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DIRECTIONAL SENSITIVITY OF HUMAN PERIODONTAL MECHANORECEPTIVE AFFERENTS TO FORCES APPLIED TO THE TEETH

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SUMMARY

1. Single-unit impulse activity from thirty-eight mechanoreceptive afferent fibres was recorded in the human inferior alveolar nerve using tungsten microelectrodes. All afferents responded to mechanical stimulation of the teeth and most likely supplied periodontal mechanoreceptors.

2. All afferents showed their highest sensitivity to forces applied to a particular tooth (the lower incisors, the canine or the first premolar). Forces with 'ramp-and-hold' shaped profiles of similar magnitudes were applied to that tooth in the following six directions: *lingual*, *labial*, *mesial* and *distal* in the horizontal plane, and *up* and *down* in the axial direction of the tooth. Both static and dynamic response components were analysed.

3. All afferents were 'slowly adapting' since they discharged continuously in response to static forces in at least one stimulation direction. Twenty-five afferents (66%) were spontaneously active in the sense that they showed an on-going discharge in the absence of external stimulation.

4. Diverse receptive fields were observed. Most afferents (74%) responded to static forces in two or three of the four horizontal directions. Likewise, all units showed excitatory responses to axial loading with a majority (74%) responding in one of the two axial directions and the remainder in both axial directions. Spontaneously active afferents generally decreased their discharge rate when stimulated in directions opposite to the directions exciting the afferent. With regard to population responses, approximately half of the afferents showed excitatory responses to each stimulus direction except for downwards, in which 86% responded.

5. Twenty-three afferents (61%) exhibited the strongest response to forces in one of the horizontal directions. Of those, a majority were most responsive to the lingual direction (52%) and some to the labial direction (30%). Accordingly, the discharge rates during force application averaged over the whole afferent sample were highest in these directions. Of the remaining afferents, most responsive to one of the axial directions, 60% showed their strongest responses to forces in the downward direction.

6. Forty-five per cent of the afferents showed wider receptive fields to the dynamic

component of the force stimulation than to the static. The direction of maximal sensitivity, however, remained the same with few exceptions.

7. It was demonstrated that even though individual periodontal mechanoreceptive afferents provide ambiguous information regarding the direction of a force applied to a tooth, populations of such afferents are well suited to give detailed directional information. It is suggested that such information may play an important role for the control of mastication.

INTRODUCTION

A prominent feature of periodontal mechanoreceptive afferent units in mammals is the dependence of their responses on the direction in which forces are applied to the teeth (Pfaffman, 1939; Ness, 1954; Hannam, 1970; Sakada & Kamio, 1971; Karita & Tabata, 1985; Loescher & Robinson, 1989). This feature is also represented in the higher order cells in the trigeminal main sensory nucleus (Kawamura & Nishiyama, 1966), the thalamus (Yokota, Koyama, Nishikawa & Hasegawa, 1988) and the somatosensory cortex (Taira, 1987). Such directional sensitivity may be important for perceptual functions, as well as for afferent modulation of oral motor behaviours. Indeed, there are recent studies suggesting specific roles for these afferents in the sensorimotor regulation of chewing movements (Lavigne, Kim, Valiquette & Lund, 1987; Inoue, Kato, Masuda, Nakamura, Kawamura & Morimoto, 1989; Morimoto, Inoue, Masuda & Nagashima, 1989).

Except for one preliminary report in man (Johansson & Olsson, 1976), studies on afferent responses to tooth loading have been performed in animals. These studies indicate problems with extrapolation of data between species and even between afferents innervating different teeth within the same species (see Discussion). Hence, to acquire data of direct relevance to human behavioural studies, it appears essential to obtain information on periodontal afferents from man. The present paper is the first in a series of studies on the afferent encoding of mechanical stimulation of the human teeth. Load force stimuli were applied to the teeth in six directions in three orthogonal planes and directional aspects of both static and dynamic responses were analysed. It will be demonstrated that even though individual periodontal mechanoreceptive afferents cannot unambiguously encode the direction of a force applied to a tooth, populations of such afferents provide detailed directional information. A portion of the results have been reported in a preliminary communication (Trulsson, Olsson & Johansson, 1990).

METHODS

Subjects and general procedure

Eleven healthy subjects (five males, six females, ages 20–50), participated in this study 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 experimental 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 of one 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 either the left or the right inferior alveolar nerve using a coated tungsten needle electrode (Vallbo & Hagbarth, 1968; also cf. Johansson & Olsson, 1976). The electrode had a shaft diameter of 0·2 mm and a free tip of 5–15 μm. The impedance was 100–400 kΩ measured *in situ* at 1 kHz.

The manual handling of the electrode was guided by the landmarks used in dental practice when blocking the mandibular nerve. To facilitate the search for the nerve, electrical square-wave pulses (0·2 ms duration, 0·1–1 mA) of negative polarity were occasionally delivered through the electrode. Paraesthesias in the mucosal or cutaneous zones of the lip indicated that the electrode was close to the nerve and subjects indicated this by pointing at various symbols presented on a chart. When the nerve had been impaled near its entrance to the mandibular foramen, the position of the electrode was carefully adjusted until impulse responses in a single afferent to mechanical stimulation of the teeth could be discriminated. The electrode was left in a recording position supported only by the surrounding tissue. The minute electrode adjustments occasionally evoked short-lasting and localized paraesthesias in the lip or dull 'aching' sensations in particular teeth. No persistent paraesthesias or other complications were reported following the recording session.

Mechanical stimulation

For each afferent, the tooth that gave the strongest discharge when mechanically stimulated by a manually held probe (stimulation force 0·5–1 N) was defined as the '*receptor bearing tooth*'. Forces were applied to this tooth in six directions, to examine the directional sensitivity of the afferent. The probe was equipped with force transducers (DC-200 Hz) and a small nylon sphere (diameter 1 mm) was attached to its end. The forces were applied to a nylon cube attached to the top of the tooth as shown in Fig. 1*A*. The cubes were mounted on individual copper attachments which in turn were cemented (*Miradapt*™, *Johnson & Johnson Dental Products Company, USA*) to the incisors, the canine and the first premolar on the recording side prior to the experiment. The weight of the attachment, the cube and the cement was about 0·3 g. The probe was nominally oriented perpendicular to the tested cube surface for force application. Because the frictional coefficient between the cube and the nylon sphere was very low (< 0·15) the maximum deviation from a true perpendicular force application was $\pm 8{\cdot}5$ deg; at larger angles, slips occurred. Forces in the upward direction were applied through a nylon loop fixed to the copper attachment. In this way, forces were applied close to orthogonal orientations in six directions: four directions in the horizontal plane (*lingual*, *labial*, *mesial* and *distal*) and in the axial directions of the tooth (*down* and *up*).

Force profiles that consisted of three phases, a *force increase*, a *static phase* and a *force decrease* back to zero force (Fig. 1*B*), were manually applied by the experimenter who was guided by visual feedback via an oscilloscope. The force increase lasted for $0{\cdot}46 \pm 0{\cdot}13$ s (mean ± S.D.), the static phase for $1{\cdot}9 \pm 0{\cdot}4$ s and the force decrease for $0{\cdot}16 \pm 0{\cdot}05$ s. The experimenter attempted to produce a 250 mN force during the static phase. The actual force amplitude during this period was measured to be 267 ± 22 mN. There were no significant differences in the various stimulation directions in the force amplitudes applied ($P > 0{\cdot}2$, Kruskal–Wallis analysis of variance). During the loading ramp the force rate averaged $0{\cdot}6 \pm 0{\cdot}2$ N/s and, again, there were no significant differences for the various stimulation directions ($P > 0{\cdot}1$, Kruskal–Wallis).

A single stimulation sequence included one force application in each of the six directions at a minimum inter-stimulus interval of 2 s. Two to five such sequences were delivered and the order of tested directions was varied within the sequences.

Data collection and processing

The nerve signal was displayed on an oscilloscope, fed into an audio monitor and, together with the force signal, stored on magnetic tape (DC-5 kHz). Data were subsequently analysed using a flexible laboratory computer system. The nerve and force data were sampled at 12·8 kHz and 800 Hz, respectively (12 bits A/D resolution). Triggering of action potentials was performed using a previously described algorithm (Edin, Bäckström & Bäckström, 1988) implemented in the analysis program.

For each force stimulation, the *dynamic response* was defined as the mean impulse firing rate from the start of the force ramp (determined from the second order time derivative of the force) until

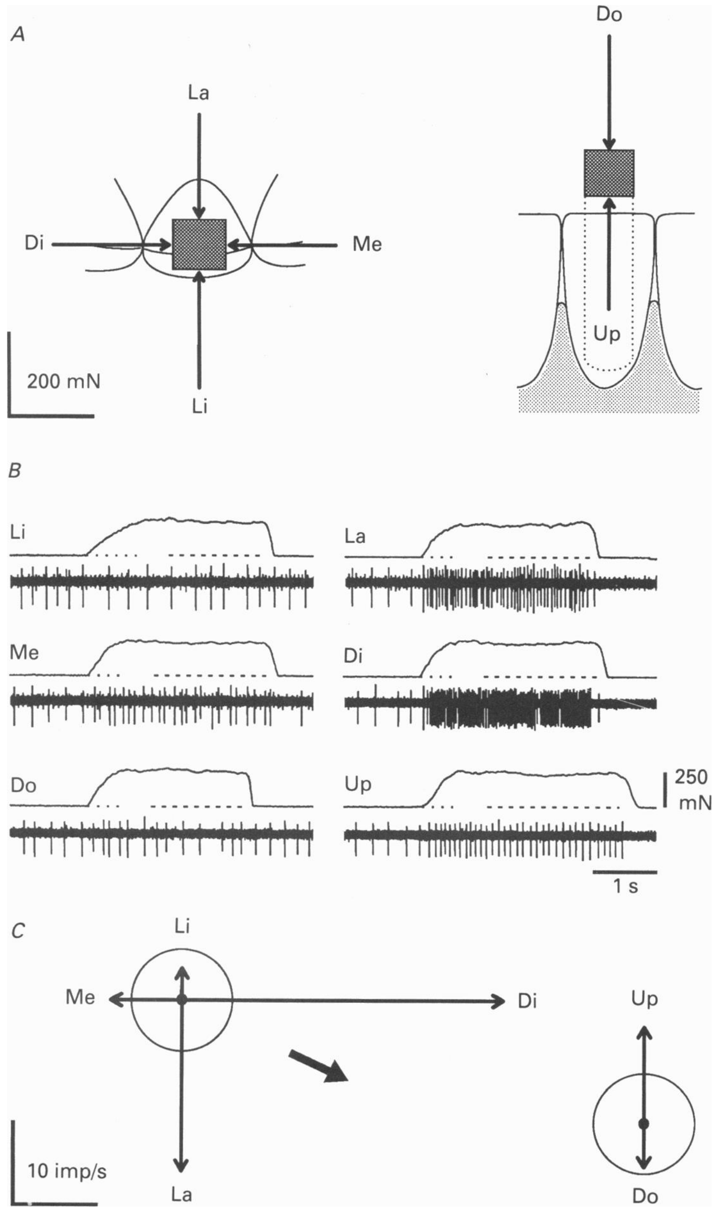

Fig. 1. Responses of a single afferent unit to forces applied in six directions to the lower central incisor. *A*, the tooth is shown in the horizontal plane (left) and in a vertical plane (right). The static force (mean of five stimulations) in each of the six directions are represented by the vectors. The forces were applied to each of the five free faces on a nylon cube (3 × 3 × 3 mm; shaded) cemented to the tooth 1 mm above its edge using a copper attachment (dotted contour). The upwards force (Up) was applied with a nylon loop affixed to the copper attachment (not shown). *B*, examples of neurograms from a single afferent with the corresponding force records above. Dotted and dashed horizontal lines indicate the intervals during which the dynamic and static responses were measured, respectively. The noise level of the nerve records corresponds to approximately 20 μV (peak to peak). *C*, vectorial presentation of the static responses to stimulations in the horizontal plane (left) and in the axial directions (right). The lengths of the vectors are

90 % of the static force was reached. The *static 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 static force. The spontaneous afferent discharge was assessed during the 2–5 s time period prior to the application of the first test in the sequence. For each afferent, the dynamic and static responses reported are averaged data from all force stimulations in a given direction. This treatment was justified since the afferent responses did not vary appreciably between the tests. The coefficient of variation (S.D./mean value) for the repeated tests in the most sensitive stimulation direction ranged from 0·06 to 0·20 for all afferents tested (mean coefficient of variation 0·10). All individual tests were inspected to positively identify weak responses to force stimulations in spontaneously discharing afferents. An afferent was considered responsive if an increase or decrease in discharge rate was observed in a majority of the tests.

In addition to linear regression analysis (least-squares fit), non-parametric statistics were used as detailed in the Results section (Siegel & Castellan, 1988); a P value $< 0·05$ was considered statistically significant. Reported means and standard deviations are point estimates of data pooled from all subjects.

RESULTS

Thirty-eight stable recordings of mechanoreceptive afferents sensitive to forces applied to the teeth of the lower jaw were obtained in twelve experimental sessions on three female and two male subjects (two to six afferents/experiment). Twenty afferents showed their maximal responses to forces applied to the central incisor, seven to the lateral incisor stimulation, nine to canine stimulation, and two responded maximally to first premolar stimulation. In addition, a number of afferents were isolated which responded to mechanical stimulation of cutaneous, transitional or mucosal zone of the lower lip or the gingiva of the lower jaw. Because none of these responded to tooth loading, they will not be considered further in the present report. Accordingly, the present results are most likely based on signals originating in periodontal receptors (but see Linden, 1990).

Figure 1*B* shows examples of responses in a single afferent to forces applied to an incisor tooth in each of the six stimulation directions. The static responses are illustrated as vectors in Fig. 1*C* with vector lengths proportional to the averaged static discharge rate and vector directions determined by the stimulus direction. All afferents were considered 'slowly adapting' since they showed on-going responses during the entire static phase of stimulation in at least one of the stimulus directions. Twenty-five afferents (66 %) showed an on-going discharge without any external forces applied to the teeth (e.g. Fig. 1*B*). The level of this spontaneous activity is indicated in the figures by a circle with a radius scaled to the mean firing rate (e.g. Fig. 1*C*).

Directional influences on the static afferent responses

Stimulation directions eliciting static responses

Like the afferent shown in Fig. 1, most afferents showed increased discharge rates to stimulations in more than one direction. However, the receptive fields varied

proportional to the mean impulse frequency during five stimulations in each direction and the direction of the vector represents the stimulus direction. The spontaneous discharge rate is represented by the circle with the radius indicating its intensity. Vectors longer and shorter than this radius illustrate increased and decreased firing, respectively. The thick arrow represents an estimate of the most efficient excitatory stimulus direction in the horizontal plane, i.e., the 'preferred direction'. Force directions: Li = lingual, La = labial, Me = mesial, Di = distal, Do = downward and Up = upward.

considerably among the afferents as exemplified in Fig. 2 by six afferents (*A–F*). There no obvious systematic differences in the response characteristics of afferents related to the various teeth.

All but three afferents (92%) responded to horizontally applied forces. The histogram to the left in Fig. 3*A* shows the distribution of afferents with regard to the

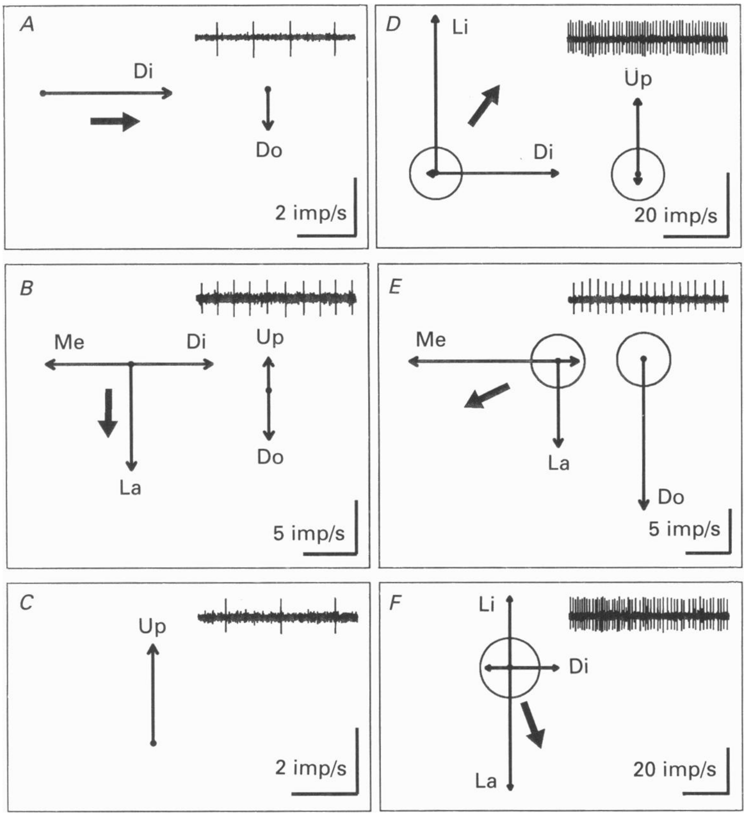

Fig. 2. Receptive fields of six afferents based on static responses. *A* and *B*, a canine tooth and a central incisor afferent. *C*, a central incisor afferent only responding to upward force. *D* and *E*, lateral and central incisor afferent. Note that the spontaneous activity was decreased by the loading in non-excitatory directions. *F*, a central incisor afferent which was most excited in two opposite directions (labial and lingual). This 'bidirectional' afferent was not tested in the axial directions. *A–F*, inserted neurograms show examples of recordings of action potentials in the most sensitive stimulation direction during the static phase of stimulation. Sweep length, 1 s. For further details see legend to Fig. 1*C*.

number of stimulation directions evoking *excitatory* responses in the horizontal plane. Out of the seven afferents responding in one direction only (e.g. Fig. 2*A*), four were spontaneously active. Twelve out of fifteen afferents responding in two (adjacent) directions (e.g. Fig. 2*D* and *E*) and eight out of thirteen afferents responding in three directions (e.g. Figs 1, 2*B* and *F*) were spontaneously active. One of these was 'bidirectional' (cf. Loescher & Robinson, 1989) showing increased firing in three directions with the strongest responses in opposite directions (Fig. 2*F*). However, most spontaneously active afferents showed a decreased discharge rate in stimulation directions opposite to excitatory directions (e.g. Figs 1, 2*D* and *E*).

All afferents that were tested in both axial directions ($n = 27$) showed excitatory responses to forces applied in at least one of these directions (Fig. 3*A*, right

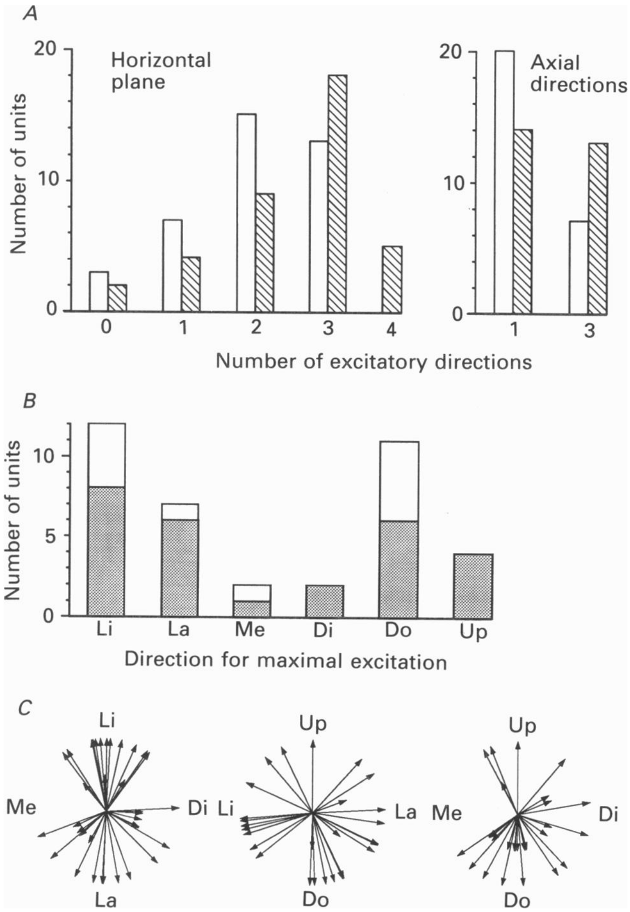

Fig. 3. *A*, distribution of afferents with respect to the number of stimulation directions evoking excitatory responses in the horizontal plane (left) and the axial directions (right). Open and hatched columns refer to static and dynamic responses, respectively. *B*, stimulation directions showing the strongest static responses. The shaded columns refer to afferents tested in all six directions and open columns to afferents not tested in the upward direction. *C*, the 'preferred direction' of individual afferents projected to the horizontal plane (left panel; $n = 35$) and two orthogonal vertical planes (middle and right panel; $n = 27$). Long arrows refer to afferents showing their strongest responses in one of the directions represented in the plane whereas short arrows refer to afferents with the strongest responses in another plane. *B* and *C*, data based on static responses.

histogram). Three afferents discharged when loaded only in the axial directions (e.g. Fig. 2*C*). To evoke responses to horizontal loads in these afferents, the forces had to be increased from the test level (on average 267 mN) to approximately 400 mN. Fourteen out of the twenty afferents showing excitation in one axial direction (Fig.

3*A*) were spontaneously active and their discharge rate decreased when the tooth was loaded in the opposite direction (Figs 1, 2*D* and *E*). Four of the seven afferents showing responses in both directions (e.g. Fig. 2*B*) were spontaneously active.

Inverse correlations were regularly found between the discharge rates elicited by forces in opposite directions ($P < 0{\cdot}001$–$0{\cdot}05$, Spearman rank correlation analysis; data from all afferents pooled). Thus, for afferents showing a strong discharge when loaded in one direction, the discharge when loaded in the opposite direction was generally smaller and for spontaneously active afferents it often involved a decrease of the on-going activity. In contrast, no significant correlations were found between discharges evoked for any other pairs of stimulation directions.

Stimulation direction providing the strongest responses

Figure 3*B* illustrates the distribution of the afferent sample with regard to the stimulation direction that evoked the strongest afferent response. The number of afferents was unevenly distributed among the six stimulus directions ($P < 0{\cdot}02$; Chi-square goodness-of-fit test). For most afferents, the strongest responses were evoked by lingual, labial or downward stimulations. The static response rate in the most sensitive stimulation direction was $22{\cdot}4 \pm 13{\cdot}9$ imp/s, and was not significantly different for different stimulus directions ($P > 0{\cdot}3$, Kruskal–Wallis).

'Preferred direction'

The force direction which would excite an afferent most effectively was estimated by vectorial addition of the vectors representing excitatory responses (e.g. Figs 1*C* and 2). Hence, it was assumed that the response magnitude varied continuously with the stimulation direction in quadrants defined by directions exhibiting excitatory responses. Figure 3*C* shows the obtained '*preferred direction*' for each of the afferents projected onto the horizontal plane, and the two vertical planes. In the horizontal plane the 'preferred directions' were distributed around the circumference of the tooth showing a bias toward the lingual and labial directions. In the vertical aspect, the 'preferred direction' was clearly biased downwards (19/27).

To assess the accuracy of the estimation of the preferred direction, the method was applied to the data of Karita & Tabata (1985; Figs 2 and 3) and Loescher & Robinson (1989; Fig. 3) using four stimulation directions (lingual, labial, mesial and distal) out of the twenty-four or twelve actually used by these authors. The preferred direction obtained did not deviate more than 20 deg from the direction of measured maximum response.

Population responses

Figure 4*A* summarizes the responses of all recorded afferents responding to static forces applied to the teeth in each of the six stimulation directions. As noted above, when only the most sensitive stimulation direction for each unit was taken into account, no directional differences in static responses were observed. In contrast, when responses in all directions were considered, the excitatory response was clearly direction dependent ($P < 0{\cdot}05$, Kruskal–Wallis; open columns in Fig. 4), and was stronger in the lingual and labial directions than in other directions ($P < 0{\cdot}001$; Mann–Whitney, lingual and labial directions tested *versus* the other directions). There were no such directional differences with regard to the decline in firing rate of spontaneously active afferents ($P > 0{\cdot}1$; Kruskal–Wallis; filled columns in Fig. 4). The relative frequency of afferents responding in the various directions are shown in Fig. 4*B*. Stimulation in any given direction excited about half of the afferent population except for the down direction in which a higher fraction (86%) of the

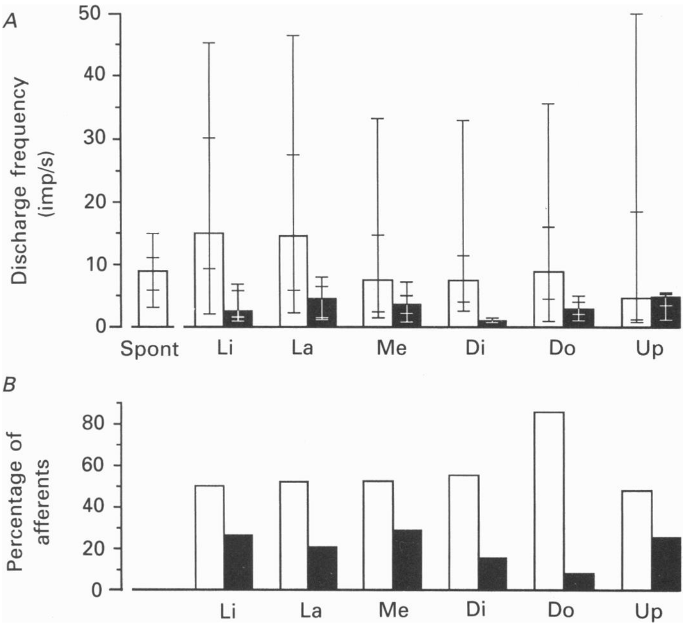

Fig. 4. *A*, magnitude of static responses obtained for the various stimulation directions. Columns show the median value and the horizontal bars indicate the 25th and 75th percentile and the range. Open columns refer to excitatory responses and filled columns to decreases in firing rate for spontaneously active afferents. For each of the spontaneously active afferents the response was expressed as the absolute value of the change in the discharge frequency caused by the mechanical stimulation. The single left column (Spont) gives the intensity of the spontaneous discharges for all spontaneously active afferents ($n = 25$). *B*, percentage of afferents showing excitatory (open columns) and inhibitory (filled columns) responses to stimulation in the different directions. Data based on static responses recorded from thirty-eight afferents except in the upward direction where $n = 27$.

afferents increased their firing ($P < 0{\cdot}05$, Chi-square). A somewhat lower fraction of the spontaneously active afferents (some 20%) showed decreases in firing rate and no directional differences were found for those ($P > 0{\cdot}5$, Chi-square).

The capacity to encode the direction of forces applied to an individual tooth was further analysed using an approach similar to the one introduced by Georgopoulos and his colleagues to represent the activity of a population of neurons in the motor cortex of the monkey (Fig. 5; see Georgopoulos, Caminiti, Kalaska & Massey, 1983). A neuronal population vector (dashed line with arrow-head) was calculated for the six stimulation directions and viewed in the sagittal, horizontal, and frontal plane. Each population vector represents the vectorial summation of individual afferent vectors (represented by thin continuous lines with common origin). The direction of the individual afferent vector was the 'preferred direction' of the afferent (see Fig. 3C), and the length of the vector represented the size of the static response to the current stimulation direction. As can be seen, the obtained population vectors correspond surprisingly well to the applied stimulation directions.

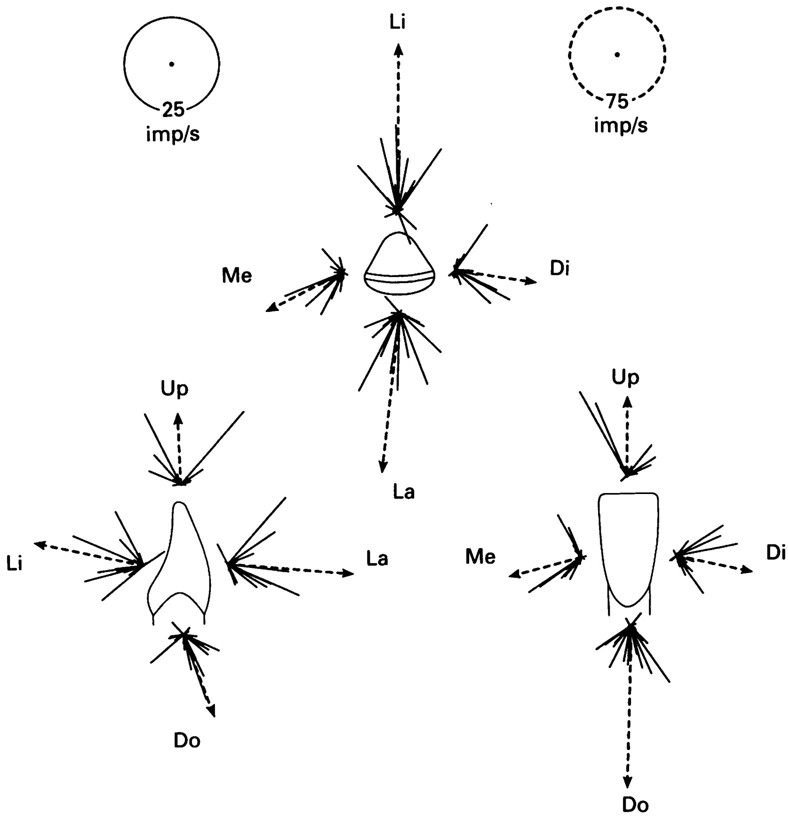

Fig. 5. Estimated capacity of the population of recorded periodontal afferents to encode force direction shown as a neuronal population vector (heavy dashed lines with arrowhead) calculated for six force stimulation directions and viewed in the sagittal (left), horizontal (middle) and frontal (right) planes. The separate clusters all represent the same neuronal population composed of individual afferent vectors (thin lines with common origin), and refer to the various stimulation directions also represented by their position relative to the tooth. The direction of each individual afferent vector thus represents the 'preferred direction' of the afferent as in Fig. 3C, whereas the length of the vector represents the size of the static response to the current stimulation direction. For spontaneously active afferents which decreased the discharge rates the orientation of the response vectors are opposite to the 'preferred direction'. Note the separate calibrations for the individual afferent vectors and the resultant vector (upper left and right circle, respectively).

Directional influences on the dynamic afferent reponses

As seen in Fig. 3A, the number of stimulation directions exhibiting dynamic excitatory responses during the loading ramp (on average 4·1) was higher than those evoking static excitatory responses (on average 3·3). This difference was accounted for by seventeen afferents (45 %). Five of these afferents actually responded in all six directions during the force increase. Such an omni-directional receptive field was not observed in any afferent for the static responses. Despite the wider receptive fields for the dynamic responses, the preferred directions and estimates of the neural

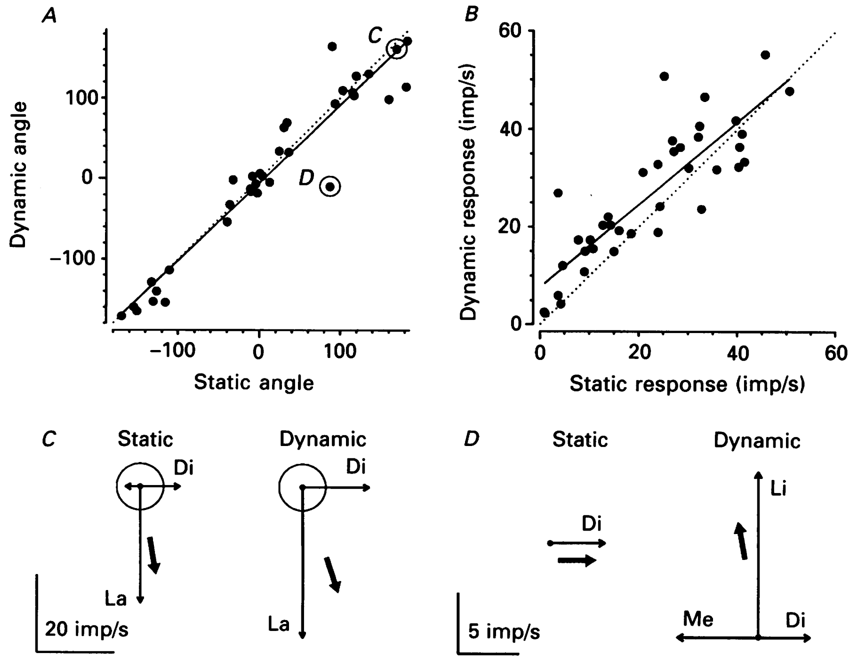

Fig. 6. Dynamic responses compared to static responses. *A*, relationship between the 'preferred directions' of the static and the dynamic responses in the horizontal plane. (0 deg, lingual; 180/−180 deg, labial; −90 deg, mesial and 90 deg, distal direction). *B*, relationship between the dynamic response and the corresponding static response in the direction showing the strongest static response. *A* and *B*, each symbol represents one afferent. The dotted lines indicate equal angles (*A*) or mean response rate (*B*) and the continuous lines linear regression. *C* and *D*, static (left) and dynamic (right) receptive fields for stimulation in the horizontal plane. A central incisor afferent (*C*) showing similar static and dynamic responses. A canine afferent (*D*) showing a static response in only one direction (distal) and dynamic responses in three directions (mesial, lingual and distal). The encircled symbols in *A* marked with *C* and *D* represent the afferents illustrated in *C* and *D*, respectively. For further details, see legend to Fig. 1*C*.

population vectors were similar to those shown in Figs 3*C* and 5 for the static responses.

Figure 6*A* compares the 'preferred directions' of the static and the dynamic responses in the horizontal plane for each afferent by plotting the two directions against each other (0 deg = lingual direction). The obtained relationship was largely linear (correlation coefficient (r) = 0·96) with a slope close to one and with zero intercept. Thus, the receptive fields were rather similar for the static and the dynamic responses (e.g. Fig. 6*C*). An exceptional afferent is shown in Fig. 6*D*, whose static response was confined to one direction (*distal*), whereas dynamic responses appeared in three directions (*mesial*, *lingual* and *distal*). Moreover, the dynamic responses were stronger in the two directions for which static responses were not elicited (*mesial* and *lingual*).

Figure 6*B* illustrates the relationship between the static response in the most responsive direction and the dynamic response in the same direction. There was a strong positive correlation between these two response parameters ($r = 0.84$; $P < 0.001$, linear regression analysis).

DISCUSSION

In the present study we analysed the directional sensitivity of 'slowly adapting' human mechanoreceptive afferents responding to mechanical stimulation of teeth in the lower jaw. The various afferents showed diverse and generally wide receptive fields both to static and dynamic phases of directional force stimulation. The receptive fields defined by static responses typically included two to four of the six tested directions and for nearly half of the sample the receptive field was even larger if defined from dynamic responses. Still, the individual afferents showed clear and similar directional preferences during both static and dynamic phases of force stimulation. Moreover, the present findings strongly indicate that detailed directional information of both static and dynamic tooth loads are encoded in the *population responses* of the human periodontal afferent neurons.

In the horizontal plane, most afferents showed a pronounced sensitivity to forces in the labial or particularly in the lingual direction, and in the vertical plane there was a preference for downward forces. The majority of the receptors related to the front teeth of the lower jaw thus seem well suited to register load forces striking the crown directly or obliquely from above. These directions probably represent the most important force directions during biting and chewing. Hence, this directional bias may reflect a functional adaptation (Sato, Maeda, Kobayashi, Iwanaga, Fujita & Takahashi, 1988; also cf. Tabata & Karita, 1986).

Mechanical stimulation

The mechanical stimulation was applied using a hand-held instrument implying that the amplitude and the rate of the force varied between the tests. However, it seems unlikely that this factor significantly influenced the results regarding the directional sensitivity. First, the actual stimulation force was continuously measured and the force feedback provided to the experimenter made the stimulations surprisingly reproducible (see Methods). Second, each test was generally repeated five times for each stimulation direction and the evoked responses were averaged. Third, it was observed that the differences in force stimulation between consecutive tests caused only small differences in receptor discharges compared to the large differences in discharge related to stimulation directions (cf. the relationship between intensity of static stimulation and discharge rate; Johansson & Olsson 1976). Moreover, the maximum error of the stimulus direction was controlled to less than ± 8.5 deg. For the lifting forces applied with the nylon loop, however, larger directional errors may have occurred because the direction was only visually guided.

Population encoding of force direction

From the present study it is obvious that single periodontal afferents provide ambiguous information about the direction of a force applied to a tooth due to the broad receptive fields. Nevertheless, accurate information about the direction of the force is clearly expressed in the activity of a population of periodontal afferents (Fig. 5). Hence, it appears as if the population of periodontal afferents has the capacity to continuously provide information regarding the direction and probably the point of attack and the magnitude of the resultant forces striking the individual tooth. It is conceivable that this information might be used in the moment-to-moment modulation of the motor programs controlling mastication.

Mastication is modulated by primary afferents (Thexton, Hiiemae & Crompton, 1980; Lund, Rossignol & Murakami, 1981) and in animals as well as in humans the intraoral receptors seem to be of particular importance (Inoue *et al.* 1989; Kapur, Garrett & Fischer, 1990). Considering the specific contribution from periodontal receptors, Lavigne *et al.* (1987) and Morimoto *et al.* (1989) concluded that inputs from these receptors contribute to the dynamic adjustment of the jaw movements during the slow closing phase of the masticatory cycle. It seems likely that the differentiated information provided by the periodontal afferents is used in the detailed expression of the masticatory programs in terms of the three-dimensional mandibular movement path and in optimizing the force distributions on the teeth. Indeed, during execution of purposeful phasic movements it appears that operating motor programs (i.e. 'central pattern generators') control the flow of information in the sensory and motor systems that are engaged in the current task (e.g. Gracco & Abbs, 1985; Olsson, Sasamoto & Lund, 1986; Rossignol, Lund & Drew, 1988; Johansson, 1991).

It should be noted that the 'preferred direction' used in the estimation of the population responses in this study is an approximation based on only six stimulation directions. It seems highly unlikely, however, that data from more stimulation directions would substantially alter the population characteristics as they emerged in the present study. Indeed, despite a relatively small afferent sample and few stimulation directions, the obtained population responses correspond remarkably well to the applied stimulation directions.

Mechanisms underlying the receptive fields

No two periodontal afferents showed identical receptive fields. A similar diversity in spatial sensitivity profiles has been observed in animal studies (e.g. Ness, 1954; Hannam, 1970; Sakada & Kamio, 1971; Karita & Tabata, 1985). The receptive terminals of the afferents in the present study most likely resided among the collagen fibres of the periodontal ligament (Byers, 1985; Byers & Dong, 1989). The hypothesis that the directional characteristics may reflect the location of the receptor within the ligament (Cash & Linden, 1982) could not be verified by Loescher & Robinson (1989). Rather they suggested that the lack of a simple relation between receptor location and preferred direction is linked to the intricate radial arrangement of the collagen fibres of the ligament (cf. Sloan, 1979).

One afferent in the present study showed a 'bidirectional' receptive field similar to those reported in the cat (cf. Mei, Hartmann & Roubien, 1975; Loescher & Robinson, 1989; but see Karita & Tabata, 1985). It has been suggested that the bidirectional receptive field could be the result of fibre branching in the primary afferent terminal region or merely reflect the mechanical loading patterns in a complex collagen arrangement (Loescher & Robinson, 1989). Another possibility is that the expression of a bidirectional receptive field in the human jaw may be a consequence of interdental relations. The distribution of 'preferred directions' in the horizontal plane showed a bias towards lingual and labial directions (cf. Fig. 3) and there were generally stronger population discharges in these directions (cf. Figs 4*A* and 5). These observations may relate to a stabilization of the tooth by the interdental contacts, increasing the stiffness in the mesial and distal direction favouring the appearance of bidirectional responses in the lingual and labial direction (Fig. 2*F*). Afferent responses to stimulation of teeth adjacent to the most sensitive tooth (i.e. the assumed receptor bearing tooth) will be addressed in a separate report.

Human observations in relation to earlier animal results

The present results regarding the extent of the receptive fields are in general agreement with earlier findings in the cat (Sakada & Kamio, 1971; Karita & Tabata, 1985). Sakada & Kamio (1971) found that 61% of the periodontal afferents of the canine tooth were sensitive to three or four out of five tested directions (same test directions as ours except Up). More recently, Karita & Tabata (1985) examined the directional sensitivity of 328 canine afferents by manually applying forces in eight horizontal directions at nominal intervals of 45 deg. Of the afferents, 8% were classified as having a 'broad' receptive field (more than 180 deg), 87% as a 'medium' type (90–180 deg), and 5% as a 'narrow' type receptive field (less than 90 deg). The majority of the afferents in the present study would be classified as 'medium' or 'broad', i.e. 80% of the afferents showed static responses in more than one of the four horizontal directions implying that the response fields of these afferents must have been larger than 90 deg. Moreover, in agreement with the present results, the receptive fields defined with dynamic stimulation in the cat seem to be larger than those defined with static forces (cf. Karita & Tabata, 1985 and Loescher & Robinson, 1989). Data on the periodontal mechanoreceptors in the dog (Hannam, 1970), however, suggest narrower receptive fields than observed in the cat and in the present study. Whether these discrepancies reflect functional adaptation or methodological differences is difficult to determine, at present.

Most animal studies describe both 'rapidly adapting' and 'slowly adapting' mechanoreceptive afferents that respond to tooth loading (cf. Hannam, 1982; Linden, 1990; but see the pioneer study by Pfaffman, 1939). In contrast, we have found only 'slowly adapting' afferents. Whether this discrepancy is due to species differences or not has yet to be established. However, the difference may be due, at least partly, to methodological factors. The three dimensional stimulation procedure adopted in this study clearly disclosed the 'slowly adapting' response features of afferents which would not have been observed had they been stimulated in the horizontal plane only, as was done in recent animal experiments (e.g., Cash & Linden, 1982; Karita & Tabata, 1985; Loescher & Robinson, 1989). Interestingly, Cash & Linden (1982) hypothesized 'that there may be only one type of mechanoreceptor and that the rate of adaptation is dependent on the location of the receptor within the periodontal tissues'. They considered 'rapidly adapting' responses to be related to receptors not optimally stimulated (cf. Linden, 1990). Thus, the present findings support the hypothesis that all periodontal mechanoreceptors responding to non-noxious forces applied to the tooth can show 'slowly adapting' properties. However, another alternative is that considerably higher forces and force rates than used in the present study may be necessary to excite and thereby disclose true 'rapidly adapting' afferents (cf. stimulation parameters used by Hannam, 1969). Another, less likely, explanation would be that the physiological muscle tremor by the experimenter when manually applying the stimulation forces might have dynamically excited the afferents during the static phase of the stimulation. However, this seems quite unlikely since (1) the dynamic sensitivity of the afferents appeared rather weak (Figs 1 and 6*B*), and (2) a careful inspection of the nerve signal during strong force tremor cycles did not reveal any obvious relationship between the muscle tremor and the afferent discharge.

Several authors have emphasized the importance of stimulating the tooth in three dimensions (e.g. Ness, 1954; Hannam, 1970). Based on the results of the present study, it is obvious that a three dimensional approach is necessary to characterize the periodontal receptors. The direction of force application is crucial when assessing the response thresholds and receptive fields, as well as the adaptation properties. For example, had axial stimulation not been applied in the present study, three afferents would have been classified as 'rapidly adapting'. Although upwards forces occur during normal function no study to date has analysed the response to such forces. Also, abutment teeth involved in the retention of dental prostheses are exposed to such forces. The present results clearly indicate that the population of tooth related mechanoreceptor afferents also code forces in this direction.

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