

# Static and Dynamic Responses of Periodontal Ligament Mechanoreceptors and Intradental Mechanoreceptors

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## SUMMARY AND CONCLUSIONS

1. The response properties of 39 periodontal ligament mechanoreceptors (PDLMs) and 12 intradental mechanoreceptors (IMs) related to the intact mandibular canine tooth were isolated by extracellular recording methods from the ipsilateral trigeminal semilunar ganglion.

2. The stimulus threshold and response magnitude of individual PDLMs depended on the direction of steady force applied to the intact canine tooth. Canine PDLMs as a population, however, did not have a preferred stimulus direction. IMs were activated only by a rapid mechanical transient applied to the intact tooth in any direction. The stimulus threshold and response magnitude of each IM were approximately equipotent in all stimulus directions.

3. Application of quantifiable ramp-and-hold stimulation showed that PDLMs can encode the intensity of steady forces as well as the rate of force ramps. Increasing the ramp rates decreased the total ramp discharge but increased the peak discharge frequency. IMs encoded only the rate of force ramps that were applied by percussion. Higher ramp rates increased both the total discharges and peak discharge frequency of IMs.

4. The dynamic response properties of PDLMs and IMs were clearly differentiated by sinusoidal vibratory stimulation. The maximum frequencies for entrainment of IM discharge at the stimulus cycle length ( $251 \pm 103$  Hz, mean  $\pm$  SD) and at any periodicity including multiples of the stimulus cycle length ( $295 \pm 100$  Hz) were significantly higher than the maximum frequencies for PDLM discharge entrainment at the stimulus cycle length ( $103 \pm 53$  Hz) and at any periodicity ( $133 \pm 62$  Hz).

5. The functional similarities of PDLMs and IMs, respectively, to slowly adapting type II mechanoreceptors and Pacinian corpuscle receptors in the skin are discussed. Our present findings, which complement earlier anatomic and behavioral evidence, strongly suggest that IMs subserve nonnociceptive and nonpain functions. Both PDLMs and IMs may provide a continuum of dynamic afferent inputs necessary for tactile sensibility of teeth.

## INTRODUCTION

Our laboratory reported, in an earlier qualitative study (Dong et al. 1985), the first evidence of physiologically identified intradental mechanoreceptors that have fast-conducting large myelinated A-beta parent axons. This finding was consistent with short-latency tooth pulp-evoked potentials and unit responses that have been recorded throughout the trigeminal brain stem nuclear complex and in the thalamus and cortex (reviewed by Dong and Chudler 1984 and Dong et al. 1990). The adequate stimuli for intradental mechanoreceptors are rapid mechanical transients applied to the intact tooth. These receptors lack spatial directionality and can respond to high-frequency tooth vibration (e.g.,

256 Hz). Because nerve endings in teeth can provide sensory information that is nonnociceptive, the assumption that pain is the only sensation evoked by mechanical or thermal stimulation of the tooth must be questioned. Although low-intensity electrical stimulation of the tooth can elicit nonpainful sensations (Chatrian et al. 1982; McGrath et al. 1983), the sensations (if any) elicited by activation of intradental mechanoreceptors using natural stimuli are still unknown. This gap in our knowledge is due in part to the difficulty of performing psychophysical studies that must account for the confounding effects produced by coactivating mechanoreceptors in the periodontal ligament. To design behavioral experiments that can assess the sensory contribution of each receptor population, we need a better understanding of the differences in static and dynamic response properties between intradental mechanoreceptors (IMs) and periodontal ligament mechanoreceptors (PDLMs).

The structure and static response properties of PDLMs have been studied in some detail. The most structurally complex periodontal ligament (PDL) receptors are unencapsulated, branched Ruffini-like sensory endings, and the least complex receptors are free unmyelinated and small myelinated axons. No encapsulated receptors are found within the PDL of the rat, hamster, or dog (Byers 1985; Kannari et al. 1991; Sato et al. 1992); coiled Ruffini receptors occur only rarely in the monkey and cat (Byers and Dong, 1989); and encapsulated receptors have not been found in systematic surveys of cat canine PDL (Loescher and Holland 1991; Millar et al. 1989) or were extremely rare (Byers and Dong 1989; Byers et al. 1986). The current consensus among investigators is that virtually all PDL mechanoreceptors are Ruffini terminals. The stimulus threshold, response latency, discharge frequency, and adaptation properties of PDLMs, unlike those of IMs, depend on the direction in which force is applied to the tooth. When forces are applied in the direction of maximum response sensitivity, more rapidly adapting PDLMs have significantly higher thresholds than slowly adapting PDLMs (reviewed by Loescher and Robinson 1989). Slow adaptors have a range of discharge frequencies that is graded in relation to the magnitude of the applied force (Hannam 1969; Hannam and Farnsworth 1977). Hannam (1969) suggested that some PDLMs are sensitive to dynamic forces; the peak discharge frequency during the ramp phase of stimulation is increased as the rate of loading to reach a fixed steady force is increased. The force threshold of PDLMs is

decreased with increasing rates of force application (Linden and Millar 1988b; Loescher and Robinson 1989).

The present study provides evidence of the physiological differences between IMs and PDLMs in the intact tooth. Particular emphasis is given to studying the two receptor populations when subjected to quantitated dynamic forces in the form of sinusoidal and ramp stimulation. The results support the hypothesis that the IMs and PDLMs provide a continuum of dynamic afferent inputs necessary for tactile sensibility of teeth. Such sensory inputs may provide information about the texture of food during mastication and about severe abrasion or percussion of tooth enamel.

## METHODS

### *Animal preparation*

Twenty adult cats ( $3.4 \pm 0.8$  kg, mean  $\pm$  SD) were prepared for extracellular recording in the trigeminal semilunar ganglion (SLG). Each animal was anesthetized initially with thiopental sodium (40 mg/kg, i.p.). Anesthesia was maintained subsequently by periodic infusion of thiopental sodium (5–10 mg) through the femoral vein. After completion of all surgical procedures, a regimen of injections for thiopental sodium and gallamine triethiodide (3–4 mg/kg) was used during the recording session to maintain anesthesia and to suppress the jaw-opening reflex. Procedures to assure that each cat was anesthetized adequately throughout the recording session were described in previous reports (Dong and Chudler 1984; Dong et al. 1990). End-tidal  $\text{CO}_2$  concentration was measured and maintained between 4.0 and 4.5% while the animals were artificially ventilated. Lactated Ringer solution with 5% dextrose was infused continuously to maintain fluid and electrolyte balance. Rectal temperature was monitored and maintained between 37 and 39°C by a circulating water blanket.

The head of each cat was stabilized by holding it in a stereotaxic apparatus; the mandible was allowed to move freely about the temporomandibular synovial joint. The mandibular division of the SLG was exposed for recording extracellular activity by an extensive craniotomy, hemispherectomy, removal of a bony ridge overlying part of the SLG using fine rongeurs, and careful dissection of dura overlying the SLG using an operating microscope at  $\times 40$  magnification. Two additional cats were prepared for recording canine tooth pulp-evoked potentials in the SLG. A 5- to 7-mm length of canine tooth pulp between the apical foramen and crown was dissected free and mounted on platinum hook electrodes for bipolar stimulation. Dehydration of the exposed pulp was minimized by intermittent application of Ringer solution onto its surface.

### *Mechanical tooth stimulation*

An electromechanical vibrator or shaker (Ling Dynamic Systems, 102) and power amplifier (LDS, TPO25) were used to deliver calibrated mechanical stimuli to the intact ipsilateral mandibular canine tooth. The vibrator was equipped with an impedance head (Bruel-Kjaer, 8001) that housed an accelerometer for providing signal feedback to a sine program controller (LDS, SPC-4) as well as a piezoelectric force transducer. An 8-mm-long flat-faced stimulus probe (2.5 mm diam) that made contact with the mesial (anterior) side of the tooth was attached to the driving platform of the impedance head. The force gauge was located close to the driving point, giving a stiff, low-mass coupling to the probe test point. The sine program controller provided a sinusoidal signal for vibration and used the feedback signals from the accelerometer to provide a constant peak acceleration or integrated the accelerometer feedback signal to provide constant peak velocity or

displacement at one sinusoidal frequency or across a range of frequencies (i.e., 10–450 Hz applied at 100 Hz/min). The impedance head was also used to determine the mechanical resistance of the tooth-mandible to being set in motion; it provided the necessary measurements of applied forces and accelerometer feedback signals for maintaining constant velocity across a sinusoidal frequency range (see RESULTS). Acceleration, velocity, and displacement calibration for the sinusoidal vibration measurement system (accelerometer and sine program controller) was performed periodically by using a vibration reference signal source such as an electromagnetic exciter driven by a stabilized oscillator at a frequency of 159.2 Hz (Bruel-Kjaer, 4294). The electromechanical shaker and power amplifier were also controlled by a trapezoid generator (Haer, 40-95-7) that was driven by a positive-pulse square-wave stimulator to produce trapezoid stimuli of varying frequency, amplitude, duration, and ramp rise and fall times. Displacement and associated velocity of the tooth and mandible was measured independently by a piezoelectric film transducer (Pennwalt, Kynar Piezo Film) that had a high sensitivity to deformation, a flat frequency response over a wide range, highly damped resonance frequencies, and low mechanical impedance. One end of the piezoelectric film was held by a clamp on a stereotaxic carrier, and the other end was placed on the distal (posterior) side of the mandibular canine tooth under tension. The displacement-voltage relationship of the transducer was determined by visual measurement of the film displacement during ramp-and-hold and low-frequency sinusoidal stimuli and by applying calibrated displacement steps with a piezoceramic translator/manipulator (WPI, PM 20 N/B). The electromechanical shaker-impedance head-stimulus probe assembly and the piezoelectric film transducer were held by stereotaxic carriers that were mounted next to the stereotaxic head frame on a slotted cast-aluminum plate.

All forces applied to the intact mandibular canine tooth by the electromechanical shaker were directed along its mesial (anterior)-distal (posterior) plane. The stimulus probe tip was placed in contact with the mesial surface on the tip of the tooth crown; the piezo-film transducer was placed on the opposing distal surface. A search stimulus consisting of 10- to 20-Hz sinusoidal vibration was used to activate IMs or PDLMs. No spontaneous discharges were observed when the tooth was in its unloaded or rest position. Because the probe was not cemented to the tooth during the search stimulation, the probe made contact with the tooth only during half of each sine wave cycle. This resulted in both percussive stimulation (i.e., light taps) at the onset of probe-tooth contact and smoothly increasing or decreasing stimulation during each half-cycle. Our earlier study showed that the adequate stimulus for IMs was a mechanical transient (Dong et al. 1985). The search stimulus favored the isolation of PDLMs that were responsive to forces applied in the mesial-to-distal direction. After isolating a unit, the stimulus probe was temporarily removed so that hand-held aesthesiometers (Somfy-tec) with a calibrated range of 0–50 gram-force (0–491 mN) could be used to determine the directional sensitivity and approximate thresholds in different stimulus directions. Sinusoidal vibratory and ramp-and-hold stimulation were applied with the stimulus probe cemented to the mesial tooth surface by dental resin; however, a gap of 0.5 mm between the probe and tooth was needed before delivery of percussive ramp stimulation for IM units.

### *Recording procedures*

Signals related to calibrated mechanical stimulation were monitored on digital meters or oscilloscopes and stored digitally on magnetic tape. Signals recorded from the electromechanical stimulation system included voltages linearly proportional to the following: 1) sinusoidal stimulus frequency; 2) vibrator-probe acceleration, velocity, and displacement; 3) force; and 4) piezo-film dis-

placement. Additional signals recorded included sine waves from the vibrator controller, trapezoid waveforms from the ramp-and-hold generator, and synchronization (trigger) pulses from the square-wave stimulator.

In two cats, tooth pulp-evoked potentials (TPEPs) were recorded from the SLG surface with monopolar macroelectrodes (100  $\mu\text{m}$  tip diam) and were referenced to an indifferent platinum needle electrode inserted into the dorsal neck muscles. Monophasic pulses of 0.2 ms duration were delivered at a rate of two per second to the tooth pulp-stimulating electrodes ( $<5\text{ K}\Omega$  interelectrode impedance). A photoelectric stimulus isolation unit connected in series with the stimulator provided a constant current source for pulse stimulation. The TPEPs were led into a high-impedance probe and AC preamplifier with a frequency response of 30 Hz–3 KHz (3 dB down points, 6 dB/octave slope). The amplified signals and stimulator synchronization pulses were led to a computer for signal averaging. Each averaged record represented a summation of 64 successive trials and contained 1,024 data points (5  $\mu\text{s}$ /point sampling rate). Averages of TPEPs and calibration pulses were displayed on an oscilloscope, stored on magnetic disks, and subsequently plotted on an  $X$ - $Y$  plotter. In 20 cats, extracellular action potentials from the SLG were recorded through glass micropipette electrodes filled with 0.5 M sodium acetate and Pontamine sky blue dye (15–20 M $\Omega$  impedance,  $<0.5\text{ }\mu\text{m}$  tip diam). The location of the reference electrode and procedure for signal amplification, except for a frequency response of 100 Hz–3 KHz, were the same as those described above. Single-unit activity was displayed on an oscilloscope alongside signals related to calibrated mechanical stimulation and stored digitally on magnetic tape for subsequent data analysis.

### Data analysis

Annotated isopotential contour plots of TPEPs recorded from the SLG surface were constructed by graphics software (Surface II Graphics System, R. J. Sampson). A one-way analysis of variance was used to determine the significant main effect of stimulus direction on the threshold of PDLMs. The Student's  $t$  test (2-tail) was used to determine significance between various dynamic response properties of IMs and PDLMs (e.g., maximum frequency of discharge entrainment at the stimulus cycle length).

All unit discharges were screened before frequency analysis by a dual time-amplitude window discriminator regardless of single- or multiple-unit activity in the recording. Peristimulus time histograms of unit discharges were generated relative to mechanical stimulation with hand-held probes, and poststimulus time histograms were generated in relation to the onset of ramp and to the onset of stationary (hold) stimulation. The total spikes and average spikes per second were determined for both the ramp and plateau periods. Although displacement of the tooth was measured relative to a freely moving mandible, it was not possible to measure the actual displacement of the tooth in its bony socket in the *in vivo* preparation. The steady force and the rate of force applied to the tooth were used as the independent stimulus variables rather than tooth-mandible displacement and velocity. Instantaneous frequency (1/time interval) histograms were generated to examine the dynamic responses of IM and PDLM units. Single-unit discharges were processed in an interspike interval-to-voltage converter (Bak, ISI-1). The amplitude of each output pulse was directly proportional to the inverse of the interspike interval time and was displayed on the  $Y$  axis of a digital oscilloscope as a point. The instantaneous discharge frequency was plotted against voltages that were linearly proportional to ramp force or sine wave frequency on the  $X$  axis. All oscilloscope  $X$ - $Y$  displays were stored digitally on magnetic disks, and a "dot plot" program produced hard copies of the  $X$ - $Y$  functions.

### Classification criteria for dental receptors

Several criteria were used to initially differentiate IMs from PDLMs and to verify that IMs originated from the intact mandibular canine tooth. The intradental impulse collision test and nerve block test used in our earlier study (Dong et al. 1985) to establish the intradental origin of IMs were not employed here because implantation of stimulating and recording electrodes and of canulae for infusing a nerve blocking coolant would damage PDL receptors. Mechanoreceptors whose intradental origins were verified by electrophysiological tests in our previous study had response properties unlike those of PDLMs (Karita and Tabata 1985; Loescher and Robinson 1989; Tabata and Karita 1986). The following response profile was observed for every IM in both the earlier and present studies. 1) An IM was activated only by a rapid mechanical transient (i.e., light tap from aesthesiometer probe tip). 2) Only rapidly adapting discharges of one to three spikes were evoked by contact, and sometimes by retraction of the stimulus probe. No additional discharges were evoked by either steady force or displacement after initial contact with the stimulus probe. 3) An IM responded to a rapid mechanical transient applied in any direction (omnidirectional) and did not show directional selectivity to stimulation (stimulus threshold and response magnitude were approximately equipotent in all stimulus directions). We also determined that the receptive field of each IM was restricted to the mandibular canine tooth. Application of the same static and dynamic forces to adjacent gingiva, perioral tissues, and other teeth such as the incisors and molars did not evoke a response from an IM receptor. Activation of joint afferents by opening and closing the jaw also did not elicit IM discharges. Because mandibular canine IM units were isolated for study within a somatotopically organized region in the SLG (Amano et al. 1987; Arvidsson 1975; Shigenaga et al. 1989), it was unlikely that we recorded from non-mandibular units activated by dynamic stimulus forces transmitted through the mandibular canine tooth to nerve endings in other intraoral structures. In contrast to the response profile of IMs, the following response characteristics were observed in PDLMs. 1) A PDLM was activated by steady force or displacement. 2) Slowly adapting responses were usually evoked by such stimulation. 3) A PDLM displayed directional selectivity to stimulation.

### RESULTS

The optimal site in the SLG for sampling neurons that innervate the ipsilateral mandibular canine tooth pulp was identified from maps of the topographic amplitude distribution of TPEPs. As shown in Fig. 1, TPEPs were recorded from the epidural surface of the mandibular division (III) of the SLG and represented on an annotated isopotential contour map. The first positive wave or A-beta component of the TPEP, which has an average peak latency of 1.7 ms, was recorded at 0.5-mm intervals along a rectangular grid of points and was measured from baseline to peak amplitude. The location of the largest amplitudes, which reflect the origin of the current generator source, was at the center of the mandibular division and corresponded to the site from which canine IMs were most frequently isolated in our previous study (Dong et al. 1985). Thirty-nine PDLMs and 12 IM units were isolated for study from the SLG area circumscribed by the 4- $\mu\text{V}$  isopotential contour line in Fig. 1. No functional segregation of these neurons was observed within this area. None of the units exhibited spontaneous discharges, and all responded to a search stimulus of sinusoidal

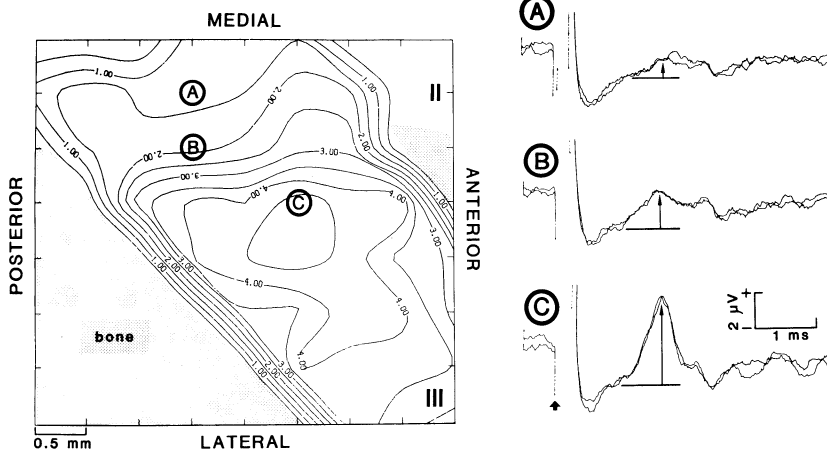


FIG. 1. Surface (epidural) distribution of canine tooth pulp-evoked potentials on the mandibular division (III) of the trigeminal ganglion. No potentials were observed on the maxillary division (II). Potentials were recorded from a rectangular grid of points equally spaced in the anterior-posterior and medial-lateral directions at 0.5-mm intervals. Pairs of evoked potentials were recorded from each locus, and each evoked potential represented an average of 64 trials. An isopotential contour map was constructed from the baseline to peak amplitude measurements of the first positive wave or A-beta component ( $\rightarrow$ ). Contour lines are displayed in incremental steps of 0.5  $\mu$ V and superimposed on the X-Y recording grid. Pairs of overlapping traces (A-C, right) are representative of 3 isopotential contour levels (A-C, left). Short arrow: stimulus onset and subsequent stimulus artifact.

dal vibration applied along the mesial (anterior)-distal (posterior) plane of the canine tooth.

The canine PDLM and IM units were initially differentiated by the response criteria described above (see METHODS). Mechanical stimulation delivered by hand-held aesthesiometers was used to assess the stimulus threshold and relative response magnitude in each of five stimulus directions. For each PDLM, the response magnitude measured as the peak discharge per second was not similar in all directions of stimulation at suprathreshold intensity ( $>50$  mN). Among the 39 PDLMs studied, 34 had no response to stimulation in one or more of the five directions tested. In every case, the lowest stimulus thresholds were associated with the direction(s) of maximum response sensitivity. PDLM stimulus threshold for a given direction was determined by slowly applying force until discharges were detected by the investigators. Thresholds determined by manual stimulation were higher than thresholds determined by ramp-and-hold stimulation (see below). Canine PDLMs as a population did not appear to have a preferred direction of stimulation. The mean stimulus thresholds for forces applied in each direction were the following: mesial to distal,  $26 \pm 19$  (SD) mN; distal to mesial,  $22 \pm 18$  mN; labial to lingual,  $15 \pm 13$  mN; lingual to labial,  $18 \pm 14$  mN; crown to root,  $20 \pm 14$  mN. No significant main effect of stimulus direction on the threshold of the PDLM population was concluded by using an ANOVA. The difficulties of delivering controlled percussive forces by a hand-held aesthesiometer and of detecting rapidly adapting IM discharges (1–3 spikes) evoked by such stimulation precluded accurate measurement of IM stimulus thresholds. However, the response magnitude measured as the total discharge was identical in all directions of stimulation at suprathreshold intensity ( $>50$  mN).

### Responses to ramp-and-hold stimulation

Eleven PDLMs that were maximally sensitive to manual stimulation of the canine tooth in the mesial-to-distal direction were studied further by trapezoidal ramp-and-hold stimulation. The stimulus threshold for ramp-and-hold forces applied in the mesial to distal direction from an unloaded (resting) tooth position was  $9.7 \pm 5.8$  (SD) mN. No discharges were observed when the tooth was in its unloaded position. The relationship between steady (plateau)

forces and static responses for each PDLM is summarized in Fig. 2. All PDLMs, except one PDLM that adapted completely during the ramp, exhibited higher mean discharge rates in response to increments of steady force. The stimulus-response function was steepest when steady forces were applied at various levels  $<20$  mN. Under static force, the PDLMs (except 1) displayed either a slowly adapting or nonadapting response (see example in Fig. 3). The interspike intervals of PDLMs were generally uniform rather than variable in length, and consequently, the interval distribution of the adapted discharge was Gaussian (normal) rather than Poisson (random). Figure 3 illustrates the normal interspike distribution of the adapted discharge of a PDLM. A  $\chi^2$  analysis for goodness of fit of a normal distribution (Zar 1984) at several levels of applied steady force

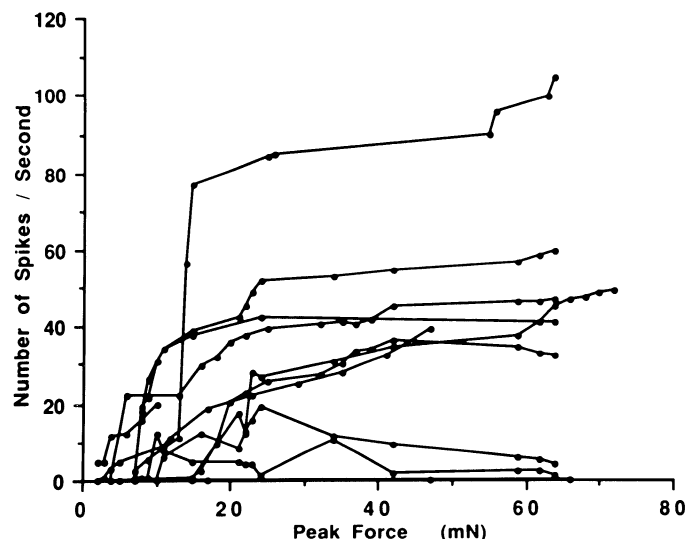


FIG. 2. Response of periodontal ligament mechanoreceptors (PDLMs) to steady force stimulation. Ramp-and-hold stimuli were tested on 11 PDLM units; force was applied to the canine tooth from its unloaded (resting) position and in the mesial (anterior)-to-distal (posterior) direction. All peak forces were reached on completion of force ramps that had a short duration of 125 ms and rates ranging from 16 to 576 mN/s. The peak force was held steady for 5 s, and the average number of spikes per second at the plateau force was calculated. All PDLMs, except 1 that adapted completely during the ramp, demonstrated graded static responses to increments of peak force. Intradental mechanoreceptors did not discharge during application of a steady force to the tooth and thus are not represented in this graph.

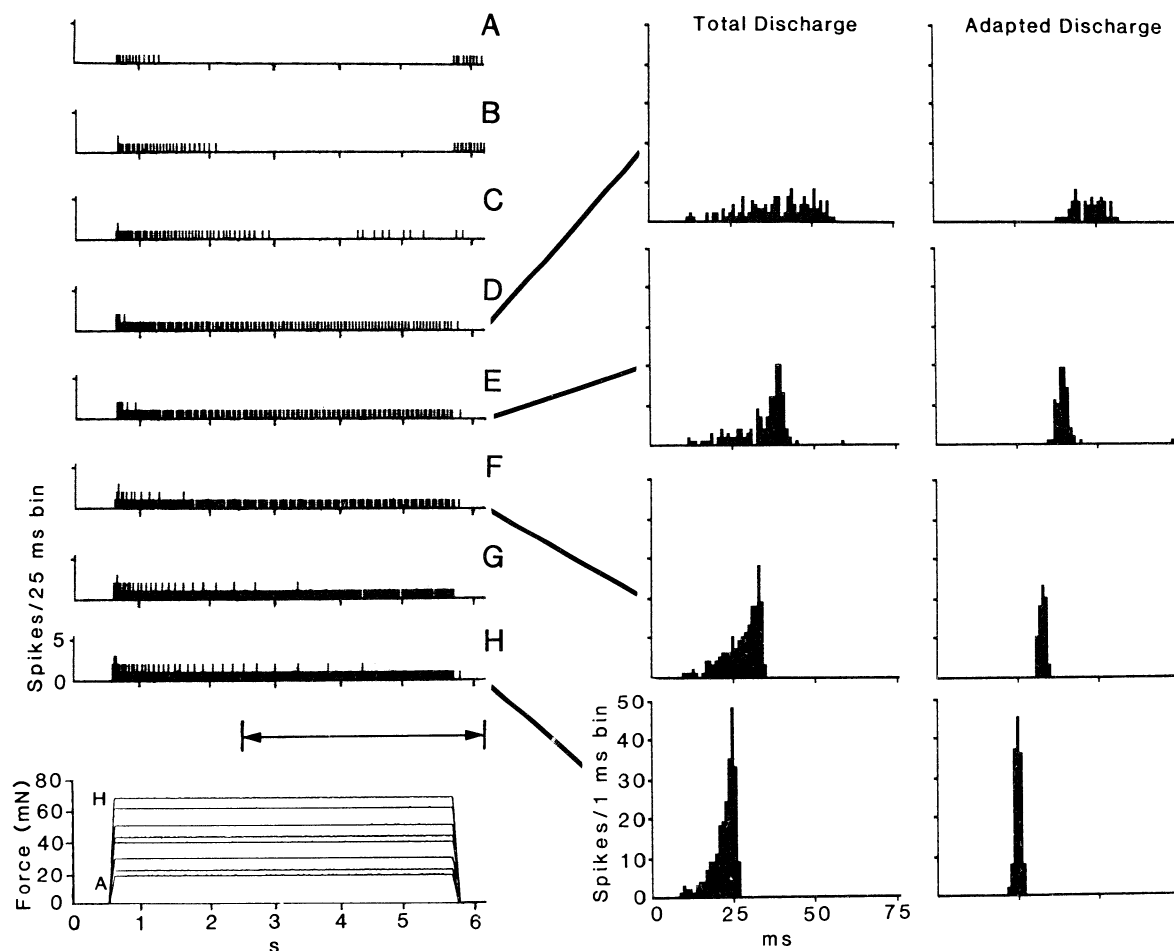


FIG. 3. Discharge adaptation of a periodontal ligament mechanoreceptor (PDLM) to steady force stimulation. Ramp-and-hold stimuli were applied to the canine tooth from its unloaded position and in the mesial-to-distal direction. All peak forces (A–H, bottom left) were reached on completion of force ramps with a 125-ms duration and rates ranging from 144 mN/s (A) to 544 mN/s (H). The peak force was held steady for 5 s. Peristimulus time histograms (left) illustrate the discharge rate and pattern in response to increments of steady force. This PDLM unit displayed a slowly adapting response during static force; discharges were also observed after release of smaller steady forces (A and B). Time interval histograms (right) show the distribution of interspike intervals for several levels of steady force (D–F and H); both the total discharge after onset of peak force and the adapted discharge after 2 s of peak force onset ( $\leftrightarrow$ ) were analyzed. Note the general shortening of interspike intervals for both the total and adapted discharges in response to increments of steady force. The interval distribution of the adapted discharge was normal as determined by a  $\chi^2$  analysis for goodness of fit of normality. In each case (D–F and H), the null hypothesis that the intervals came from a normal population was tested and not rejected ( $P > 0.05$ ). Values of the  $\chi^2$  distribution were 20.67, 11.32, 9.96, and 2.89, respectively.

(Fig. 3, D–F and H) showed that the null hypothesis in each case was true ( $P > 0.05$ ); that is, the interspike intervals came from a normal population. Three IMs were tested with percussive ramp-and-hold stimulation applied in the mesial-to-distal direction. The stimulus threshold of the IMs was  $32 \pm 13$  (SD) mN and was significantly higher than that of PDLMs (Wilcoxon rank-sum test,  $S = 33$ ,  $P < 0.01$ ). IMs did not encode steady forces because their evoked discharges adapted completely during percussive ramp stimulation.

The responses of the same PDLMs and IMs to dynamic force stimulation of the tooth in the mesial-to-distal direction are illustrated in Figs. 4 and 5. In Fig. 4, the total number of discharges during each ramp was measured and plotted against the respective ramp force rate (millinewtons per second). For each unit, a set of ramp force rates was applied to reach a fixed suprathreshold peak force. Because these PDLMs (except 1) discharged during both the ramp-and-

hold phases of the stimulus, their total ramp discharges were reduced as would be expected by higher ramp rates (shorter effective stimulus duration). For a given ramp rate, however, a wide range of total ramp discharges or responsiveness was observed for the PDLM population. In contrast, the total ramp discharges of IM units were increased from one to two or three discharges by higher ramp rates. IM activation, however, required a force ramp that was applied by percussion to the tooth. Evidence of dynamic responses in both PDLMs and IMs was obtained from analysis of mean instantaneous or peak discharge frequencies at different ramp force rates. As shown in Fig. 5, three PDLMs and one IM were each presented with three different ramp rates, and the resulting instantaneous discharge frequency was plotted against the ramp force for each ramp rate. The three PDLMs illustrated in Fig. 5 (A–C) represent units with widely different responsiveness (total ramp discharges) to a given ramp rate. In every case, the

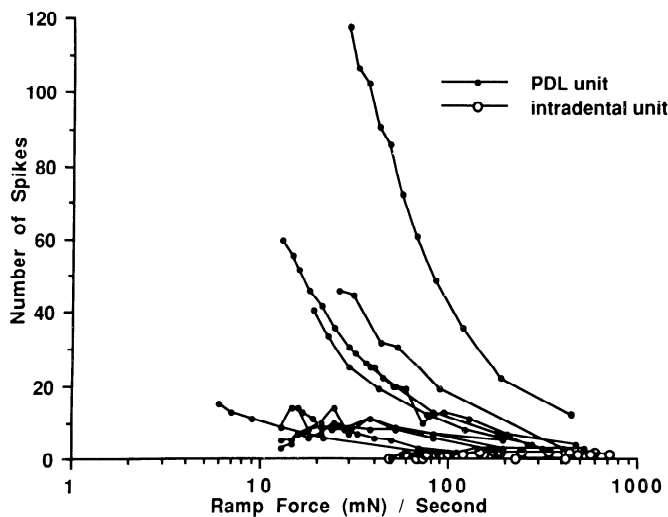


FIG. 4. Response of intradental and periodontal ligament mechanoreceptors to dynamic force stimulation. Ramp-and-hold stimuli were tested on 11 periodontal ligament mechanoreceptor (PDL) and 3 intradental mechanoreceptor (IM) units; force was applied to the canine tooth from its unloaded position and in the mesial to distal direction. Response from 2 IM units was evoked only by tooth percussion, which required a distance of 0.5 mm between the stimulus probe and tooth before delivering ramp force stimulation. For each unit, a set of ramp force rates was applied to reach a fixed suprathreshold peak force (range of 10–66 mN for all units). The total number of spikes evoked during each ramp was measured and plotted against the respective ramp rate. Total ramp discharges of IM units were increased from 1 to 2 or 3 discharges by higher ramp rates; total ramp discharges of slowly adapting PDL units were reduced as would be expected by higher ramp rates (shorter ramp durations). Despite differences in stimulus threshold and onset of ramp discharges, note the different responsiveness (total ramp discharges) between PDL units for a given ramp rate.

stimulus force-response functions were displaced upward by increasing the ramp force rate. The upward displacement of the curves indicates that the increased instantaneous discharge frequency was due to increased ramp rates and not to ramp forces, which were the same for each rate. It should be noted that the ramp force-vs.-response curves did not merely steepen, which might occur if the ramp rates acted only to exceed the decay time for discharge adaptation. At the lowest ramp force rate (e.g., 13 or 30 mN/s), a bimodal distribution of interspike intervals or discharge frequencies was observed in PDLs as force increased. In Fig. 5D, an IM unit displayed a typical small increase in both total ramp discharges and instantaneous discharge frequency at higher ramp rates.

#### Responses to sinusoidal vibratory stimulation

Physiological differences between PDL and IM units were also evidenced by their dynamic responses to controlled vibratory stimulation applied along the mesial-distal plane of the canine tooth. Fourteen PDL and nine IM units were tested by applying sinusoidal vibration at various fixed frequencies as well as across a range of frequencies in which an ascending, unidirectional sweep was made while maintaining constant peak acceleration. For each unit, constant peak acceleration was increased for each successive frequency sweep to determine the maximum frequencies for discharge entrainment. At low stimulus frequen-

cies, both PDLs and IMs responded to stimulation applied in either the mesial-to-distal or distal-to-mesial direction from the unloaded tooth position; the response in either direction was most often composed of multiple discharges. Bidirectional responses and multiple discharges, respectively, were observed in PDLs below stimulus frequencies of  $48 \pm 36$  (SD) Hz and  $32 \pm 15$  Hz and were observed in IMs below frequencies of  $71 \pm 34$  and  $52 \pm 23$  Hz. These mean stimulus frequencies were higher for the IMs than PDLs but were not significantly different (*t* test,  $P > 0.05$ ). Of particular importance was the determination that the maximum frequency ( $251 \pm 103$  Hz, mean  $\pm$  SD) for entrainment of IM discharge at the stimulus cycle length (1:1) was significantly higher than the maximum frequency ( $103 \pm 53$  Hz) for entrainment of PDL discharge at the stimulus cycle length (*t* test,  $P < 0.01$ ). Moreover, the maximum frequency ( $295 \pm 100$  Hz, mean  $\pm$  SD) at which any kind of periodic entrainment could be observed visually for IM discharges including interval multiples of the stimulus cycle length (1:2, 1:3, 1:4, etc.) was also significantly higher than the maximum frequency ( $133 \pm 62$  Hz) for similar PDL discharge entrainment (*t* test,  $P < 0.01$ ).

An example of the dynamic responses of a PDL evoked by sinusoidal vibration frequencies is shown in Fig. 6. The PDL unit was readily identified by static response characteristics related to stimulus directionality, which included differential thresholds, response magnitudes, and adaptation rates (see *top right* panel). Sinusoidal frequencies from 10 to 100 Hz were applied at a constant peak acceleration of 0.2, 0.6, 0.8, or 1.5 g; the velocities and displacements ( $\frac{1}{2}$  sine wave cycle) associated with each level of constant peak acceleration were obtained from both direct measurements and a vibration nomograph. Force at each frequency was also increased by the increments in acceleration (not shown). Represented in the instantaneous discharge frequency histogram at stimulus frequencies between 10 and 18 Hz are multiple discharges evoked in each stimulus direction. Entrainment of discharge at the stimulus cycle length and at multiples of the cycle length was observed between 18 and 79 Hz at a constant peak acceleration of 0.8 or 1.5 g. Increasing the constant peak acceleration to  $>0.8$  g did not increase the frequency of discharge entrainment. High-frequency discharges were observed at resonant frequencies of tooth and mandible vibration (30–40 Hz). Shown in Fig. 7 is an example of the dynamic responses of an IM evoked by sinusoidal vibration frequencies. Percussive stimulation of the tooth in any direction evoked two or three spikes; no responses were evoked during steady force or displacement. At stimulus frequencies between 10 and 77 Hz, multiple discharges were elicited in each stimulus direction. In contrast to the PDL unit described above, the dynamic response range of the IM was considerably wider. Entrainment of discharge at the stimulus cycle length and at multiples of the cycle length was observed between 77 and 374 Hz at a constant peak acceleration of 0.4 or 0.6 g. High-frequency discharges were also observed at several resonant frequencies of tooth-mandible vibration (indicated by arrows). Increasing the constant peak acceleration to  $>0.4$  g did not increase the frequency of discharge entrainment.

Frequency tuning or cyclic entrainment of PDL and IM discharges were also studied by construction and analy-

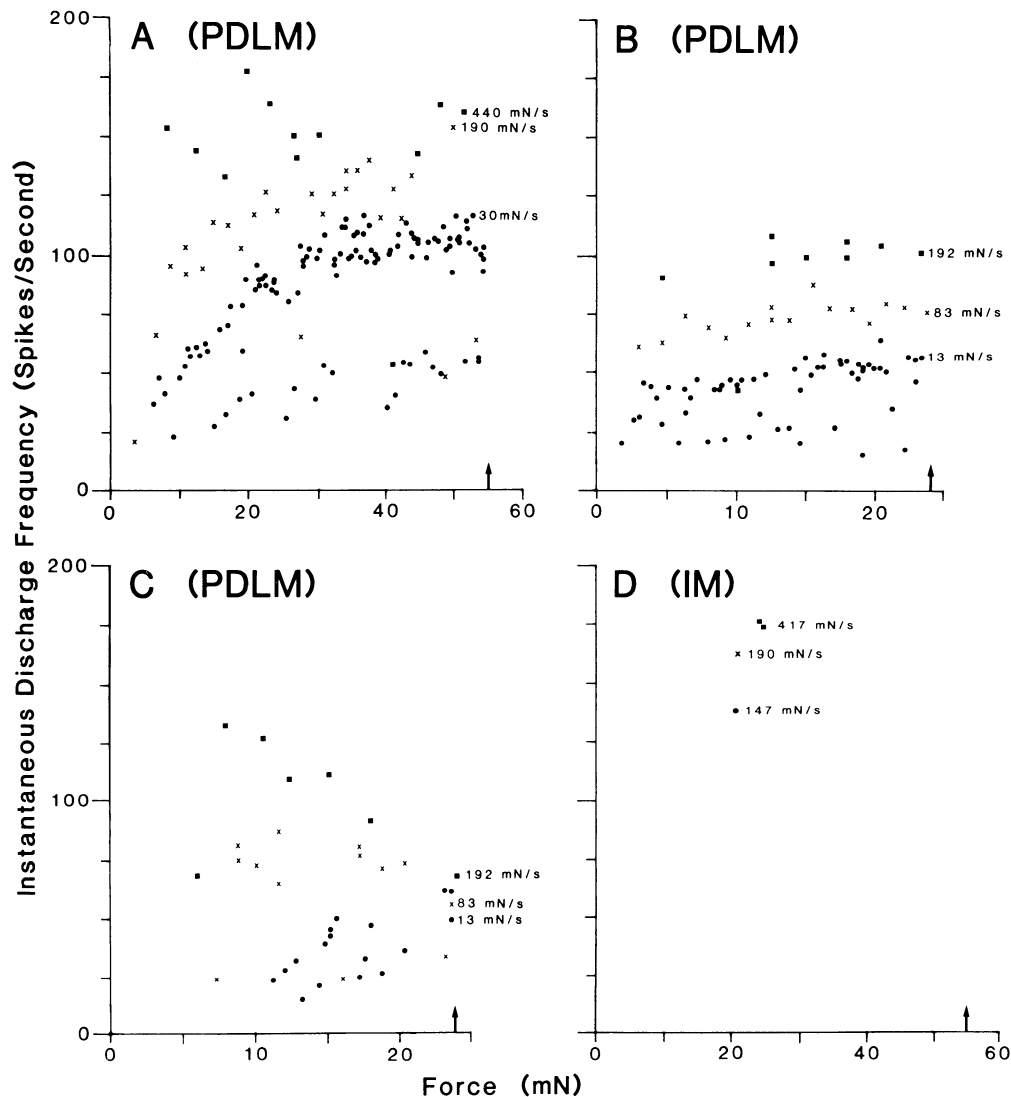


FIG. 5. Discharge of intradental mechanoreceptors (IMs) and periodontal ligament mechanoreceptors (PDLMs) as a function of ramp force at different ramp force rates. Ramp-and-hold stimuli were applied to 1 IM and 3 PDLM units; force was applied to the canine tooth from its unloaded position and in the mesial-to-distal direction. In each panel, discharges of a unit to ramp-force stimulation are plotted as symbols on an instantaneous frequency (1/time interval) histogram. Each symbol represents the reciprocal of the interval between 2 successive spikes plotted at the ramp force of the 2nd spike. Different symbols ( $\blacksquare$ ,  $\times$ ,  $\bullet$ ) are used to identify discharges associated with application of 3 ramp force rates; each ramp force rate is shown immediately to the right of a symbol type used to represent related discharges. Arrow on the ramp force scale (abscissa): termination of dynamic force stimulation and the onset of steady force stimulation (no static responses are plotted). In A–C, the frequency and pattern of discharges at different ramp force rates are representative of PDLM units with high, intermediate, and low total ramp discharges, respectively (also see Fig. 4). The low total ramp discharge (1–3 spikes) depicted in D is typical of IM units. Response from the representative IM unit was evoked only by tooth percussion, which required a distance of 0.5 mm between the stimulus probe and tooth before delivering ramp force stimulation.

sis of interval and cycle histograms. Absolute and tuning thresholds were determined at various fixed sine wave frequencies by varying the stimulus acceleration and consequently displacement, velocity, and force. The interspike interval histograms illustrated in Fig. 8, A and B, respectively, are typical of both IM and PDLM responses in that discharge entrainment gradually shifts by increasing the stimulus intensity from multiples of the sine wave period at the absolute threshold to unity with the sine wave period at the tuning threshold. One-to-one frequency tuning at 250 Hz for the IM and at 50 Hz for the PDLM was attained at higher accelerations and forces (*top* histograms) when  $\sim 100\%$  of the successive interspike intervals had an inter-

spike interval time equal to the sine wave period of 4 or 20 ms. Phase-locking of discharges to a narrow portion of the sine wave cycle was evident on analysis of the cycle histograms. Responses to successive stimulus cycles at 250 Hz for the IM and at 50 Hz for the PDLM are shown in Fig. 9, A and B, respectively. Increasing the acceleration and the force increased the percentage of cycles in which one spike was phase-locked to half the stimulus cycle. Regardless of whether the temporal firing pattern of these cells was analyzed by an interval or cycle histogram, the same stimulus strengths were needed in each case to produce near-perfect entrainment of one discharge per stimulus cycle (cf. Figs. 8A vs. 9A and Figs. 8B vs. 9B). A prominent phase shift of

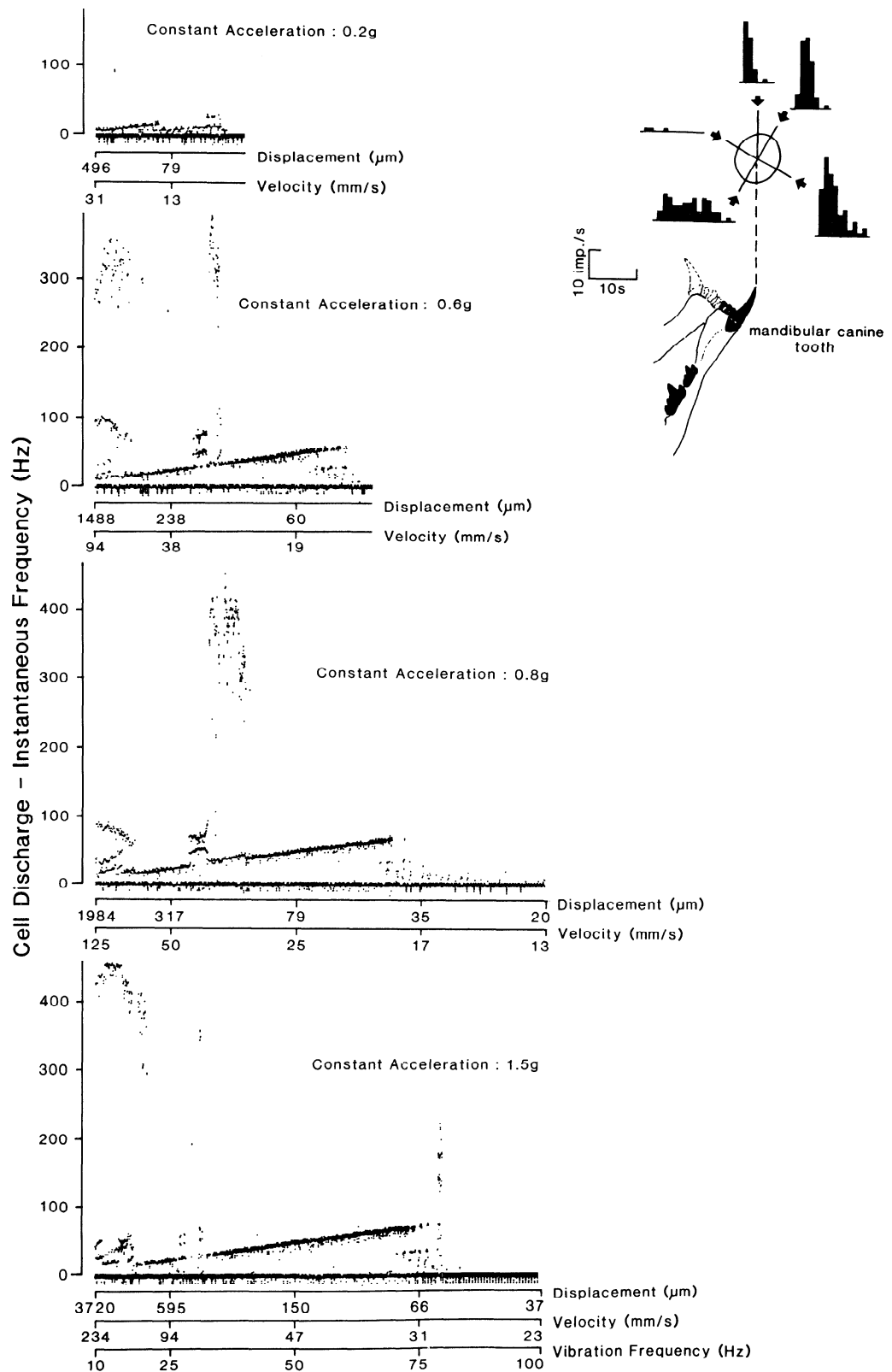


FIG. 6. Dynamic responses of a periodontal ligament mechanoreceptor to sinusoidal vibration frequencies. Static responses to sustained suprathreshold stimulation ( $>50$  mN) applied along the vertical axis of the canine tooth crown and in various directions perpendicular to the vertical axis are shown at the *top right*. Stimulus thresholds depending on the direction of applied force ranged from 4 to 10 mN. Other features associated with directional selectivity included differences in adaptation rate and in the total or peak discharge frequency. Sinusoidal stimulation was applied along the mesial-distal plane of the canine tooth. A range of sinusoidal frequencies (10–100 Hz) was applied at a constant peak acceleration of 0.2, 0.6, 0.8, or 1.5 g and at velocities and displacements ( $\frac{1}{2}$  sine wave cycle) associated with a given acceleration. Individual discharges are represented as points on an instantaneous-frequency (1/time interval) histogram. Stimuli from 10 to 18 Hz



discharges by increasing stimulus intensity was noted in PDLMs. Some IM units, like the one shown in Fig. 9A, displayed an additional one or two discharges during the opposite half cycle of stimulation. Tuning curves for PDLMs and IMs were constructed from interspike interval histograms that displayed tuning thresholds at various sine wave frequencies (e.g., Fig. 8). Each point on a tuning curve for the PDLM or IM unit in Fig. 10A represents the lowest force at a given frequency for which  $\sim 100\%$  of the successive discharges were entrained to one cycle length. Entrainment of one spike to each cycle for the PDLM and IM units in this example, respectively, was not possible at  $>100$  and  $250$  Hz. Tuning curves for both the PDLM and IM were positively accelerating such that tuning at the highest frequencies required the highest forces. It is important to note that the forces necessary for frequency tuning of IMs at  $<100$  Hz were generally lower than those forces for PDLMs. Of particular interest is evidence that the dynamic behavior of PDLMs and IMs to vibratory stimulation may be dependent on the biomechanics of the tooth-mandible structure. The mechanical impedance curves for the tooth-mandible *in vivo* are also positively accelerating like the PDLM and IM tuning threshold curves over the same sinusoidal stimulus frequency range. The mechanical impedance or resistance of the tooth-mandible to being set in motion over a range of sine wave frequencies is shown in Fig. 10B. Mechanical point impedance ( $Z$ ) is the ratio of the force ( $F$ ) exciting a structure to the resulting velocity ( $V$ ) and thus was determined by measuring the velocity and force at the same point ( $Z = F/V$ ). The velocity level of the measuring point was kept constant to measure the force that indicates the modulus of impedance as functions of frequency. The two impedance curves shown in Fig. 10B were generated at different constant velocities and have the same function over the tested frequency range.

## DISCUSSION

Physiological differences between PDLMs and IMs have been elucidated in this study by using static and dynamic mechanical stimulation. Qualitative stimulation clearly demonstrated that each IM displayed rapidly adapting responses of equal magnitude to mechanical transients applied in all tooth directions. In contrast, each PDLM exhibited directional selectivity in that its response threshold and sensitivity were dependent on the direction of tooth stimulation. Quantifiable ramp-and-hold stimulation revealed that PDLMs can modulate their discharge frequency to encode the intensity of steady forces as well as the rate of force ramps. However, IMs encoded only the rate of force ramps that were applied by percussion to the canine tooth. IMs also had fewer discharges (1–3 spikes) than PDLMs in response to the same force ramps. The dynamic response properties of PDLMs and IMs were clearly differentiated by sinusoidal vibratory stimulation. The maximum frequencies for entrainment of IM discharge at the stimulus cycle

length and at any periodicity including multiples of the stimulus cycle length were significantly higher than the maximum frequencies for similar PDLM discharge entrainment.

### *Response properties of PDLMs*

The PDLMs have many response properties that are similar to those of slowly adapting type II (SAII) cutaneous mechanoreceptors (Burgess and Perl 1973; Darian-Smith 1984; Iggo 1974). Some of these characteristic response features include: 1) discharges observed during both the dynamic and static phases of mechanical stimulation, 2) interspike intervals related to both stimulus amplitude (displacement or force) and velocity (or force rate) components, 3) spatial directionality and sensitivity, 4) Gaussian (normal) or regular interval distribution of the adapted static discharge, and 5) adapted-position (static) responses related to stimulus amplitude in a narrow dynamic range. Cutaneous mechanoreceptors with SAI response properties have been correlated to histologically identified Ruffini sensory terminals (Chambers et al. 1972). Likewise, PDLMs with SAI-like properties and perhaps even those with more rapidly adapting properties have been found to overlie Ruffini terminals (Millar et al. 1989). Linden and co-workers (Cash and Linden 1982; Linden and Millar 1988a) have suggested that only one morphological type of PDLM exists and that the threshold and adaptation property of a PDLM depend on the position of the receptor relative to the fulcrum of the tooth. However, Loescher and Robinson (1989) found no apparent relationship between the distance of the receptor from the tooth fulcrum and its arc of directional sensitivity, threshold, maximum discharge frequency, response duration, or adaptation rate. The mean force thresholds of PDLMs in our study are in general agreement with values reported in other studies of the cat canine tooth (Linden and Millar 1988b; Loescher and Robinson 1989; Pfaffmann 1939a). However, the force threshold observed in either animals (Hannam 1969; Linden and Millar 1988b; Loescher and Robinson 1989) or humans (Linden 1975; Lowenstein and Rathkamp 1955; Schoo et al. 1983; van Steenberghe and de Vries 1978) can vary widely and may be dependent on the rate of force application. The mean conduction velocities of PDLMs determined from recordings in the inferior alveolar nerve (IAN), SLG, and mesencephalic trigeminal nucleus (MS) indicate that they are supplied by A-alpha and A-beta fibers like SAI cutaneous mechanoreceptors (reviewed by Iggo 1974 and Loescher and Robinson 1989). Results from a recent study (Mengel et al. 1992) of periodontal C-fiber afferents with polymodal response properties suggest that the free unmyelinated terminals in the PDL may subserve thermal and mechanical nociception but not mechanoreception.

Our results are in agreement with those of Linden and Scott (1989), who found that the directions of maximum

evoked bidirectional responses and multiple discharges in either direction. Entrainment of 1 discharge per stimulus cycle occurred within the range of 18–72 Hz when constant peak acceleration was set at 0.8 or 1.5 g. Between 72 and 79 Hz, discharges occurred infrequently at the cycle length and more commonly at interval multiples of the cycle length (1:2, 1:3, 1:4, etc.). The points representing a 0 or negative instantaneous discharge frequency are artifacts of the interspike interval to voltage conversion apparatus.

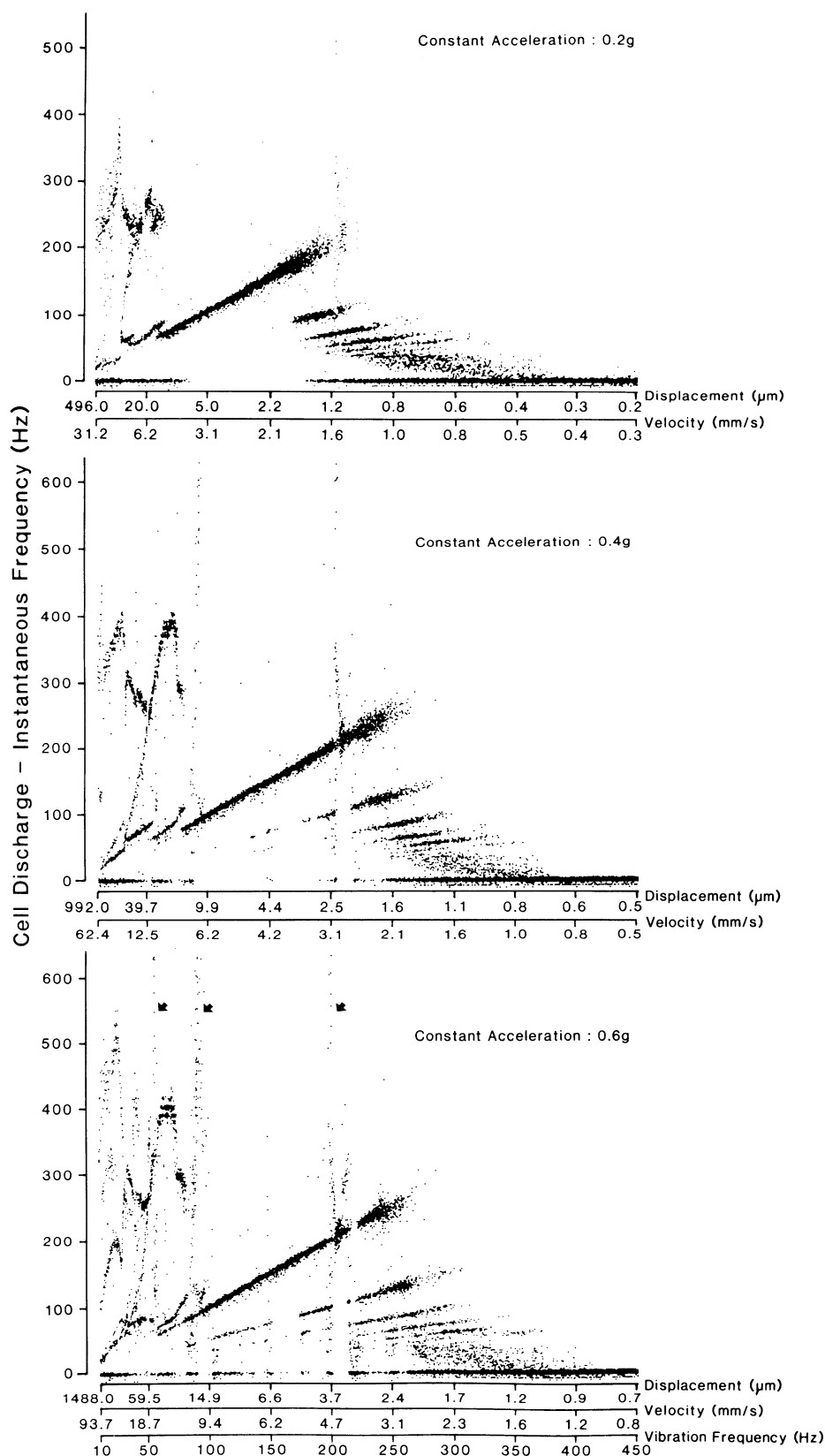


FIG. 7. Dynamic responses of an intradental mechanoreceptor to sinusoidal vibration frequencies. No responses were evoked by application of a steady force or displacement. Mechanical transients applied to the canine tooth in any direction elicited 2 or 3 discharges. Sinusoidal stimulation was applied along the mesial-distal plane of the canine tooth. A range of sinusoidal frequencies (10–450 Hz) was applied at a constant peak acceleration of 0.2, 0.4, or 0.6 g and at velocities and displacements ( $\frac{1}{2}$  sine wave cycle) associated with a given acceleration. The instantaneous frequencies (1/time interval) of the discharges are plotted against the stimulus frequency. Between stimulus frequencies of 10 and 77 Hz, multiple spikes were evoked in response to stimulation applied in either direction from the unloaded tooth position. Entrainment of 1 discharge per stimulus cycle occurred within the range of 77–207 Hz when constant peak acceleration was set at 0.4 or 0.6 g. Between the stimulus frequencies of 207 and 374 Hz, discharge occurred at the cycle length ( $\leq 253$  Hz) and at interval multiples of the cycle length. Arrows in the *bottom* panel: high-frequency discharges elicited at several resonant frequencies of tooth and mandible vibration. The points representing a 0 or negative instantaneous discharge frequency are artifacts of the interspike interval to voltage conversion devices.

sensitivity of PDLMs recorded from the SLG were equally distributed around the circumference of the canine tooth root. In contrast, Loescher and Robinson (1989) and Tabata and Karita (1986) found that the directions of maximum sensitivity of PDLMs were unevenly distributed

around the tooth; a significantly greater number of PDLMs responded maximally to forces directed through an arc in the distolingual direction. The differences among the studies may be attributed to differences in the method of cell sampling such as the isolation of single-fiber activity in the

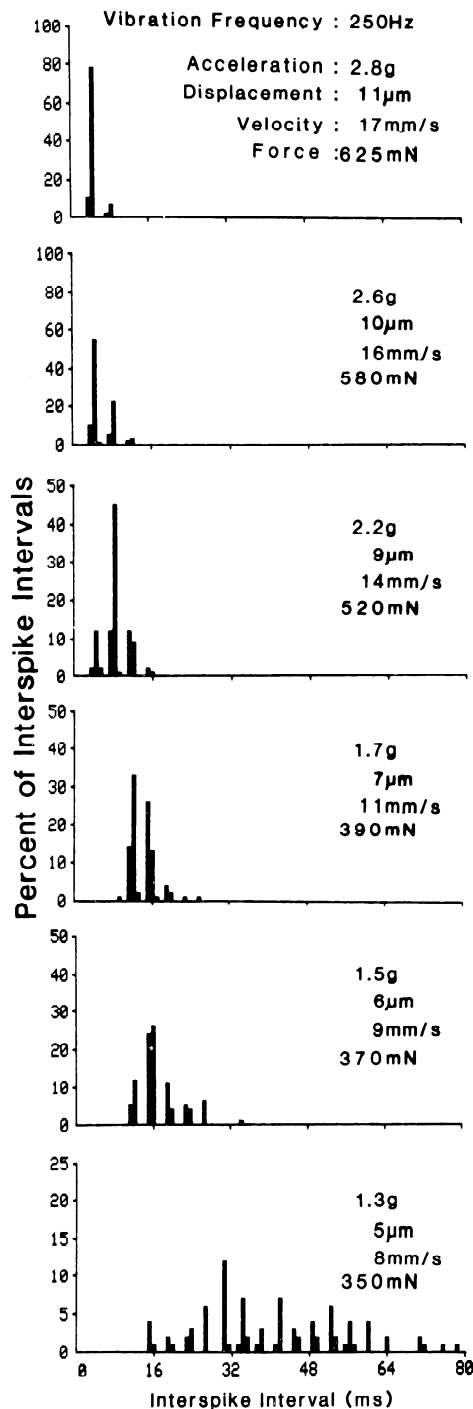
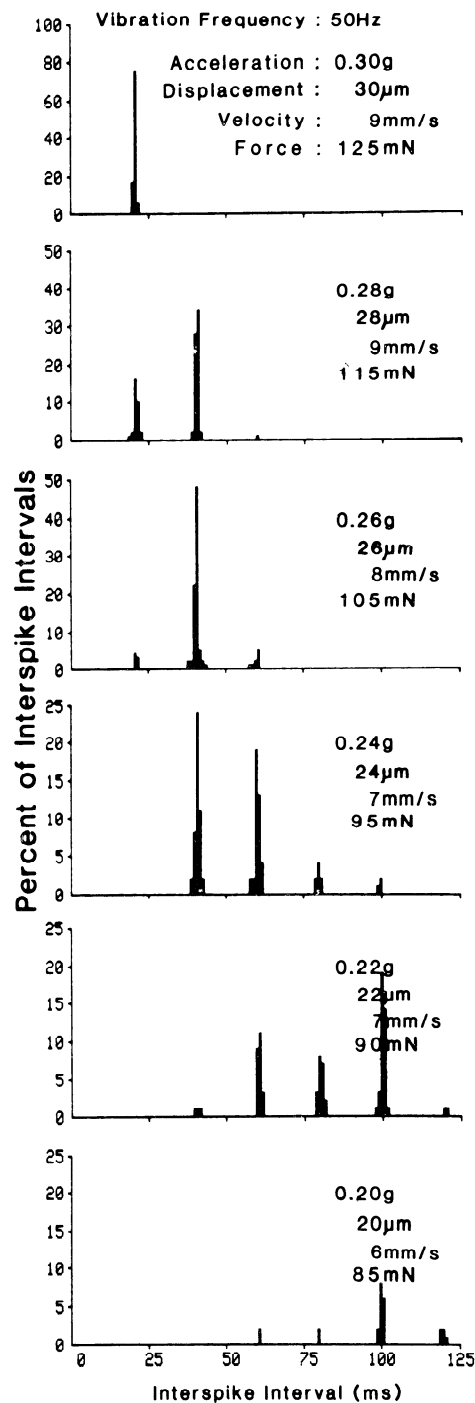
**A (IM)****B (PDLM)**

FIG. 8. Absolute and tuning thresholds of intradental mechanoreceptors (IMs) and periodontal ligament mechanoreceptors (PDLMs). Sinusoidal vibratory stimulation was applied to activate an intradental mechanoreceptor (*A*) at 250 Hz and to a periodontal ligament mechanoreceptor (*B*) at 50 Hz. One-to-one frequency tuning or entrainment of 1 spike to each sine wave cycle was possible for the IM and PDLM, respectively, at frequencies of 250 and 50 Hz but not at 275 and 75 Hz. A set of graded forces was applied along the mesial-distal plane of the mandibular canine tooth at 50 or 250 Hz. The PDLM was maximally sensitive to stimulation in either direction along this plane, whereas the IM was equally sensitive to stimulation in any direction. An interspike interval histogram was generated at each force level using 100 successive spikes, irrespective of the serial or temporal order of spike intervals and stimulation cycles and of the number of resultant cycles. The force indicated in each histogram was applied from the unloaded tooth position to either mesial or distal position ( $\frac{1}{2}$  sine wave cycle); the associated tooth-mandible acceleration, velocity, and displacement are also indicated. The absolute and tuning threshold responses for each frequency are represented, respectively, in the *bottom* and *top* histograms. The ordinate displays the relative frequency (as a percentage) of a given interspike interval (abscissa).

IAN, which projects to either the MS or SLG, as opposed to isolation of cell activity solely in the SLG. Interestingly, Linden and Scott (1989) showed that the majority of PDLMs recorded from the MS responded maximally when forces were directed through a wide arc in the mesiolabial direction. The difference in directional sensitivity between PDLMs in the SLG and MS may be related to the location of their terminals in the PDL of the canine tooth. Byers et al. (1986) and Byers and Dong (1989), using autoradiographic labeling techniques, found that cell bodies in the MS and SLG were distributed differently in the periodontal

ligament of the cat canine; the MS terminals were concentrated below and next to the base of the root (tooth apex), whereas the SLG receptors were around the middle of the root (near the tooth fulcrum). These observations are contrary to results from an electrophysiological study that showed MS terminals distributed discretely around the middle of the root and SLG terminals distributed widely over the lower half of the root (Linden and Scott 1989). Further studies will be needed to resolve this discrepancy and to determine whether the density of MS or SLG terminals is different along the circumference (i.e., mesial, distal,

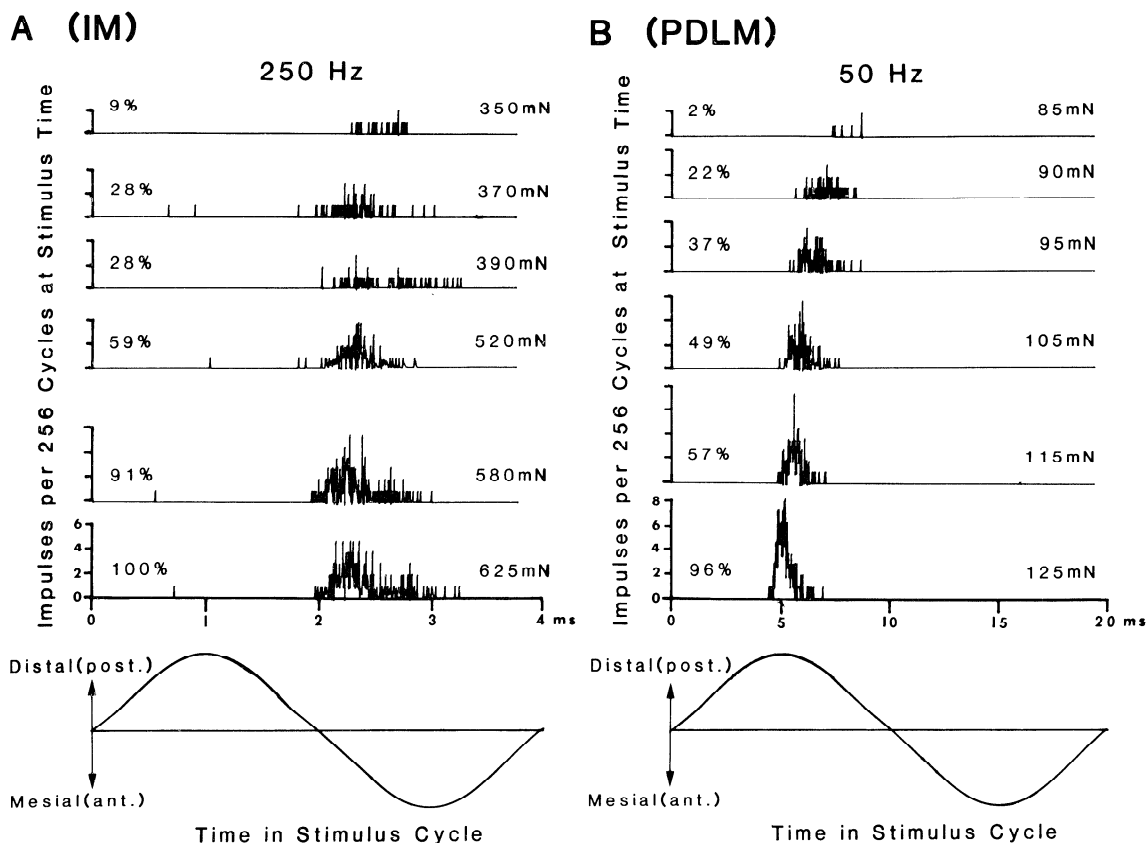


FIG. 9. Cyclic entrainment of discharge in intradental mechanoreceptors (IMs) and periodontal ligament mechanoreceptors (PDLMs). Sinusoidal stimulation at 250 and 50 Hz was applied, respectively, to the same IM (A) and PDLM (B) described in Fig. 8. A set of graded forces were applied along the mesial-distal plane of the mandibular canine tooth at 50 or 250 Hz. A cycle histogram was generated at each force level using 256 successive stimulus cycles independent of the serial or temporal order of individual spikes and stimulation cycles and of the number of resulting spikes. The force indicated in each histogram was applied from the unloaded tooth position to either the mesial or distal position ( $\frac{1}{2}$  sine wave cycle). The percentage entrainment of 1 spike within a half-cycle is indicated in each histogram. Observe 1) the phase-locking between the stimulus and response, 2) the prominent phase shift of PDLM discharges as stimulus intensity increased, and 3) the additional IM discharges in the opposite half cycle of stimulation.

lingual, labial aspects) of the tooth root than it is along the longitudinal axis of the root.

The present results confirm and extend the earlier findings of PDLM sensitivity to the dynamic component of mechanical stimulation (Hannam 1969). Increasing the rate of a given force ramp increased the peak or instantaneous discharge frequency during the ramp. The functional significance of this response property is uncertain; we need to determine whether central neurons that receive PDLM input encode ramp rates with the same fidelity and whether such neural encodement is correlated to perceptual discrimination of the same rates. We also showed that PDLM discharges can be entrained (1:1) to a sinusoidal vibration frequency as high as  $103 \pm 53$  (SD) Hz. This is in good agreement with the maximum one-to-one frequency tuning of slowly adapting (SA) cutaneous mechanoreceptors at  $\sim 128$  Hz to perpendicular sinusoidal vibration of human glabrous skin (Johansson et al. 1982). These maximum entrainment frequencies are much lower than the  $311 \pm 70$  Hz for PDLMs reported by Linden and Millar (1989) and the range of "following frequencies" for dental afferents reported by Pfaffman (1939b). In the latter studies, the possibility that the discharges entrained at higher vibration frequencies were recorded from IMs cannot be excluded

because intradental fibers were left intact. In support of this possibility, we have determined that  $251 \pm 103$  Hz was the maximum frequency for entrainment of IM discharge at the stimulus cycle length. The effects of vibration on the temporal structure of PDLMs are similar to those reported for slowly adapting mechanoreceptors in the glabrous skin of monkeys (Freeman and Johnson 1982a,b). The latter are most likely SA type I cutaneous mechanoreceptors (Phillips et al. 1990, 1992). Both types of receptors exhibited impulse phase locking and phase advance with increasing stimulus intensity. We conclude, on the basis of the static and dynamic response properties of PDLMs, that these tooth receptors detect displacement (or force), velocity (or force rate), and relatively low-frequency vibration.

#### *Response properties of IMs*

The IMs have dynamic response properties that are similar to those of cutaneous Pacinian corpuscle receptors (PCs), which detect repeated mechanical transients (vibration) or acceleration (Bolanowski and Zwislocki 1984; Burgess and Perl 1973; Darian-Smith 1984; Talbot et al. 1968). The most important of these common properties include the following: 1) lack of position (static) detection

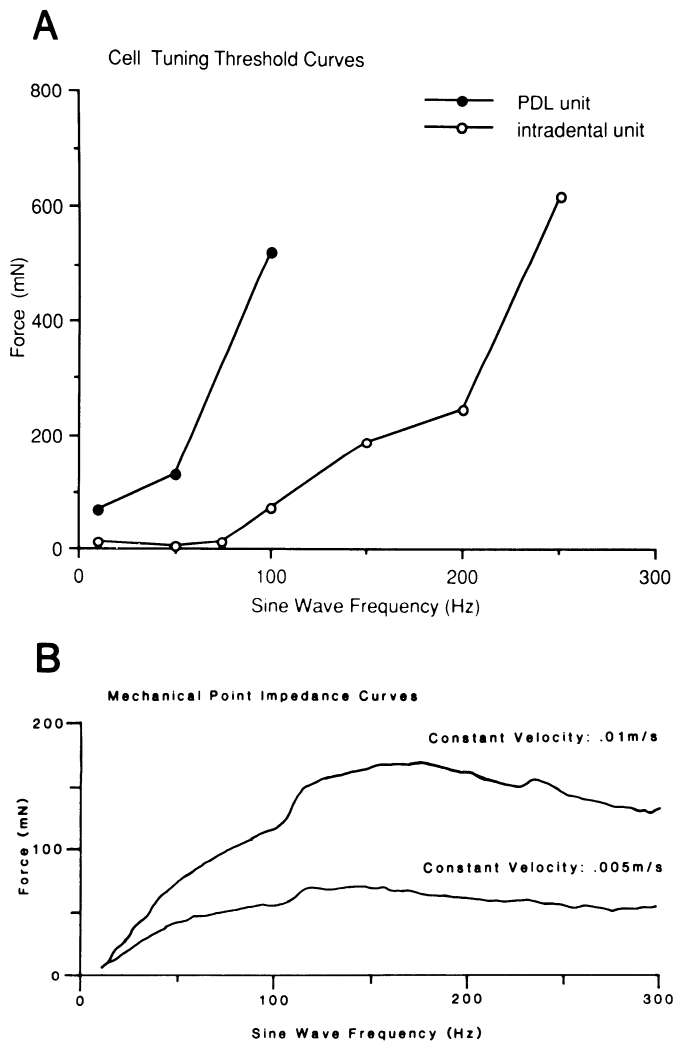


FIG. 10. Cell tuning threshold and mechanical point impedance curves. Tuning curves (*A*) were obtained from interspike interval histograms for a periodontal ligament mechanoreceptor (PDL) (●) and an intradental mechanoreceptor (IM) (○) unit. Each point represents the lowest force at a given sine wave frequency for which ~100% of the nerve impulses generated by a PDL or IM neuron were entrained to 1 cycle length. No points were plotted for the PDL unit beyond 100 Hz sinusoidal stimulation because discharges only occurred at interval multiples of the cycle length regardless of the intensity of the applied force. The mechanical impedance or resistance of the mandible and canine tooth to being set in motion over a range of sine wave frequencies is shown in *B*. Mechanical point impedance is defined as the ratio of the force exciting a structure to the resulting velocity, and it was determined by measuring the velocity and force at the same point. Accordingly, the modulus of velocity was kept constant to determine the modulus of impedance vs. frequency. The 2 impedance curves generated at different constant velocities had the same function over the sine wave frequency range.

and of spatial directionality and sensitivity, 2) few discharges (1–3 spikes) evoked during the dynamic phase of stimulation, 3) difficulty in eliciting discharges during constant-velocity (or force rate) ramp stimulation, and 4) relatively high-frequency discharge entrainment at one spike per cycle. Unlike the PCs, IMs have 1) a much lower maximum frequency for 1:1 discharge entrainment with each sine wave cycle (e.g., 251 vs. 800 Hz) and 2) positively accelerating, tuning threshold-frequency curves rather than U-shaped tuning curves with a maximum sensitivity near 300 Hz. The latter comparison is based on the assumption

that the forces applied to the tooth reflect the actual displacements of the tooth in its bony socket, which cannot be measured at this time. We have speculated that IMs might be the axially oriented, unmyelinated axons located in the fluid-filled dentinal tubules (Dong et al. 1985). Although mechanical, thermal, and chemical stimulation of the exposed dentinal surface elicits pain in humans and activates A-delta and C intradental fibers in animals, some clinical and electrophysiological evidence suggest that dentinal pain does not necessarily result from direct stimulation of dentinal nerve endings and that nociceptors in the pulp are activated by noxious stimuli applied to exposed dentin (reviewed by Närhi 1985a,b). This leaves open the possibility that at least some receptor terminals in dentin have a non-nociceptive function in the intact tooth. It should be noted that the fluid-filled dentinal tubule with its unmyelinated axon may be morphologically analogous to the PC structure, which has fluid-filled spaces surrounding the unmyelinated axon and between the lamellae (Hunt 1974). Both may provide mechanical filtering properties that prevent deformation of the nerve ending by slow displacements, and in other instances facilitate the transfer of abrupt displacements to the nerve ending (i.e., velocity vs. acceleration detection). Little is presently known about the structure and function of the neural transduction mechanism housed within the rigid dentinal tubules. It is unlikely that the “hydrodynamic” model of dentinal pain (Brännström and Aström 1972), which operates by bulk flow and displacement of dentinal tubule contents, has the sensitivity and response time that are compatible with the dynamic response range of IMs. A more plausible model in intact teeth would involve percussion or vibration of enamel and transmission of the resulting stimulus energy as sound waves through dentinal tubular walls and fluid to free nerve endings that are closely apposed to odontoblasts (Byers and Dong 1983; Byers et al. 1987). It is possible that minute changes in dentinal fluid pressure are sufficient to affect pressure-sensitive ion channels in the receptor membrane and to generate nerve impulses (see also Matthews and Hughes 1988). Our earlier study (Dong et al. 1985) demonstrated that the intradental and extradental conduction velocities, respectively, of IMs, were predominantly in the range of conduction velocities associated with myelinated A-delta and A-beta nerve fibers. This is consistent with both anatomic and physiological evidence, which has shown that 1) large myelinated A-beta fibers exist within the pulp near the tooth apex (Byers 1984; Fried and Hildebrand 1981; Holland and Robinson 1983) and 2) some intradental receptors have extradental conduction velocities that are identical to those of A-beta cutaneous nerve fibers (Cadden et al. 1983; Dong and Chudler 1984; Dong et al. 1990; Dostrovsky 1984; Hu and Sessle 1988; Lisney 1978).

A number of studies have challenged the premise that specialized intradental receptors subservise nonnociceptive and nonpain functions. Närhi et al. (1992a,b) and Matthews (1986) have failed to find intradental A-beta or A-delta fibers in the inferior alveolar nerve that respond to innocuous mechanical stimulation of the intact tooth crown (i.e., tapping or pressing in different directions). A large proportion of these A-beta and A-delta fibers did respond to mechanical or chemical stimulation of exposed

dentin (Närhi et al. 1992a,b). Methodological differences in cell sampling and tooth stimulation may partly explain these discrepant results. The existence of nociceptive intradental A-beta afferents would be entirely unique in the somatosensory system because cutaneous A-beta afferents do not subserve nociception and pain sensibility (Wiesenfeld-Hallin et al. 1984; Willer and Albe-Fessard 1983; Willer et al. 1978, 1980). Other investigators have suggested that nonpainful and painful sensations elicited by electrical stimulation of the tooth pulp depend on temporal summation (Virtanen et al. 1987) or spatial summation (Brown et al. 1985) of a single A-delta fiber population. These studies, however, were not designed to exclude the possible coactivation of IMs with A-delta or A-beta pulpal axons and the contribution of such pulpal input to nonpainful sensations. Moreover, McGrath et al. (1983) showed that tooth-pulp stimulation at the lowest currents evoked nonpainful sensations and were of constant magnitude despite changes in the frequency of stimulation.

Several lines of evidence indicate that activity recorded from IMs in the SLG are unlikely to originate from extradental sources, including the PDL. All IMs isolated in this study matched the response profile of IMs isolated in our previous study (Dong et al. 1985); the intradental origins of the IMs in the earlier study were established rigorously by impulse collision and nerve cold block tests. The receptive field of each IM was determined by applying static and dynamic mechanical forces over a wide trigeminal area and was found to be associated only with the ipsilateral mandibular canine tooth. No responses were evoked by direct stimulation of the overlying gingiva and adjacent oral mucosa. Our results do not support the possibility that IMs send collateral branches to adjacent gingival mucous membrane or skin. Although branched afferent nerves supplying the tooth pulp and adjacent periodontal tissues have been demonstrated by electrophysiological techniques (Lisney and Matthews 1978), such collateralization of primary afferents to innervate both the tooth pulp and surrounding tissues including the PDL have not been convincingly demonstrated by anatomic methods (Capra et al. 1984). Despite the fact that IMs have many response characteristics similar to PCs, the possibility that IMs were mistaken for PCs located near the tooth proper is remote. PC-like receptor structures are extremely rare in the PDL of cat (Byers and Dong 1989; Byers et al. 1986) and have not been found in several systematic studies of cat (Loescher and Holland 1991; Millar et al. 1989) and in other species (Byers 1985; Kannari et al. 1991; Sato et al. 1992). Furthermore, Barlow (1987) has demonstrated in a human psychophysical study of vibration detection thresholds that Pacinian-type frequency sensitivity was absent from the perioral facial skin. The apparent lack of cutaneous mechanoreceptors in the perioral region with Pacinian-like sensitivity will require further histological and physiological evidence for verification. Because a force ramp can generate a rapidly adapting response with few discharges from both IMs and some PDLMs (see also Hannam 1969, 1970; Linden and Millar 1988a; Loescher and Robinson 1989), IMs can be mistaken for PDLMs if identification is based solely on this common property. Unlike PDLMs, IMs were unaffected by the direction of tooth stimulation and required a percussive

ramp stimulus that contains a high acceleration component. It is also unlikely that our identification of IMs was confounded by inadvertent activation of sensory nerve endings in the mandibular periosteum. Sakada (1971, 1983) has found encapsulated endings (Golgi-Mazzoni corpuscles) and free nerve endings in the periosteum of the mental foramen region overlying the canine root; these receptors apparently have response properties similar to cutaneous rapidly adapting mechanoreceptors and their discharges were entrained to vibratory stimulation  $\leq 200$ –400 Hz. Our dynamic stimulation of teeth adjacent to the canine, which would presumably excite distant periosteal receptors by transmission of mechanical transients through bone, never excited canine IMs. Moreover, the U-shaped tuning threshold-frequency curves with a maximum sensitivity near 100 Hz that characterize rapidly adapting periosteal and gingival-oral mucosal receptors (Sakada 1971, 1983) differ from the tuning curves of IMs.

### *General conclusions*

This study has shown that PDLMs and IMs can be functionally differentiated by varying the frequency of vibratory stimulation and by applying a force ramp with or without a percussive component. Such information about the parameters of adequate stimulation for PDLMs and IMs should be useful in designing psychophysical studies that can assess the sensory contribution of each receptor population and elucidate the functional significance of dynamic responses seen in PDLMs and IMs. The experimental design should include dynamic mechanical stimulation of both vital and nonvital (pulpless) teeth and comparisons of task performance for discrimination of sinusoidal vibration frequencies and of percussive/nonpercussive ramp rates. The PDLMs and IMs appear to provide a continuum of dynamic afferent inputs necessary for tactile sensibility of teeth. We speculate that such inputs are important for protecting the structural integrity of tooth enamel from severe abrasion or percussion during activity such as biting, grasping, or gnawing and for signaling the texture of food during mastication. The electrophysiological evidence in this study along with previous anatomic evidence about the density, diversity, and complexity of intradental innervation provide strong inference that a portion of intradental input subserves sensory modalities other than nociception. Further physiological studies are needed to determine whether inputs from PDLMs and IMs converge onto the same second-order neurons in the trigeminal brain stem nuclear complex or follow separate central routes. Recent studies have demonstrated overlap of central projection sites for tooth pulp and PDL afferents (Dong et al. 1990; Tabata and Karita 1991; Tsuru et al. 1989), which might suggest a possible convergence of IM and PDL inputs onto brain stem neurons.

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