Encoding of Amplitude and Rate of Tooth Loads by Human Periodontal Afferents From Premolar and Molar Teeth

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Johnsen, Skjalg E. and Mats Trulsson. Encoding of amplitude and rate of tooth loads by human periodontal afferents from premolar and molar teeth. J Neurophysiol 93: 1889–1897, 2005. First published November 24, 2004; doi:10.1152/jn.00664.2004. Microneurographic recordings were obtained from 20 periodontal mechanoreceptive afferents in the inferior alveolar nerve while force profiles of different amplitudes and rates were applied to a premolar or the first molar in the most sensitive direction. The majority of afferents (17/20) showed a hyperbolic relationship between the steady-state discharge rate and the amplitude of the stimulating force, featuring a pronounced saturation tendency. These afferents were also characterized by a similar decline in dynamic sensitivity with increasing amplitude of background force. However, a few afferents (3/20) showed nearly linear stimulus-response relationships and a small decline in dynamic sensitivity with increasing tooth load. Quantitative models developed for all afferents successfully predicted the afferent discharge rates for novel force stimulations. Application of the transfer function to chewing forces predicted that the discharge rates of periodontal afferents rapidly increased at initial tooth contact and continued to discharge as long as the tooth was loaded. However, due to the marked saturation tendencies at higher forces, most periodontal afferents poorly encoded the magnitude of the strong chewing forces. In addition, the discharge rates of a minority of afferents continued to reflect the force profile during high chewing forces. The results revealed that periodontal afferents of posterior teeth were less sensitive at low tooth loads compared with afferents of anterior teeth. During each chewing cycle, periodontal afferents may provide information about the mechanical properties of food shortly after tooth contact that can be used to scale the muscle commands of the upcoming power phase.

INTRODUCTION

Periodontal mechanoreceptors signal information about tooth loads to the CNS. The nerve endings, often described as Ruffini-like, are located close to the collagen fibers in the periodontal ligament, anchoring the root of the tooth to the jawbone (Byers 1985). The force encoding properties of the periodontal afferents innervating the lower front teeth in humans have been described earlier (see Trulsson and Johansson 1996b). All human periodontal afferents of anterior teeth were found to adapt slowly to maintained tooth loads. Populations of periodontal afferents encode information about which teeth are loaded and the direction of forces applied to individual teeth (Trulsson 1993; Trulsson et al. 1992). Moreover, information about the magnitude of steady forces is made available in the mean firing-rate response of the afferents (Trulsson and Johansson 1994). Most afferents responding to loading of the front teeth in humans, exhibit a marked “hyperbolic” relationship between the static discharge rate and the force amplitude; the highest sensitivity to changes in static force is observed at forces <1 N. Similarly, the dynamic sensitivity is highest at low forces. Based on this data, a quantitative model for periodontal afferent responses was developed that successfully represented both the static and the dynamic response properties (Trulsson and Johansson 1994). Application of the quantitative model on recorded force profiles, obtained when subjects used their incisors to hold and split food particles, show that periodontal afferents efficiently encode food contact during biting and continuously discharge while food is held between the incisors (Trulsson and Johansson 1995). Subjects spontaneously exert low contact forces matched to the sensitivity characteristics of these periodontal afferents when holding food substances between the incisors (Trulsson and Johansson 1996a). If periodontal afferent information is not available (e.g., after administration of dental anesthesia), the control of hold forces is severely impaired. Because only a few afferents encode information about the rapid and strong force increase employed to bite through food, it was concluded that subjects rely on signals from periodontal afferents to regulate the jaw muscles primarily when they first contact, manipulate and hold food substances between the incisors (Trulsson and Johansson 1996b).

The posterior teeth, the premolars and molars, are substantially different from the front teeth. In general, they are larger and often supported by more than one root. While front teeth are used during initial food intake, when morsels are manipulated, split into smaller pieces and transported into the mouth, the posterior teeth are used during rhythmic chewing when strong axial and horizontal forces are produced by the jaw muscles to grind the food. Considering the different form and function of anterior and posterior teeth it cannot be excluded that the periodontal afferents innervating the different types of teeth are functionally different. A recent study from our laboratory has demonstrated that the receptive field properties of human periodontal afferents of anterior and posterior teeth are similar; the afferents often respond to loading of more than one tooth and are broadly tuned to the direction of tooth loading. However, analyses of the population responses made it clear that periodontal afferents supplying anterior and posterior teeth differ in their capacity to signal horizontal and vertical forces (Johnsen and Trulsson 2003a).

Very little is known about the encoding of force intensity by periodontal afferents from posterior teeth (Johansson and Ols-
son 1976; Trulsson and Johansson 1996b). Thus the purpose of the present study was to analyze the encoding of force amplitude and rate by human periodontal afferents of posterior teeth. A second goal of this study was to model the discharge rates of periodontal afferents of posterior teeth (see Trulsson and Johansson 1994) and to use the transfer functions to predict the afferent responses during chewing. An abstract of preliminary results has been published previously (Johnsen and Trulsson 2003b).

METHODS

Subjects and recording procedure

The results presented in this paper are based on data obtained from four female volunteers (ages 20–24) who participated in one or more recording sessions. The subjects were in good general health with no history of neurological disorders. At the time of the experiment, they showed no clinical signs or symptoms of any oral problem or orofacial malfunction. The teeth that were included in the study were free of dental restorations, showed normal relations to antagonistic teeth, exhibited no periodontal breakdown, and had not been exposed to any endodontic, prosthetic, or orthodontic treatment. All subjects signed informed consent and the study was approved by the Human Ethics Committee, Karolinska Institute. Subjects were comfortably seated in a dental chair in a semi-recumbent position. 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. Single-unit impulses were recorded from mecanoreceptive afferents in the human inferior alveolar nerve with the use of a coated tungsten needle electrode (Valibo and Hagbarth 1968). The impedance of the electrode was 100–400 kΩ measured in situ at 1 kHz. The nerve was approached intraorally and impaled near its entrance to the mandibular foramen (Johansson and Olsson 1976; Trulsson et al. 1992). The tooth that gave the strongest discharge when mechanically stimulated (stimulation force: 0.5–1 N) was defined as the “receptor bearing tooth” (cf. Trulsson 1993).

Mechanical stimulation

Forces were applied manually to the teeth via a probe equipped with force transducers (DC-200 Hz). The probe terminated in a small nylon sphere (1 mm diam). At the beginning of every recording session, four nylon cubes (3 mm side) mounted on copper attachments were affixed 1 mm above the cusp tips of the premolars and the first molar on the recording side (Johnsen and Trulsson 2003a). On the premolars, the cubes were centered over the crown of the tooth. On the first molar, two cubes were centered over the mesial and the distal half of the crown, respectively. One face of the cube was oriented perpendicular to the long axis of the root, and four faces were oriented perpendicular to the lingual, facial, mesial, and distal direction, respectively. For stimulus delivery, the probe was applied normal to the five free faces of the nylon cube. In addition, the four cubes were equipped with nylon loops allowing delivery of upwardly directed forces (Trulsson et al. 1992). Stimulation was applied to the receptor bearing tooth (the cube that gave the strongest response) in the direction that evoked the greatest discharge activity: lingual, facial, mesial, distal, downward, or upward.

The temporal profile of the applied force consisted of a loading ramp (force increase), a static phase (2.1 ± 0.4 s; mean ± SD), and an unloading ramp (force decrease) back to zero force. Visual feedback to the experimenter via a computer screen assisted the experimenter in delivering force profiles with the desired characteristics. One stimulation sequence generally included 8–10 force applications attaining different static phase force amplitudes (range: 0.1–5 N). One or two such sequences were delivered for each afferent. The force rates achieved during the loading ramp ranged between 0.6 and 81 N/s (peak force rate) and correlated with the force amplitude during the static phase ($r = 0.96$, $P < 0.001$; Spearman rank correlation analysis). In addition, more complex force profiles were used to stimulate some of the afferents. The experimenter applied force profiles similar to those generated by subjects instructed to split/crush half a peanut after holding it between a pair of premolars for a few seconds (“hold and split task”) (Johnsen et al. 2004; Trulsson and Johansson 1996a) as well as force profiles mimicking the forces that are developed during chewing of food (De Boever et al. 1978). Before the neural recordings, the experimenter learned to approximately reproduce these force profiles. Again, visual feedback was provided via a computer screen. For each afferent, the experimenter delivered ten force profiles to simulate the hold and split forces and the chewing forces, respectively. The minimal interval between stimuli was 2 s.

Data collection and processing

The nerve and force signals were sampled at 12.8 kHz and 800 Hz, respectively (12-bit 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.

For each force application, the steady-state response was defined as the mean discharge rate during a 1-s period starting 0.5 s after the end of the loading ramp. The steady-state force was defined as the mean applied force during the same period. For spontaneously discharging afferents, the mean discharge rate of the background activity was assessed during a 1-s period before each force application. Reported means ± SD are point estimates of data pooled from all subjects. Non parametric statistics were used as detailed in RESULTS (Siegel and Castellan 1988); $P < 0.05$ was considered statistically significant.

RESULTS

The relationship between amplitude and rate of forces applied to the teeth and the evoked afferent responses were analyzed for 20 periodontal mechanoreceptive afferents. The receptor bearing tooth was the first premolar for 13, the second premolar for 4, and the first molar (distal cube) for 3. The afferents most likely originated in the periodontal ligament because gentle probing of the gingiva surrounding the responsive teeth was ineffective in evoking afferent responses. The direction of stimulation that produced the greatest afferent responses was down for seven afferents, lingual and buccal for four afferents each, mesial for three, and distal for two afferents. All analyses of the force encoding properties of the afferents were based on stimulation in the most responsive direction. All afferents were slowly adapting (cf. Trulsson and Johansson 1996b), and a majority (14/20) showed an ongoing discharge in the absence of any external force applied to the teeth, i.e., they were spontaneously active.

Encoding of steady-state forces

Figure 1A shows examples of responses in a single afferent to forces of three different amplitudes applied to a first premolar, and B demonstrates the relationship between the steady-state force and the steady-state response for three representa-
The parameters $a$, $b$, and $c$ were determined for each afferent by an iterative procedure. The parameter $c$ was iteratively varied, and for each $c$ value, $a$ and $b$ were estimated by linear regression; the fit was optimized by maximizing the resultant correlation coefficient ($r$). The parameter $a$ (median 5.1, range, $-13-18$) essentially represents the ongoing discharge rate at zero force for spontaneously active afferents (negative values for non-spontaneously active afferents is related to various factors such as the threshold force). The parameter $b$ represents an estimate of the maximum increase in discharge rate that could be evoked by steady-state force stimulation (median: 76, range: $29-104$); and $c$, the force amplitude generating one-half this maximum rate (Fig. 2D; Table 1). As such, the parameter $c$ describes the curvature of the stimulus-response function; the three afferents showing “nearly linear” stimulus-response relationships were all characterized by high values of $c$ (Fig. 2D).

Responses to forces applied in directions other than in the most responsive one were also obtained and analyzed for two of the afferents that showed hyperbolic stimulus-response relationships (Johnsen and Trulsson 2003a). For each of these afferents, although they also exhibited some saturation tendency. All afferents except one showed a correlation coefficient $>0.94$ (Fig. 2B). Figure 2C illustrates the mean value (black solid curve) $\pm 1$ SD (black dashed curves) of all afferents shown in A. For comparison, the gray curves show corresponding data from periodontal afferents of anterior teeth (data extracted from Trulsson and Johansson 1994).

Trulsson and Johansson (1994) tested several theoretical functions for describing the stimulus-response relationships of mechanoreceptors at anterior teeth. Various versions of linear, power, logarithmic, exponential, and hyperbolic log tangent functions (cf. Chambers et al. 1972; Knibestol 1975; Kruger and Kenton 1973; Pubols and Pubols 1976; Werner and Mountcastle 1965) were also tested on the data of the present study. Several nonlinear functions with three or more parameters showed reasonably good fits for most of the afferents. However, the function finally chosen by Trulsson and Johansson (1994) on the data from anterior teeth also showed the best fit for the data from posterior teeth. Thus we chose the following function with three parameters to describe the stimulus-response relationships for all afferents

$$R_s = a + bF/(F + c) \quad (1)$$

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. The function described by Eq. 1 provided the best fit as determined by correlation coefficients as well as by visual inspection. As a further argument for its use, the function is consistent with a simple mechanical model of the periodontal ligament (see Trulsson and Johansson 1994).

FIG. 1. Responses of periodontal afferents to steady-state forces of various amplitudes applied to the receptor-bearing tooth in the direction that gave the greatest response. A: examples of force stimulation and nerve recordings of a single afferent during application of 3 different force amplitudes to a 1st premolar. The period during which the steady-state response and steady-state force was measured is marked by the time bar. B: stimulus-response relationship for 3 afferents (a–c). The curves fitted to the data are defined by Eq. 1 (in text), and the corresponding correlation coefficients ($r$) are given to the right of each curve. $c$ (curve a and b), the $c$ parameter (abscissa value) and the estimated half-maximum discharge rate (ordinate value). Due to a high $c$ value there is no $c$ in curve c. For afferents a–c, the $c$ parameter was 4.08, 1.02, and 23.16, respectively.

FIG. 2. A: steady-state stimulus-response functions for 20 periodontal afferents. Curves fitted to experimental data as for Fig. 1B. Solid and dashed curves, afferents showing a hyperbolic stimulus response function ($n = 17$) and a nearly linear function ($n = 3$), respectively. B: distribution of correlation coefficients ($r$) for all afferents ($n = 20$). C: mean value for all steady-state stimulus-response functions. Black solid and dashed lines, the means $\pm 1$ SD of all stimulus response functions shown in A. Gray solid and dashed lines, the means $\pm 1$ SD of corresponding data from anterior teeth (data extracted from Fig. 2A in Trulsson and Johansson 1994). Note the steeper curve at low force levels for the afferents of anterior teeth indicating a higher sensitivity at low forces compared with the afferents of posterior teeth. D: distribution of the $c$ parameters for all afferents. The heavy and the thin line represent data from posterior and anterior teeth, respectively (data from anterior teeth is extracted from Trulsson and Johansson 1994).
afferents, all stimulus-response relationships were similar to those obtained in the direction that gave the greatest responses, i.e., they showed marked “saturation” tendencies. However, the discharge rates were lower, as if the response intensity was scaled down.

General transfer function describing the force encoding properties

By using multiple linear regression, Trulsson and Johansson (1994) developed a general transfer function for the force encoding properties of human periodontal afferents of anterior teeth. The same transfer function was tested on the present sample and was found to be useful in predicting the temporal profile of the instantaneous discharge rate evoked by arbitrary force profiles applied to a posterior tooth in the most responsive direction. In short, the modeled discharge rate was described as the weighted sum of a static discharge rate component directly related to the amplitude of the force stimulation and a dynamic response component directly related to the rate of force change. The modeled discharge rate is graphically illustrated in Fig. 3 (dashed curve) for force profiles of three different amplitudes (top curve) applied to a first premolar. The static response component was calculated in accord with the stimulus-response relationship described by Eq. 1 and the dynamic response component was estimated by a first-degree high-pass filtering of the same transform.

The following expression fully describes the general transfer function representing the force encoding of the periodontal afferents

\[ R = a + bf + df_{HP} \]

\[ f = F/(F + c) \]

\[ f_{HP}(t) = h[f(t - T) + [f(t) - f(t - T)]] \]

where \( R \) stands for the instantaneous discharge rate, \( F \) for the applied force, and \( a–d \) are parameters. \( f_{HP} \) represents the high-pass filtered \( f \), \( h \) the filter constant, \( T \) the interval between samples, and \( \tau \) the time constant. An iterative algorithm was employed to estimate the time-constant (\( \tau \)) of the high-pass filter that resulted in the best fit (maximum \( r \); see Table 1).

### Table 1. Parameters of general transfer function developed to predict the instantaneous discharge rate of an individual periodontal afferent to forces applied to the receptor bearing tooth in the most sensitive direction

<table>
<thead>
<tr>
<th>Afferent Number</th>
<th>Tooth Direction</th>
<th>( a ), imp/s</th>
<th>( b ), imp/s</th>
<th>( c ), N</th>
<th>( d ), imp/s</th>
<th>( \tau ), ms</th>
<th>( r )</th>
<th>( d/b )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>6 lingual</td>
<td>–1.4</td>
<td>71</td>
<td>0.25</td>
<td>89</td>
<td>156</td>
<td>0.90</td>
<td>1.26</td>
</tr>
<tr>
<td>2</td>
<td>6 lingual</td>
<td>0.5</td>
<td>79</td>
<td>0.37</td>
<td>27</td>
<td>416</td>
<td>0.97</td>
<td>0.34</td>
</tr>
<tr>
<td>3</td>
<td>5 down</td>
<td>3.3</td>
<td>57</td>
<td>0.45</td>
<td>32</td>
<td>624</td>
<td>0.90</td>
<td>0.56</td>
</tr>
<tr>
<td>4</td>
<td>4 lingual</td>
<td>0.9</td>
<td>54</td>
<td>0.55</td>
<td>31</td>
<td>833</td>
<td>0.90</td>
<td>0.57</td>
</tr>
<tr>
<td>5</td>
<td>4 down</td>
<td>4.9</td>
<td>88</td>
<td>0.57</td>
<td>50</td>
<td>416</td>
<td>0.97</td>
<td>0.56</td>
</tr>
<tr>
<td>6</td>
<td>4 down</td>
<td>14.7</td>
<td>24</td>
<td>0.63</td>
<td>13</td>
<td>624</td>
<td>0.92</td>
<td>0.52</td>
</tr>
<tr>
<td>7</td>
<td>4 distal</td>
<td>1.4</td>
<td>87</td>
<td>0.83</td>
<td>87</td>
<td>124</td>
<td>0.97</td>
<td>0.99</td>
</tr>
<tr>
<td>8</td>
<td>4 buccal</td>
<td>4.9</td>
<td>58</td>
<td>1.02</td>
<td>33</td>
<td>624</td>
<td>0.98</td>
<td>0.57</td>
</tr>
<tr>
<td>9</td>
<td>4 down</td>
<td>4.0</td>
<td>67</td>
<td>1.13</td>
<td>36</td>
<td>624</td>
<td>0.95</td>
<td>0.53</td>
</tr>
<tr>
<td>10</td>
<td>4 down</td>
<td>1.5</td>
<td>49</td>
<td>1.27</td>
<td>59</td>
<td>249</td>
<td>0.96</td>
<td>1.20</td>
</tr>
<tr>
<td>11</td>
<td>4 mesial</td>
<td>5.9</td>
<td>59</td>
<td>1.57</td>
<td>29</td>
<td>624</td>
<td>0.97</td>
<td>0.50</td>
</tr>
<tr>
<td>12</td>
<td>4 down</td>
<td>8.8</td>
<td>70</td>
<td>2.39</td>
<td>35</td>
<td>1249</td>
<td>0.98</td>
<td>0.49</td>
</tr>
<tr>
<td>13</td>
<td>4 mesial</td>
<td>2.8</td>
<td>61</td>
<td>2.68</td>
<td>50</td>
<td>312</td>
<td>0.96</td>
<td>0.81</td>
</tr>
<tr>
<td>14</td>
<td>4 buccal</td>
<td>3.1</td>
<td>63</td>
<td>2.95</td>
<td>72</td>
<td>312</td>
<td>0.95</td>
<td>1.14</td>
</tr>
<tr>
<td>15</td>
<td>4 down</td>
<td>7.4</td>
<td>81</td>
<td>3.33</td>
<td>87</td>
<td>249</td>
<td>0.97</td>
<td>1.07</td>
</tr>
<tr>
<td>16</td>
<td>6 buccal</td>
<td>5.9</td>
<td>112</td>
<td>4.08</td>
<td>87</td>
<td>124</td>
<td>0.97</td>
<td>0.77</td>
</tr>
<tr>
<td>17</td>
<td>5 mesial</td>
<td>7.3</td>
<td>62</td>
<td>4.79</td>
<td>47</td>
<td>624</td>
<td>0.96</td>
<td>0.76</td>
</tr>
<tr>
<td>18</td>
<td>5 distal</td>
<td>10.3</td>
<td>86</td>
<td>8.37</td>
<td>51</td>
<td>416</td>
<td>0.98</td>
<td>0.60</td>
</tr>
<tr>
<td>19</td>
<td>4 lingual</td>
<td>13.1</td>
<td>67</td>
<td>17.08</td>
<td>187</td>
<td>624</td>
<td>0.91</td>
<td>2.78</td>
</tr>
<tr>
<td>20</td>
<td>5 buccal</td>
<td>1.9</td>
<td>78</td>
<td>23.16</td>
<td>303</td>
<td>24</td>
<td>0.89</td>
<td>3.87</td>
</tr>
</tbody>
</table>

The discharge rate is calculated as the weighted sum of a static and a dynamic response component according to Eq. 2. Teeth 4–6 are the first premolar, second premolar, and first molar, respectively. The “relative dynamic sensitivity” is represented by \( d/b \).

![Fig. 3](https://via.placeholder.com/150)

**Fig. 3.** Quantitative modeling of instantaneous discharge rate evoked by force profiles applied to a 1st premolar in the direction that gave the greatest responses of the afferent. Example of records (3 single trials) from a spontaneously active afferent showing a hyperbolic stimulus-response relationship (\( c = 1.02 \)). From above, the curves refer to stimulation force, modeled static response component (plus spontaneous activity), modeled dynamic response component, predicted instantaneous discharge rate (---) superimposed on empirically observed instantaneous discharge rate (—), and recorded nerve signal, respectively, as a function of time.
20 periodontal afferents were included in the modeling and the regression values are shown in Table 1. All data obtained with various amplitudes and rates of force (force sampled at 800/s) were used when estimating the parameters of the transfer functions except for a few trials which were deliberately excluded to evaluate the model (see following text). For a more detailed description of the development of the transfer function, see Trulsson and Johansson (1994).

As the parameters $d$ and $b$ represented the gain of dynamic and static discharge response components, respectively, a measure of the relative dynamic sensitivity of each afferent was obtained by the ratio $d/b$ (see Table 1). This index varied across the afferents, ranging from 0.3 to 3.9. Two of the afferents with nearly-linear stimulus response relationships showed the highest ratios (see afferent 19 and 20 in Table 1). Thus a significant positive correlation was found between the relative dynamic sensitivity and the $c$ parameter ($r_c = 0.45, P < 0.05$; Spearman rank correlation analysis). No significant correlation was found between the relative dynamic sensitivity and the $b$ parameter ($r_b = 0.15, P > 0.5$; Spearman), but an inverse correlation was found between the relative dynamic sensitivity and the time constant, $\tau$ ($r_\tau = -0.65, P < 0.002$; Spearman).

Predictive value of the transfer function

For each afferent, the predictive value of the fitted transfer function was assessed. Specifically, the predicted profile of instantaneous discharge rate for two to three randomly selected force stimulations was compared with the empirically observed discharge rates. These trials included different force amplitudes and rates and were excluded during the development of the transfer function. For all afferents ($n = 20$), the model predicted the actual receptor discharge with a high degree of accuracy (correlation coefficients, $0.89 < r < 0.98$).

In addition, for five of the afferents (4 hyperbolic and 1 nearly linear afferent), the predictive value of the model was also tested on more realistic complex loads that differed substantially from the trapezoidally shaped force profiles used in the development of the transfer functions. Figure 4 shows examples of force profiles produced by the experimenter to imitate the forces produced by a subject when holding and splitting a morsel between a pair of premolars ($A$ and $B$) (Johnsen et al. 2004; Trulsson and Johansson 1996a) and when chewing on food ($C$). Figure 4A shows a recording from a nearly linear afferent ($c = 8.37$), and $B$ and $C$ show recordings from two different hyperbolic afferents ($c = 2.39$ and 4.08, respectively). Superimposed on the discharge rates actually observed (---), the - - - in Fig. 4 illustrate the simulated discharge rates (computed for the very same force profiles using the previously developed transfer functions). As shown, they provided an excellent match to the measured discharge rates ($r$ values 0.91–0.96; all 10 trials included for each afferent). The good correspondence indicates that the transfer functions provide an adequate description of the afferent responses even for the more complex loads used by subjects in realistic masticatory tasks.

The more complicated force profiles in Fig. 4, $A$ and $B$, consisting of a steady-state force followed by a strong force pulse, reveal different response characteristics of the nearly-linear and the hyperbolic afferents. The discharge rate of the nearly linear afferent (Fig. 4A) reflects the force profile, both for the steady-state force and the following strong force pulse. However, due to the high static and dynamic sensitivity at low tooth loads, and the parallel decrease in sensitivity at higher loads, the discharge rate of the hyperbolic afferent (Fig. 4B) is relatively high during the steady-state force and weakened during the strong force pulse. Also note the strong initial response of the hyperbolic afferent to the chewing-like force profiles in Fig. 4C. Even though the force is first increasing and then decreasing rapidly the strong initial response is followed by a quite stable saturated response until the force is released from the tooth.

Simulation of periodontal afferent responses to chewing-like force profiles

Figure 5 illustrates simulated afferent responses to force profiles obtained during “chewing” on a rubber-coated force transducer held between the first molars on one side. Ten different force profiles ranging from 3 to 52 N are shown at the top. Below the force trace the simulated time-varying discharge rates of 10 representative afferents are shown. Each horizontal row represents the simulated discharge rate profile for one individual afferent (numbered 1–20 according to Table 1). The steady-state stimulus-response relationships for afferents 1–16 all featured pronounced saturation tendencies (hyperbolic afferents), whereas afferents 19 and 20 showed nearly linear relationships.

Application of the transfer function to these time-varying force profiles predicted that the discharge rates of periodontal...
The afferents rapidly increased at initial tooth contact due to their high static and dynamic sensitivity at low force levels. The afferents continued to discharge as long as the tooth was loaded. However, due to the marked saturation tendencies at higher forces, most afferents (1–16) poorly encoded the magnitude of the strong chewing forces and the force changes occurring at these high loads (also cf. Fig. 4C). The discharge rates of a minority of afferents (19 and 20), however, continued to reflect the force profile reasonably well also during the high chewing forces.

Some of the chewing-like force profiles shown in Fig. 5 were considerably higher compared with the forces used in the development of the models (<15 N; see Fig. 2A). Thus a considerable extrapolation was necessary when using the models on higher chewing forces. Nevertheless, for the following reasons, we still argue that the transfer functions are useful in predicting the instantaneous discharge rates of periodontal afferents in addition to those of higher forces. First the afferents with hyperbolic stimulus-response relationships were anticipated to reach saturation at the higher forces exerted during chewing; the static forces yielding half the estimated maximum steady-state discharge rate were on average only 1.7 N (cf. c parameter in Table 1). Second, the afferents showing the nearly linear stimulus-response relationships would still be partly sensitive to the higher forces and rates encountered during chewing; the force levels at which these afferents attained half their estimated maximum discharge rate during steady loads ranged from 8 to 24 N.

**DISCUSSION**

The present study on human periodontal afferents analyzed the encoding of forces of various amplitudes and rates applied to posterior teeth. A majority of the afferents (17/20) showed a hyperbolic relationship between the steady-state discharge rate and the amplitude of the stimulation force, featuring a pronounced saturation tendency. These afferents were also characterized by a similar decline in dynamic sensitivity with increasing amplitude of background force applied to the tooth. However, a few afferents (3/20) showed nearly linear stimulus-response relationships and a small decline in the dynamic sensitivity with increasing background force.

**Limitations of the study**

In the present experiments, the exact site of termination for the mechanoreceptor under study is not known. However, there are several reasons to believe that the sample of afferents studied supplied receptors located in the periodontal ligament of the teeth (cf. Trulsson and Johansson 1996b). First none of the afferents responded to gentle probing of tissues surrounding the tooth (gingiva, mucosa, etc.), i.e., they were specific for tooth loading (see also Trulsson 1993). Second, other afferents responding to light mechanical stimulation of perioral and intraoral structures, e.g., cutaneous, transitional, or mucosal zone of the lip or the gingiva (cf. Johansson et al. 1988), were not sensitive to tooth loading (Trulsson et al. 1992). Third, their overall response characteristics were very similar to those of the mechanoreceptors definitively shown to terminate in the periodontal ligament of the cat (cf. Cash and Linden 1982; Linden 1990).

The search strategy adopted in these experiments to identify afferent units was optimized for low-threshold mechanoreceptive afferents (cf. Trulsson et al. 1992). Thus other types of afferents that may contribute to dental mechanosensitivity (e.g., high-threshold periodontal afferents and intra-dental afferent) were not studied and will not be further discussed.

**Sensitivity to steady-state forces of periodontal afferents of anterior and posterior teeth**

Except for one recording published by Johansson and Olsson (1976), existing data on the afferent encoding of the magnitude of tooth loads was collected from periodontal afferents supplying the incisors and canines. Recordings in a number of species (Hannam and Farnsworth 1977; Ness 1954; Pfaffmann 1939) including human (Trulsson and Johansson 1994) showed that most periodontal afferents from anterior teeth displayed strongly curved steady-state stimulus-response relationships featuring a gradually decreasing sensitivity to increments in force.

The general shape of the steady-state stimulus-response functions found in the present study was similar to that described for human periodontal afferents of anterior teeth (Trulsson and Johansson 1994). Thus the stimulus-response
functions for all human periodontal afferents are well described as a constant times \( F(F + c) \), where \( F \) represents the steady-state force. For both posterior (17/20) and anterior teeth (15/19) (Trulsson and Johansson 1994), a majority of the afferents showed a hyperbolic, strongly saturating, stimulus-response relationship. However, compared with afferents of anterior teeth, the afferents of posterior teeth showed a reduced sensitivity at low tooth loads. This is illustrated in Fig. 2C by the steeper average stimulus response curve for afferents of anterior (gray curve) compared with that of posterior teeth (black curve). For afferents from posterior teeth, the forces yielding half the estimated maximal discharge rates (c-parameter) were on average 1.7 N, which is four times higher compared with afferents from anterior teeth (0.42 N) (Trulsson and Johansson 1994).

Afferents demonstrating nearly linear steady-state stimulus-response relationships were found in a small proportion of both posterior (3/20) and anterior teeth (4/19) (Trulsson and Johansson 1994). The forces that yielded half the estimated maximal discharge rates (c-parameter) ranged between 8 and 23 N for the afferents of posterior teeth and between 5 and 22 N for afferents of anterior teeth (Trulsson and Johansson 1994). Thus the nearly linear afferents of posterior and anterior teeth showed a similar sensitivity to changes in steady-state forces applied to the teeth.

Importantly, if individual afferents with curved stimulus-response relationships were loaded in a nonoptimal direction, the discharge rate still showed the same saturation tendency, but at lower levels. These observations were in line with results from periodontal afferents of anterior teeth (cf. Fig. 3 in Trulsson and Johansson 1994) and suggest that the proportion of saturating afferents is not changed when considering the whole population response, i.e., also when nonoptimally stimulated afferents are included.

**Dynamic sensitivity of periodontal afferents of anterior and posterior teeth**

The estimated relative dynamic sensitivity (dlb in Table 1) of the afferents in the present study (median: 0.68, range: 0.34–3.87) was significantly lower compared with afferents from anterior teeth (median: 2.17, range: 0.54–17.73; \( P < 0.001; \) Mann-Whitney) (extracted from Table 1 in Trulsson and Johansson 1994). Furthermore, the time constant (\( \tau \) in Table 1; median: 416 ms, range: 24–1249 ms), characterizing the high-pass filter in the transfer function, was significantly longer compared with afferents from anterior teeth (median: 124 ms, range: 17–624 ms; \( P < 0.01; \) Mann-Whitney) (extracted from Table 1 in Trulsson and Johansson 1994). Thus when forces are applied to the crowns of the teeth, the dynamic sensitivity of periodontal afferents of posterior teeth is both lower and slower compared with afferents of anterior teeth. The lower dynamic, and static, sensitivity of periodontal afferents of posterior teeth may reflect a functional adaptation to the faster and stronger forces that are developed during motor activities involving the posterior teeth.

**Biomechanical considerations**

Similar to the periodontal afferents from the anterior teeth, a strong attenuation of the dynamic sensitivity with increased background force was observed for the hyperbolic afferents in the present study. The parallel attenuation of the dynamic and static sensitivities suggests the operation of a common mechanism to account for a global reduction in sensitivity as the tooth load increase. Trulsson and Johansson (1994) discovered that the \( F(F + c) \) transform is compatible with a biomechanical model of the periodontal ligament, implying that transduction of stress is accomplished by “squeezing” of the mechanosensitive nerve endings, which are interspersed among the collagen fibers of the ligament. According to this model, the difference among afferents regarding the static (c parameter) and dynamic sensitivity may be explained by local variations in the viscoelastic properties of the tissues interleaved between the nerve endings and the collagen fibers (Trulsson and Johansson 1994). The difference in static and dynamic sensitivity between afferents of different types of teeth may be explained by local variations at the site of the nerve endings or by factors affecting the stiffness of the tooth, such as differences in periodontal fiber architecture and the anatomy and size of the tooth root. Indeed, the periodontal ligaments of molars and incisors from rats and bovines have been found to have different biomechanical properties, indicating that periodontal fiber architecture is different between different types of teeth (Komatsu and Chiba 1993; Pini et al. 2004).

**Periodontal afferent encoding of tooth loads during mastication**

To understand how periodontal afferents contribute to the control of oral motor behaviors, such as biting and chewing, a description of the information they carry to the brain during these behaviors is essential. For technical reasons, intraoral recordings are not easily made from human periodontal afferents during oral motor functions. However, the quantitative model of the force-encoding properties of periodontal afferents described in the preceding text provides a means by which such a description can be obtained.

Earlier studies on human periodontal afferents of anterior teeth describe simulated afferent responses during holding and biting of food using the front teeth (hold-and-split task) (Trulsson and Johansson 1995). Due to high static and dynamic sensitivity at low tooth loads, hyperbolic periodontal afferents of anterior teeth are predicted to respond distinctly to the small force produced by initial food contact, to exhibit a maintained response when the subject gently holds the food between the teeth (hold phase), and exhibit only a moderate increase in the discharge rate to a rapid force increase required to split the food (split phase). Similar responses to this type of force profiles were expected for the hyperbolic afferents in the present sample. Some of the force profiles used in the present study to evaluate the transfer function were similar to the bite force profiles produced by subjects during a hold-and-split task (Fig. 4, A and B). Except for the rather sluggish dynamic response to initial tooth contact, the response profile shown by the hyperbolic afferent in Fig. 4B was akin to that expected for hyperbolic afferents of anterior teeth (Trulsson and Johansson 1995). Furthermore, in similarity to the periodontal afferents of anterior teeth, a minority of the afferents of posterior teeth (nearly linear afferents) possessed the capacity to encode the rapid and strong force increase required to bite through food (see Fig. 4A).
While the anterior teeth are used during initial food intake, when morsels are manipulated, split into smaller pieces, and transported into the mouth, the posterior teeth are used during rhythmic chewing when strong forces are produced by the jaw muscles to grind the food. During normal chewing of mixed food, the forces exerted on one posterior tooth rarely exceed 50–70 N (De Boever et al. 1978). The simulations of periodontal afferent responses to chewing-like force profiles (≤52 N) obtained in the present study predicted that the discharge rates of hyperbolic afferents rapidly increased after initial tooth contact. The afferents continued to discharge as long as the tooth was loaded, but due to the marked saturation tendencies at higher forces, these afferents poorly encoded the magnitude of strong chewing forces and the force changes occurring at these high loads (cf. afferents 1–16 in Fig. 5). The hyperbolic afferents showed their highest discharge rates shortly after initial tooth contact and the discharge rates decreased to a saturated level, even if the force continued to increase. Indeed, response saturation of the periodontal afferents have been described in anesthetized rabbits, while chewing on a rubber tube (Appenteng et al. 1982). However, the nearly linear afferents constitute a subpopulation of periodontal afferents that encodes forces over a wide intensity range (cf., afferents 19–20 in Fig. 5), including the forces developed during the power phase of chewing (De Boever et al. 1978).

Periodontal afferent signals in the intensive control of mastication

Several investigations have indicated that periodontal afferents are important for the control of jaw muscles during biting and chewing (see Lund 1991; Trulsson and Johansson 1996b; Türker 2002). Human periodontal afferents signal detailed information about spatial changes of tooth loads and contribute to the spatial control of mastication, and these effects have been discussed extensively in earlier published papers (Johnsen and Trulsson 2003a; Trulsson and Johansson 1996b).

Given their high sensitivity, at low tooth loads, most periodontal afferents are particularly well suited to encode in detail the temporal changes in the force that occur immediately after contact with food, e.g., while food is being positioned for biting and during the early contact phase of each chewing cycle. From this information, and information about the movement of the jaw, the mechanical impedance of the food can be derived. The jaw movement is hypothetically available either from peripheral mechanoreceptors or through internal representations of the jaw closure commands (e.g., “afferent copies”). Accordingly, signals from the periodontal afferents may modulate the motor commands, given the existent mechanical impedance. This would take place in a predictive feed-forward (“open loop”) manner based on learned relationships between patterns of afferent signals and appropriate efferent signals (cf. Johansson 2002). Indeed, jaw actions observably adapt to the changing mechanical properties of a bolus during mastication (cf. Hidaka et al. 1997; Inoue et al. 1989; Plesh et al. 1986; Schwartz et al. 1989; Thexton et al. 1980).

The hypothetical function of early “state information” in the control of forthcoming jaw actions brings to mind that served by tactile afferents in the human finger tips during grasping and manipulation of small objects. Immediately after contact with an object, tactile afferents encode various mechanical contact provisions including information about the frictional characteristics of the object (Johansson and Westling 1987; Westling and Johansson 1987). Such information is used to trigger the release of motor commands for subsequent phases of manipulative maneuvers and to predictively modify the force output to the physical properties of the object (e.g., Johansson 2002).

These principles are also expressed in the control of chewing-like movements in humans. Ottenhoff et al. (1992a,b) have shown that “additional muscle activity” (AMA) required during the power phase to overcome impedance of the food is largely parameterized in advance on the basis of sensory experiences during the preceding chewing cycle. Memory of food’s resistance in the previous cycle is used to predictively scale the muscle commands that initiate the power phase. It is also used to regulate the strength of a sensory mediated “reflex” increase in muscle activity, elicited by food resistance; a maximum output strength of the reflex contribution to the AMA is set (Ottenhoff et al. 1992b). Signals in periodontal afferents may contribute both to information about food resistance gained during the previous cycle and to the reflex-mediated component of the AMA (Ottenhoff et al. 1992b).

A recent study on anesthetized rabbits performing rhythmic jaw movements confirm that a “facilitatory masseteric response” (FMR; equivalent to the AMA in humans) often precede tooth contact; this supports the operation of a feed-forward control mechanism (Komuro et al. 2001). The blocking of periodontal afferent input by cutting dental nerves did not affect the FMR, whereas blocking information from muscle spindle afferents, innervating the jaw closing muscles, abolished the FMR component preceding tooth contact. Earlier animal studies have shown that combined destruction of periodontal afferents and muscle spindle afferents diminish the FMR almost completely, whereas destruction of either one of both afferents did not completely diminish the FMR (Inoue et al. 1989; Lavigne et al. 1987; Morimoto et al. 1989). These results suggest that the timing of the predictive component of FMR may be controlled in the main by information from muscle spindles, whereas the magnitude of FMR is under the control of both muscle spindles and periodontal receptors (Komuro et al. 2001).

Interestingly, deprivation of periodontal afferent information by cutting the nerves to the teeth significantly reduced the buildup speed of the masticatory force during chewing (Hidaka et al. 1997). Thus information acquired by periodontal afferents early after contact during each chewing cycle (early “state information”) may be used to scale the muscle commands of the ensuing power phase to the current food impedance.

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