Receptive Field Properties of Human Periodontal Afferents Responding to Loading of Premolar and Molar Teeth

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INTRODUCTION

Periodontal mechanoreceptive afferents inform the brain about temporal, spatial, and intensive aspects of forces acting on the teeth. The force encoding properties of periodontal afferents supplying the anterior teeth (the incisors and canines) have been described for a number of species (see Hannam 1982; Linden 1990) including humans (see Trulsson and Johansson 1996). The human periodontal afferents have been found to adapt slowly to maintained tooth loads. Investigations on the spatial aspects of the force-sensitivity profiles of these afferents (i.e., their receptive fields) show that most afferents are broadly tuned to direction of force application, and about half respond to forces applied to more than one tooth (Trulsson 1993; Trulsson et al. 1992). Populations of periodontal afferents, nevertheless, reliably encode information about both the individual teeth stimulated and the direction of forces applied to those teeth (Edin and Trulsson 1992; Trulsson et al. 1992). Very limited information, however, is available on the human periodontal afferents supplying the teeth posterior to the canines (Johansson and Olsson 1976; Trulsson and Johansson 1996).

Afferent information about forces acting on the teeth is important for the sensorimotor regulation of mastication (see Lund et al. 1998). Because chewing mostly involves postcanine teeth, it is surprising that only a few animal studies report data on the force-encoding properties of periodontal afferents innervating these teeth (Appenteng et al. 1982; Linden 1978; Tabata and Hayashi 1994; Tabata and Karita 1986). Appenteng et al. (1982) found that the majority of afferents supplying the rabbit molars was rapidly adapting. On the other hand, in the cat and rat, the majority was reported to be slowly adapting (Linden 1978; Tabata and Hayashi 1994; Tabata and Karita 1986). Whether the apparent discrepancy in receptor classification is due to a true species difference or simply reflects differences in methodology, such as differences in the stimulus force applied to the teeth, is difficult to discern (see Trulsson and Johansson 1996). However, the limited information available on the receptive properties of these afferents suggests major species differences. For example, in the cat and rat only 5% of the periodontal afferents show “multiple-teeth” receptive fields. In the cat, these afferents supply the anterior teeth (Tabata and Karita 1986), whereas in the rat, they are restricted to the posterior teeth (Tabata and Hayashi 1994). This dissimilarity may, at least in part, be attributed to the different arrangements of the teeth in the two species. The human

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dentition is strikingly different from that of the animals investigated in earlier studies, both with regard to the anatomy of the individual teeth and their interdental relations. Thus to acquire data of direct relevance to human oral function, it is essential to obtain information on periodontal afferents in humans.

The purpose of the present study was to analyze the receptive fields of human periodontal mechanoreceptive afferents supplying the postcanine teeth. Forces of controlled amplitude and direction were applied to individual premolars and the first molar in the lower jaw to characterize the directional sensitivity of individual afferents.

It was found that the basic discharge characteristics of the human periodontal afferents innervating postcanine teeth are similar to those of the afferents innervating the anterior teeth: All afferents are slowly adapting and a majority are spontaneously active. Most afferents are broadly tuned to direction of force application and about half respond to forces applied to several teeth. The present findings also demonstrate that periodontal afferents innervating different types of teeth along the dental arch differ in their capacity to signal horizontal and vertical forces, respectively. Some of the results have been reported in a preliminary communication (Johnsen and Trulsson 2001).

Methods

Subjects and general procedure

Data were obtained in 12 experimental sessions on four healthy female subjects (ages 20–24). The volunteers participated after giving their informed consent in accordance with the Declaration of Helsinki. The study was approved by the local ethical committee.

The subject was comfortably seated in a dentist’s chair during the session, which lasted about 4 h. To allow intra-oral nerve recordings, the mouth was kept open in a stable position by the support of a trimmed thermoplastic block placed between the upper and lower molars on the side contralateral to the recording side. A horizontal plate was attached to this block to control movements of the tongue.

Recording procedure

Recordings were obtained from single mechanoreceptive afferents in the inferior alveolar nerve on either side by means of an insulated tungsten microelectrode (Valbo and Hagbarth 1968). The electrode had an exposed tip of 5–15 μm and the impedance was 100–400 kΩ measured in situ at 1 kHz. The nerve was approached through the oral cavity and was impaled near its entrance at the mandibular foramen (Johansson and Olsson 1976). For a more detailed methodological description, see Trulsson et al. (1992) and Trulsson and Johansson (1996).

Mechanical stimulation

Prior to nerve recording, copper attachments supporting nylon cubes (3-mm side) at their tops were cemented (Miradapt, Johnson and Johnson Dental Products) to the first and second premolars and the first molar on the recording side. The attachment for the premolars was equipped with one cube each that was centered over the crown of the tooth. The attachment for the molars, on the other hand, was equipped with two cubes that were centered over the mesial and the distal half of the crown, respectively (Fig. 2B). The cubes were oriented such that the four free faces were perpendicular to the lingual, facial, mesial, and distal directions, respectively, and the upper free face was perpendicular to the long axis of the tooth. A nylon loop was fixed to each cube to enable the application of upward-directed forces.

A probe equipped with transducers for continuous force measurement (DC-200 Hz), and a small nylon sphere (1 mm diam) at its end was used to manually apply mechanical stimuli normal to the free faces of the nylon cubes (maximum directional error was ± 8.5°) for details, see Trulsson et al. 1992). In this way, forces were applied close to orthogonal orientations in six directions: four directions in the horizontal plane (lingual, facial, mesial, and distal) and two vertical directions (down and up).

When a stable single-unit recording was obtained, the handheld probe was used to apply forces (ca. 250 mN) to the different cubes to identify the tooth that gave the strongest discharge. This tooth (cube) was defined as the “most sensitive tooth” (MST). Forces were applied to this tooth (cube) in the six stimulation directions to examine the directional sensitivity of the afferent. If the recording was still stable after the completion of the directional sensitivity test of the MST, the responses when stimulating adjacent teeth were obtained. Thus for afferents that were kept isolated for the whole protocol, each of the four cubes was loaded in four horizontal directions (lingual, facial, mesial, and distal) and two axial directions (down and up); i.e., in total 24 stimulus sites. For the first molar, data were collected when each of two cubes (the mesial and distal) were loaded separately. However, in the analysis of the directional sensitivity of the MST and of the responses to loading of adjacent teeth, only the cube that gave the strongest response was considered. To test whether afferents responding to tooth loads also respond to mechanical stimulation of the gingiva, a hand-held dental probe was used to produce gentle indentations of the gingiva surrounding the examined teeth.

The temporal profile of the stimulus consisted of a force increase, a static phase (2.0 ± 0.3 s; mean ± SD), and a force decrease back to zero force. On average, the amplitude of the load force plateau during the static phase was 252 ± 24 mN; the force profile was maintained via visual feedback provided to the experimenter via a computer screen. For each cube, a single stimulation sequence included one force application in each of the six directions. The minimal interval between stimuli was 2 s. Two to five such sequences were delivered to each cube, and the order of directions tested was varied within the sequences.

Data collection and processing

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). Individual action potentials were identified off-line using previously described algorithms (Edin et al. 1988). 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.

The static afferent response was defined as the mean firing rate during the period starting 0.5 s after the end of the loading ramp and ending during the unloading ramp when the force had dropped to 90% of the plateau level (duration: 1.5 ± 0.3 s). The spontaneous afferent discharge was assessed during the 2- to 5-s period prior to the application of the first stimuli in the sequence. For each afferent, the static responses were averaged for all force applications in a given direction and cube.

In addition to linear regression analysis (least-squares fit), nonparametric statistics were used as detailed in the Results section (Siegel and Castellan 1988). Mardia-Watson-Wheeler and Rayleigh tests were used for comparison of vector data (Batschelet 1981). A P value
RESULTS

Single-unit recordings were obtained from 45 mechanoreceptive afferents in response to forces applied to three adjacent teeth: the first premolar, the second premolar, and the first molar on the recording side. None of the afferents responded to gentle probing of the gingiva, suggesting that the present results are based on signals originating from periodontal receptors. For each afferent, stimulation of one of the teeth (the MST) was found to excite the afferent most strongly. The first premolar, the second premolar, and the first molar were the MSTs of 23, 13, and 9 of the afferents, respectively (Fig. 1). All afferents showed a continuous slowly adapting response during the entire static phase of stimulation in at least one of the stimulus directions. Twenty-nine of the afferents (64%) were spontaneously active in the sense that they showed an on-going discharge (8.6 ± 3 imp/s) without any external forces applied to the teeth. As can be seen in Fig. 1, the proportion of spontaneously active afferents decreased from the first premolar (74%) to the second premolar (62%), and the first molar (44%).

Figure 2A shows a set of responses from a single afferent to forces applied to the first premolar, second premolar and the first molar (mesial and distal cube) in each of the six stimulation directions. The direction and magnitude of the applied forces are illustrated as vectors in Fig. 2B. Figure 2C gives the static excitatory responses to the various stimulation directions.
The response was strongest when the first premolar was loaded in the downward direction; this tooth was thereby defined as the MST. Smaller responses were elicited when the second premolar and the first molar were loaded.

**Directional sensitivity to forces applied to the MST**

**STIMULATION DIRECTIONS ELICITING STATIC RESPONSES.** When loading the MST, the afferents typically showed excitatory responses in two to four of the six stimulation directions (on average: 2.9 ± 1.0 directions; see examples in Fig. 2 and 3). No difference in this respect was found between the afferent populations for the different teeth (P > 0.3, Kruskal-Wallis).

All but one afferent (98%) responded to horizontally applied forces. In the horizontal plane, 9, 21, and 14 afferents showed responses in one, two and three directions, respectively. No afferent responded to loading in all four horizontal stimulus directions. In the vertical directions of the tooth, 38 afferents (84%) showed responses in one of the two directions. One afferent responded to forces applied in both directions (see Fig. 3C), and six afferents showed no discharge at all in the vertical directions.

**STIMULATION DIRECTION PROVIDING THE STRONGEST STATIC RESPONSES.** Figure 4A illustrates the distribution of the afferent sample with regard to the stimulation direction that evoked the strongest afferent response. The three diagrams present data from the first premolar, the second premolar, and the first molar, respectively. A clear difference in the distribution can be seen between the three teeth. For the first premolar, second premolar, and first molar, the strongest responses were evoked for most afferents by downward, mesial, and lingual loading, respectively. The relative frequency of afferents showing their maximal response in the down direction decreased from the first premolar (35%) to the second premolar (15%) and the first molar (0%). None of the afferents showed their maximal response in the upward direction. The static response rate in the most sensitive stimulation direction was 17.7±10.7 imp/s and was not significantly different for different directions or teeth (P > 0.6, Kruskal-Wallis).

**PREFERRED DIRECTIONS.** Vectorial addition of the vectors representing excitatory responses was used to estimate the force direction that would excite the afferent most effectively. The direction of the resultant vector was termed the preferred direction (see Trulsson et al. 1992). The preferred directions (in the horizontal plane) for the afferents illustrated in Figs. 2C and 3 are indicated by heavy arrows. Figure 4B displays the preferred directions for the afferent populations at the first premolar (n = 23), the second premolar (n = 13), and the first molar (n = 9) projected onto the horizontal plane, the frontal and sagittal planes, respectively. Solid vectors refer to afferents showing their strongest responses in one of the directions represented in the plane. Dashed vectors refer to afferents with the strongest responses in another plane. The heavy arrows, termed population vectors, are derived from a summation of all preferred directions in that plane. Note that the population vectors are only shown when a significant directional bias is present in the afferent sample (i.e., P < 0.05, Rayleigh). A and B: the graphs illustrate the afferents at the 1st premolar (n = 23), the 2nd premolar (n = 13), and the 1st molar (n = 9), respectively.
The preferred directions of the afferents at the first and second premolar showed a quite even distribution in the horizontal plane \((P > 0.05, \text{Rayleigh})\) and a clear bias downward in the vertical plane (note the population vectors directed downward; \(P < 0.05–0.001\)). For the afferents at the first molar, however, the picture was somewhat different: in the horizontal plane, the preferred directions were significantly biased in the distal-lingual direction \((P < 0.01, \text{Rayleigh})\). In the frontal and the sagittal planes, a directional bias was seen in the lingual and the distal directions, respectively \((P < 0.05–0.01)\).

A comparison of the distribution of the preferred directions between different teeth in each plane revealed the following: in the horizontal and the frontal planes, the distributions of preferred directions at the first premolar were significantly different from the distributions at the first molar \((P < 0.01, \text{Mardia-Watson-Wheeler})\). In the sagittal plane, the distribution of preferred directions at the second premolar was found different from the distribution at the first molar \((P < 0.05, \text{Mardia-Watson-Wheeler})\).

**Population responses.** Figure 5A displays the relative frequency of afferents showing excitatory responses in the various stimulation directions. The top three rows display the afferents at the first premolar \((n = 23)\), second premolar \((n = 13)\), and first molar \((n = 9)\), respectively. A comparison between the different teeth for each direction revealed no statistically significant differences between teeth \((P > 0.05, \chi^2)\). There was, however, an obvious dissimilarity between the premolars and the molar. For the premolars, stimulation in any of the horizontal directions activated close to half \((35–69\%)\) of all afferents. For the molar, forces in the distal and lingual directions activated 100 and 78% of the afferents, respectively. In the downward direction, the relative frequency of afferents showing a response decreased from 91% for the first premolar, 77% for the second premolar to 67% for the molar.

Figure 5B summarizes the responses of the afferents showing excitatory responses to static forces applied to the three different teeth in each of the six stimulation directions. If considering all excitatory responses in any of the six directions for each tooth (see Fig. 5B, right), the response was significantly different between teeth \((P = 0.01, \text{Kruskal-Wallis})\). The afferents from the first premolar showed a stronger response compared with the second premolar \((P < 0.05)\) and the first molar \((P < 0.01, \text{Mann-Whitney})\). A comparison between the different teeth for each stimulus direction showed a significant decrease in the response only in the down direction \((P < 0.01, \text{Kruskal-Wallis})\). In the down direction, the afferents from the first premolar showed a stronger response compared with the second premolar \((P < 0.05)\) and the first molar \((P < 0.01, \text{Mann-Whitney})\).

**Afferent responses to loading of teeth adjacent to the MST**

Of the 45 afferents tested to loading of the MST, 35 were also tested to forces applied to all involved teeth, i.e., the first premolar, the second premolar, and the first molar. Eighteen, 12, and 5 of these afferents responded to loading of one, two and three teeth, respectively. Thus about half of the tested afferent \((17/35)\) responded to stimulation of more than one tooth. Examples of afferents showing multiple-tooth receptive fields are shown in Fig. 2 and Fig. 3. A, C, and D. A common feature of all these afferents is that the crowns of the involved teeth were adjacent and in mechanical contact.

**Stimulation sites and directions eliciting static responses.** The number of activated afferents falls off rapidly with the distance from the MST. Less than half of the tested afferents responded when forces were applied to the first adjacent tooth. Furthermore, not one of the nine afferents tested at the second adjacent tooth in the mesial location responded. That is, afferents with the first molar as the MST never responded to loading of the first premolar.

**Fig. 5.** A: percentage of afferents showing excitatory responses when loading the MST in the 6 different directions. B: magnitude of responses obtained in the various stimulation directions. Columns show the median value and the horizontal bars indicate the 25th and the 75th percentile and the range. The single columns to the right gives values for all directions (All) for the respective tooth. A and B, top to bottom: graphs show data for the 1st premolar \((n = 23)\), the 2nd premolar \((n = 13)\), and the 1st molar \((n = 9)\), respectively.
For the afferents showing multiple-tooth receptive fields, the number of horizontal stimulation directions (i.e., 4 tested directions) exhibiting static excitatory responses was similar for the MST (1.8 ± 0.7) and the adjacent teeth (1.7 ± 0.6; Mann-Whitney, P > 0.5). For the MST, there was no difference in the number for afferents responding to stimulation of more than one tooth and afferents responding to stimulation of only the MST (2.0 ± 0.8; P > 0.3, Mann-Whitney).

**Stimulation directions providing the strongest responses.**

Figure 6A illustrates the horizontal stimulus direction that evoked the strongest afferent response when stimulating the adjacent mesial (Me) teeth, the MST and the adjacent distal (Di) teeth, respectively. For the MST, the afferents were approximately evenly distributed with respect to directional preferences. For the adjacent teeth, however, there were pronounced directional preferences. For the teeth mesial to the MST, most afferents showed their strongest responses to distal and lingual loading. In contrast, for the teeth distal to the MST most afferents exhibited their strongest responses in the mesial direction. Thus when adjacent teeth were stimulated most afferents responded most strongly when the stimulus direction was toward the MST, i.e., when the MST was pushed by the adjacent teeth.

For the multiple-tooth afferents, the static firing rate in the most sensitive stimulation direction was significantly lower for the adjacent teeth (7.1 ± 5.3 imp/s) than for the MST (19.4 ± 8.9 imp/s; P < 0.001, Mann-Whitney). For all afferents, there was a gradual decline in the response strength with distance from the MST (see examples in Figs. 2 and 3). On loading the MST, the afferents responding to only this one tooth showed a significantly lower firing rate (12.2 ± 6.2 imp/s) in the most sensitive direction than those afferents responding to more than one tooth (P < 0.1, Mann-Whitney).

**Preferred directions for teeth adjacent to the MST.** Figure 6B shows the preferred directions in the horizontal plane for all multiple-tooth afferents when loading the MST (middle) and the first adjacent tooth in the mesial location (left) and the distal location (right), respectively. For the MST, the preferred directions were evenly distributed around the circumference of the tooth (P > 0.05, Rayleigh). For the first adjacent tooth in the mesial (Me1) or distal (Di1) location from the MST, the preferred directions were biased toward the location of the MST (Me1 P = 0.03; Di1 P = 0.01, Rayleigh). More specifically, 6 of 7 afferents for loads to Me1, and 9 of 10 for loads to Di1, had a preferred direction component pointing toward the MST. Only one afferent each for the first adjacent teeth exhibited preferred directions that pointed away from the MST.

**Afferent responses to loading of two different sites at the molar.**

Fourteen afferents showed static excitatory responses to loading of the first molar. All of these responded to loading of both the mesial and the distal cube attached to the tooth. Four and five of the afferents showed their strongest responses to loading of the mesial and distal sites on the molar, respectively. Thus the molar was the MST for 9 of the 14 afferents. Five afferents responded most vigorously to loading of the first premolar.

For half of the afferents (7/14), the number of stimulation directions (of the 6 directions tested) eliciting a static response differed for the mesial and the distal stimulation sites (see examples in Figs. 2 and 3, C and D). On average, however, the number of directions evoking a static response was identical for the two sites (2.3 ± 1.2 directions; P > 0.9, Wilcoxon).

For all afferents except one, the direction for maximal excitation was the same for the mesial and distal stimulation sites. The static response rate in the most sensitive stimulation direction was 10.6 ± 7.3 imp/s and was not significantly different for the two sites (P > 0.7, Wilcoxon).

Figure 7A shows the preferred directions in the horizontal plane at the mesial and distal stimulus sites for all afferents responding to loading of the first molar. When all afferents were considered, no directional bias was observed for the preferred directions at the mesial or the distal stimulus sites (P > 0.05, Rayleigh), and no difference was found in the distribution of preferred directions at the two sites (P > 0.9, Mardia-Watson-Wheeler). Interestingly, the afferents with the molar as the MST (n = 9; solid arrows in Fig. 7A; also cf. Fig. 4B, bottom left) showed a clear directional bias in the distal-lingual direction, whereas all afferents with a premolar as the MST...
In the present experiments, the exact site of termination of the afferent under study was not known. There are, however, strong reasons to believe that the afferents supplied mechanoreceptors located in the periodontal ligaments of the premolar and molar teeth. First, all afferents were specific for tooth loading, i.e., none of the afferents responded to gentle probing of tissues surrounding the tooth. Second, other afferents that were observed during the experiments and responded to mechanical stimulation of gingiva or other intraoral tissues were not sensitive to tooth loading (cf. Trulsson 1993 and Trulsson and Johansson 1996). Thus for each periodontal afferent, the tooth defined as the MST was considered to be the receptor-bearing tooth (Trulsson et al., 1992).

In these experiments, the first premolar was the MST for the highest number of afferents followed by the second premolar and the first molar (see Fig. 1), indicating a decreasing innervation of the periodontal ligaments distally along the dental arch. During the search for single-unit recordings, care was taken to stimulate all test teeth to the same extent. Thus it is unlikely that the unit sample suffers significant bias toward particular teeth. These results are in line with our earlier studies on the anterior teeth in which the central incisor was the MST for the highest number of afferents followed by the canine, the lateral incisor and the first premolar (cf. Fig. 2A in Trulsson and Johansson 1996). Moreover, 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 with anterior teeth. Thus even if the size of many of the teeth (and their periodontal ligaments) increase distally along the dental arch the number of periodontal receptors seem to decrease. This finding emphasizes the importance of a well-developed mechanoreceptive innervation of the anterior part of the mouth. The front teeth are involved in initial stages of food intake when morsels are manipulated, split into smaller pieces, and moved into the mouth. Sometimes the front teeth are even used as a “third hand” in manipulative tasks or as a precision cutting tool. These tasks most likely rely heavily on sensory information as those involving the densely innervated fingertips of the hand (Johansson and Vallbo 1983).

**Basic discharge characteristics of periodontal afferents from posterior teeth**

The receptive field properties of periodontal afferents responding to forces applied to human incisors and canines have been described earlier (Trulsson 1993; Trulsson and Johansson 1996; Trulsson et al. 1992). The present experiments on postcanine teeth were designed in a similar way to allow comparison between anterior and posterior teeth. As expected, the
Basic discharge characteristics were found to be similar for afferents supplying different types of teeth: all afferents showed a slowly adapting response to loading of the MST (at least in 1 stimulus direction), and a high proportion of the afferents were spontaneously active. The response characteristics are similar to that of the Ruffini endings (SA II) described in the skin (Chambers et al. 1972; Knibestål and Vallbo 1970). Indeed, Ruffini-like nerve endings have been observed in close relation to collagen fibers in the periodontal ligaments of both anterior and posterior teeth in several types of species (Byers 1985; Byres and Dong 1989; Sato et al. 1988; Schulze et al. 1993), including man (Lambrichts 1992; Maeda et al. 1990).

Interestingly, the fraction of spontaneously active afferents seem to decrease from the anterior teeth (71%) (Trulsson and Johansson 1996) and the first premolar (74%) to the second premolar (62%) and the first molar (44%). Hannam (1969) suggested that the spontaneous discharge in periodontal afferents is due to a sustained tension in the periodontal ligament. If this is correct, it would imply that the tension in the collagen fibers in the periodontal ligament of anterior teeth is higher, or more variable, compared with the posterior teeth.

"Multiple-tooth" receptive fields

In the present study, about one half (17/35) of the periodontal afferents from the posterior teeth responded to stimulation of more than one tooth. A common feature of all "multiple-tooth" afferents was that the involved teeth were adjacent and their crowns were in mechanical contact. All afferents showed their highest response rate when stimulating the MST with a gradual decline in the response when loading the adjacent teeth. As such, these results match our earlier findings on anterior teeth in humans (Trulsson 1993) and indicate that the extended receptive fields are generated by mechanical coupling between neighboring teeth rather than by branching of single afferents to more than one tooth (Hannam 1970; Tabata and Karita 1986). For the teeth bordering the MST, the preferred directions were biased toward the MST (see Fig. 6B), indicating that most afferents (15/17) were activated when the MST was pushed by the adjacent teeth. Interestingly, two afferents (2/17) exhibited preferred directions opposite to the MST, implying that the MST was pulled by the adjacent teeth. Thus both interdental contacts between tooth crowns and the transseptal fiber system may be involved in the mechanical coupling generating "multiple-tooth" receptive fields (Trulsson 1993; but see Tabata et al. 1995).

The present results on multiple-tooth afferents from posterior teeth are in sharp contrast the information available from animal experiments. In the cat and rat, only 5% of the periodontal afferents respond to loading of more than one tooth. For the cat, the receptive fields of the multiple-tooth afferents are observed mainly at the incisor teeth, whereas for the rat they are restricted to the molars (Tabata and Hayashi 1994; Tabata and Karita 1986). Most likely, these dissimilarities can be attributed to the different anatomical arrangements of the teeth in the two species. In contrast to the cat, the rat has no canines or premolar teeth, and its incisors are located far away from the molars. Likewise, the different anatomy of the human dentition is probably the reason for the different results obtained in animals and humans.

Considering the human first molar, the afferent responses in the present experiments were remarkably similar when loading the two stimulus sites at the tooth. Both the intensity and the directional sensitivity of the afferent response when loading one side of the tooth was preserved to a great extent when loading the other side. The population of periodontal afferents with the molar as the MST showed a strong directional bias in the distal-lingual direction (see Figs. 4B and 7A). This extreme directional bias could possibly hamper the ability of the CNS to encode the direction of forces striking the tooth in other directions. However, the afferents responding to loading of the molar, but with a neighboring tooth as the MST, showed a strong directional bias in the mesial direction. Thus the lack of sensitivity in the mesial direction for periodontal receptors at the molar is compensated for by receptors at other teeth, emphasizing the view that information from a single tooth cannot be interpreted in isolation. Rather the multiple-teeth sensitivity profiles of the receptive fields for many periodontal afferents is most likely an advantage for the capacity to encode both directional and intensive aspects of forces acting on teeth (Edin and Trulsson 1992; Trulsson 1993).

Directional sensitivity of periodontal afferents innervating different types of teeth

An exquisite sensitivity to changes in the direction of tooth loads is common for all human periodontal afferents. However, the present experiments also show that periodontal afferents supplying anterior and posterior teeth differ in their capacity to signal horizontal and vertical forces, respectively. For the afferents from the incisors and canines, the preferred directions in the horizontal plane are distribution around the circumference of the tooth showing some bias toward the lingual and the labial directions (see Fig. 3C in Trulsson et al. 1992). A somewhat similar distribution, without any obvious directional bias, was found for the preferred directions of the afferents from the premolars. A clearly different distribution, however, was found for the afferents from the first molar, showing a significant bias in the distal-lingual direction (see Fig. 4B, bottom left).

The responsiveness to vertically directed forces is clearly higher for afferents from anterior teeth compared with afferents from posterior teeth (Trulsson et al. 1992). If considering only the upward-directed forces, only two afferents (4%) at the posterior teeth responded. This is in sharp contrast to the anterior teeth showing excitatory responses to upward-directed forces in about 50% of the afferents (Trulsson et al. 1992). The low sensitivity to upward-directed forces for premolars and molars becomes evident in Fig. 4B (middle and right) showing an upward-directed response component only for two afferents at the first premolar. For comparison with afferents from the incisors and canines see, Fig. 3C in Trulsson et al. (1992).

The distribution of the preferred directions in Fig. 4B also nicely displays the diminishing sensitivity to downward-directed forces from the first premolar to the molar. Note how the resultant vectors (heavy arrows) gradually move from a downward direction for the first premolar to a more horizontal direction for the molar. The decreasing sensitivity of periodontal afferents to downward-directed forces distally along the dental arch is a result of both a lower
fraction of activated afferents and a lower firing rate in these afferents.

The shift from a high sensitivity in most directions for the receptor population at the anterior teeth to a more restricted sensitivity profile for the receptors at the molars may reflect the unique functions of the different types of teeth. As discussed earlier, the front teeth are involved in initial stages of food intake when morsels are manipulated, split into pieces, and transported into the mouth. The main function of the molars, on the other hand, is to grind the food during forceful chewing. Interestingly, studies on tooth displacement during oral function indicate that the lower first molar tilts in a lingual direction during clenching and biting (Miura 1998; Siebert 1981). Hence, the directional bias of the afferents at the molar may very well reflect a functional adaptation to the load forces that normally act on the tooth.

Periodontal afferent signals in the spatial control of mastication

During chewing, when food particles are ground into smaller pieces, strong axial and, in particular, horizontal forces are exerted onto the premolar and molar teeth. The periodontal receptors at premolars and molars are well suited to encode in detail the temporal and spatial changes of these tooth loads. Most likely, signals from periodontal receptors play a role in biasing the excitability of relevant elements of the motor- and/or pre-motoneuron pools such that the jaw-closing action spatially match the current contact pattern between the food and the dentition. Such a mechanism, working on a moment-to-moment basis, would necessarily take into account the direction of the contact forces at individual teeth and their changes. Indeed, to efficiently handle food, activation of the jaw muscles must be coordinated to produce jaw actions that are spatially adapted to the food’s distribution in relation to the teeth. During mastication, the spatial information provided by the periodontal receptors at the time of initial contact between the food particles and individual teeth may also contribute to an early predictive parameterization of the jaw action vector (Trulsson and Johansson 1996). Accordingly, dyssynchronization in chewing has been observed after denervation of intraoral receptors including periodontal receptors. The absence of sensory input results in reduced masticatory force and distorted spatial control of jaw movements during chewing (Inoue et al. 1989; Lavigne et al. 1987).

In an upcoming study on periodontal afferents from premolars and molars, we will describe the afferent encoding of amplitude and rate of tooth loads and discuss their role in the intensive control of mastication.

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