

From the Department of Prosthetic Dentistry
Institute of Odontology
Karolinska Institutet, Stockholm, Sweden

HUMAN PERIODONTAL MECHANORECEPTORS

FUNCTIONAL PROPERTIES AND ROLE IN
JAW MOTOR CONTROL

Skjalg E. Johnsen



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OPPONENT:

Professor Pål Brodin, University of Oslo,
Institute of Oral Biology,
Oslo, Norway

EXAMINING COMMITTEE:

Associate Professor Håkan Olausson, University of Gothenburg,
Department of Clinical Neurophysiology,
Gothenburg, Sweden

Professor Hans Forssberg, Karolinska Institutet,
Institute of Women and Childrens Health,
Stockholm, Sweden

Professor Kaj Fried, Karolinska Institutet,
Institute of Odontology, COB
Huddinge, Sweden

SUPERVISOR:

Associate Professor Mats Trulsson, Karolinska Institutet,
Institute of Odontology, Department of Prosthetic Dentistry,
Huddinge, Sweden

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ABSTRACT

Periodontal mechanoreceptors signal information about tooth loads to the central nervous system and are considered to be important for the control of oral motor behaviors, like biting and chewing. Surprisingly, very little is known about the functional properties of periodontal mechanoreceptors at posterior teeth. In this thesis, the technique of microneurography was used on humans to record from single nerve fibers in the inferior alveolar nerve responding to forces applied to the teeth. The basic discharge patterns of human periodontal mechanoreceptors of posterior teeth were analyzed. Receptive field properties, directional sensitivity and encoding of force amplitude and rate were studied. Further, to evaluate the strength of the synaptic coupling between periodontal afferents (and other orofacial mechanoreceptive afferents) and jaw muscle motoneurons, the microneurography technique was combined with electromyography recordings. Finally, in behavioral experiments, the importance of periodontal mechanoreceptors in the regulation of force levels used to hold and split morsels between different types of teeth was attested.

The present results indicate that the innervation of the periodontal ligament is weaker for the posterior teeth compared to the anterior teeth. When the posterior teeth were loaded, all periodontal afferents responded with a slowly adapting response, i.e., they all continued to discharge during sustained tooth loads in at least one direction. The teeth were stimulated in six different directions in the horizontal and vertical planes and the afferents typically responded in two to four of the six directions. However, distally along the dental arch, the afferents showed weaker sensitivity in the vertical directions and a bias in disto-lingual direction for the 1st molar. When stimulating teeth adjacent to the receptor bearing tooth (RBT) about half of the afferents responded to loading of one or two more teeth. This is most likely due to transmission of forces to the RBT because of interdental contacts between the teeth. Thus, mechanical coupling between teeth rather than branching of single nerve fibers explains the multiple-tooth receptive fields.

The majority of the afferents of posterior teeth exhibited a marked curved relationship between the steady-state discharge rate and the amplitude of the stimulated force, featuring a pronounced saturation tendency. Compared to afferents from anterior teeth, these afferents were less sensitive at low force levels. The afferents of posterior teeth were also characterized by a decline in the dynamic sensitivity with increasing force. A quantitative model based on this data revealed that these afferents poorly encode the magnitude of stronger chewing forces. However, a minority of the afferents showed a nearly linear stimulus-response relationship and a small decline in dynamic sensitivity with increased tooth load. Thus, this afferent group will continue to reflect the force profile during higher chewing forces.

Strong synaptic coupling between single periodontal afferents and motoneurons of the jaw muscles demonstrated the importance of these receptors for a successful execution of oral function, like mastication. This coupling was mainly unilateral except for the central incisor.

The use of periodontal afferent signals in controlling manipulative and power elements of a biting behavior was studied in a simple hold-and-split task using different types of teeth. The forces used to hold the morsel between the teeth increased distally along the dental arch. Importantly, the difference in hold forces for the various teeth could be explained by the different sensitivity characteristics of the periodontal

afferents innervating anterior and posterior teeth. Blocking the sensory input from periodontal afferents increased the magnitude and variability of the hold forces for all types of teeth suggesting that periodontal afferent information is important for the fine motor regulation of the jaw when morsels are manipulated and positioned between the teeth to be prepared for chewing.

LIST OF PUBLICATIONS

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HUMAN PERIODONTAL MECHANORECEPTORS

Functional properties and role in jaw motor control

Skjalg E. Johnsen

*The Department of Prosthetic Dentistry
Institute of Odontology
Karolinska Institutet, Huddinge, Sweden*

1 INTRODUCTION

The normal regulation of oral functions, such as biting and chewing, is dependent on information from several sensory organs, including the periodontal mechanoreceptors (see Anderson et al. 1970; Lund 1991; Trulsson and Johansson 1996a). The periodontal mechanoreceptors signal information about forces applied to the teeth and are located among the collagen fibers in the periodontal ligament, which attach the root of the tooth to the alveolar bone.

These receptors and their functional properties have been analyzed in both animal (see Hannam 1982; Linden 1990) and human (see Trulsson and Johansson 1996a) studies. However, only the receptors associated with anterior teeth have been studied. Very limited information is available about the receptors of posterior teeth in both animal and human (Appenteng et al. 1982; Johansson and Olsson 1976; Trulsson and Johansson 1996a). During food intake, the anterior teeth are the first to come into contact with the food before it is taken into the mouth. The posterior teeth grind the food during rhythmic chewing and prepare it for swallowing. During such sequences, information from the periodontal mechanoreceptors about forces acting on the teeth and direction of the force stimulation are likely to be transported to the central nervous system (CNS) from both anterior and posterior teeth. Surprisingly, no reports about the functional properties of posterior periodontal mechanoreceptors are available and the understanding of these receptors is therefore sparse. Thus, the purpose of the current work was to describe how the periodontal mechanoreceptors of posterior teeth function and further demonstrate the importance of these receptors in the regulation of jaw actions and manipulative tasks.

1.1 OROFACIAL MECHANORECEPTORS

Mechanoreceptors are specialized neural sense organs that respond to mechanical deformation of structures in which they lie. In the orofacial area in humans, recordings have been done from the mechanoreceptive afferents innervating the facial skin, lip and tongue (Johansson et al. 1988; Nordin and Hagbarth 1989; Edin et al. 1995; Trulsson and Essick 1997). In the facial skin and lip, three different types of mechanoreceptors have been described: Fast adapting type I (FA I) - Meissner, slowly adapting type I (SA I) - Merkel and slowly adapting type II (SA II) - Ruffini. The type I receptors have small and well-defined receptive fields, while the type II receptors demonstrate larger and less well-defined receptive fields. The rapidly adapting receptors adapt quickly to maintained skin deformation, in that they only respond to changes in skin deformation. Slowly adapting receptors, continuously respond to a maintained skin deformation and are also dynamically sensitive. Thus, there is a lack of fast adapting type II receptors (Pacinian) in the orofacial region (see Johansson et al. 1988). In the tongue, an additional deep tongue receptor has been reported which has a larger receptive field and exhibits a high force threshold. Most likely these receptors are muscle spindles located deep in the muscle of the tongue (Trulsson and Essick 1997). The periodontal mechanoreceptors are a specialized group of mechanoreceptors that respond to forces applied to the teeth.

1.2 PERIODONTAL MECHANORECEPTORS

1.2.1 Histology

The trigeminal nerve is the fifth cranial nerve and is mainly sensory, although it has a small motor region. Leaving the brain and entering the trigeminal ganglion (Gasserian ganglion) it divides into three branches: ophthalmic nerve, maxillary nerve and mandibular nerve. The maxillary nerve penetrates the rotundum foramen and divides into branches that innervate for example the teeth of the upper jaw. The lingual and inferior alveolar nerves are main branches from the mandibular nerve. The lingual nerve is exclusively sensory while the inferior alveolar nerve becomes purely sensory after entering the mandibular foramen. In the mandibular canal, the inferior alveolar nerve gives branches off to the teeth and gingiva of the lower jaw. The small branches then enter the periodontal ligament and innervate the tooth and surrounding structures. Continuing in the mandibular canal the inferior alveolar nerve enters the mental foramen and innervates the skin of the lower lip, the cheek and the mucosa through the mental nerve.

The afferents innervating the periodontal ligament have their cell bodies located in either the trigeminal ganglion or the trigeminal mesencephalic nucleus (Beaudreau and Jerge 1968; Gottlieb et al. 1984). Receptors closest to the apex of the tooth have cell bodies in the trigeminal mesencephalic nucleus while those located in the middle of the root have cell bodies in the trigeminal ganglion (Byers and Dong 1989). The different location of sensory input in the brain stem might indicate different functional roles between these two groups of afferents (Olsson and Westberg 1989).

There are several studies on the termination of the nerves in the periodontal ligament. A variety in structure from being large, complex with extended “fingers” into the collagen fibers to more simple Ruffini-like receptors, including preterminal axons and free-endings have been reported. However, studies by Byers (1985), suggest that the periodontal mechanoreceptors in the ligament of rat are Ruffini-type, supplied by myelinated fibers and are unencapsulated. Other publications have confirmed the occurrence of ‘Ruffini-like’ endings in close relation to the collagen fibers in animal (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 in human (Maeda et al. 1990; Lambrechts et al. 1992).

The periodontal ligament of incisors and molars from rats and bovines have been found to have different biomechanical properties, thereby indicating that periodontal fiber architecture varies between different types of teeth (Komatsu and Chiba 1993; Pini et al. 2004). Byers and Dong (1989) studied the distribution of periodontal receptors labeled in the trigeminal ganglion in monkeys, and found a reduced incidence of receptors (about half) around posterior teeth compared to anterior teeth. In another study on the same species, Hassanali (1997) found a decreased number of labeled neurons in the trigeminal ganglion for posterior teeth (incisor 50%, canines 42% and molars 8%). This is supported by Passatore et al. (1983) who reported a greater representation of incisors compared with molars in the trigeminal mesencephalic nucleus of the rabbit.

1.2.2 Physiology

In the periodontal ligament, collagen fibers attach the root of the tooth to the alveolar bone. Nerve endings are located between the collagen fibers and will respond when the part of the ligament in which they lie is put into tension, in that they are sensitive to stretch of the collagen fibers (Cash and Linden 1982). So when the tooth is mechanically stimulated, the collagen fibers, and consequently the periodontal mechanoreceptors are affected leading to a response in the receptor. The conduction velocities of the afferent fibers range from 26 to 87 m/s, with a mean of 54 m/s, placing them within the A- β group of fibers (reviewed by Anderson et al 1970; Hannam 1982; Linden 1990).

Pfaffmann (1939) described the periodontal mechanoreceptors as slowly adapting when responding to loading of teeth. However, most animal studies classify periodontal afferents into both rapidly and slowly adapting (cf. reviews by Hannam 1982; Linden 1990). Linden and Millar (1988a,b) found that receptors just apical to the tooth fulcrum have the highest threshold to a force applied to the crown, and those nearer the apex the lowest. A grading of threshold was apparent for receptors between these two extreme positions. In addition, a grading of adaptation time was described, with the most rapidly adapting receptors near the fulcrum and the most slowly adapting ones at the apex, indicating that there may only be one type of mechanoreceptor within the ligament. If a stimulus, such as a displacement, is applied to a slowly adapting unit in the periodontal ligament then the receptor might well behave as a rapidly adapting mechanoreceptor if its not optimally stimulated. A finding that was confirmed in reviews by Hannam (1982) and Linden (1990).

However, in human the converse applies with only slowly adapting periodontal mechanoreceptors being reported. In human, a non-optimally stimulated slowly adapting receptor can easily be mistaken for a rapidly adapting one (see Trulsson and Johansson 1996a for review). Periodontal mechanoreceptors are very sensitive to the direction of the tooth loading (Johansson and Olsson 1976; Trulsson et al. 1992). Trulsson et al. (1992) used six stimulus directions (four in the horizontal plane and two in the vertical plane) to elucidate the slowly adapting response properties of the periodontal mechanoreceptors. They also reported that without stimulation in the six different directions some afferents would easily have been misclassified as rapidly adapting. In most animal studies, only horizontal stimulus directions have been used and no study has reported forces directed in the upward direction.

Since Pfaffmann (1939) found that the periodontal mechanoreceptors in the cat were directionally selective, there have been many descriptions of the directionality of response fields of the periodontal mechanoreceptors recorded from primary afferent neurons in a variety of species: man (Johansson and Olsson 1976; Trulsson et al. 1992), rabbit (Ness 1954; Appenteng et al. 1982), dog (Hannam 1969a, 1970) and cat (Jerge 1963; Sakada and Kamio 1971; Mei et al. 1975; Linden 1978). The studies showed that the afferent units could be excited by mechanical stimulation applied over a range of angles diverging from the most sensitive direction. In humans, Trulsson et al. (1992) demonstrated that the periodontal afferents of anterior teeth exhibited a slightly more preferred direction lingually and labially for horizontally directed forces. For vertically directed forces there was a bias in the downward direction. However, the population response was about equal in all six tested directions except for a higher response frequency in the downward direction. In general, the afferents responded in two to four

out of the six tested stimulus directions. Thus, periodontal afferents of anterior teeth are broadly tuned for directional response to tooth load. In the cat, Karita and Tabata (1985) examined the directional sensitivity of the canine and classified 87% of the afferents as having a medium receptive field (90-180 deg). Also, in cat and on a canine tooth Sakada and Kamio (1971) found that 61% of the afferents were sensitive to three or four out of five tested directions. Whereas in dog, Hannam (1970) suggested a directionally narrower receptive field than that observed in cat or human.

Multiple-tooth receptive fields, i.e., periodontal afferents that respond to forces applied to several teeth, have been reported in both human (Trulsson 1993) and animal (Hannam 1970; Sakada and Kamio 1971; Tabata and Karita 1986; Tabata et al. 1994, 1995). Tabata and Karita (1986) reported that only 5% of the afferents in cat had receptive fields of more than one tooth while on the same species Sakada and Kamio (1971) found 58% and Tabata et al. (1994) 34%. In dog, Hannam (1970) found 21%. The mechanism underlying the multiple-tooth receptive field is unclear. Sakada and Kamio (1971) claimed that the receptive field is formed by branching of the afferent fiber in cat, while in dog, Hannam (1970) explained it as a result of a displacement of the receptor bearing tooth. Trulsson (1993) proposed that the human multiple-tooth receptive fields are due to mechanical coupling between the teeth and that both interdental contacts and the transseptal fiber system may be involved. This hypothesis was later supported by Tabata et al. (1994, 1995) in cat.

When a force is applied to a tooth the periodontal mechanoreceptors encode the magnitude and the rate of the force applied. Pfaffmann (1939), Ness (1954), Hannam (1969a), Johansson and Olsson (1976) and Trulsson and Johansson (1994), with the two latter in human, observed that the afferent discharge rate most often depend nonlinearly on the amplitude of the applied force. In 1939, Pfaffmann reported that the discharge of periodontal afferents was affected by the rate of force application. Hannam (1969a) in dog and Fujita (1987) in man further demonstrated an increase in the discharge rate when the rate of force application increases. In cat, Hannam and Farnsworth (1977) noticed that most information about static force amplitude is encoded at forces below 0.7N. This was later supported by Trulsson and Johansson (1994) analyzing afferents of anterior teeth in human. The study reported that most of the afferents (80%) exhibited a hyperbolic relationship between the amplitude of the stimulation force and the steady-state response, featuring a pronounced saturation tendency. The periodontal afferents exhibited highest sensitivity to changes in static force levels below 1N. Moreover, the dynamic sensitivity decreased with increasing amplitude of static background force. Further on, about 20% of the afferents exhibited a nearly linear relationship showing little decrease in dynamic sensitivity with increased force. In addition, they also developed a general transfer function making it possible to predict the instantaneous discharge rate of individual afferents.

The only reports on the functional properties of periodontal afferents from posterior teeth are from Johansson and Olsson (1976), recording from one 1st premolar in human and Appenteng et al. (1982), recording from the trigeminal ganglion of anesthetized rabbit. Johansson and Olsson (1976) reported that the periodontal afferent from the 1st premolar was directionally sensitive and slowly adapting while Appenteng et al. (1982) only stimulated the molar in one direction and found mostly rapidly adapting receptors. The shortage of information about the functional properties of posterior periodontal mechanoreceptors reveal the importance of the present work.

1.2.3 Role during oral motor behaviors

Basic features of masticatory behaviors can be generated by the CNS in the absence of sensory input (Dellow and Lund 1971; Nozaki et al. 1986). Kobayashi et al. (2002) studied mastication in an osteopetrotic mouse, which is a mutant with no tooth eruption. The study found several differences in mastication from those in normal mouse, but the basic rhythm and pattern of mastication was similar. They proposed that the central pattern generator (CPG) developed in the absence of teeth and periodontal mechanoreceptors. However, signals from mechanoreceptive afferents are required for an efficient and adaptive execution of the masticatory sequence. Several reports indicate the importance of periodontal afferents in the control of jaw muscles during biting and chewing (Lund 1991; Trulsson and Johansson 1996a; Türker 2002).

The afferent nerve fibers of the periodontal mechanoreceptors have reflex connections to the jaw muscles. Experiments in man with a tap on the labial surface of an upper incisor during clenching showed a series of inhibitory and excitatory reflexes in masseter muscle activity (Van der Glas et al. 1985). Brodin et al. (1993) also stimulated an upper incisor using both pushes and taps. The taps elicited a short-latency inhibitory reflex, which increased as the taps became stronger, often followed by an excitatory peak. Pushing the tooth on the other hand evoked a long-latency excitatory response that increased with stronger pushes, followed by a short-latency inhibitory response. In both studies after applying local anesthesia to the tooth the inhibitory and excitatory effects decreased greatly, indicating that mainly the periodontal mechanoreceptors mediate these reflexes. The differences found in the latency indicate that there might be several parallel sensory-motor pathways. In another investigation by Türker and Jenkins (2000), reflex responses induced by tooth unloading of static force of 2N in the horizontal direction on a maxillary incisor tooth was studied. Both inhibitory and excitatory effects on the human masseter muscle could be seen. Also, after the application of anesthesia around the stimulated tooth the responses changed. On the contrary, only the inhibitory responses were abolished and they concluded that the excitatory responses from the tooth unloading not could be periodontal mechanoreceptive afferent induced, but rather from muscle spindles. When stimulating in the axial direction differences between incisor and molar could be seen (Brinkworth et al. 2003; Brinkworth et al. 2004). With brisk axial stimulation of the incisor an inhibition followed by a late excitation was the most common response of the masseter muscle. Slowly rising stimuli did not produce any excitatory reflex activity. Anesthesia of the periodontal ligament reduced both the inhibitory and excitatory response, concluding that the responses were due to the periodontal mechanoreceptors. However, excitation was the primary response for the molars. Anesthesia of the periodontal ligament had little effect on the response and the authors claimed that the muscle spindles and not the periodontal mechanoreceptors were primarily responsible for the reflex activity after stimulation of the 1st molar in the axial direction.

Neurons in the medial reticular formation that generate the rhythmic bursts of jaw muscle activity are called a CPG. The masticatory CPG generates the basic pattern of rhythmic jaw muscle activity during chewing. It is believed that the CPG may also be involved in adjusting the gain of reflexes by changing the excitability of interneurons of the reflex pathways (Lund 1991).

Rhythmic jaw movements are modulated by sensory feedback of masticatory force and the direction of force load to the tooth from mechanoreceptors in the periodontal

tissues (Appenteng et al. 1982; Lavigne et al. 1987; Inoue et al. 1989). Lavigne et al. (1987) found that the amplitude and duration of the masseteric burst increased when an obstacle was introduced between the opposing molars during fictive mastication. They proposed that periodontal mechanoreceptors provided positive feedback to jaw-closing muscles during mastication. After bilateral combined section of the maxillary and inferior alveolar nerves, Lavigne et al. (1987) and Inoue et al. (1989) showed that trigeminal deafferentation modifies jaw-closing muscle activity. This reduction was ascribed mainly to the loss of periodontal sensation. However, Morimoto et al. (1989) showed that the response to test strips was not completely abolished by the denervation of the nerves in the anesthetized rabbit. When the muscle spindles were additionally blocked by lesioning the mesencephalic trigeminal nucleus, the remaining facilitatory response of the masseteric electromyography (EMG) bursts was nearly eliminated and the masseter muscle hardly responded to an application of the strip during cortically induced rhythmic jaw movements (CRJM). Thus, muscle spindle afferents from the jaw-closing muscles, as well as the periodontal receptors were likely to be involved in the regulation of the jaw-closing muscle activities during chewing.

Hidaka et al. (1997) found that the masticatory force was basically regulated in proportion to the hardness of the chewing substances. The force duration was insensitive to the change in strip hardness. The build up speed of force changed in a hardness-dependent manner, i.e. the harder the strip, the faster the build up speed of force. After denervation of the maxillary and inferior alveolar nerves, the masticatory force was found to build up more slowly. This finding may be accounted for by the loss of periodontal sensation. It could be that both periodontal afferents and muscle spindles were responsible for the hardness-dependent change, and that removing only one of them does not have much effect alone.

When anesthetized rabbits were chewing on thin plastic strips Komuro et al. (2001) reported that 'facilitatory masseteric responses' (FMR) often occurred prior to contact of the teeth to the strip from the second masticatory cycle, but never in the first cycle. This finding supports the concept of a feed-forward control mechanism that modulates FMR timing. Furthermore, the FMR preceding the force onset disappeared after making a lesion in the mesencephalic trigeminal nucleus, where the ganglion cells of the muscle spindle afferents from the jaw-closing muscles are located. In contrast, no such change occurred after blocking periodontal afferents by deprivation of both the maxillary and the inferior alveolar nerves. The authors therefore concluded that the putative feed-forward control of the FMR was mainly dependent on sensory inputs from the muscle spindles. They further suggested that it was probable that the timing of the FMR is mostly controlled by the muscle spindles, while the magnitude of the FMR was controlled mainly by the muscle spindles and partly by the periodontal receptors (Komuro et al. 2001).

In human, Ottenhoff et al. (1992a,b; 1993) found that when food-simulating force was given to the mandible, using a computer-controlled device, while subjects were making rhythmical open-close jaw movements, an 'additional muscle activity' (AMA; equivalent to the FMR in animal) was induced in the masseter muscle along with the muscle activity required for the basic rhythmical movements of the jaw. This AMA appeared before the onset of the force from the second cycle with force, although it did not appear in the first cycle with force. AMA is regarded as the muscle activity that was made in preparation for anticipated force. They suggested that a pre-programmed activity would be generated when a peripheral trigger was present. The sensory

information about the bolus size in the previous masticatory cycles might affect the onset of the AMA in the following masticatory cycles. This has also been demonstrated by Johansson and Westling (1988) in the hand and arm during lifting task with precision grip. The weight adaptation primarily relied on stored information from the previous lift. If weight of the lifted object had changed unexpectedly, erroneous weight programming occurred in the hold phase until information about the new weight had been collected.

Furthermore, Trulsson and Johansson (1996b) asserted that the periodontal mechanoreceptors of anterior teeth in human were important in manipulative tasks like holding and positioning food for biting. It was found that the forces used to hold a peanut between the incisors coincided with the range over which periodontal afferents are most sensitive to changes in force. Anesthesia of the periodontal tissues resulted in both much higher and variable hold forces. In a study on human subjects lacking periodontal mechanoreceptors, such as patients with osseointegrated implants or dental prosthesis, the subjects also used much higher hold force levels (Trulsson and Gunne 1998). These observations demonstrate the importance of periodontal mechanoreceptors in the regulation of low hold force levels when food is held and manipulated between anterior teeth.

1.3 AIMS OF THE PRESENT INVESTIGATION

- Describe the basic discharge characteristics of human periodontal afferents of posterior teeth.
- Analyze the receptive field properties and directional sensitivity of human periodontal afferents of posterior teeth.
- Analyze the encoding of force amplitude and rate of human periodontal afferents from posterior teeth and describe their discharge properties during chewing.
- Investigate the strength of the synaptic connection between periodontal afferents and other orofacial mechanoreceptive afferents and jaw muscle motoneurons.
- Describe the role of periodontal afferents during natural biting tasks using anterior and posterior teeth.

2 METHODOLOGICAL CONSIDERATIONS

2.1.1 Subjects and general procedure

Healthy subjects between 20 and 40 years of age participated in these studies. All subjects signed informed consent and the studies were approved by the Human Ethics Committee, Karolinska Institutet.

The teeth that were included in the studies were free of major dental restorations, showed normal relations to antagonistic teeth, exhibited no periodontal breakdown, and had not been exposed to any endodontic, prosthetic or orthodontic treatment. During the experiments subjects were comfortably seated in a dental chair.

2.1.2 The microneurographic method

In **Papers I, II and III**, the microneurographic technique developed by Vallbo and Hagbarth (1968) was used. A trimmed thermoplastic block was placed between the upper and lower molars on one side to keep the mouth open in a stable position. A horizontal plate, attached to the block, prevented contact between the tongue and electrode. The electrode had an exposed tip of 5-15 μm and the impedance was 100-400 k Ω , measured *in situ* at 1 kHz. The inferior alveolar nerve was approached through the oral cavity and was impaled near its entrance to the mandibular foramen (Johansson and Olsson 1976; Trulsson et al. 1992). The lingual nerve was approached in a similar way slightly medial to the inferior alveolar nerve. To facilitate the search for the chosen nerve, low-intensity electrical pulses were intermittently delivered through the electrode. Paresthesia indicated that the electrode approximated the nerve. When a nerve fascicle was penetrated the electrode was carefully adjusted until impulse responses in a single afferent were obtained.

2.1.3 Mechanical stimulation techniques

Copper attachments with nylon cubes at their tops were affixed 1 mm above the 1st premolar, 2nd premolar and 1st molar. On the 1st and 2nd premolar one cube was cemented centrally over the crown on each tooth while on the 1st molar two cubes were cemented centrally over the mesial and distal half of the crown. The cubes enabled stimulation in five free faces, while using a nylon loop fixated in the copper attachment enabled stimulation in an upward direction (see Fig. 1). Totally, this allowed four stimulation directions in the horizontal plane (lingual, facial, mesial and distal) and two stimulation directions in the vertical plane (up and down). The maximum directional error was $\pm 8.5^\circ$ (for details, see Trulsson et al. 1992). When a stable single-unit recording was attained, forces of ca. 250mN were applied to the different cubes to identify the tooth that gave the strongest discharge, which was defined as the receptor bearing tooth (RBT, see **Paper I**). By applying forces to this tooth and the neighboring teeth, the size of the receptive field was attested. The receptor bearing tooth was then stimulated in the six different directions to examine the directional sensitivity of the afferent. In the direction that evoked the strongest response a stimulation sequence of generally 8-10 force applications, attaining different static phase force amplitudes, (range 0.1 -15 N) were applied (**Paper II**). In **Paper III**, a probe was used to apply the force directly on the tooth crown and therefore the stimulus directions were restricted to

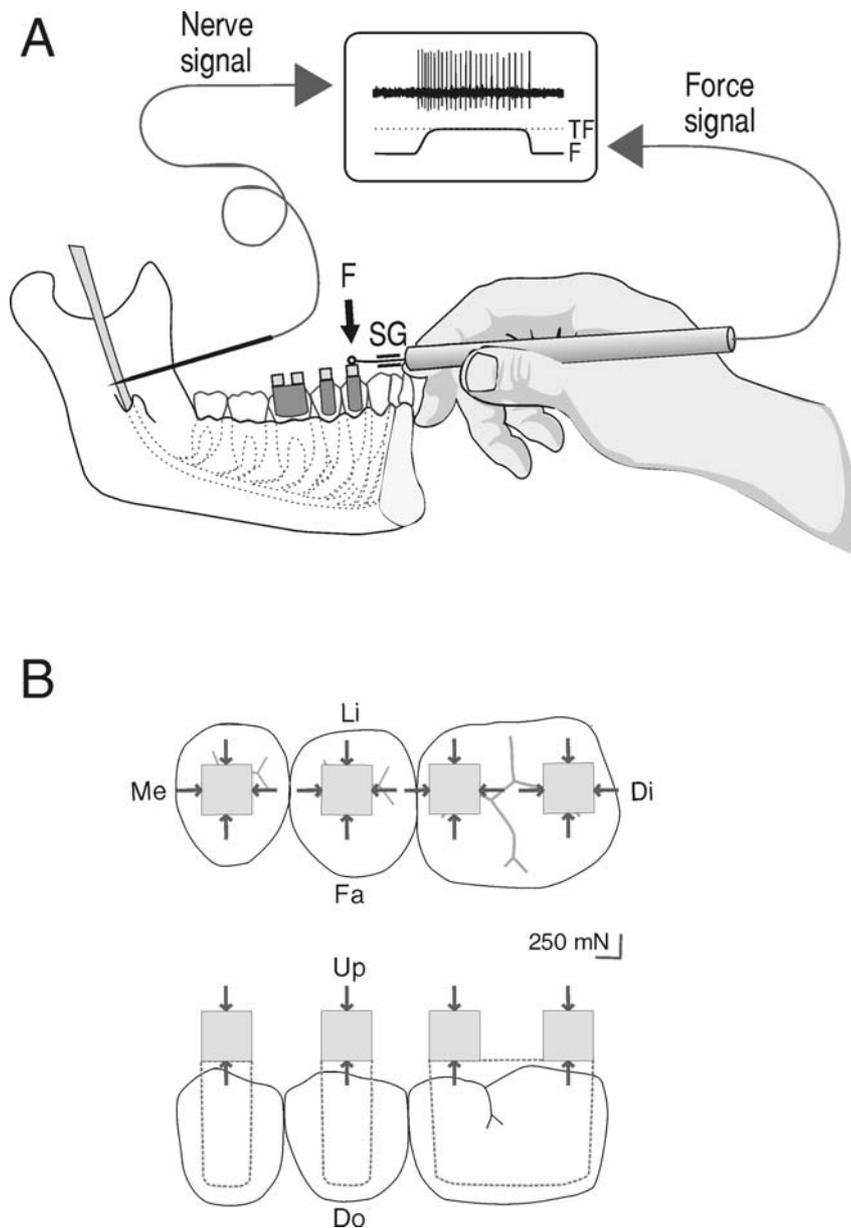


Figure 1. **A.** On the tracing of the lower jaw, as seen from the median plane (left), is indicated the position of the tungsten microelectrode in the inferior alveolar nerve. A probe equipped with strain gages (SG) for continuous force measurement was used to apply the force. The force signal (F), a target force (TF) for the experimenter, and the nerve signal were displayed on a computer screen during the experiment. **B.** The forces were applied in each of the six directions represented by arrows: Me, Li, Di, Fa, Up and Do. Me=Mesial, Li=Lingual, Di=Distal, Fa=Facial, Up=Upward, Do=Downward.

downward, lingual and facial directions. The mesial and distal surfaces were not easily assessable and the tooth could not be lifted upwards.

2.1.4 Recording EMG from jaw muscles

In **Paper III**, surface EMG was recorded from the masseter and anterior temporal muscles bilaterally using disposable Ag/AgCl surface electrodes placed over the belly of the masseter muscle and at the anterior edges of the temporal muscle. The electrical activity of the suprahyoid muscles (DIG) was recorded by placing one electrode on either side of the suprahyoid region to gather an overall activity of all the jaw openers. To record intramuscular activity a Teflon[®] insulated bipolar multiunit EMG wire electrode was inserted to a depth of about 1 cm into the anterior portion of the masseter muscles on both sides (Scutter and Türker, 1998). The multiunit EMG recording illustrates the masseter activity with minimal cross talk from the mimic muscles that overlie the masseters. EMG activity was amplified, filtered (bandwidth 8 Hz - 5 kHz), digitized at 3.2 kHz (surface EMG) or 6.4 kHz (intramuscular EMG) and stored on computer with the nerve signal.

2.1.5 Recording of biting forces

In **Paper IV**, half a peanut rested on a transducer-equipped bar and the forces used were recorded. The subjects were instructed to hold the peanut between the central incisor, canine, 2nd premolar or 1st molar and the respective antagonist for 3 seconds before splitting it.

2.1.6 Data analysis

The nerve and force signals were sampled at 12.8 kHz and 800 Hz, respectively (12 bits resolution) using a flexible data-collection/analysis computer system (SC/ZOOM, Section for Physiology, IMB, Umeå University). The reliability of each nerve recording was established using the spike recognition software incorporated in the SC/ZOOM system. In addition, all spikes were visually examined on an expanded time scale before they were accepted as representing unitary activity. The instantaneous discharge rate was calculated as the inverse of the time interval between consecutive action potentials.

In **Paper III**, the EMG data was full wave rectified and averaged around the time of the nerve spike, so that the peak of the action potential became trigger-time zero (Milner Brown et al. 1973). Resultant averaged EMG data were also normalized to the mean EMG value. CUSUMs have then been built from the averaged EMG trace (integration of the differences in each bin value from the mean bin value; Ellaway 1978) to highlight subtle changes in the EMG and to visualize the effect of the nerve unit autocorrelogram peaks on the motoneuron pool. CUSUM reveals any time locked EMG modulation related to the discharge of the nerve spike. However, even though this method helps visualize the modulation in the EMG, it is not a statistical approach and hence cross correlogram calculations are used to indicate any significant correlation between the peaks and troughs in the averaged EMG records and the peaks and troughs in the nerve spike train autocorrelogram.

3 RESULTS AND DISCUSSION

In our studies all periodontal afferents were slowly adapting and continued to discharge in response to static forces in at least one simulation direction. This is in line with the findings by Pfaffmann from 1939. However, several animal studies have described both rapidly and slowly adapting afferents (see Hannam 1982; Linden 1990), which can be due to differences in the species. However, as described by Linden (1990), a non-optimally stimulated slowly adapting afferent can easily be mistaken for being rapidly adapting. As previously mentioned, only the report of Trulsson et al. (1992) have stimulated the afferents in three dimensions, all other missing at least the upward direction. An afferent being most sensitive in the upward direction could then behave like a rapidly adapting in other directions because the afferent is not optimally stimulated (see Trulsson and Johansson 1996a).

3.1.1 Receptive field properties and directional sensitivity of periodontal afferents of posterior teeth (Paper I)

To study the receptive field properties and directional sensitivity of periodontal afferents of posterior teeth ramp-and-hold shaped force profiles of ca. 250mN was applied in six different directions: lingual, facial, mesial and distal in the horizontal plane and up and down in the vertical direction of the tooth (see Fig. 2). When loading an afferent, one particular tooth (the lower 1st premolar, 2nd premolar or the 1st molar) showed the strongest response being the RBT. The RBT typically showed excitatory responses in two to four out of the six tested directions demonstrating that the afferents are broadly tuned to direction of force application. Further, the number of periodontal afferents and their sensitivity to tooth loads decreased distally along the dental arch. The RBT was the 1st premolar for 23, the 2nd premolar for 13, and the 1st molar for 9 afferents, indicating a decreased innervation of the periodontal ligament distally along the dental arch. This is in line with a report by Trulsson (1993) on anterior teeth in which the central incisor was the RBT for the highest number of afferents, followed by the canine, the lateral incisor and the 1st premolar. The decreased innervation distally along the dental arch is supported by Byers and Dong (1989) who found a reduced incidence of receptors around the posterior teeth compared to anterior teeth, studying receptors with their cell bodies in the trigeminal ganglion in monkey.

All the periodontal afferents showed slowly adapting responses in at least one stimulus direction and a majority was spontaneously active, like the anterior teeth. However, the number of spontaneously active afferents seemed to decrease posteriorly from 71% for the anterior teeth (Trulsson and Johansson 1996a), 74% for the 1st premolar, 62% for the 2nd premolar and 44% for the 1st molar. Interestingly, Hannam (1969b) suggested that spontaneous activity was a result of sustained tension in the periodontal ligament. If this is correct our results may indicate that the tension of the collagen fibers in the periodontal ligament is lower for posterior teeth than anterior.

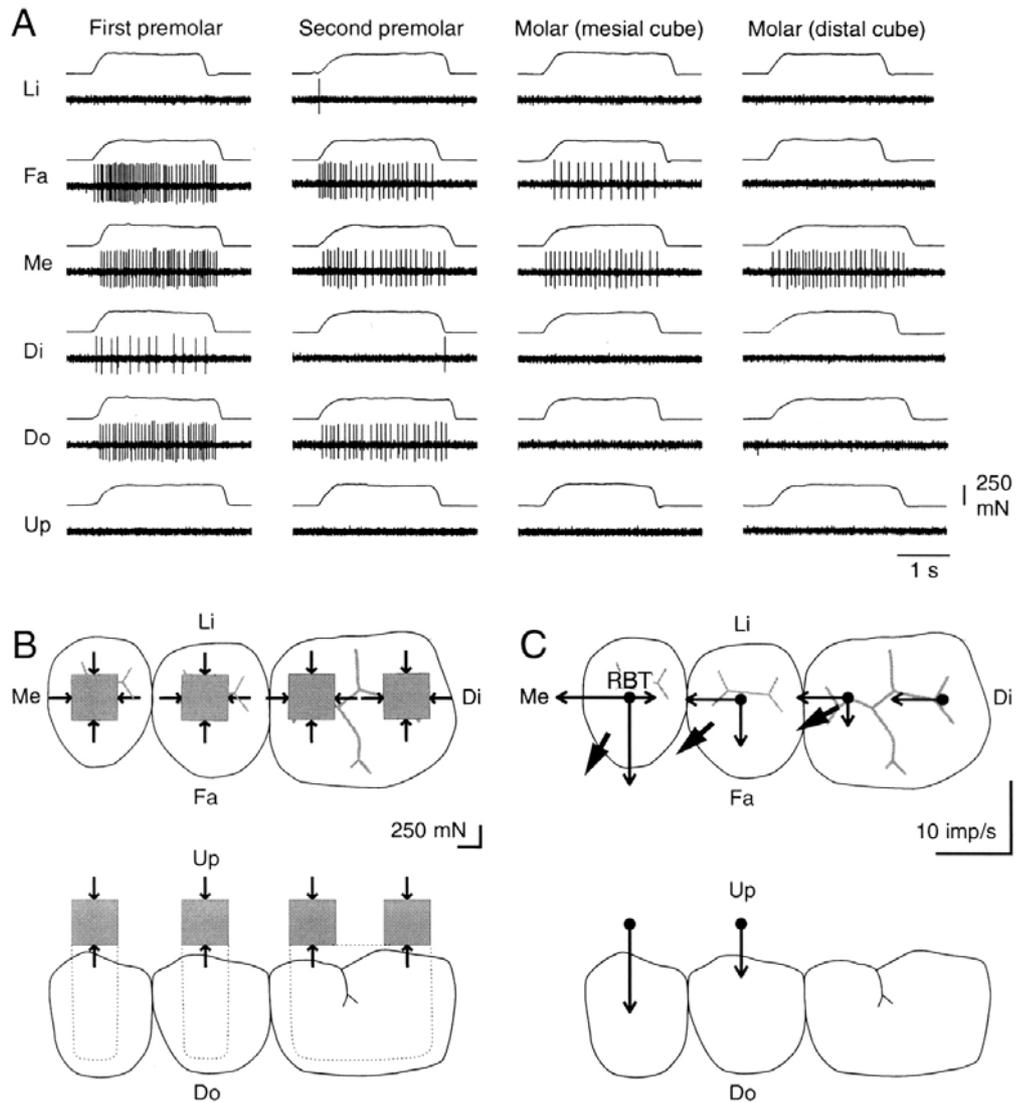


Figure 2. Responses of a single periodontal afferent to forces applied in six directions to the 1st premolar, 2nd premolar and 1st molar (mesial and distal cube). **A.** examples of neurograms with the corresponding force records above. In **B** and **C** the three teeth are shown in a horizontal plane and in a sagittal plane. **B.** the static forces (mean of 3 stimulations) in each of the six directions and for each of the three teeth are represented by the vectors. The forces were applied to each of the five free faces on a nylon cube (3x3x3 mm; shaded) positioned on the tooth 1 mm above its edge by the use of a copper attachment (dotted contour). The upward force was applied via a nylon loop affixed to the copper attachment (not shown). **C.** vectorial presentation of the static responses to force stimulations in six directions to each cube. The length of the vectors is proportional to the mean impulse frequency during three stimulations in each direction, and the direction of the vector represents the stimulus direction. The thick arrow represents an estimate of the most efficient excitatory stimulus direction in the horizontal plane, i.e., the 'preferred direction'. The position of the dot represents the center of the cube used for mechanical stimulation. Force directions: Li = Lingual, Fa = Facial, Me = Mesial, Di = Distal, Do = Downward, Up = Upward. RBT= 'receptor bearing tooth'.

About half of the tested afferents (17/35) responded to loading of more than one tooth. All these afferents showed their highest response rate when stimulating one particular tooth, i.e. the RBT, with a gradual decline in the response when loading the adjacent teeth. A common feature of all these afferents was that the involved teeth were adjacent and the crowns of the teeth were in mechanical contact. The teeth adjacent to the RBT almost always had their preferred direction towards the RBT. Thus, the response profiles of these afferents indicated that multiple-tooth receptive fields were due to mechanical coupling between teeth rather than branching of single afferents to innervate several teeth. However, for the few afferents with their preferred direction away from the RBT the multiple-tooth receptive fields were most likely due to the transseptal fiber system (Trulsson 1993; Tabata et al. 1995). The 1st molar was equipped with two cubes centered over the mesial and distal half of the crown. However, no differences in directional sensitivity could be seen for the afferents when forces were applied to different sites of the same tooth.

In contrast to the afferents of anterior teeth (Trulsson et al. 1992), the afferents of posterior teeth show a weak sensitivity in vertical directions and the 1st molar shows a clear directional bias in the disto-lingual direction. Anterior teeth are involved in initial stages of food intake, when morsels are manipulated, split into pieces, and transported into the mouth, whereas the molars grind the food during forceful chewing. The bias for the 1st molar in the disto-lingual direction, is in line with studies on tooth displacement during oral function, which has reported that the 1st molar tilts in the lingual direction during clenching and biting (Siebert 1981; Miura 1998).

Interestingly, including receptive fields of more than one tooth, the 1st molar responded in a disto-lingual direction when being the RBT but, when a premolar was the RBT the 1st molar responded in a mesial direction (see Fig. 7 **Paper I**). This compensatory effect for lack of sensitivity in the mesial direction when the 1st molar was the RBT, demonstrates that the information from a single tooth should not be interpreted in isolation. During mastication not only are the afferents around the directed stimulated tooth activated but also the afferents around the adjacent teeth. Edin and Trulsson (1992) used artificial neural networks to demonstrate that the population response in human periodontal afferents contained detailed information about the direction of applied forces and which tooth that was loaded. The overlapping of peripheral receptive fields is characteristic for all sensory systems and most likely it improves the accuracy of spatial representation (Johansson and Vallbo 1980).

The proportion of afferents showing multiple-tooth receptive fields in humans (52% for anterior teeth and 49% for posterior teeth) conflicts with the results from animal experiments. Tabata and Karita (1986) reported that only 5% of the afferents in cat had multiple-tooth receptive fields while on the same species Sakada and Kamio (1971) found 58% for the slowly adapting afferents and Tabata et al. (1994) 34%. In dog, Hannam (1970) found 21%. The differences between human and animal studies are most likely explained by anatomical variations in the dentition, for example the rat has no canines or premolar teeth, and its incisors are located far away from the molars. In human the teeth often have interdental contacts between adjacent crowns, whilst animals often demonstrate spacing between the teeth.

This study suggests that human periodontal afferents from anterior and posterior teeth differ in their capacity to respond to horizontal and vertical forces.

3.1.2 Encoding of force amplitude and rate of periodontal afferents of posterior teeth (Paper II)

The encoding of force amplitude and force rate by human periodontal afferents at posterior teeth was studied on the RBT and in the most responsive direction, described in **Paper I**. As in **Paper I**, a comparison with human anterior afferents (Trulsson and Johansson 1994) was made and further the quantitative model they developed was also tested on the afferents of posterior teeth. This model enabled the prediction of the instantaneous discharge rate for individual afferents. Following the affirmation that this model could predict the discharged rate, a prediction of how these mechanoreceptive afferents at posterior teeth signal during simulated chewing will be proposed.

The relationship between the steady-state discharge rate and the amplitude of

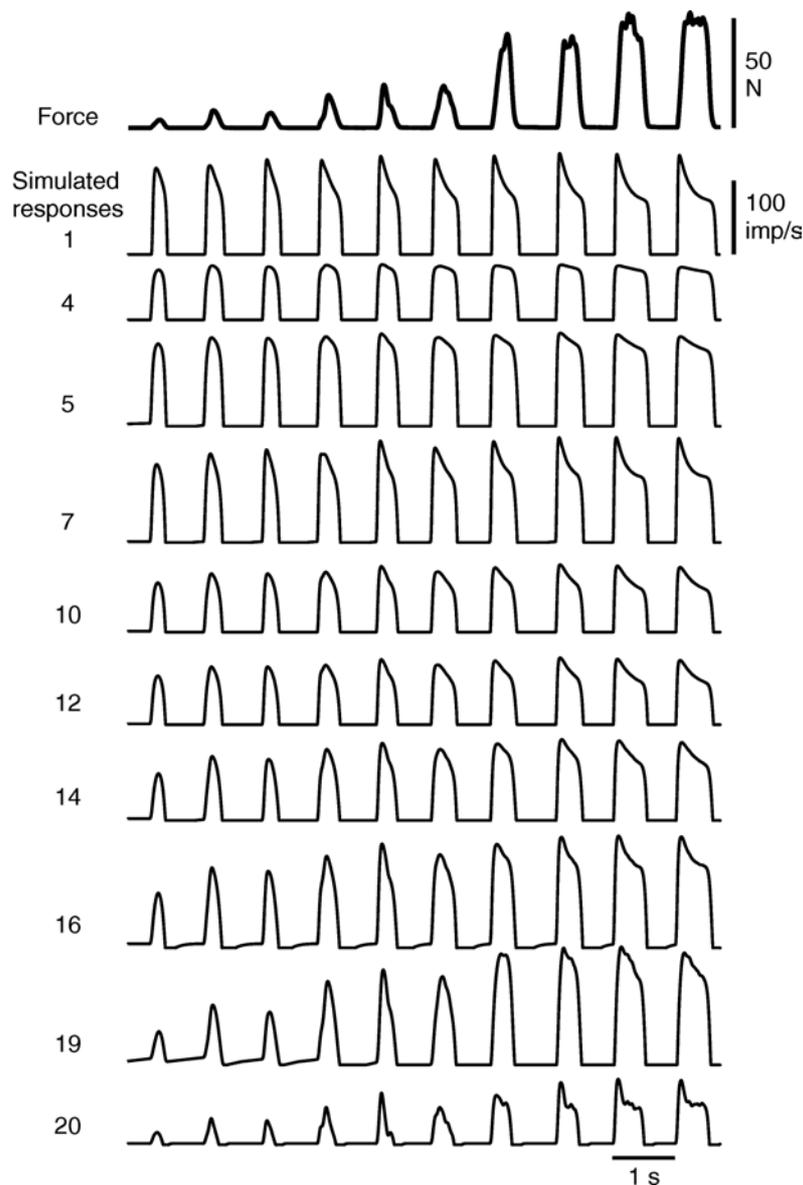


Figure 3. Simulated periodontal afferent responses to force profiles recorded during “chewing” on a force transducer placed between a pair of molars. Ten different “chewing” force profiles with peak forces ranging from 3 N to 52 N are shown at the top. Below the force traces, the simulated afferent responses are shown. Each horizontal row of curves represents the simulated responses for one afferent (numbered 1-20 according to Table 1, **Paper I**). Afferents 1-16 all featured hyperbolic stimulus-response relationships, whereas afferents 19 and 20 showed nearly-linear relationships.

stimulation force exhibited a marked curved (negatively accelerating) relationship for a majority of the afferents (85%). These hyperbolic afferents feature their highest static and dynamic sensitivity at low force levels and exhibit a strong saturation tendency. In contrast, a minority of the afferents (15%) showed nearly linear stimulus-response relationship and a little decline in the dynamic sensitivity with increasing force. The mathematical function, described by $R_s = a + bF/(F+c)$, where R_s stands for the steady-state response, F for the steady-state force, and a , b and c are parameters estimated for each afferent, was used to fit the curves in accord with the experimentally obtained data. All afferents except one showed a correlation coefficient above 0.94 ($0.89 < r < 0.98$). For afferents from posterior teeth, the forces yielding half the estimated maximal discharge rates (c -parameter) were on average 1.7N, which is four times higher than afferents from anterior teeth (0.42N; Trulsson and Johansson 1994).

These results are in line with Trulsson and Johansson (1994), who also reported that a majority of the mechanoreceptive afferents was hyperbolic (about 80%) and a minority was nearly linear (about 20%). Saturating stimulus-response relationships have also been shown in animal studies (Pfaffmann 1939; Ness 1954; Hannam 1969a; Hannam and Farnsworth 1977) and Hannam (1969a) described in dog that one of six afferents were non-saturating.

The present report reveals that periodontal afferents from posterior teeth are less sensitive to low tooth loads than afferents from anterior teeth.

Periodontal afferent encoding of tooth loads during mastication

For technical reasons intraoral recordings from human periodontal afferents are very difficult to perform during oral motor functions. However, by using the quantitative model that successfully described the instantaneous discharge rate for individual afferents, such a description could be achieved. By chewing on a rubber coated force transducer held between the 1st molars on one side, ten different force profiles ranging from 0.3N to 52N were recorded. Fig. 3 shows the different force profiles followed by the simulated discharge rate profile for one individual afferent on each row (numbered 1-20). The first eight rows illustrate hyperbolic afferents with highest sensitivity for low force levels while afferents 19 and 20 are more linear. Applying the force profiles to the quantitative model predicted that the discharge rates of periodontal afferents rapidly increased at initial tooth contact due to their high static and dynamic sensitivity at low force levels. All afferents will continue to discharge as long as the tooth is loaded. However, due to saturation tendencies at higher force levels, the first eight afferents will poorly encode the magnitude of strong chewing forces and the force changes occurring at these high forces. On the other hand, the nearly linear afferents (19-20) will continue to respond to the changes, also for the high chewing forces.

3.1.3 Synaptic coupling between periodontal afferents (and other orofacial afferents) and jaw muscles (Paper III)

Papers I and II have described the exquisite sensitivity to low forces for the periodontal afferents. The CNS receives information about which direction the tooth is loaded and for what forces. This sensory information is important for the motor control of the jaw. Thus, one would expect a strong coupling between the periodontal afferents and the jaw muscles. Brodin et al. (1993) have previously described this connection by

tapping or pushing on an upper central incisor in humans. The muscle responses were then the result of a stimulation of several afferents. The present study (**Paper III**) investigated if responses in the jaw muscles could be seen as a result of stimulation of a single periodontal afferent. For comparison, the effect on the muscles elicited by other orofacial mechanoreceptors was also studied.

Single mechanoreceptive afferents from the periodontal ligament, gingiva, red lip, mucosa, hairy skin and tongue were analyzed (see Fig. 4). Both fast and slowly adapting afferents were found in the skin of the face and the red zone of the lip (FAI,

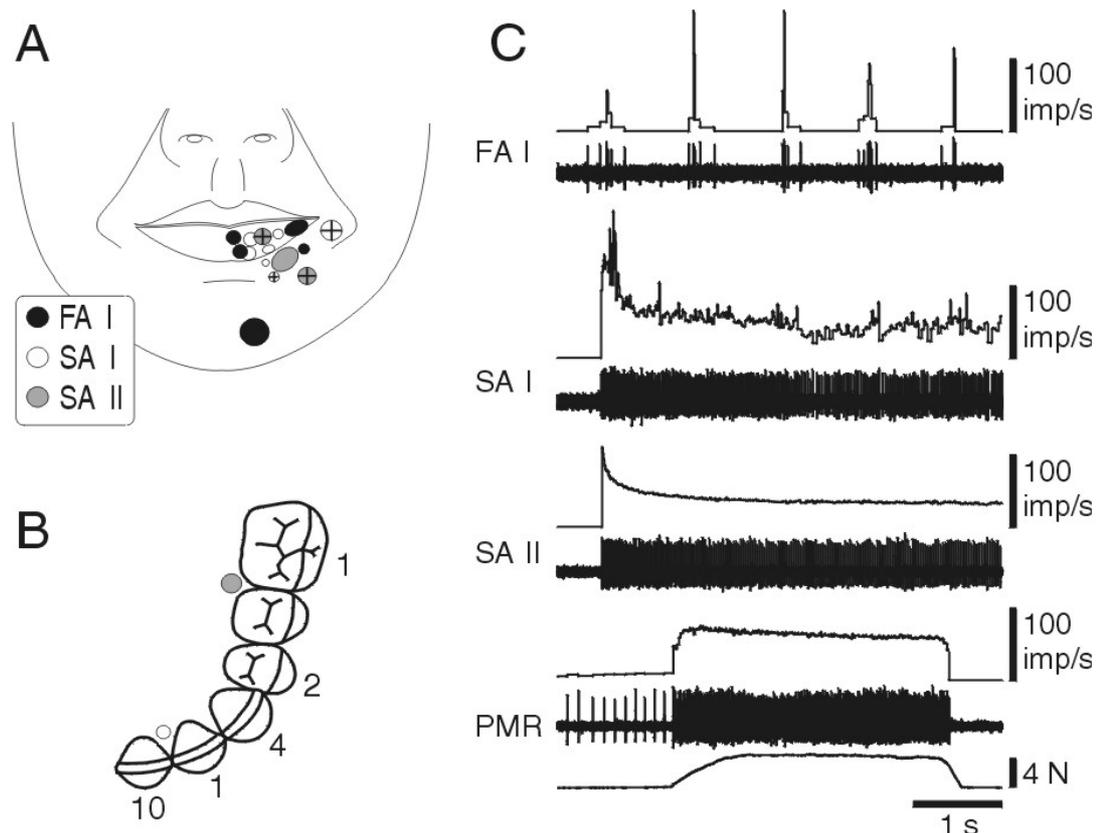


Figure 4. Receptive field and response characteristics of mechanoreceptive afferents in the human inferior alveolar nerve. **A.** Schematic drawing of the face illustrating the location and relative size of 15 receptive fields of three different types of afferents (FA I, SA I and SA II) in the facial skin, red lip and mucosa. The receptive fields marked with a cross indicate that these fields were located inside the mouth on the mucosa of the lower lip. **B.** Schematic drawing showing the lower teeth on the left side. The incisors, the canine, the premolars and the first molar are shown from bottom to top. The figures next to the teeth indicate the number of periodontal mechanoreceptors (PMRs) that showed the strongest responses when loading that particular tooth. The receptive fields located on the lingual side of the teeth show the approximate location and extension of two slowly adapting mechanoreceptors (1 SA I and 1 SA II) in the gingiva. **C.** Examples of recordings (instantaneous discharge frequency and neurogram) from four different types of afferents; FA I, SA I, SA II and PMR. The first five seconds of a two-minute recording is shown for each afferent.

SAI and SAI, cf. Johansson et al. 1988). Intra-orally in the mucosa and gingiva only slowly adapting afferents could be identified (SAI and SAI). For the periodontal afferents almost all (17/18) showed slowly adapting properties in at least one stimulation direction. One afferent was only sensitive to dynamic stimuli and responded when taps were applied to the tooth. Such afferent could easily be mistaken for a rapidly adapting type, but most probably the afferent was not optimally stimulated since we only applied forces in three directions (downward, lingual and facial; see Trulsson and Johansson 1996a). The decreasing sensitivity distally along the dental arch could be attested even here, the RBT was an incisor for 11 units, a canine for 4 units, a premolar for 2 units and a molar for 1 unit (Table 1). In the tongue FAI, SAI, SAI and deep tongue receptors were identified (cf. Trulsson and Essick 1997).

Receptor	RMemg	RM-mu	RTemg	Demg	LMemg	LM-mu	LTemg	Total	% Resp	No of units
31	3	6	1	7	3	9	3	32	46	10
32	1	-	-	1	1	1	1	5	56	1
33	1	2	2	2	-	4	1	12	43	4
34	1	-	-	1	-	2	-	4	29	2
36	-	-	-	-	-	-	-	-	-	1
TOTAL	6	8	3	11	4	16	5	53	42	18
% Response	33	44	17	61	22	89	28			

Table 1. Percentage of significant responses for each muscle is calculated by dividing the total number of responses of a particular muscle to the total number of units recorded (n = 18) and multiplying the result by 100 (columns). Percentage of significant responses for different units were calculated similarly, total responses/(number of units x 7) x100. Number of units was multiplied by seven since there were seven muscles, each of which is capable of significant correlation. 31 is lower left central incisor PMR; 32 is lower left lateral incisor PMR; 33 is lower left canine PMR; 34 is lower left first premolar PMR; 36 is lower left first molar PMR. RMemg is the surface EMG from the right masseter; RM-mu is the intramuscular multi unit EMG from the right masseter; RTemg is the surface EMG from the right temporalis; Demg is the surface EMG of the digastric muscle; LMemg is the surface EMG of the left masseter; LM-mu is the intramuscular multi unit EMG from the left masseter; LTemg is the surface EMG from the right temporalis. Although stimulation of the molar PMR induced a very large modulation in all muscles tested, we have decided to ignore this result since it is very much likely that many receptors (including the spindles) are simultaneously activated by the tap stimulus

The nerve signals in the afferents around the lip, tongue and gingiva generated modulation in several jaw muscle EMGs with a success rate of about 20%. Interestingly, the periodontal afferents and deep tongue receptors showed the strongest coupling with a success rate of more than 40%. The synaptic couplings were particularly strong in the ipsilateral side, except for the central incisor that also generated a strong response on the contralateral side. The strong coupling between the periodontal afferents and the jaw muscle motoneurons suits the role that the jaw muscles practice during mastication. In similar to this study, a coupling between mechanoreceptors and motoneurons has been shown for finger digits (McNulty et al

1999; McNulty and Macefield 2001). The lack of FAII:s in the orofacial region has previously been described by Johansson et al. (1988).

The significant modulation of the jaw muscles, especially by the periodontal mechanoreceptors and deep tongue receptors demonstrate their importance in controlling jaw muscle activity so that oral functions such as mastication are executed successfully.

3.1.4 Forces applied by anterior and posterior teeth during hold-and-split tasks (Paper IV)

The hold-and-split forces exerted by the upper central incisor, canine, 2nd premolar and 1st molar were recorded and analyzed to characterize human biting behavior. Half-a-peanut rested on a transducer-equipped plate, which the subjects held between two antagonist teeth (see Fig. 5). They were instructed not to use more force than necessary and after three seconds they were told to split the peanut.

The forces used to hold the peanut increased posteriorly from 0.60N for the incisor, 0.77N for the canine, 1.15N for the 2nd premolar and 1.74N for the 1st molar. The difference of hold forces between anterior and posterior teeth can be explained by the difference in sensitivity for the teeth as discussed in **Paper II**. Fig. 8 illustrates the distribution of hold forces for anterior and posterior teeth together with sensitivity curves for periodontal afferents of anterior and posterior teeth. Interestingly, the distribution of hold forces are skewed to coincide with the range over which the periodontal afferents are most sensitive to changes in force.

After the hold phase, the split phase started with a distinct rapid ramp force increase causing the peanut to split. The split force increased together with the peak force rate distally along the dental arch. This resulted in a constant split phase duration that did not differ between anterior and posterior teeth. The split force is likely to be affected by the mechanical properties of the food and the anatomical structures of the teeth. While an incisor is sharp and will split the food the molar will crush the food. Since the test food (peanut) was the same for all teeth the difference in split force is most likely explained by the mechanical cleaving effect of the different teeth. The force rate is determined by the nervous system. However, from this experiment it is difficult to know if the higher force rates for the posterior teeth depend on higher split forces or the use of posterior teeth instead of anterior teeth.

Blocking the periodontal afferents by using anesthesia demonstrated the importance of the input from these afferents in the present behavioral task. The average hold force for all teeth and subjects was 3.5 times higher after anesthesia. In the split phase no statistically significant differences were seen for the quantitative measures. However, tendencies for a lower peak force rate and higher split phase duration was seen for all tested teeth. Considering the small sample ($n=4$) this might imply that the periodontal mechanoreceptors could also be important in the regulation of not only low hold forces but also in forthcoming higher forces used to split the food. This has previously been shown in the chewing rabbit by Hidaka et al. (1997).

Trulsson and colleagues (Trulsson and Johansson 1996b; Trulsson and Gunne 1998) have used the same hold-and-split task to attest the importance of the periodontal mechanoreceptors for anterior teeth in humans. Trulsson and Johansson (1996b) also blocked the input from the periodontal mechanoreceptors in human by using

anesthesia, whilst Trulsson and Gunne (1998) used subjects that lacked periodontal mechanoreceptors. Both reported much higher hold forces in the absence of normal signals from periodontal mechanoreceptors.

The present study demonstrated higher hold forces for posterior teeth than anterior teeth. This is explained by the less sensitivity for low force levels for afferents of posterior teeth than afferents of anterior teeth.

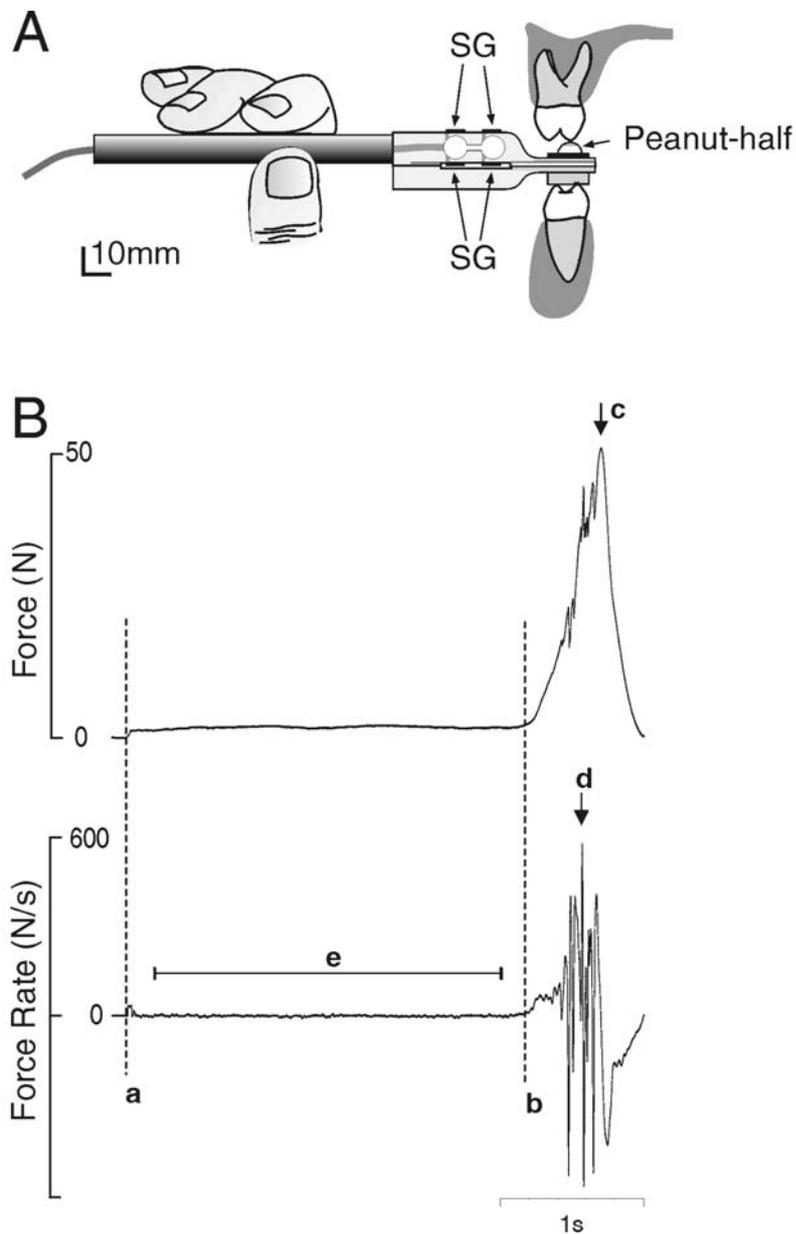


Figure 5. A. Apparatus used to record the forces exerted on the morsel. The peanut rested on a horizontal plate of duralumin with a thin piece of rubber affixed to it and equipped with strain gauges (SG) for force measurement. B. Example of single trial force profile recorded from a 1st molar during the hold-and-split task (upper trace). The lower trace illustrates the force rate. Events of interest include: *a* initial food contact; *b* onset of the split phase; *c* point at which maximum split force was attained; *d* point at which maximum of peak split force rate was attained; *e* interval beginning 0.2s after initial contact with the food and ending 0.2s prior to the onset of the split phase.

4 PERIODONTAL AFFERENTS FROM ANTERIOR AND POSTERIOR TEETH

The four articles presented here address the functional properties of periodontal mechanoreceptors and their role in motor control of the jaw. The role of periodontal mechanoreceptors in the regulation of oral functions has been extensively discussed (see Anderson et al. 1970; Hannam 1982; Linden 1990; Lund 1991; Trulsson and Johansson 1996a). However, few articles have described the mechanoreceptors of

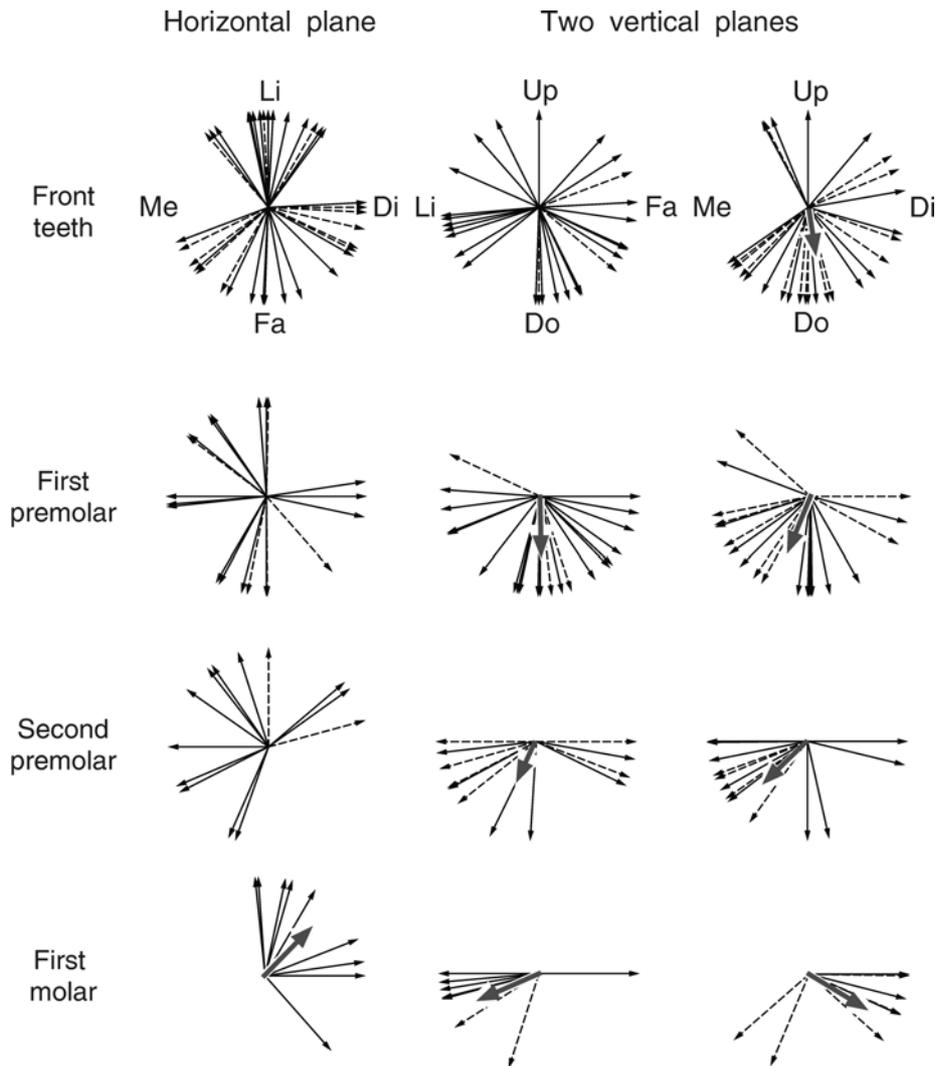


Figure 6. The 'preferred direction' of individual afferents projected to the horizontal plane (left panel) and two orthogonal vertical planes (middle and right panel). Solid arrows refer to afferents showing their strongest responses in one of the directions represented in the plane, dashed arrows refer to afferents with the strongest responses in another plane. For each cluster of vectors showing a significant directional bias ($P < 0.05$, Rayleigh) a resultant vector was calculated (heavy gray arrows). The data for the front teeth (incisors and canines) is from Trulsson et al. 1992. In the horizontal plane, the preferred directions of the afferents at the front teeth and the premolars are quite evenly distributed around the circumference of the tooth. The afferents at the molar, however, show a clear directional bias in the disto-lingual direction. In the vertical planes, a lower sensitivity to upward and downward directed forces is evident for the posterior teeth.

posterior teeth (Johansson and Olsson 1976; Appenteng et al. 1982) and further differences between anterior and posterior teeth. The mechanoreceptors of anterior and posterior teeth do indeed demonstrate similarities but there are also important differences.

First of all, as demonstrated in **Papers I, II and III**, the number of afferents decreased distally along the dental arch indicating a weaker innervation for posterior teeth than anterior. This finding is supported by several histological studies (Passatore et al. 1983; Byers and Dong 1989; Hassanali 1997). The difference between anterior and posterior teeth demonstrates the importance of a well-developed innervation for the anterior part of the mouth. When food is taken into the mouth, the morsel will be split into smaller pieces by the front teeth before it is moved to posterior parts of the dentition. Sometimes the front teeth are even used as a ‘third hand’ in manipulative tasks, or as a precision cutting tool. Proper execution of such tasks relies heavily on sensory information as those involving execution of comparable manipulative tasks performed by the densely innervated fingertips of the hand (Johansson and Vallbo 1983).

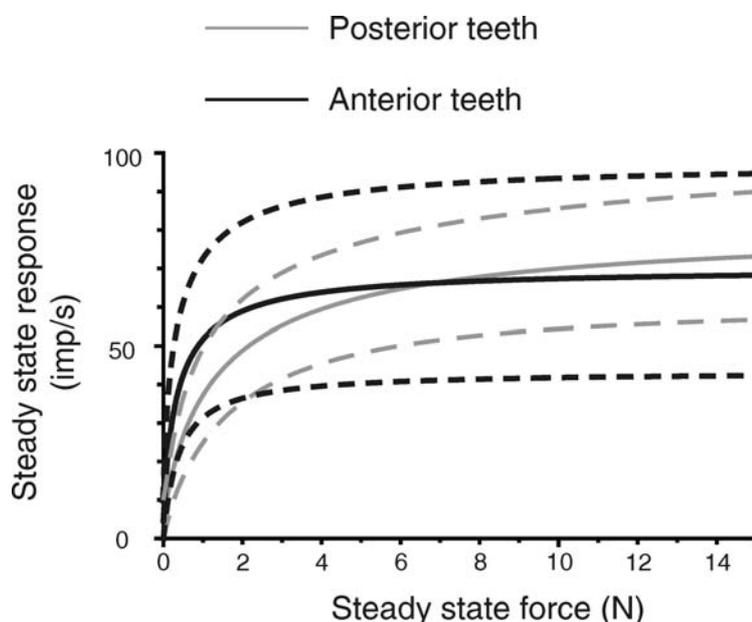


Figure 7. Mean value of all steady-state stimulus response functions for afferents at the posterior (gray curves) and anterior teeth (black curves, respectively). The solid and dashed lines represent the mean \pm 1 SD of the stimulus response functions (data obtained from 19 periodontal afferents of anterior teeth Trulsson and Johansson 1994 and 20 periodontal afferents of posterior teeth Paper II).

Secondly, afferents from the 1st molar have a biased directional sensitivity in the disto-lingual direction (**Paper I**), in contrast to the afferents of anterior teeth that are more broadly tuned (Trulsson et al. 1992; Fig. 6). In addition, for the upward direction there is a sharp difference between anterior and posterior teeth. Only 4% of the afferents at posterior teeth responded in upward direction while for afferents at anterior teeth about 50% responded (Trulsson et al. 1992). The difference in directional sensitivity may reflect the unique functions of different teeth. When anterior teeth are involved in manipulation of food at initial food intake and splitting it into pieces, forces are applied to them in all directions. The molars, on the other hand, grind the food during more powerful chewing and prepare it for swallowing. At the end of a chewing cycle when the molars approach the intercuspal position from a posterior and lateral position, they are likely to experience distal and lingually directed forces upon contact with the antagonist. Further, studies on tooth displacement during oral function indicate a tilt of the 1st molar during chewing and biting in a lingual direction (Siebert 1981; Miura 1998). Thus, the sensitivity of the afferents in the lingual direction for the molar may reflect a functional adaptation. However, it could also be that the CNS will not

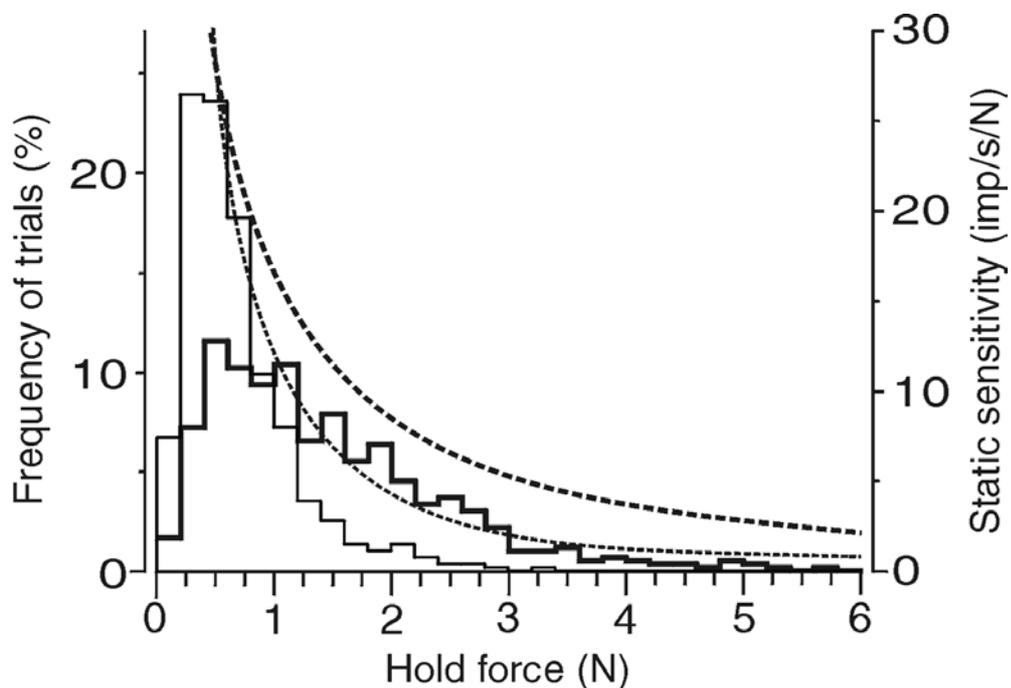


Figure 8. Frequency distribution of hold forces pooled over subjects. Thin line histogram represents data from anterior teeth (i.e. central incisor and canine) and thick line histogram represents data from posterior teeth (i.e. 2nd premolar and 1st molar). The superimposed curves represent the sensitivity to changes in steady-state force stimulation of two populations of human periodontal afferents. The thin and thick dashed curves show the first force differential for the steady-state discharge rate (mean values) as a function of force amplitude for periodontal afferents from anterior and posterior teeth, respectively. Data was obtained from 19 periodontal afferents of anterior teeth (Trulsson and Johansson 1994) and 20 periodontal afferents of posterior teeth (**Paper II**).

only get detailed information about the direction of the force but also where on the dental arch the force is applied. Indeed this has been demonstrated by Edin and Trulsson (1992) for anterior teeth. During mastication, not only will the periodontal afferents that innervate the tooth be activated by the force, but also afferents innervating adjacent teeth. Overlapping receptive fields are a distinguishing feature for all sensory systems and can improve the spatial representation by a population of afferents (see Johansson and Vallbo 1980).

Thirdly, the receptors of posterior teeth are less sensitive to low static and dynamic forces than anterior teeth. Fig. 7 shows the mean value of all steady-state stimulus response functions for anterior and posterior afferents. In this figure the curve for anterior afferents are steeper for lower forces than for posterior afferents. This difference in sensitivity is further confirmed in **Paper IV** during hold-and-split tasks. Subjects use lower hold forces for anterior teeth than posterior teeth and Fig. 8 illustrates the frequency distribution of hold forces for anterior and posterior teeth together with sensitivity curves for periodontal afferents of anterior and posterior teeth. The subjects chose to use hold forces within a range in which the periodontal afferents are most sensitive to changes in force. 90% of the hold forces are below 1.2N for anterior teeth whilst the corresponding value for posterior teeth is 2.7N. Lack of sensory input from periodontal mechanoreceptors in humans clearly deteriorates the motor control when performing manipulative tasks (see Trulsson and Johansson 1996b; Trulsson and Gunne 1998; **Paper IV**). An increase in hold forces and difficulties in controlling the morsel demonstrate the importance of the periodontal mechanoreceptors in fine motor control.

Immediately after contact with an object, tactile afferents in the hand encode various mechanical properties of the object that will be used to trigger the release of motor commands (Johansson and Westling 1987). In the oral cavity, most of the periodontal afferents are extremely sensitive to low force levels. That is upon tooth contact, information about the spatial distribution of food in relation to the dentition and information about mechanical properties of the food will be signaled to the brain. This early 'state information' from the periodontal afferents can be used to modulate a forthcoming motor command. Hidaka et al. (1997) reported that cutting the nerves to the teeth and thereby preventing input from periodontal afferents, reduced the build up speed of the masticatory force during chewing. Thus, information from periodontal afferents early after contact during each chewing cycle may be used to scale the muscle commands. This would take place in a predictive feed-forward ('open loop') manner, which has been described by Ottenhoff et al (1992 a,b) in humans. They showed that 'additional muscle activity' (AMA) required to overcome the impedance of the food is parameterised in advance on the basis of sensory experiences from the previous chewing cycles. In anaesthetized rabbits, performing rhythmical jaw movements, Komuro et al. (2001) reported that blocking of the periodontal afferents did not have much effect on the 'facilitatory masseteric response' (FMR), whereas blocking information from the muscle spindles abolished the FMR. Several earlier studies have demonstrated that combined destruction of periodontal afferents and muscle spindle afferents is necessary to diminish the FMR completely (Lavigne et al 1987; Inoue et al. 1989; Morimoto et al 1989).

All together this gives a picture of the periodontal mechanoreceptors as an important factor in the regulation of oral functions and the differences in sensitivity for afferents of anterior and posterior teeth might be ascribed to functional adaptation. The

anterior part of the mouth and the teeth are the first to be in contact with the food and at this stage much information about the morsel is collected which may be used to scale the muscle commands for forthcoming jaw actions.

5 CONCLUSIONS

1. All human periodontal afferents from posterior teeth adapt slowly to maintained tooth loads and a majority is spontaneously active.
2. The number of periodontal afferents responding maximally to loading of posterior teeth is lower compared to anterior teeth indicating a weaker innervation of the periodontal ligament posteriorly.
3. Periodontal afferents are directionally sensitive and respond typically in two to four out of six tested directions. Distally along the dental arch, the afferents showed weaker sensitivity in vertical directions and a bias in disto-lingual direction for the 1st molar.
4. When teeth adjacent to the receptor bearing tooth (RBT) are loaded, about half of the afferent population respond to loading of one or two more teeth. The multiple tooth receptive fields are explained by mechanical coupling between teeth rather than branching of single nerve fibers.
5. A majority of the afferents from posterior teeth exhibit a marked curved ('negatively accelerating') relationship between the steady-state discharge rate and the amplitude of the stimulating force, featuring a pronounced saturation tendency. However, compared to afferents from anterior teeth, these afferents are less sensitive at low force levels. In addition to a decline in static sensitivity at higher loads, they also show a decline in the dynamic sensitivity with increasing amplitude of background force.
6. A minority of the afferents exhibits a nearly linear stimulus response relationship and almost a maintained dynamic sensitivity with increasing background force.
7. Most human periodontal mechanoreceptors will poorly encode force changes at normal chewing forces due to their pronounced saturation tendencies at these high force levels. On the other hand, a small group of afferents will continue to respond to changes in the force profile even for higher chewing forces.
8. The combination of microneurography of single afferent nerve fibers and EMG recordings revealed a strong synaptic coupling between the periodontal mechanoreceptors and the motoneurons of the jaw muscles. This coupling was mainly unilateral except for the central incisor. The strong coupling between the afferents and muscles acting on the jaws supports the important role of periodontal mechanoreceptors in the control of the human jaw.
9. The forces used by subjects to hold and manipulate food morsels between the teeth increased distally along the dental arch. The difference in hold forces for the various teeth can be explained by the different sensitivity characteristics of the periodontal afferents innervating anterior and posterior teeth.
10. Blocking the sensory information from the periodontal afferents by the use of anesthesia, severely disrupts the control of the hold forces for all types of teeth. Thus, periodontal mechanoreceptors are important in the regulation of the forces used to hold and manipulate morsels between the teeth.

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