they were anesthetized (Trulsson and Gunne 1998).

Together, such findings indicate that individuals rely on signals from the PMRs to regulate their jaw muscles, especially when they first make contact with, manipulate, and hold pieces of food between the teeth with gentle forces. Thus, a plausible hypothesis is that soon after contact between the food and teeth, somatosensory information concerning the spatial distribution of pieces of food, as well as their physical properties (e.g., hardness), is collected, processed and thereafter employed by the brain to control subsequent activities of the jaw muscles (see Trulsson and Johansson 1996a, Trulsson 2006). Moreover, various types of dental status and treatment may alter the function of PMRs. For example, reduction of the support provided by periodontal tissue is associated with a decrease in the number of PMRs, as well as with enhanced mobility of the tooth. In addition, fixed tooth-supported bridges reduce the mobility of the teeth involved and individuals with implant-supported bridges lack PMRs.

Aims

The general aim of this thesis work

The general aim has been to improve the understanding of the role of the periodontal mechanoreceptors in regulating jaw function and of how disturbance of the sensory information provided by these receptors due to disease or dental treatment influences masticatory behavior. In the latter context the focus has been on prosthetic treatments, i.e., tooth-supported and implant-supported fixed prostheses.

Specific aims

The specific aims of the individual studies were as follows:

Study I

- To examine how a reduction of the periodontal ligament due to periodontitis, which is associated with altered mechanoreceptive innervation of the teeth, affects masticatory behavior.

Study II

- To describe the role played by periodontal afferents in connection with holding and biting by teeth at different locations along the dental arch.

Study III

- To determine whether periodontal mechanoreceptors influence the power of the jaw actions in connection with the splitting of a morsel of food and whether different force rates are employed to split morsels of varying hardness.

Study IV

- To assess the ability of individuals with tooth- or implant-supported bridges to regulate the low contact and high biting forces required for holding and splitting food between the teeth, respectively.

Study V

- To describe motor performance during a novel manipulation-and-split task and to assess the extent to which control of this intraoral motor task is dependent on information supplied by periodontal mechanoreceptors.

Materials and Methods

Subjects

The motor behavioural experiments were carried out on volunteers. All participants were in good general health, with no history of neurological disorders; exhibited no symptoms of dental, oral or oro-facial problems or malfunction; and had normal inter-maxillary relationships at the time of these studies. *Study I* involved individuals with natural dentition, but with reduced support of periodontal tissue around at least one pair of opposing anterior teeth, as well as an age-matched control group. All of the participants in *Studies II* and *III* had natural healthy dentition. In *Studies IV* and *V*, individuals with bimaxillary tooth-supported fixed bridges or implant-supported fixed bridges, as well as age-matched controls with natural teeth were included.

Study I

In *Study I* the test group consisted of 11 subjects (6 women and 5 men with a mean age of 58 (range 41-74) years) suffering from advanced periodontal breakdown. As determined by assessment of available intraoral radiographs, destruction of their alveolar bone ranged between 30 and 70% (55 (12) %, mean (SD)) and was similar for the opposing mandibular and maxillary incisors. The clinical loss of attachment for the 11 maxillary and 11 mandibular central incisors examined was measured 1.8 - 9.2 mm (5.5 (2.3)) mm.

The control group consisted of an equal number of periodontally healthy subjects, matched by gender and age to the test group (6 women and 5 men, mean age 61 (44-75) years). Their corresponding loss of clinical attachment was 1.5 (0.5) mm.

None of the teeth examined in either group had been exposed to any endodontic or prosthetic treatment. Probing of gingival pockets did not result in extensive bleeding, nor were there any radiographic signs of apical pathology or earlier apical surgery.

Study II

Study II involved 20 subjects (12 women and 8 men, mean age 25 (range 22-40) years) with healthy natural dentition. The teeth employed in the task (the upper right central incisor, the canine tooth, the second premolar, the first molar and their antagonists) were all free from major dental restoration, exhibited normal mobility and no periodontal breakdown, and had not been subjected to any endodontic or prosthetic treatment. Four of these individuals (2 women and 2 men, mean age 25 (22-29) years) also repeated the same experimental task following administration of local anesthesia to their teeth.

Study III

In *Study III* 15 subjects (10 women and 5 men, mean age 24 (20-41) years) with healthy natural dentition participated. The teeth involved in the task (i.e., upper right central incisor and its antagonists) exhibited normal mobility and no periodontal breakdown, were free from major restoration, and had not been subjected to any endodontic or prosthetic treatment.

Study IV-V

Study IV involved three groups of 10 subjects each. The "bridge group" consisted of 10 individuals (5 women and 5 men, mean age 70 (61-83) years) with tooth-supported fixed bridges of the metal-ceramic type that had extensions of at least 10 units (including the abutment teeth and pontics) in both the upper and lower jaws. These bridges were supported by 4-9 (mean 6.7) abutment teeth in each jaw and had been in place for a mean of 53 (range 8-246) months. The "implant group" contained 10 participants (3 women and 7 men, mean 72 (67-77) years) with implant-supported fixed bridges of the metal-acrylic type (with the exception of one individual with a metal-ceramic bridge in the upper jaw) with extensions of at least 10 units (including dental implant abutments and pontics) in both the upper and lower jaws. These bridges were supported by 4-6 (mean 5.0) dental implants (ad modum Brånemark®) in each jaw and had been in use for an average of 77 (range 1-240) months. The "natural group" consisted of 10 age-matched control volunteers (3 women and 7 men, mean age 67 (62-72) years) with healthy natural dentition and no known history of periodontal disease. Their upper and lower front teeth had not been subjected to any endodontic or prosthetic treatment. All of these participants visited their dentists on a regular basis.

Study V involved the same three groups of 10 subjects as *Study IV*, except that one of the subjects in the "natural group" was different. This natural group consisted of 4 women and 6 men with a mean age of 66 (61-72) years.

Methodological considerations

Equipment

Studies I-IV

Two similar, custom-built apparatuses were employed to measure force in *Studies I-IV*. Each apparatus consisted of a bar handle connected to two duralumin blocks that terminated in two parallel, rectangular plates, similar to an apparatus employed previously (Trulsson and Johansson 1996b, Trulsson and Gunne 1998). The upper duralumin block contained strain gauge force transducers that continuously monitored the forces applied to the plate and the apparatus was designed so as to insure that force measurement was independent of where the force was applied to the plate (Lockerly, 1971). A morsel of food was placed on the free end of the upper plate (Fig 2a).

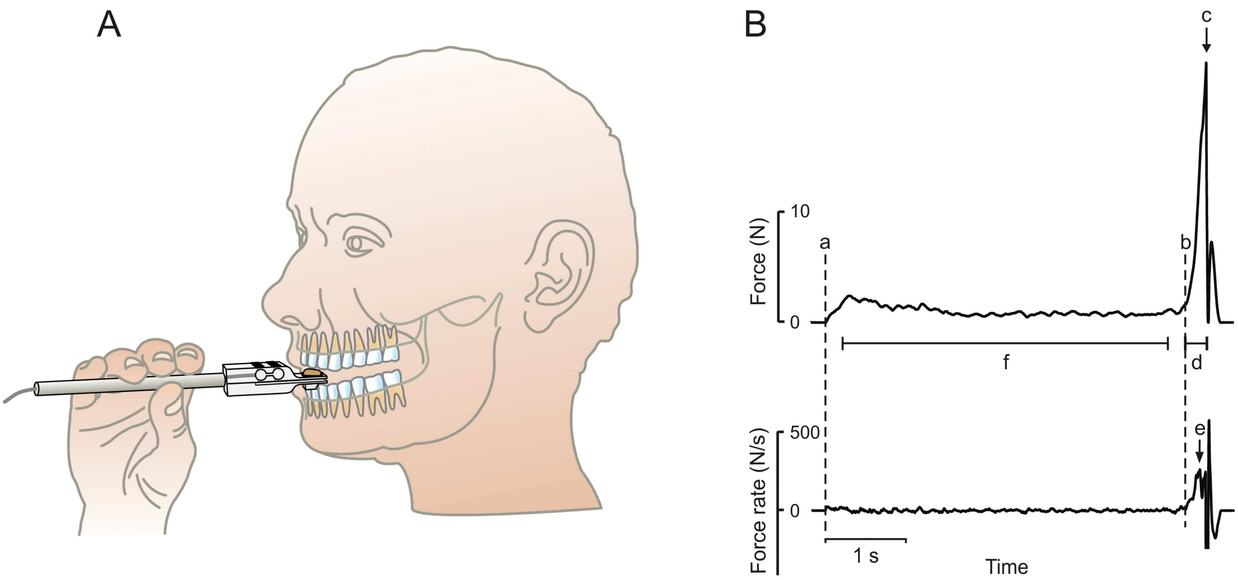

Figure 2. (**A**) The hand-held apparatus employed to record the bite forces exerted on the morsel of food during performance of the hold-and-split task. The morsel rested on the upper horizontal plate and the apparatus was positioned between the upper and lower right central incisors. The lower plate had an anterior stop designed to facilitate positioning in the mouth. (**B**) A representative force profile (upper trace) and force rate profile (lower trace) for a subject with natural teeth holding and splitting a peanut. a) initial contact with the food; b) initiation of splitting; c) the split force and end of the split phase; d) duration of the split phase; e) peak rate of split force; and f) the hold phase, i.e., the interval beginning 0.2 s after initial contact with the food and ending 0.2 s prior to the onset of the split phase.

Study V

In this case a custom-built device designed to monitor jaw movements in all three dimensions was utilized to track vertical movements of the incisor point of the lower jaw with respect to the upper jaw. This device consisted of a lightweight frame that rested on the upper part of the bridge of the nose and was held in place by spectacle frames whose ends were connected by an adjustable velcro strap placed around the head. A multiple array of magnetic sensors located on the arms projecting from this frame next to the cheeks tracked the three dimensional position (with a resolution of 0.1 mm) of a magnet (10x5x5 mm in size) attached to the labial surface of the mandibular incisors (with light-curing composite material), independently of the posture of the head (Fig 3a). The sensors were positioned at right angles to the horizontal Frankfurt plane (i.e., the line between the inferior border of the orbita and the tragus of the ear) of each subject. This jaw-tracking device interfered minimally with oral functions and allowed free movement of the head.

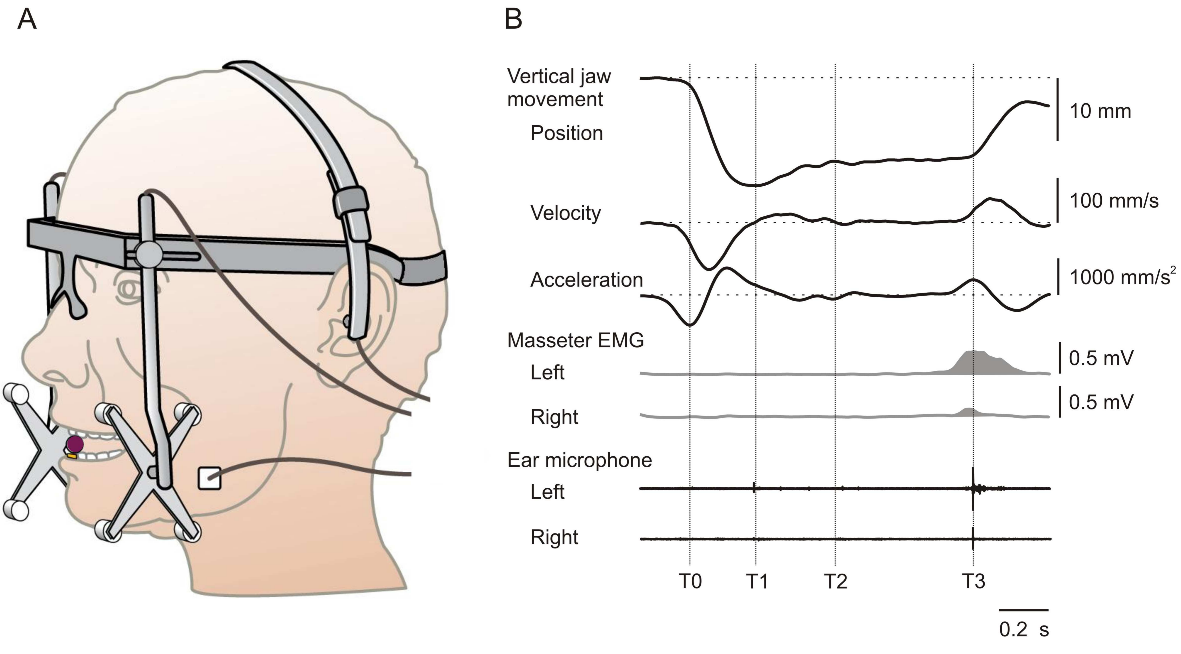

Figure 3. (**A**) The custom-built device for monitoring movements of the lower jaw with reference to the upper jaw during the manipulation-and-split task. Magnetic sensors located on arms projecting from the frame tracked the position of a magnet attached to the labial surface of the mandibular incisors in three dimensions. EMG signals were recorded bilaterally from the centers of the masseter muscles with bipolar surface electrodes. Sounds related to the cracking of food were recorded bilaterally with microphones inside earplugs mounted on a headset. (**B**) Representative recordings made during the manipulation-and-split task performed by a subject with natural dentition. From top to bottom the curves depict: position; velocity and acceleration of the vertical movement of the mandible; muscle activity (the r.m.s.-processed EMG) from the left and right masseter muscles; and sound recordings from the left and right ear microphones. The events of interest are the following: The onset of the jaw opening phase (T0). End of the opening phase, and start of the contact-establishing phase (T1). End of the contact-establishing phase, and start of the contact phase (T2). End of the contact phase, and start of the jaw-closing phase (T3). The split of the candy was detected as rapid closing of the mandible that coincided with both elevated activity in the masseter muscles and sound in the ear-microphones.

Bipolar surface electrodes were used to record EMG signals bilaterally from the centers of the masseter muscles. After cleaning the skin thoroughly with a solution of alcohol, gel was applied to these electrodes and they were then attached with double-sided adhesive tape.

Sounds originating from the cracking of food were recorded bilaterally by a custom-built device consisting of microphones inside earplugs mounted on a headset. These earplugs were positioned firmly at the entrance to the auditory meatus and the two microphones calibrated prior to the experimental session with each subject.

Behavioral tasks, experimental procedures and test food

All investigations were performed with the subjects seated comfortable in an office chair (*Study I*) or dental chair (*Studies II-V*) in a quiet room.

Study I

These subjects performed a **hold-and-split task** (developed by Trulsson and Johansson (1996b)) that involved holding the force measurement apparatus in their preferred hand, placing half of a peanut on top of the upper plate and then positioning this food horizontally between a pair of opposing central incisors. The subjects were instructed to hold the peanut between their teeth and not use more force than necessary to control the peanut. Approximately 3-4 seconds later, they were told to split the peanut. Each subject performed this task 15 times.

Study II

This investigation involved the same hold-and-split task as in *Study I,* except that in this case the subjects performed this task using four different types of teeth – the upper right central incisor, the canine tooth, the second premolar and the first molar. Furthermore, three series of tests were performed during each session to determine whether previous experience influenced the holding behavior and whether this behavior changed with time. In each of these series five trials were performed utilizing each type of tooth. Thus, each subject performed the hold-and-split task a total of 15 times with each tooth.

In addition, four of the subjects returned on a later occasion to perform one more series of hold-and-split tasks before and after achievement of local anesthesia in the upper (by local infiltration of an anesthetic) and lower teeth (by blockage of the inferior alveolar nerve at the mandibular foramen) on the right side of the jaw. When the teeth were anesthetized, the instructor helped the subjects position the apparatus in their mouth in order to obtain optimal contact between the peanut and specific teeth.

Study III

Again, the same hold-and-split task as in *Study I* was performed, but in this case with two different kinds of food – half a peanut, as in *Studies I* and *II*, and a piece of a biscuit (approximately 6x10 mm in size; Digestive; Göteborgskex, Kungälv, Sweden). In addition, each subject performed a series of hold-and-split tasks both before and after application of local anesthetic to their upper and lower incisors (by local infiltration). In each series 15 pieces of biscuit and 15 peanuts were tested in a semi-random order, so that, each subject performed the hold-and-split task a total of 60 times (30 times each with and without periodontal anesthesia). The subjects were aware at all times of the type of food being used.

Study IV

The protocol in this case was identical to that in *Study III*, except that the piece of biscuit was somewhat larger (approximately 8x12mm; Digestive Oliv, Göteborgskex, Kungälv, Sweden) and no anesthesia was employed. Each subject performed the hold-and-split task 10 times with the half of a peanut and 10 times with the piece of biscuit in a semi-random order. As in *Study III*, the subjects were aware at all times of the type of food being used.

Study V

This investigation involved a novel **manipulation-and-split task** that involved positioning a spherical chocolate dragée (with a diameter of 10 mm and weight of approximately 0.80 g; Marianne chokladdragé; Cloetta Fazer, Helsinki, Finland) between the front teeth and then splitting it into two parts of similar size.The candy was placed between the tongue and mid-section of the hard palate by the subjects themselves, after which they closed their mouths and maintained their teeth in the intercuspal position. Each subject was subsequently instructed to move the piece of candy with their tongue to their front teeth and thereafter to split it into two equal sized parts. After splitting, the subjects spit the pieces of candy into a cup held by the experimenter. Each subject performed this task 15 times.

In all five studies, each subject performed 5 or 6 practice trials in order to familiarize him- or herself with the task prior to the actual experimental session.

Data collection and calculations

The hold-and-split task

The variation in bite force with time was monitored employing a PC software system for data acquisition and analysis (SC/Zoom (*Studies I-III*) or WinSC/WinZoom (*Study IV*); Umeå University, Physiology Section, IMB, Umeå, Sweden). Force measurements at several different time-points during each individual trial (see Fig 2b) were used for subsequent calculations.

The average hold force was defined as the mean value during the period, beginning 0.2 s after initial contact with the food (a) and ending 0.2 s before the onset of splitting (b). The splitting phase was characterized by a distinct and rapid increase in force (b to c), which eventually split the morsel. The moment of initial contact (a) and the onset of splitting (b) were both reliably identified by the computer from the force-rate signal, as confirmed by manual checking. The splitting force (c) was defined as the peak force prior to the moment the morsel split, which was indicated by a rapid decline in force that also marked the end of the splitting phase. The duration of the splitting phase (d) was defined as the time from the onset (b) to the end of this phase (c) and the mean force rate as the elevation in force during this period divided by its duration. The peak split force rate (e) was identified by the computer.

In *Studies III* and *IV* the rate of enhancement in force during the early part of the splitting phase was analyzed by measuring the time required for the force to increase 1, 2, 3 and 4 N (*Study III*) or 1, 2, and 3 N (*Study IV*) relative to that applied at the beginning of this phase.

For each subject, the data from all trials in each series involving one type of tooth, condition and/or food group were combined to obtain a subject mean for each parameter, and these values were subsequently employed for statistical analyses.

The manipulation-and-split task

The weight of the larger piece of candy resulting from each split (measured with a precision of 0.01g) was compared to half of the weight of the original piece (0.40 g). An equal split was considered to be ideal; deviation by more than 50% from this ideal split (i.e., cases in which the larger piece weighed more than 0.60 g) was classified as unsuccessful; and deviation of more than 75% (with the larger piece weighing more than 0.70 g) was designated as a failed split.

Jaw movements and EMG and sound signals were collected and analyzed with a PC-based software system for data acquisition and analysis (WinSC/WinZoom).

Several measurements of time and position from each individual trial were of interest (Fig 3b): The **onset of jaw-opening** (T0) was defined as the time-point during the beginning of mandible opening at which maximal vertical acceleration (peak negative value) occurred and the **end of the opening phase** (T1) and **beginning of the contact-establishing phase** (T1) was considered to have been reached when the vertical velocity became zero for the first time thereafter. The **end of the contact-establishing phase** (T2) and **start of the contact phase** (T2) was defined as the time-point at which the vertical velocity first became zero after the beginning of the former. The point of maximal vertical acceleration (peak positive value) prior to the split was designated as the **end of the contact phase** (T3) and **start of the jaw-closing phase** (T3). The split of the morsel was detected as a rapid closing movement of the mandible that coincided with both increased EMG activity and a clear sound in the ear-microphones. All of these time-points were identified by the computer and subsequently checked manually for error.

Data from all 15 trials for each individual subject were combined to calculate a subject mean for each parameter and these values utilized for statistical analyses.

Statistical analyses

In *Study I* the non-parametric Mann-Whitney U test was used to compare the test and control groups with respect to: holding force, variability in the holding force (holding force SD), splitting force, the rate of change in the splitting force and duration of the splitting phase. A P-value <0.05 was considered to be statistically significant.

In *Studies II* and *III* multivariate and repeated-measures analysis of variance (ANOVA), respectively, was utilized to compare the major force parameters (holding force, variability in holding force (*Study II*), splitting force, mean force rate, peak force rate and duration) with the different types of teeth (incisor, canine, premolar and molar; *Study II*) and with the two different types of food (biscuit and peanut; *Study III*), as well as before and after anesthesia. If the ANOVA indicated a significant main effect ($P < 0.05$), post hoc analysis was performed using an Unequal N HSD test. A P-value <0.05 was considered to be statistically significant.

In *Studies IV* and *V* linear mixed models were used to evaluate the effect of dental status (natural teeth, tooth-supported bridges or implant-supported bridges) and type of food (biscuit and peanut in *Study IV*) on; holding force, variability in holding force, splitting force, duration of the splitting phase and peak and mean rates of increase in the splitting force (*Study IV*), as well as median splitting performance, mandibular position at T1 to T3, peak velocity during jaw-opening and duration of the different individual phases (T0-T3) (*Study V*). In cases of significant interaction, planned pairwise comparisons were then performed.

Certain of the variables (holding force and duration of the splitting phase in *Study IV* and median splitting performance, mandibular position at T1 to T3 and number of unsuccessful and failed splits in *Study V*) displayed skewed distributions and were therefore transformed for analysis on a log-scale.

Wilcoxon's signed ranks test was applied to compare the time required for the force to increase 3 N during the early part of the splitting phase with the biscuit and peanut within the groups in *Study IV*.

Ethical approval

- *Studies I* and *II* were pre-approved by the local ethics committee at Karolinska University Hospital in Huddinge, Sweden (Dnr: 492/00).
- *Studies III, IV* and *V* were pre-approved by the regional ethical review board in Stockholm, Sweden (Dnr: 04-715/4).

Prior to participation, written informed consent was obtained from each of the participants in accordance with the Declaration of Helsinki.

Results and Discussion

Holding and splitting food (Studies I-IV)

All of the subjects in the different groups examined exerted relatively steady forces during the holding phase, followed by a rapid elevation in force until the morsel was split (the splitting phase). However, some noteworthy differences between the groups were observed with respect to the level of holding force, variability in this level and the rate of force increase during the splitting phase.

Holding forces

… using different types of teeth (Study II)

The mean levels of holding force for the three test series performed were very similar, suggesting stable holding behavior for all of the teeth examined and allowing the data for all three series to be pooled to obtain a single mean value for each tooth in each subject. The mean holding force increased distally from the incisor (0.60 (0.27) N (mean (SD))), to the canine tooth (0.77 (0.45) N), to the premolar (1.15 (0.72) N), to the molar (1.74 (0.76) N) (Fig 4). Except for the incisor compared to the canine tooth, these differences were all statistically significant (P<0.001 to <0.01).

… in subjects with loss of support by periodontal tissue (Study I)

In subjects with loss of support by the periodontal tissue the holding forces was almost three times higher than for the periodontally healthy controls (1.10 (0.36) and 0.40 (0.22) N, respectively; P<0.001) (Fig 4). The periodontally impaired group also employed more variable holding forces, as reflected in both the within-trial variance (i.e., the variation in force during the holding phase; P <0.01) and the between-trial variance (i.e., the variation in mean holding force for the different trials; P <0.001).

… during periodontal anesthesia of the teeth (Studies II* and *III)

Following periodontal anesthesia in *Study II*, the mean holding forces exerted by all of the teeth examined were elevated on an average of 3.5-fold (P<0.05) (Fig 4). In addition, the mean holding forces varied considerably between anesthetized subjects, spanning a range 3.4 times greater than that observed in the absence of anesthesia.

In *Study III*, the mean holding forces during anesthesia (1.51 (0.71) N in the case of biscuits and 1.31 (0.58) N for peanuts) were found to be approximately twice those observed under normal conditions (0.79 (0.57) N and 0.66 (0.42) N, respectively) (P < 0.01 for both foods) (Fig 4). With or without anesthesia the mean holding forces for these two food substances did not differ significantly.

… in subjects with tooth- or implant-supported bridges (Study IV)

The holding forces for the pieces of biscuit were 0.69 (0.52-0.88) (median (25-75 percentile)) N for the natural group, 1.13 (0.85-1.36) N for the bridge group and 1.98 (1.30-3.01) N for the implant group. In the case of the peanut, the corresponding forces were 0.79 (0.62-0.93) N, 1.47 (1.11-1.65) N and 2.02 (1.53-3.19) N. Thus, the subjects with tooth- or implant-supported bridges applied nearly twice as much (1.3 N) and approximately 2.5-fold higher (2.0 N) holding force, respectively, over both foods than those with natural dentition (0.74 N; P<0.001) (Fig 4). Furthermore, the individuals with implants employed significantly higher holding forces over both foods than those in the bridge group (P=0.003).

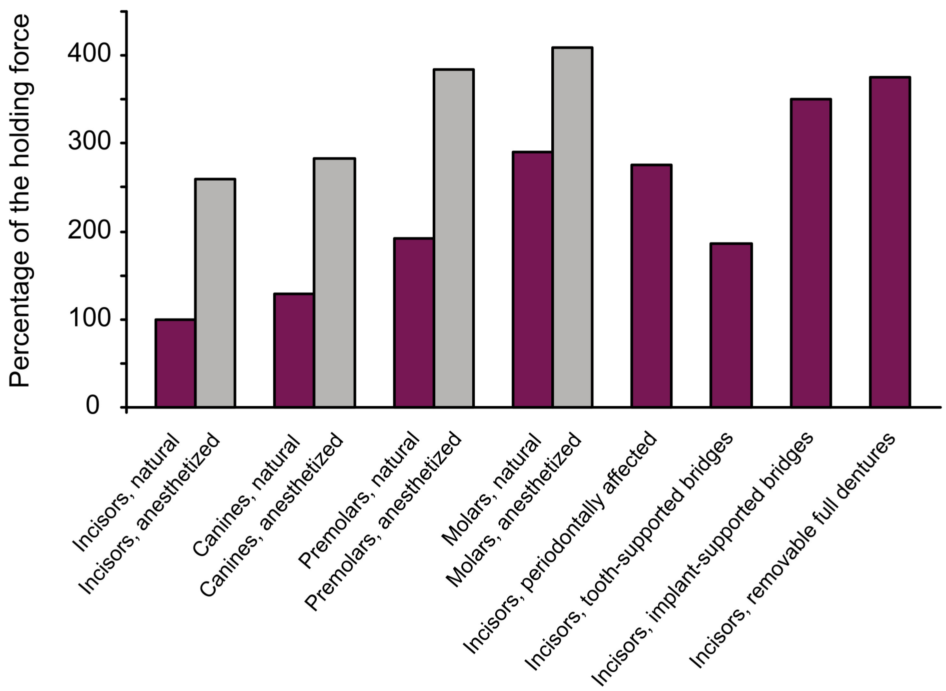

Figure 4. Relative holding forces (with peanuts) for the different types of teeth, conditions and prosthetic treatments in relationship to natural incisor teeth with normal periodontal sensibility. These data are from *Studies I, II, III* and *IV* and the investigations by Trulsson and Johansson (1996b; anesthetized incisor teeth) and Trulsson and Gunne (1998; implant-supported bridges and removable full dentures). In cases of more than one study on the same group, the mean of all relevant studies is presented.

The holding forces observed here in individuals with healthy natural dentition (0.40-0.79 N for incisor teeth in *Studies I-IV*) are comparable to those reported previously (0.59-0.63 N; Trulsson and Johansson 1996b, Trulsson and Gunne 1998), while the holding forces for the posterior teeth (1.15 N for premolars and 1.74 N for molars; *Study II*) were significantly higher. The use of such holding forces by individuals with natural teeth are easily explained by the pronounced sensitivity of PMRs at these low force levels (<1 N in the case of anterior teeth and < 3 N for posterior teeth; see Fig 1). Apparently, individuals with natural teeth automatically adjust the forces of their bite during the holding phase so as to optimize the information supplied by PMRs (see Trulsson and Johansson 1996a, Johnsen and Trulsson 2005, Trulsson 2006).

When sensory input from the teeth is blocked by administration of a local anesthetic to the periodontium, considerably higher and more variable holding forces are observed (*Studies II* and *III*), in line with the report by Trulsson and Johansson (1996b) of an average holding force of 2.3 N during periodontal anesthesia. Similar impairment of force control during holding and manipulation of food has also been observed in individuals lacking PMRs, e.g., patients with fixed prostheses supported by osseointegrated dental implants (2.6 N) or with removable complete dentures supported by the oral mucosa (2.2 N) (Trulsson and Gunne 1998).

The use of significantly higher forces (1.1 N) by individuals with reduced support from periodontal tissue around the teeth than by those with intact support (0.40 N) in *Study I* can be explained by lowered sensitivity of the teeth as a consequence of fewer functioning periodontal receptors. However, their partially remaining innervation of the periodontal ligament allows the application of lower holding forces by the former subjects in comparison to individuals in whom sensory input from the PMRs is totally lacking (i.e., as a result of periodontal anesthesia in *Studies II* and *III* and the presence of implant-supported bridges in *Study IV*). Interestingly, the enhanced tension on the remaining ligament, which might possibly excite the mechanoreceptors present to a higher degree, appears not to be able to compensate functionally for the loss of periodontium.

The holding force exerted by the participants with tooth-supported bridges was nearly twice as high and more variable than that used by those with natural dentition (1.3 versus 0.74 N over both foods) (*Study IV*), which can be explained by a number of factors. First, the reduced support for the abutment teeth from periodontal tissue which was rather common among the subjects with tooth-supported fixed prostheses, probably leads to the utilization of higher holding forces (see *Study I*). Secondly, the rigid mechanical coupling between the abutment teeth included in the bridge results in lower mobility (higher stiffness) of these individual teeth when force is applied to the prosthesis (Picton 1990, Nyman and Lang 1994), thereby necessitating higher bite (holding) forces to generate the same degree of tooth movement and thus the same level of PMR stimulation. Finally, a force applied to the incisors in a fixed full bridge will affect not only the anterior, but also the posterior abutment teeth (premolars and molars) in which the PMRs are less sensitive to alterations in force (see Johnsen and Trulsson 2005). Accordingly, the differing sensitivities of PMRs associated with different types of teeth (see *Study II*) may influence the holding forces produced by subjects with tooth-supported bridges.

Nonetheless, the holding force exerted by the participants with tooth-supported bridges was only approximately two-thirds of that used by those with implant-supported bridges (1.3 versus 2.0 N over both foods). This difference can reasonably be attributed to differences in the availability of sensory information concerning the bite forces applied. Subjects with tooth-supported bridges still have PMRs, even if these are stimulated by applied forces to a lesser extent than normal (see above), whereas individuals with dental implants, lack PMRs and must thereby utilize some other, less sensitive sensory systems for the regulation of holding forces. Such alternative sensory systems could include mechanoreceptors located in the mucosa, periosteum, bone sutures, temporomandibular joints and/or muscle spindles in the jaw muscles (see the Introduction). Indeed, in monkeys the primary afferents from muscle spindles are highly active shortly after initial contact with food and may very well be capable of providing information about contact forces (Lund et al 1979, Larson et al 1981).

The splitting phase

The force required to split the morsels of the two different types of food used here ranged between 9-13 N for biscuits and 18-35 N for peanuts, with no differences between any of the groups examined, except for between the different types of teeth in *Study II*. The differences in split forces between the different studies probably reflected primarily variations in the size of the piece of biscuit and batch of peanuts used. Indeed, origin, year of harvest, roasting time, salt content and other manufacturing parameters are known to influence the hardness of peanuts (Smyth et al 1998, McKiernan and Mattes 2010)

The force required to split the peanut in *Study II* differed for the various types of teeth examined, increased distally along the dental arch from the incisor (18.9 (2.6) N (mean (SD))), to the canine tooth (20.3 (3.5) N), to the premolar (30.1 (9.8) N), to the molar (34.9 (10.7) N). All of these differences between teeth were statistically significant ($P<0.001$), except for the differences between the incisor and canine tooth and between the premolar and molar. At the same time, the duration of the splitting phase was surprisingly similar for all of the teeth (with an overall mean of 0.47 (range 0.43-0.52) s, so that the rate of increase in force was higher for the posterior teeth than the anterior. The peak rate of increase in force increased posteriorly, from the incisor (181 (100) N/s; mean (SD)), to the canine tooth (226 (124) N/s), to the premolar (319 (214) N/s), to the molar (379 (220) N/s).

The mean rate of increase in force (mean force rate) during splitting of the peanuts in *Study I* was significantly lower for the subjects with reduced support from periodontal tissue (61 (35) N/s) than for those in whom this support was intact (117 (68) N/s) ($P<0.005$). This lower force rate was correlated to a splitting phase that was approximately twice as long as for the periodontally healthy ($P<0.01$).

Study III revealed that with normal periodontal sensibility the mean force rate when splitting biscuits was only approximately two-thirds of that attained when splitting peanuts ($P<0.001$). In the case of the biscuits this rate was unchanged by periodontal anesthesia, whereas with the peanuts the force rate was reduced upon anesthesia ($P<0.05$). Since the splitting forces were the same under both conditions, periodontal anesthesia led to prolongation of the splitting phase with the peanuts ($P<0.05$).

For participants with tooth- or implant-supported bridges or natural dentition, *Study IV* showed that when splitting biscuits the mean force rate was only about half of that attained when splitting peanuts ($P<0.001$), which corresponded to a longer splitting phase in the case of the peanuts ($P<0.001$). However, the maximal force rate exerted during the splitting phase (the peak force rate) with biscuits was found to be similar for the three groups, with no significant difference between the two foods for subjects with tooth- or implant-supported bridges, while those with natural dentition exhibited a peak force rate that was almost twice as high when splitting the peanuts compared to biscuits (P<0.001).

These latter findings from *Studies III* and *IV* indicate that with normal periodontal sensibility the increase in bite force is adjusted for the hardness of the food. However, the higher mean (and peak) split force rate observed for the peanuts might also be interpreted as constituting evidence that individuals actively adjust the force of attack during the splitting phase, to suit the hardness of the food. This would be correct if the increase in force during the splitting phase were linear with time, but the rate of this increase during the initial part of the splitting phase clearly accelerates with both peanuts and biscuits. Thus, subjects could use exactly the same accelerating increase in force with both types of food and because higher force is required to split the peanut, the mean (and peak) split force rate is higher and the duration of the splitting phase longer in this case (Fig 5a). To determine whether our subjects actually utilized different force trajectories when splitting peanuts and biscuits, the time required to increase the force by 1, 2, 3, and 4 N (*Study III*) or 1, 2, and 3 N (*Study IV*) from the initiation of the splitting phase was measured (Fig 5b). Interestingly, in *Study III*, the increase from 2 to 3 N and from 3 to 4 N with the peanut took less time than with the biscuit (Fig 6a), resulting in a steeper slope for the peanut (P < 0.05). In *Study IV* the time required to enhance the force by 3 N was also shorter for the peanuts in participants with healthy natural dentition (P=0.010) (Fig 6c). However, for the individuals with natural dentition subjected to periodontal anesthesia (*Study III*), as well as for those with tooth- or implant-supported bridges (*Study IV*), no such difference between the two foods during this early stage of splitting could be observed (Fig 6b, d and e).

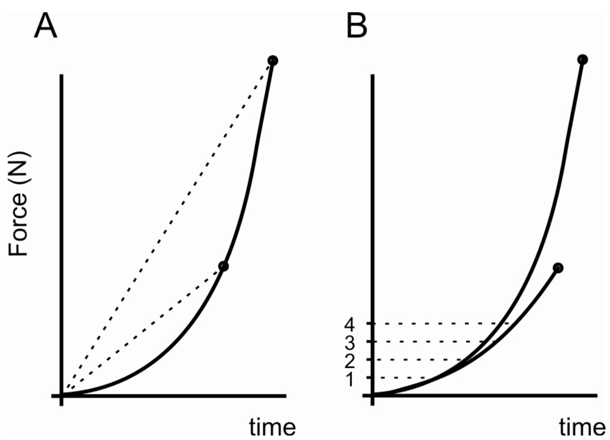

Figure 5. Schematic illustration of two different hypothetical strategies that could be employed by the nervous system to reach different split forces. The curves indicate force trajectories during the split phase and the filled circles the time-point at which the morsel is split. (**A**) Two morsels of food split at different levels along the same force trajectory. As a consequence of the curvature of this force trajectory, the morsel that is split at the highest force will also demonstrate the most rapid mean increase in force (indicated by the dashed lines) and the longest split phase. (**B**) Two morsels of food split at different levels (filled circles) along different force trajectories. As in (A), the morsel split at the highest force exhibits the most rapid mean increase in force and the longest split phase. To determine whether the subjects actually produced different force trajectories when splitting peanuts and biscuits, the time required to increase the force by 1, 2, 3, and 4 N (*Study III*) or 1, 2 and 3 N (*Study IV*) from the initiation of the splitting phase was measured.

The observation that the forces required to split the two items of food did not differ between our groups of subjects indicates that these forces are determined primarily by the physical properties of the food itself. However, the anatomical shape (sharpness) of the occluding teeth also influences the force required to split morsels to a certain extent. Thus, the positive correlation observed in *Study IV* between the splitting forces for biscuits and peanuts indicates that individuals who required high biting force to split one of these foods must develop high force to split the other as well. Similar correlation, both before and during periodontal anesthesia, could be seen in *Study III*. It can be assumed that the incisors of the subjects who had to apply higher force to split the food were less sharp. This is important to note, however, that since there were no differences in the mean group split forces in any of the studies *(Studies I-IV)*, it can be assumed that the average cutting efficiency of the incisors of the individuals in these groups was similar.

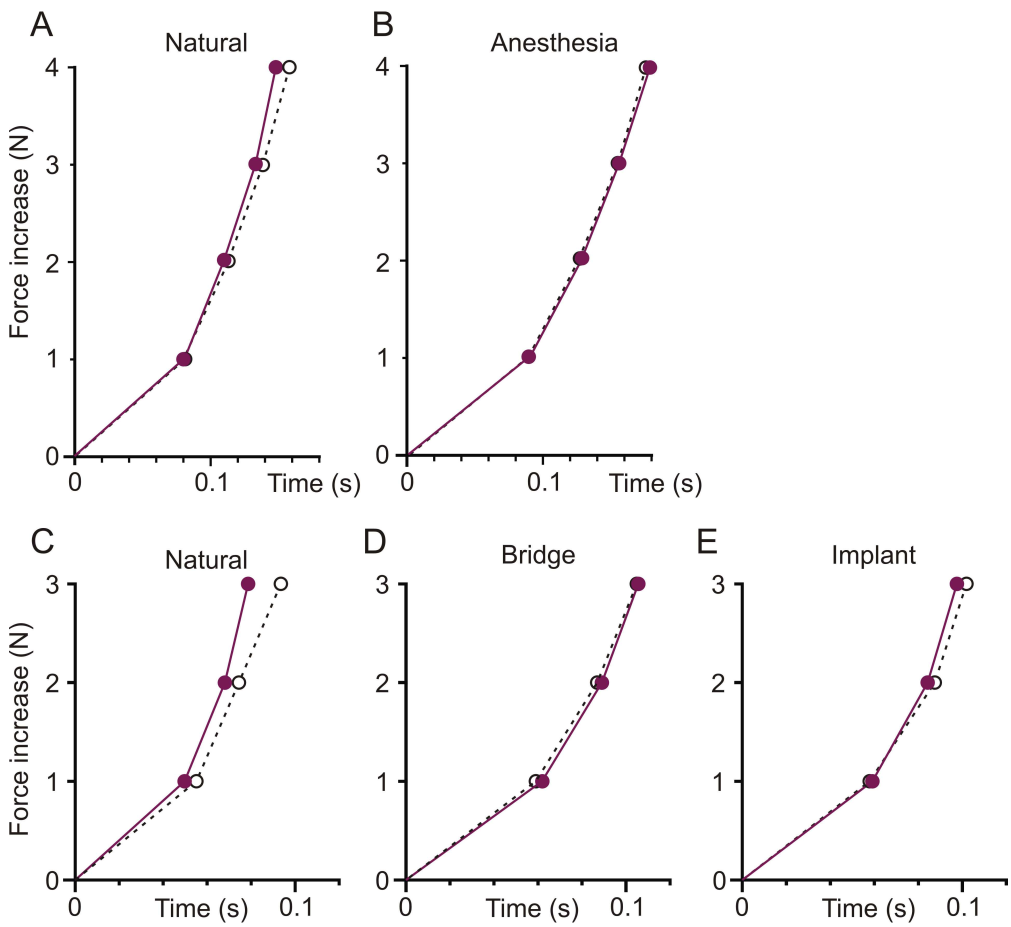

Figure 6. Force trajectories during the early stage of the split phase. (**A-B**) From initiation to achievement of a 4-N increase in force by subjects with natural teeth and normal periodontal sensibility (**A**) or local anesthesia (**B**) (*Study III*). (**C-E**) From initiation to achievement of a 3-N increase in force **by** subjects with natural teeth (**C**), tooth-supported bridges (**D**) or implant-supported bridges (**E**) (*Study IV*). The filled circles connected with a plum colored line indicate the mean (A-B) or median value (C-E) for peanuts, while the unfilled circles connected with a dashed black line indicate the corresponding values for biscuits. Note the shorter time required for the participants with natural dentition to attain the 4 -and 3-N increases with peanuts than with biscuits (A) and (C).

These observations confirm the hypothesis that when splitting harder morsels of food, individuals with natural dentition elevate both the duration and rate of force production to achieve higher splitting forces. Thus, when the PMRs are intact, the nervous system can adapt the rate at which the force is elevated to achieve efficient biting of different types of food. This adaptive mechanism appears to be absent from both subjects with anesthetized teeth and those with bridges supported by teeth or dental implants.

Food manipulation and positioning for biting (Study V)

When instructed to split the candy, all of our subjects immediately moved their mandibles vertically (the jaw-opening phase) to make room for this candy. During the opening and subsequent contact-establishing phase, the candy was moved forward and positioned between the central incisors with the tongue. It was then retained between the front teeth (contact phase) while its position was being finally adjusted so that its relationship to the incisal edges of the teeth was optimal for splitting into two pieces (see Fig 7). Although similar pattern was observed for all subjects in all three groups, there were some notable differences indicative of impaired positioning and splitting performance in individuals with bridges supported by teeth or dental implants.

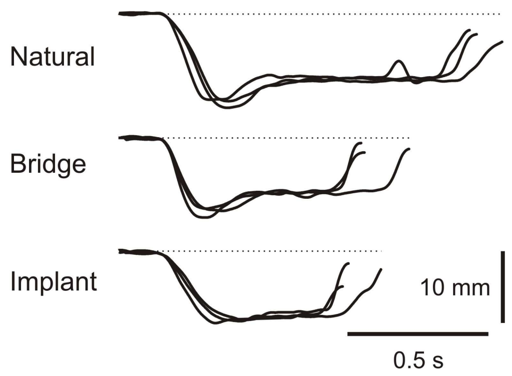

Figure 7. Representative recordings of vertical jaw movement during performance of the manipulation-and-split task by subjects in the natural, bridge and implant groups. Three superimposed trials for each subject are shown.

Splitting performance

The splitting performance was assessed by comparing the weight of the largest piece of candy produced to the “ideal split” (see Methodological considerations). The individuals with natural dentition deviated by an average of 14% (13-20) (median (25-75 percentile)) from the ideal, which was significantly better than the deviations of the individuals with bridges supported by teeth (30% (20-35); P=0.005) or dental implants

(28% (23-33); P=0.034). There was no statistically significant difference between the bridge and implant groups in this respect.

For those with natural dentition, only 9% of the splits were classified as unsuccessful (i.e., deviating by >50% from the ideal split), while the corresponding values for the bridge and implant groups were 30% (P=0.002) and 24% (P=0.015) respectively, with no statistically significant difference between these latter two groups. Similarly, the proportion of failed splits (with a deviation of >75% from the ideal split) was 0% for the natural group, 18% for the bridge group and 8% for the implant group.

This more efficient splitting by individuals with natural dentition reflects a superior capacity to position the spherical piece of candy between the teeth and fine-tune the direction of the bite force vector to split it down the middle. Most likely, this capacity is dependent on intact dental sensitivity and, indeed, PMRs provide detailed information concerning the spatial location and direction of forces applied to teeth (Trulsson et al 1992, Trulsson 1993, Johnsen and Trulsson 2003).

An important role for PMRs in this context can explain the relatively poor performance by subjects with tooth- and implant-supported bridges. A tooth-supported bridge transmits a force load to all abutment teeth and their periodontium in a complex manner (Weinberg 1957a, b), probably altering the pattern of PMR signaling from the abutment teeth and reducing the ability to determine the exact location and direction of forces applied to a tooth. Thus, it is reasonable to assume that it is more difficult for individuals with tooth-supported bridges to achieve the position and direction of bite forces that are most favorable for splitting the candy.

Subjects with implant-supported bridges have no PMRs and must rely on other, less sensitive sensory systems to obtain information concerning contact of the teeth with food (Trulsson and Gunne 1998, *Study IV*), which explains their relatively poor splitting performance. These findings are in line with those by Trulsson and Gunne (1998) concerning the performance of a hold-and-split task by subjects with either implant-supported bridges or removable prostheses supported by the oral mucosa. While applying hold or split forces both of these groups dropped the food morsel from the force transducer at a high frequency similar to that of dentated subjects who had undergone periodontal anesthesia (Trulsson and Johansson 1996b). Moreover, some of the individuals with implant-supported bridges reported that they could not feel the location of the food morsel or where contact was made, comments similar to those often made by periodontally anesthetized participants (Trulsson and Johansson 1996b).

Mandibular movements

The peak vertical velocity during the opening phase for the different groups was very similar, i.e., 73 (27) mm/s (mean (SD)) for the natural group, 76 (24) mm/s for the bridge group and 66 (28) mm/s for the implant group. The vertical positions of the mandible at T1, T2 and T3 were also more-or-less identical for these three groups (12.7 (3.7), 10.1 (2.5) and 9.4 (2.3) mm for the natural group; 12.6 (2.8), 9.7 (1.0) and 8.9 (0.9) mm for the bridge group; and 12.7 (4.4), 10.1 (2.9) and 9.6 (2.3) mm for the implant group). Thus, vertical movements of the mandible during a manipulation-and-split task do not appear to be affected by the presence of tooth- or implant-supported bridges.

Temporal aspects

The total time utilized for the manipulation-and-split task, from the onset of the jaw-opening phase to onset of the jaw-closing phase (T0 to T3 = total duration) was longer in the case of the natural group (1.47 (0.27) s), than for the bridge (1.16 (0.33) s, P=0.053) or implant groups (1.08 (0.42) s, P=0.018), with no statistically significant difference in total duration between the bridge and implant groups (Fig 8a). When this difference was examined in more detail by analyzing the durations of the various phases of the biting behavior (Fig 8b-d), a significant interaction between phase and group (P=0.048) was observed. The duration of the jaw-opening phase (T0 to T1) was nearly identical for the three groups (0.35 (0.09) s for the natural group, 0.30 (0.08) s for the bridge group and 0.33 (0.11) s for the implant group (Fig 8b)), as well the duration of the contact-establishing phase (T1 to T2) (0.23 (0.07) s, 0.21 (0.07) s and 0.24 (0.10) s, respectively (Fig 8c). In contrast, the duration of the contact phase (T2 to T3) differed significantly (P=0.014) being 0.89 (0.22) s for the natural group, 0.65 (0.29) s for the bridge group and 0.51 (0.31) s for the implant group (Fig 8d)). Pairwise comparisons revealed that the natural and bridge groups differed with 0.24 s (P=0.063), the natural and implant groups differed with 0.38 s (P=0.004) and the bridge and implant groups differed with 0.15 s (P=0.248). When expressed as a percentage of the total duration, the duration of the contact phase also differed between the natural and implant groups (57 versus 41%; P<0.001) and between the implant and bridge groups (41 versus 50%; P=0.040), but not between the natural and bridge groups.

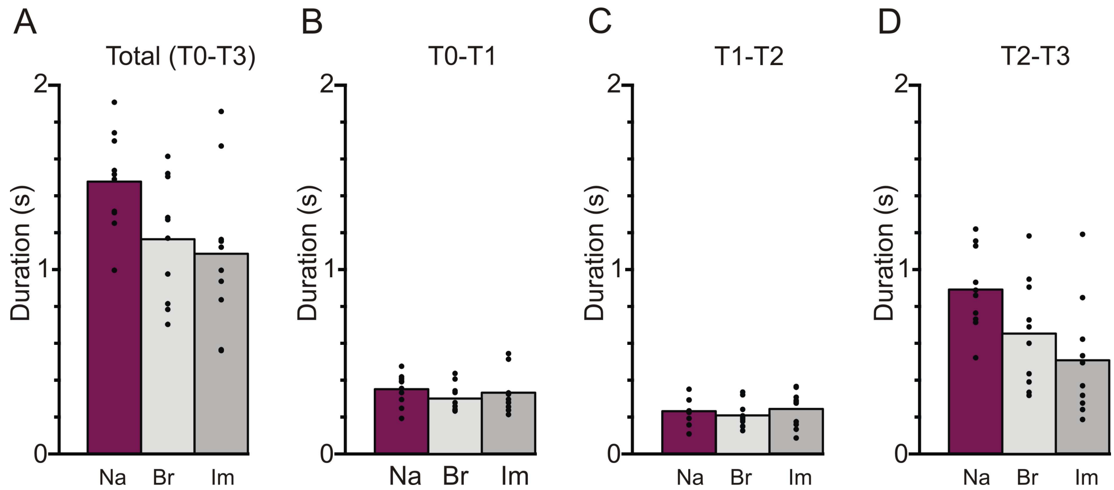

Figure 8. Total task and phase durations for subjects in the natural (Na), bridge (Br) and implant (Im) groups during the manipulation-and-split task. (**A**) total duration of the task (T0-T3). (**B**) duration of the opening phase (T0-T1). (**C**) duration of the contact-establishing phase (T1-T2). (**D**) duration of the contact phase (T2-T3). The height of each bar indicates the mean value for all of the subjects in a group and the filled circles mean values for individual subjects.

One plausible explanation for these differences in the duration of the contact phase is that individuals with natural teeth take time to collect spatial information concerning the contact between the food and dentition, for processing by the CNS to achieve accurate control of the point of attack and direction of the bite forces required to split the food, whereas individuals with tooth- or implant-supported bridges do not. Thus, when sensory information from the PMRs is available, the contact phase is prolonged. This interpretation agrees with the observations by Trulsson and Johansson (1996b) that when instructed to immediately split a morsel of food between their front teeth, subjects chose to hold this morsel (for a mean of 86 ms) with low force (mean 0.58 N) directly after contact, prior to the split. With normal periodontal sensibility, those brief holding phases were observed in approximately half of the trials, but following anesthesia of the teeth, only 14% of the trials involved brief holding. This holding of food momentarily with a low, relatively steady force prior to applying the high biting forces suggests that processing of information about contact between the food and teeth is occurring prior to execution of the split.

General discussion

Intense regulation of the large biting forces used to split food

Treatment of edentulous individuals with a prosthesis supported by osseointegrated dental implants results in considerable improvement of function and comfort and the reliable survival and success rates of this treatment have indeed made it a worldwide success (Brånemark et al 1977, Adell R et al 1990, Zarb and Schmitt 1990a, b, Lindquist et al 1996, Lekholm et al 1999). The ability and efficiency of chewing by individuals with implant-supported bridges has been shown to be as good as in individuals with natural dentition and their maximal biting forces are equivalent (and sometimes suggested to be even higher) (Haraldson 1979, Haraldson and Carlsson 1979, Karlsson and Carlsson 1993).

However, some noteworthy differences in chewing between subjects with implant-supported bridges and dentated individuals have been documented by Haraldson (1983), i.e., those with implant-supported bridges exhibited impaired regulation of jaw muscle activity in response to the gradual changes in food consistency that occur during chewing. These results, which have been confirmed recently by Grigoriadis and coworkers (2010), can probably be attributed to the lack of sensory information from the PMRs which is required for the CNS to adjust the neural output to the masticatory muscles. This proposal is consistent with observations that in experimental animals, blockage of the sensory input from the PMRs by anesthetizing or cutting the nerves innervating the teeth significantly attenuates the enhancement of jaw muscle activity caused by placing an obstacle between the teeth during rhythmic chewing (Lavigne et al 1987, Inoue et al 1989, Morimoto et al 1989).

In rabbits, Hidaka and coworkers (1997) found that blocking the sensory information provided by periodontal receptors by cutting the nerves from the teeth significantly reduces the rate at which the masticatory force is build up during chewing. Similarly, in *Study III*, the rate of force increase during splitting of peanuts was lowered significantly by application of a local anesthetic to the teeth. Moreover, adjustment of this rate to the hardness of food only occurred when periodontal sensibility was normal.

The role of PMRs in this context is further confirmed by the observation in *Study IV* that adaptation of the rate of increase in force to the hardness of the food occurred in individuals with unaffected natural dentition, but not in those with tooth- or implant-supported bridges, even though all of the participants were aware at all times of the type of food they were biting on. Most likely, signals from other oro-facial receptors, such as muscle spindles, also contribute to adaptation of muscle activity to food hardness. Indeed, muscle spindles in the jaw muscles of monkeys respond strongly during voluntary biting. Their primary afferents, which are highly active shortly after initial contact with the food, may be especially capable of signaling information about this contact (Lund et al 1979, Larson et al 1981).

In contrast to the situation during food holding and manipulation, when informational feed-back is employed to maintain stable contact with the food, the single biting stroke involved in splitting of food is such a rapid motor action that its regulation probably relies on predictive, feed-forward sensory-motor mechanisms based on earlier experience of the relationships between patterns of receptor signaling and appropriate efferent signals (see Wolpert and Flanagan 2001, Flanagan et al 2006, Johansson and Flanagan 2009). The present findings support the hypothesis that information concerning intrinsic food properties collected soon after initial food contact by the PMRs is employed in a feed-forward manner to adjust the levels of subsequent bite forces (see Trulsson and Johansson 1996b). Indeed, such a function of “early state information” in controlling forthcoming jaw actions is supported by both human and animal studies (Ottenhoff et al 1992a, b, Komuro et al 2001). **It can therefore be suggested that the receptors in the periodontal ligament are involved via feed-forward sensory-motor mechanisms in regulation of the large bite forces used to split food between the teeth.**

Intense regulation of the small biting forces employed to hold and manipulate food

Studies II and *III*, together with the report by Trulsson and Johansson (1996b), demonstrate that the holding forces utilized during a hold-and-split task are within the range where the periodontal mechanoreceptors are most sensitive to changes in force (i.e., < 1 N for anterior teeth and < 3 N for posterior teeth; see Fig 1). Blockage of the sensory information provided by the PMRs by anesthetizing the teeth significantly elevates both the magnitude and variability of these holding forces. Moreover, the findings of *Study IV*, along with those by Trulsson and Gunne (1998), show that individuals with implant-supported prostheses (i.e., lacking PMRs) apply significantly higher and more variable holding forces than naturally dentated subjects, actually behaving in a manner similar to individuals with natural dentition who have been subjected to local anesthesia of their teeth (*Studies II* and *III*, Trulsson and Johansson 1996b). Subjects with tooth-supported bridges apply holding forces whose levels and variability are intermediate between those generated by individuals with natural dentition and those with implant-supported bridges, indicating an impaired, but to some extent remaining ability to control the magnitude of holding forces.

Together, these findings suggest that, **via a feed-back sensory-motor mechanism, the PMRs play an important role in regulating the level of force applied when holding and manipulating food between the teeth prior to biting.** When sensory information from the PMRs is unavailable, some other, less sensitive system of regulation in the oro-facial region must be relied on (see the Introduction).

Spatial regulation of biting forces

Study V, in which the ability to control spatial aspects of jaw motor function when manipulating and splitting food was evaluated, revealed that individuals with natural dentition performed significantly better than those with tooth- or implant-supported bridges in producing an “ideal” split of a spherical piece of candy. Furthermore, the naturally dentated participants held this candy for a significantly longer period of time prior to splitting it (the contact phase) than those with tooth- or implant-supported bridges, presumably because the former utilized this time to process spatial information from the PMRs concerning tooth-food contact so as to optimize the position of the candy and fine-tune the direction of the bite force vector. Thus, the relatively poor performance of subjects with tooth- or implant-supported prostheses indicates **the significance of unimpaired sensory information from the PMRs for spatial control of jaw action**.

For individuals with natural dentition, sensory information provided by the PMRs is proposed to be used in a feed-forward manner to trigger the release of pre-programmed motor commands for splitting the candy. When predicted sensory information about contact, optimal position and direction of tooth load is received by the CNS, the appropriate motor program is executed and efferent output designed to effectively split the candy down the middle sent to the different jaw-closing muscles. However, in individuals with bimaxillary implant-supported prostheses, no such spatial information about tooth-food contact can be sent and is probably therefore not expected in these individuals. This means that their predicted sensory information during this task is restricted to information about contact with the food, and when this is received by the CNS, the motor program to split the morsel is initiated. This can explain the significantly shorter contact phase used by these subjects in the manipulation-and-split task in *Study V*. Holding the candy between the teeth for a longer period does not provide any more information that can be used to improve the positioning and direction of the bite force vector, so the CNS simply does not wait to trigger the motor commands to split the candy, which then occurs, but with less precision than in individuals with natural teeth.

In contrast to the findings in *Study V*, lack of tactile sensibility in other parts of the body (e.g., anesthetized fingers performing manipulation tasks) results in prolonged duration of the task, in addition to impaired performance (Johansson and Westling 1984). The shorter time used for the manipulation-and-split task by our subjects with implant-supported bridges might reflect reception of sufficient information concerning tooth-food contact to execute the motor command to split the food. This may involve the phenomenon referred to as **osseoperception** (see Klineberg et al 2005, Jacobs and van Steenberghe 2006, van Steenberghe and Jacobs 2006, Trulsson 2006), which is probably the receiving of sensory information concerning contact forces (dynamic loading) to the artificial teeth on osseointegrated dental implants from remote receptors in other tissues activated through transmission of vibrations in the jawbone. Osseoperception would allow individuals with bimaxillary implant-supported bridges to still receive such information.

In contrast, several investigations have demonstrated that the threshold for passive detection (i.e., detection of load applied to a tooth) for implants is approximately 10 to 50-fold higher than that of natural teeth (see Jacobs and van Steenberghe 2006). Yoshida (1998) reported that static detection thresholds for individuals with dental implants is approximately 10-fold higher than for those with natural teeth, whereas the dynamic (vibration) detection thresholds are similar for dental implants and natural teeth. Administration of a local anesthetic to the teeth and to the implants raises the detection threshold for dentated individuals, but does not alter this threshold in those with dental implants. This suggests that the latter receive information about dynamic loads (vibration) from receptors distant from the implant and, moreover, that vibrations are transmitted more effectively across the dental implant to the bone than from the tooth through the periodontal ligament to the bone.

A general hypothesis and future perspectives

On the basis of the findings documented here and the earlier proposal by Trulsson and coworkers (Trulsson and Johansson 1996b, Trulsson and Gunne 1998, Trulsson 2006), it is hypothesized that the PMRs signal detailed information concerning intense and spatial aspects of the forces involved in tooth-food contact. This sensory information is processed by the CNS in a feed-back manner (moment-to-moment control) to regulate the levels and directions of the bite forces used during manipulative actions. Furthermore, information provided by the PMRs is also used in a predictive feed-forward manner to adjust and adapt the motor program employed to split food using large biting forces. In other words, the sensory information sets the parameters of the motor program in such a manner that the rate of increase in force is adjusted to the intrinsic properties (e.g., hardness) of the food and the bite force vector is optimized for the location of the food relative to the teeth.

The sensory information received by the CNS during tooth-food contact and related aspects of motor control of the jaw are summarized in Table 1 and 2, respectively. Note that the reduced motor control exhibited by subjects with different types of prostheses is correlated to the reduction in sensory information received by the CNS. This information is provided by the PMRs in individuals with natural teeth and tooth-supported bridges, whereas corresponding information may be signaled via osseoperception in individuals with implant-supported bridges.

The findings in *Studies IV* and *V* reveal that if PMRs are located around teeth connected in a fixed bridge, their presence does not appear to provide a major advantage with respect to spatial control during food positioning for biting, or adaptation of the rate of force increase to the hardness of food during biting. It can thereby be proposed that whenever possible, connecting individual teeth in rigid constructions should perhaps be avoided in order to preserve the rich sensory information provided by the PMRs as required for normal functioning of the masticatory system.

Table 1. Sensory information proposed to be received by the CNS concerning tooth contact and the intensity and direction of forces in relationship to dental status.

	Sensory information		
Dental status	Dynamic * tooth contact	Intensity of small forces	Direction of forces
Natural teeth	+	+	+
Tooth-supported bridges	+	(+)	
Implant-supported bridges	+		

* rapid force changes

Table 2. Motor control ability in relationship to dental status (based on the results from *Studies I-IV*)

	Motor control			
Dental status	Timing of action	Amplitude of small bite forces	Rate of large bite force production	Direction of bite forces
Natural teeth	+	+	+	+
Tooth-supported bridges	+	(+)		
Implant-supported bridges	+			

Main findings

- Reduced support by periodontal tissue resulting from a history of periodontitis impairs regulation of masticatory forces, as reflected in larger and more variable holding forces, as well as in a lower mean rate of force increase during the splitting phase of a hold-and-split task (*Study I*).

- Different types of teeth apply different holding forces during a hold-and-split task, with these forces increasing distally along the dental arch. The levels of holding force employed coincide with the range over which the periodontal afferents of anterior and posterior teeth are most sensitive to changes in force. During periodontal anesthesia (i.e., blockage of the sensory information provided by periodontal mechanoreceptors), the magnitude and variability of the holding forces are elevated for all types of teeth (*Study II*).

- When larger bite force is required to split a morsel of food, both the duration and the rate at which the bite force is produced are enhanced. Furthermore, adaptation of the rate of increase in the bite force to the hardness of the food occurs with normal periodontal sensibility, but not during periodontal anesthesia (*Study III*).

- Individuals with tooth- or implant-supported fixed bridges in both jaws exhibit impaired regulation of the low forces utilized to manipulate and hold food between the teeth. Moreover, during splitting of food these same individuals do not adapt the rate of bite force production to the hardness of the food (*Study IV*).

- Individuals with natural teeth are significantly better than those with bimaxillary tooth- or implant-supported bridges at splitting a spherical piece of candy into two parts of similar size. In addition, individuals with tooth- or implant-supported bridges exhibit altered motor behavior in connection with the manipulation-and-split task employed here, as reflected in their significantly shorter contact phase prior to performance of the split (*Study V*).

Conclusions

The studies included in this thesis demonstrate the significance of sensory information provided by periodontal mechanoreceptors for normal motor control of biting.

- Intact periodontal mechanoreceptor function is necessary for normal motor control of low bite force levels, as well as normal regulation of the rate of bite force production when holding and splitting food between the teeth (*Studies I-IV*).
- Adaptation of the rate of bite force production to the hardness of food is dependent on adequate sensory information from the periodontal mechanoreceptors (*Studies III* and *IV*).
- Appropriate sensory information provided by the periodontal mechanoreceptors plays an important role in fine tuning and spatial adjustment of the manipulative forces involved, e.g., in positioning a spherical piece of food between the front teeth and subsequently splitting it with a high degree of precision (*Study V*).

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Populärvetenskaplig sammanfattning

Att äta är en av våra mest grundläggande behov. För att kunna svälja födan rör vi underkäken och använder de bitkrafter som behövs för att bita av och tugga utan att behöva tänka på det. Dessa exakta och noggrant koordinerade rörelser styrs automatiskt av hjärnan utifrån information som den ständigt får från ett stort antal olika sinnesorgan i och runt munnen.

Runt varje tand finns hundratals sinnesorgan, så kallade periodontalreceptorer, som bär det största ansvaret för att hålla hjärnan uppdaterad om de belastningar som tänderna utsätts för. Varje tand sitter förankrad i käkbenet via en rothinna och har därmed en viss rörlighet. När en tand belastas, t.ex. i samband med bitning eller tuggning stimulerar dessa rörelser de kringliggande periodontalreceptorerna. Dessa sinnesorgan informerar hjärnan om tidpunkten, storleken och lokaliseringen av belastningen på tanden, så att bitning och tuggning kan styras effektivt. Periodontalreceptorerna är mest känsliga när tänderna utsätts för små krafter, som när de först får kontakt med mat och man sedan håller eller flyttar omkring matbiten i munnen.

Det finns fortfarande många detaljer om hur vi biter och tuggar som inte är helt klarlagda. Dessutom saknas kunskap om hur denna reglering sker hos individer som förlorat delar av tändernas benstöd (och därmed också en del av sina periodontalreceptorer) eller som har fått behandling för förlorade tänder med tandstödda eller implantatstödda broar. I tandstödda broar sammanbinds flera tänder i en styv konstruktion vilket minskar varje enskild tands rörlighet och därmed sannolikt också den information som erhålls av kringliggande receptorer. I fallen med implantstödda broar där konstgjorda tänder sitter fast förankrade i käkbenet med hjälp av titanskruvar (dentala implantat), saknas både rörlighet och periodontalreceptorerna.

Denna avhandling syftar till att bättre förstå periodontalreceptorernas roll vid reglering av bitkrafter och käkrörelser samt att ta reda på hur denna reglering påverkas när benstöd förlorats (p.g.a. tandlossning) eller av insättning av broar. För att uppnå detta syfte har frivilliga personer med friska tänder (både med och utan lokalbedövning som tystar periodontalreceptorerna) och med tand- eller implantstödda broar utfört olika bituppgifter som innebär att placera, förflytta, hålla fast och bita av olika typer av föda samtidigt som deras bitkrafter och underkäksrörelser registrerats med specialdesignad utrustning.

I studierna har det tydligt framkommit att opåverkad information från periodontalreceptorerna är nödvändig för normal kontroll av riktningen och intensiteten hos de små krafter som vi använder för att förflytta och hålla fast föda mellan tänderna inför avbitningen. För att reglera motoriken använder hjärnan här den sensoriska informationen kontinuerligt under rörelsen, så kallad feed-back reglering. Information från periodontalreceptorerna är också nödvändig för att anpassa hastigheten på bitkraftsökningen till matens hårdhet under en avbitning. Direkt vid kontakten mellan tand och föda signaleras information om födans egenskaper (t.ex. hårdhet) som används för att i förväg justera kraftparametrar i det motoriska program som används vid avbitning, så kallad feed-forward reglering. Individer som har förlorat benstöd eller har tand- eller implantatstödda broar uppvisar tydliga avvikelser i samband med sådana uppgifter på grund av deras försämrade respektive uteblivna information från periodontalreceptorerna.

Förhoppningen är att fortsatt forskning om sensorimotorisk reglering av orala funktioner kan leda till utveckling av nya metoder för diagnostik av oral funktion och till förbättrade möjligheter att utvärdera kliniska behandlingsmetoder för funktionell rehabilitering av tandförluster.

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